Research Report

Color Opponency in Synaesthetic Experiences

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ABSTRACT—Grapheme-color synaesthesia is a rare condition in which perception of a letter or a digit is associated with concurrent perception of a color. Synaesthetes report that these color experiences are vivid and realistic. We used a Stroop task to show that synaesthetically induced color, like real color, is processed in color-opponent channels (red-green or blue-yellow). Synaesthetic color produced maximal interference with the perception and naming of the real color of a grapheme if the real color was opponent to the synaesthetic color. Interference was reduced considerably if the synaesthetic and real colors engaged different color channels (e.g., synaesthetic blue and real red). No dependence on color opponency was found for semantic conflicts between shape and color (e.g., a blue lemon). Thus, the neural representation of synaesthetic colors closely resembles that of real colors. This suggests involvement of early stages of visual processing in color synaesthesia and explains the vivid and realistic nature of synaesthetic experiences.

In a classic Stroop (1935) task, the subject is instructed to name the ink color of a word that refers to a color. Reaction times are longer if the meaning of that color word differs from the ink color (e.g., if "red" is written in blue ink) than if the meaning and the ink color are the same. The Stroop task can also be applied to study grapheme-color synaesthesia, in which perception of a letter or a digit is associated with concurrent perception of a color; synaesthetes report that these perceptions are vivid and realistic. In the case of synaesthesia, the time needed to name the ink color of a grapheme is shorter if the synaesthetic color of that grapheme is the same as the ink color (congruent condition)

Address correspondence to Danko Nikolić, Department of Neurophysiology, Max-Planck Institute for Brain Research, Deutschordenstrause 46, 60528 Frankfurt am Main, Germany, e-mail: danko@ mpih-frankfurt.mpg.de. than if the two colors are different (incongruent condition; Dixon, Smilek, Cudahy, & Merikle, 2000; Mattingley, Rich, Yelland, & Bradshaw, 2001; Odgaard, Flowers, & Bradman, 1999; Palmeri, Blake, Marois, Flanery, & Whetsell, 2002). These findings indicate interactions (interference, facilitation, or both) between the real and the synaesthetic colors, provide empirical evidence that these synaesthetic experiences are real, and suggest that synaesthesia occurs without voluntary control (Cytowic, 1989; Hubbard, Arman, Ramachandran, & Boynton, 2005; Palmeri et al., 2002). However, it is unknown at which level of processing the interactions between real and synaesthetic colors occur.

Studies based on functional magnetic resonance imaging provide evidence for activation of the color-specific area V4/V8 of the visual cortex during synaesthetic experiences (Hubbard et al., 2005; Hubbard & Ramachandran, 2005; Nunn et al., 2002; Sperling, Prvulovic, Linden, Singer, & Stirn, 2006). Neurons of these areas are responsible for processing of visual stimuli and have color-opponent receptive fields: Cells excited by red are inhibited by green (and vice versa), and cells excited by blue are inhibited by yellow (and vice versa; Chichilnisky & Wandell, 1999; Hubel & Livingstone, 1987; Hurvich & Jameson, 1955, 1957; Zeki, 1980). In the present study, we exploited this color opponency of hue-selective cells to identify the site of interactions between real and synaesthetic colors. We modified the Stroop task by creating two types of incongruent conditions. In one, the real color was opponent to the synaesthetic color (i.e., red vs. green or blue vs. yellow). We hypothesized that in this case, the two colors would likely involve the same color channels (Zeki, 1977). In the other incongruent condition, the real color was not opponent to the synaesthetic color (e.g., red vs. blue), and we hypothesized that the two colors would be processed by different channels (i.e., independently). We also hypothesized that if synaesthesia-induced colors are processed by opponent channels, there will be longer reaction times in the color-naming task when synaesthetic and real colors are opponent than when they are independent.

EXPERIMENT 1

Method

Subjects

Our experimental group consisted of 6 color-grapheme synaesthetes (4 women and 2 men) who were 25 to 41 years old (average age = 31.7 years). Five of the subjects had additional forms of synaesthesia: Three had visual sensations when hearing music, 1 had tactical sensations induced by music, and 1 had color experiences induced by smell, taste, and pain. In all the synaesthetic subjects, vowels induced stronger color experiences than consonants. Four of these synaesthetes (T.O., I.H., K.L., and K.T.) were associators (Dixon, Smilek, & Merikle, 2004; Smilek, Dixon, Cudahy, & Merikle, 2001); that is, they reported seeing the colors on an "internal screen" or "in the mind's eye." The other 2 (C.G. and N.B.) were projectors, seeing colors projected onto the graphemes in external space. We made this distinction on the basis of the subjects' subjective reports. One of the projectors (N.B.) reported projecting only strong synaesthetic colors, but not weak ones (i.e., she projected colors to vowels but not to consonants). Another subject (K.T.) saw the colors projected externally but reported that they had a fixed spatial position relative to her body and were detached from the locations of the graphemes. This defined her as an associator. As in previous studies (Baron-Cohen, Harrison, Goldstein, & Wyke, 1993; Dixon et al., 2000; Mattingley et al., 2001), the colors associated to graphemes had high test-retest reliability in all the synaesthetes (test-retest period = 9-50 weeks).

The control group consisted of 12 nonsynaesthetic subjects (2 control subjects per synaesthete) who were matched to the synaesthetes by gender and also by age (± 1 year; average age = 31.3 years).

Procedure

The consistency of the synaesthetes' color associations over time was tested by asking them to view graphemes and select the corresponding colors from a book with 5,500 colors (Kueppers, 2003). Subjects did not know in advance that they would be retested later for the same color associations. Three judges agreed that the colors were chosen with high consistency over time.

For each synaesthete, the five graphemes with the strongest grapheme-color associations were used to create stimuli for three conditions (see Fig. 1). In the *congruent* condition, the color of each grapheme was the same as the synaesthetic color; in the *incongruent opponent* condition, the color of each grapheme was opponent to the synaesthetic color (i.e., at the opposite side of the color wheel); and in the *incongruent independent* condition, the color of each grapheme and the synaesthetic color were represented by different opponent-color channels (i.e., 90° offset relative to each other; see Fig. 1b). In the *baseline* condition, a grapheme that did not have a synaesthetic color

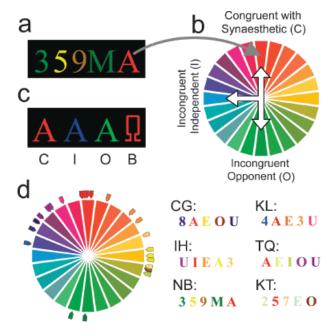


Fig. 1. Stimulus design for the Stroop task. For each synaesthetic subject, we selected the five graphemes with the strongest grapheme-color associations; an example from 1 subject is shown in (a). The synaesthetic color for each grapheme and corresponding incongruent colors were then located on a color wheel (b) to create the stimuli for three out of four experimental conditions: congruent ("C"), incongruent independent ("I"), and incongruent opponent ("O"). The examples in (c) illustrate the color of the letter A in each of these conditions for the subject whose grapheme-color associations are shown in (a). In addition, in the baseline ("B") condition, an Ω-shaped grapheme was presented; none of the synaesthetes experienced synaesthetic associations to that grapheme. The color wheel in (d) shows the distribution of all the investigated synaesthetic colors: to the right are their associations to the graphemes for each synaesthetic subject. The synaesthetic colors were not distributed uniformly around the color wheel, but tended to cluster around the pure colors (the vertical and horizontal axes).

association (Ω -shaped grapheme; see Fig. 1c) was substituted for the original grapheme and presented in that grapheme's synaesthetic color (i.e., the color used in the congruent condition). This condition allowed us to estimate the speed with which subjects named grapheme colors in the absence of synaesthesia.

A color wheel (Fig. 1b) that is close to the psychological color wheel was used as a freeware Windows application implemented in the farbwert.exe program (Kircher, n.d.). The experiment took place in a dimly lit room with a computer running the visual stimulation tool ActiveSTIM (Nikolić, 2003). The graphemes were presented on a high-contrast CRT computer monitor in Times New Roman font against a black background. Subjects' distance from the monitor was freely adjustable (typically ~ 1 m, corresponding to a stimulus size of about 2.7°). Subjects uttered the names of the colors into a microphone so that we could measure the latency of their vocal responses. The signal from the microphone was processed by a threshold discriminator connected digitally to the stimulation software.

All subjects were naive with respect to the purpose of the experiment and the hypotheses. In a pseudorandomized sequence, five graphemes were presented 10 times each in each of the four stimulation conditions, resulting in a total of 200 trials. Subjects were instructed to name the real color of each grapheme as quickly as possible, but were also told to keep their response accuracy at a high level. All trials were presented within one block (i.e., without a break and with a 1-s intertrial interval). The entire procedure lasted about 25 min. Synaesthetes were paid for participation (€30), and control subjects were unpaid volunteers. Prior to the experiment, each subject completed 15 practice trials (five graphemes presented in all three colors). To compare synaesthetes' response latencies in the baseline condition with control subjects' response latencies, for each stimulation condition we averaged the results for the 2 control subjects matched to each synaesthete. This allowed us to maintain an orthogonal repeated measures experimental design. All pair-wise comparisons were one-tailed.

Results and Discussion

For all subjects, the accuracy of responses was very high (more than 98% of responses correct). Because of the small number of incorrect responses, there were no differences in the results when the incorrect responses were excluded from analysis.

The time it took for synaesthetes to name the colors of the graphemes varied significantly across the four experimental conditions, $F(3,20)=5.9, p=.005, \eta^2=.47$ (see Fig. 2a). Post hoc pair-wise comparisons indicated that color naming was faster in the congruent condition than in the incongruent conditions, confirming results of previous studies (Mattingley et al., 2001; Palmeri et al., 2002): congruent vs. incongruent independent, $t(5)=3.55, p=.008, p_{\rm rep}=.96, \eta^2=.72$; congruent vs. incongruent opponent, $t(5)=4.07, p=.005, p_{\rm rep}=.97, \eta^2=.77$.

The difference between the two incongruent conditions was also significant. Subjects named the colors significantly faster in the incongruent independent condition than in the incongruent opponent condition (difference of $104 \, \mathrm{ms}$), $t(5) = 4.47, p = .003, p_{\mathrm{rep}} = .97, \, \eta^2 = .80$. Thus, the interference induced by synaesthetic colors was stronger when the real color of the grapheme was opponent to the synaesthetic color than when it was independent.

As expected, the nonsynaesthete control group did not show any significant differences in response times across the same four stimulation conditions, F(3, 44) < 1 (Fig. 2b), and it is important to note that these response times were not different from those of the synaesthetes in the baseline condition (difference of 8 ms), t(5) < 1. Therefore, for synaesthetes, the baseline condition was a good point of comparison for determining whether the synaesthetic colors in the other three conditions interfered with the color-naming task (i.e., response time was longer than the baseline) or facilitated this task

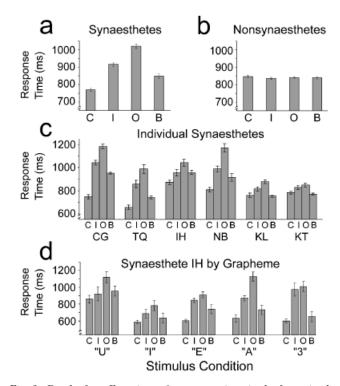


Fig. 2. Results from Experiment 1: response times in the four stimulation conditions averaged across all graphemes and all synaesthetes (a), the control subjects' response times for the same stimuli (b), response times in the four conditions computed individually for each of the 6 synaesthetes (c), and the response times for the five different graphemes for a typical subject (I.H.) whose responses were highly representative of the entire group (d). Error bars represent standard errors of the means.

(i.e., response time was shorter than the baseline). Synaesthetes' response times were longer in the independent condition than in the baseline condition (average difference of 67 ms), $t(5) = 4.11, p = .005, p_{\rm rep} = .97, \eta^2 = .77$, and were shorter in the congruent condition than in the baseline condition (difference of 78 ms), $t(5) = 2.35, p = .032, p_{\rm rep} = .91, \eta^2 = .53$ (Fig. 2a).

In summary, opponent incongruent colors produced much stronger interference than did independent incongruent colors (171 ms/67 ms = ~2.5-fold difference), and congruent synaesthetic colors facilitated the process of naming the real colors of graphemes. These results were robust, as the main findings reached significance for each individual synaesthete (all $Fs \geq 3.2$, all $ps \leq .02$, $p_{\rm rep}s \geq .93$, $\eta^2s \geq .05$), and a clear separation between the opponent and independent conditions was detected in 25 of the total of 30 individual graphemes. Figure 2c shows the average response times for each of the 6 synaesthetic subjects, and Figure 2d shows the average response times for the five individual graphemes for 1 representative subject. Results were consistent with a previous study (Dixon et al., 2004) in that the 2 subjects with the strongest effects were those who were classified as projectors (subjects C.G. and N.B.).

Volume 18—Number 6 483

EXPERIMENT 2

Method

In Experiment 2, we investigated semantic, rather than synaesthetic, associations between shape and color. We used the same Stroop task as in Experiment 1 except for the following differences. The stimuli were designed on the basis of commonly known everyday associations between shape and color. For example, a lemon is yellow or maybe green, but is never red or blue, and the shape of a heart is associated almost exclusively with red and not with other colors. Given these semantic associations, one can expect interference in the Stroop task if the color of the displayed object is incongruent with the usual color of that object (Martino & Marks, 1999; Walker & Smith, 1984). However, we propose that these semantic associations are qualitatively distinct from synaesthetic associations and thus do not involve the opponent-color system. To test this hypothesis, we presented each stimulus object in Experiment 2 in the normally associated color, in a color that was incongruent with and opponent to the associated color, and in a color that was incongruent with but nonopponent to the associated color (see Fig. 3a).

Subjects

Four of the synaesthetes from Experiment 1 and 8 of the corresponding control subjects participated in Experiment 2. The average age was 33.5 years for synaesthetes and 33.1 years for control subjects.

Procedure

The methods were the same as those used for the synaesthetic Stroop task except for the following differences. Only three objects were used for this experiment (a heart, a lemon, and a smiley face), and each appeared in only three stimulation conditions, as there was no baseline condition. Every stimulus was presented 25 times, resulting in a total of 225 trials. Effects in this experiment were much smaller than the effects in Experiment 1, and they were also smaller than the variability in the average response times across individual subjects. For that reason, significant differences in response times could be detected only if individual responses were normalized relative to each subject's average response time. In Experiment 1, there was no change in the outcome when a similar normalization method was applied.

Results and Discussion

In this experiment, response accuracy was again very high (more than 98% of responses were correct). As hypothesized, response times varied significantly across the stimulation conditions: synaesthetes, F(2, 9) = 41.8, p < .0001, $\eta^2 = .90$; nonsynaesthetes, F(2, 21) = 94.4, p < .0001, $\eta^2 = .89$ (analyses based on normalized data; see Fig. 3). There were no differences in

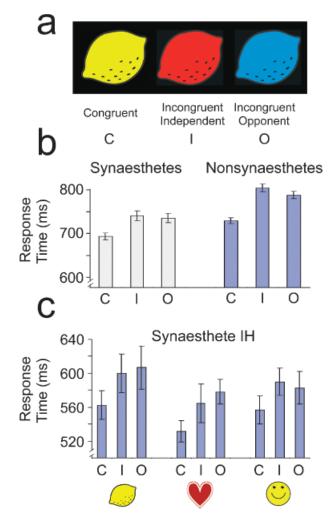


Fig. 3. Example stimuli (a) and results (b, c) from Experiment 2. The three experimental conditions are indicated by "C" (congruent), "I" (incongruent independent), and "O" (incongruent opponent). The graphs show response times averaged across the three shapes, for the synaesthetes and the nonsynaesthetes (b), and a typical subject's (synaesthete I.H.) response times for each shape in each condition. In (c), the objects' shapes are indicated on the abscissa and are drawn with their congruent colors. Error bars represent standard errors of the means.

performance between the synaesthetes and the nonsynaesthetes, $F(1, 18) = 1.81, p > .19, p_{\rm rep} < .73$; therefore, further analyses could be conducted by pooling their responses into a single data set.

The pair-wise comparisons indicated that the congruent condition differed significantly from the other conditions (both ts>8.1, ps<.0001, $p_{\rm rep}s>.99$, $\eta^2s=.86$). The difference between the incongruent independent and incongruent opponent conditions was small (13 ms) but significant, t(11)=2.4, p=.02, $p_{\rm rep}=.93$, $\eta^2=.31$ (analysis based on normalized data), but this difference was in the direction opposite the effect found in Experiment 1 (see Fig. 3b). These results are highly consistent with those of a previous study on the role of color opponency in the classical Stroop task (Laeng, Lag, & Brennen, 2005) and indicate that color opponency affects semantic

484 Volume 18—Number 6

associations between shape and color differently than synaesthetic associations. The average increase in response time for the incongruent conditions (relative to the congruent condition) was 57 ms, which is in the same range as the difference between the baseline and incongruent nonopponent (independent) conditions in Experiment 1.

GENERAL DISCUSSION

We conclude that synaesthetic color experiences interfere maximally with the perception and naming of real colors if the real and synaesthetic colors are opponent to each other; interference is much reduced when the two colors are incongruent but nonopponent (i.e., encoded by different color-opponent channels). By contrast, if synaesthetic and real colors are identical, the color-naming process is facilitated, resulting in response times that are shorter than those for graphemes that do not evoke color associations (and shorter than the response times of nonsynaesthetes).

These findings indicate that the color experiences induced by grapheme-color synaesthesia involve color-opponent channels and thus, most likely, neurons at early stages of visual processing (V1 to V4/V8). This interpretation agrees with the findings of recent functional magnetic resonance imaging studies (Hubbard & Ramachandran, 2005; Sperling et al., 2006) and is consistent with claims that experiences evoked by grapheme-color synaesthesia have a perceptual basis (Smilek et al., 2001; Ramachandran & Hubbard, 2001). Because the results were highly consistent across all of our synaesthetes (projectors as well as associators), they can be considered representative for the entire population of grapheme-color synaesthetes. In addition, comparison between Experiments 1 and 2 indicates clearly that semantic associations and synaesthetic color associations depend on entirely different mechanisms. Thus, the results of our study provide strong psychophysical evidence for involvement of color-opponent channels and, hence, early visual areas in the generation of synaesthetic color experiences.

The results from Experiment 2 enable us to explain the findings that incongruent but nonopponent colors did interfere with color naming. The magnitude of this interference was much smaller than the magnitude of the interference caused by opponent colors and was in the same range as the interference in the semantic shape-versus-color task, suggesting that semantic associations between graphemes and colors can explain the interference between nonopponent colors. The lifelong experience of synaesthesia is likely to create strong semantic associations between the graphemes and colors (e.g., "I know that my A is red"). Therefore, our results indicate that the color interactions in the present Stroop task have two components: The stronger component reflects synaesthesia proper and depends on color opponency, and the weaker component reflects knowledge about the synaesthetic associations and is independent of color opponency.

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Volume 18—Number 6 485

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Volume 18—Number 6