PERCEPTION

CONTRAST AFFECTS THE STRENGTH OF SYNESTHETIC COLORS

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ABSTRACT

Grapheme-color synesthesia is an automatic, involuntary experience of seeing colors when viewing numbers, letters or words on a printed page. Previous research has demonstrated that synesthesia is a genuine perceptual phenomenon, but crucially, all of these experiments have used high-contrast letters and numbers. Our synesthete, JC, anecdotally reported that the strength of his synesthetic colors varied depending on whether the graphemes were presented in high or low contrast. To test this, we asked JC to rate the strength of his experiences to letters of different contrasts on three different dates. JC's ratings of the strength of his synesthetic colors consistently declined monotonically with contrast, suggesting that his synesthetic colors were reduced or absent at low contrasts. To more precisely quantify the impact of this, we then tested JC on modified versions of our embedded figures task (Ramachandran and Hubbard, 2001a) and crowding task (Ramachandran and Hubbard, 2001b) by presenting displays with varying contrast between the graphemes and the background. Behavioral data in the contrast variant of our embedded figures task showed that JC performed significantly better than controls at high contrast, replicating our previous findings. However, at low contrast this advantage was eliminated, consistent with his reports of weaker or absent colors. A similar, but weaker pattern of results was found in the modified version of our crowding task. These results suggest that JC's synesthetic colors may be elicited at contrast dependent stages of visual processing. We propose that regions of the fusiform gyrus specialized for letter and number grapheme recognition that have been shown to respond in a contrast dependent manner mediate JC's synesthetic colors. However, whether this is true for all grapheme-color synesthetes or is only true of the group we refer to as lower synesthetes, remains to be seen.

Key words: synaesthesia, contrast, VWFA, cross-activation

INTRODUCTION

Grapheme-color synesthesia is an automatic, involuntary experience of seeing colors when viewing numbers, letters or words on a printed page (see, e.g., Cytowic, 1989, 2002; Ramachandran and Hubbard, 2001b; Rich and Mattingley, 2002 for reviews). For example, looking at the letter E will elicit the experience of a red overlay for our synesthete JC, while viewing an O elicits a blue percept. A number of recent studies (Dixon et al., 2000; Mattingley et al., 2001; Mills et al., 1999) have used modified versions of the Stroop interference paradigm to demonstrate that grapheme-color synesthesia is automatic, and perhaps obligatory. However, because Stroop interference can arise from either perceptual or conceptual processes (MacLeod, 1991), it provides only a coarse-grained tool for exploring the neural substrates of synesthetic experience.

The application of perceptual paradigms to the study of synesthesia can begin to dissociate perceptual and cognitive factors in synesthesia. Our previous research compliments the results from Stroop paradigms and suggests that grapheme-color synesthesia is a truly perceptual experience, as opposed to a conceptual or metaphorical process (Ramachandran and Hubbard, 2001a, 2001b). First,

we found that synesthetic subjects perform significantly better than controls in identifying which of four shapes composed of graphemes was embedded in a display containing other distracting graphemes (Ramachandran and Hubbard, 2001a), in a manner akin to color "pop-out" or texture segregation. Subjects were presented with screens filled with distracter letters or numbers and target graphemes arranged into a shape. When the displays were presented for a brief time (one second), control subjects found it difficult to search the entire display, resulting in poor performance on this task. For synesthetes, however, who report that they perceive colored shapes against a colored background, this presentation time allowed for significantly better identification of the embedded figure. Control experiments with a subset of synesthetic subjects using typographical symbols such as "&" and "$" that did not evoke colors showed no such difference between synesthetes and non-synesthetes.

Second, we have tested synesthetic subjects on a "crowding" paradigm in which their synesthetic colors were expected to aid them in identifying a central target grapheme. In non-synesthetic subjects, numbers or letters presented in the periphery were difficult to identify if presented in the presence of flanking graphemes (crowding).

This effect is attenuated by presenting the target graphemes in a different color than the flanking graphemes (Kooi et al., 1994). We find that synesthetic subjects were significantly better at identifying the target grapheme than controls (Ramachandran and Hubbard, 2001b), suggesting that synesthetic colors act in a manner similar to real colors to reduce the magnitude of the crowding effect.

Whereas we have used synesthetic color differences to facilitate performance on perceptual tasks, Smilek et al. (2001) manipulated color congruency to show that a number grapheme was harder to identify when the background color was congruent with the synesthetic color than when it was incongruent. For example, a 4, which their synesthete C experienced as blue, was harder to identify when presented against a blue background than against a red background. Subsequent results by Palmeri et al. (2002) have shown that synesthetic colors can aid in the detection of a singleton in a visual search task. Palmeri et al. showed that, when the target and distracter elicited similar colors (searching for a 6 among 8 sec), search was difficult (search slopes were about 28 msec/item). However, when synesthetic colors differed between target and distracter (searching for a 2 among 5 sec), their synesthetic subject WO was more efficient in his visual search (search slopes were about 15 msec/item). In control subjects, no such difference was observed.

Crucially, in all of these experiments, target graphemes were presented at high contrast against the background [the only exception being the Smilek et al. (2001) study, but contrast was not varied systematically]. In discussions with our synesthete, JC, he reported that the strength of synesthetic colors varied as a function of contrast. That is, when presented with a black grapheme on a white background or a white grapheme on a black background, JC reported that his synesthetic colors were substantially stronger than when presented with a dark gray grapheme on a light gray background. He commented, "It's really strange, I'm not getting my colors as strongly", "The color seems detached," and "It feels a bit like neon".

Interestingly, JC noted that his synesthetic colors were not eliminated equally strongly all across the letter, but rather that the synesthetic colors were perceived at low intensity for certain critical portions of the letter, but not for others (Figure 1). For example, JC noted that at 30% contrast the usual yellow color of "F" was weaker but present for the two horizontal bars, and absent for the vertical bar. At 5% contrast, he reported that only the tips and junctions of the "F" were colored. When "H" was presented at 5% contrast, he perceived his usual green color, but unequally over the letter. The upper left portion of the "H" was colored with an intermediate strength, but the lower right portion was barely colored at all.
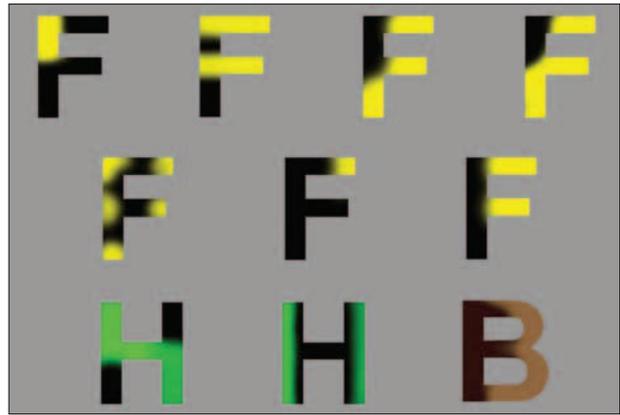

Fig. 1 – *Images depicting which regions of letters that JC reported to be colored, when presented at low contrasts. Letter 'F' at 40%, 30%, 10%, 10% (on a second occasion), 5%, 4% and 2% contrast levels; 'H' at 30% and 5%; 'B' at 30%. Percentages are nominal black levels.*

These observations may provide a novel tool for identifying the representational level at which synesthetic colors arise. To understand this issue, a bit of terminology is in order. *Inducer* refers to the stimulus that elicits synesthetic colors, while *concurrent* refers to the extra synesthetic experience (Grossenbacher and Lovelace, 2001). In grapheme-color synesthesia, the grapheme would be the inducer and the colors the concurrents. To date, synesthesia research has focused on the question of whether the synesthetic concurrents are perceptual. However, very little work has been done to address the question of whether the synesthetic *inducer* is perceptual or conceptual (but see Ward and Simner, 2003 for a discussion of similar issues in lexical-gustatory synesthesia). Simply showing that synesthetic colors are elicited when subjects view letters or numbers is not adequate to resolve these questions. In addition to perceptual processes, visual presentation of a grapheme (for example 'F') automatically elicits a host of cognitive processes, including phonemic representations of the letter name ('eff'), and higher-level representations, such as that 'F' is the sixth letter of the alphabet.

Some preliminary evidence suggests that, at least for some synesthetes, the inducer is the percept of the grapheme, rather than other higher-order cognitive processes. We have previously reported that Roman numerals and clusters of dots are not effective in eliciting synesthetic colors (Ramachandran and Hubbard, 2001a, 2001b) and that manipulation of font modulates the exact quality of the synesthetic experience (Ramachandran and Hubbard, 2003). Both of these findings suggested that the form of the grapheme was critical for the experience of colors. Our new findings that JC's synesthetic colors can be modulated by contrast further argues against the possibility that his synesthetic colors are elicited by conceptual representations, which should be contrast-invariant. Instead, our results suggest that

JC's synesthetic colors arise from contrast sensitive stages of perceptual processing, most likely in the fusiform gyrus (although there may be other synesthetes for whom this is not true, see Ramachandran and Hubbard, 2001b; Hubbard et al., 2005).

Similarly, the finding that only edges, bars or segments are synesthetically colored when viewing low-contrast graphemes is consistent with certain feature-based models of letter recognition (e.g., Boles and Clifford, 1989) which emphasize the importance of lines, junctions and free ends, although the precise correspondence depends on which feature model is employed. For example, in the case of the "F", the most important features would be the two horizontal lines (*vs.* three for an 'E'), the presence of the one L-junction and one T-junction, and the three free ends. These components were the ones that were most likely to retain their color for JC, which further suggests that the percept of the grapheme is critical for eliciting his synesthetic colors.

In the following experiments, we sought to demonstrate this effect more clearly and to measure the exact dependency of synesthetic colors on contrast. We will return to the implications of these findings for the representational level, and especially the neural basis, of the synesthetic inducer in the discussion.

EXPERIMENT 1

Subjective Rating Data

In order to assess the effect of contrast on the strength of JC's synesthetic colors, we wanted to test as wide a range of synesthetic experiences as possible. We therefore asked JC to identify what colors he experienced and how strongly he experienced those colors for high contrast (black on white) graphemes. We then chose graphemes that elicited the strongest and weakest experiences of red, green, yellow and blue. JC reported strong color experiences for E, H, F and O (red, green, yellow and blue, respectively) and weak experiences for D, S and J (red, yellow and blue; no letter was reported as eliciting a weak green experience). To test the effect of contrast on the strength of synesthetic colors, we randomly presented one of these letters at fixation for two seconds at various levels of contrast, and asked JC to rate the strength of his experiences.

Methods

Subjects

We tested synesthetic subject JC at three time points separated by approximately one month (February 20, March 7 and May 2, 2002). Because of the subjective nature of these experiments, collection of control subjects data was not appropriate.

Apparatus

Stimuli were presented on a 17" Iiyama VisionMaster Monitor (1024 × 768, 75 Hz) using Macromedia Director 7.0 (Macromedia, San Jose, CA, USA).

Stimuli and Methods

Letters were presented at fixation for two seconds in varying contrasts. Letters were approximately 3.8 cm (1.5") tall at a viewing distance of 60 cm (24"), subtending a visual angle of 2.3° × 3.6° (width × height) so that discriminability would not be a limiting factor. We tested 11 contrasts (nominally 100%, 80%, 60%, 40%, 20%, 10%, 5%, 4%, 3%, 2% and 1%) in both black and white. Letters were presented on a neutral gray background (18.4 cd/m^2). Luminance values were collected using a Tektronix J18 photometer and ranged from 0 cd/m^2 (black) to 90 cd/m^2 (white). Weber contrast therefore varied between − 1.0 and 3.89. We also included catch trials where no letter was presented (0% contrast). We presented a total of 161 trials per block (7 letters × 2 colors × 11 contrasts + 7 catch trials), and tested JC on 4 blocks per session for a total of 644 trials[1]. JC was asked to rate his subjective color experience on a scale from 0 to 5, with 0 being no color experience and 5 being as strong as a color in the real world. Each session lasted approximately 1 hour.

Results

Mean subjective rating data for each letter averaged over all three testing sessions as a function of contrast is presented in Figure 2. Subjective color strength decreases monotonically with decreasing contrast for each letter. This monotonic decrease was consistent over different letters, though the maximum rating for each letter was different, consistent with JC's early reports that some letters elicited stronger color experiences than others. JC accurately reported the identity of the letter at all contrasts. We find that JC shows highly significant effects of contrast [all Fs (10, 462) > 140, $p < .0001$] and letter [all Fs (5, 462) > 13, $p < .0001$] in each session, and a marginal contrast by letter interaction [session 1, F (50, 462) = 1.56, $p < .05$; session 2, F (50, 462) = 1.31, $p = .08$; session 3, F (50, 462) = 1.34, $p = .07$]. The lack of a clear interaction is probably due to the

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[1]Due to a programming error, the letter F was not presented in the first two sessions, except for the black 100% contrast condition. Since these were identical to the catch trials, we analyze these trials with the catch trials.
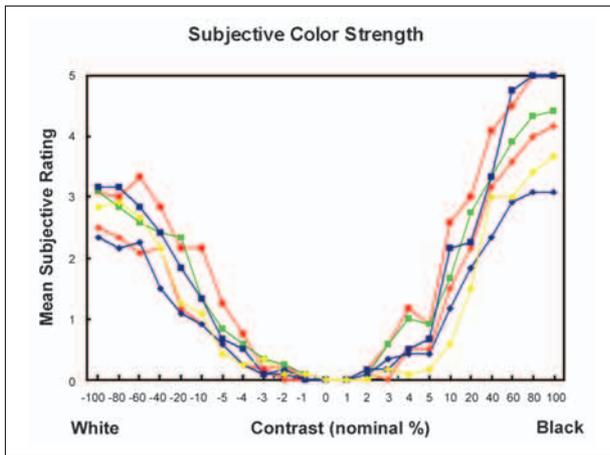
Fig. 2 – *Subjective strength ratings for JC's colors at different contrasts (nominally -100% to 100%, where black is indicated by numbers less than 0 and white by numbers greater than 0) averaged over all three testing sessions. Each line indicates JC's subjective strength rating for one letter where the color indicates the color experienced. Squares indicate graphemes that elicit strong experiences (E, O and H) and diamonds graphemes that elicit weak color experiences (D, J and S).*

fact that black and white letters show different patterns of contrast responses. When we block by color (black or white), this interaction is significant in all three sessions for black letters [all Fs (50, 198) > 2, p < .001] but not white letters [all Fs (50, 198) < 1.35, p > .05]. Blocking by color affected neither the highly significant effect of contrast nor letter. Analyses grouped over all three sessions revealed that the main effects of contrast [F (10, 1518) = 477.19, p < .0001], and letter [F (5, 1518) = 49.41, p < .0001] and the contrast by letter interaction [F (50, 1518) = 2.91, p < .0001] were all significant. Overall, these data demonstrate that JC's colors vary with contrast, and that those letters reported as having higher strength in the high-contrast condition showed a greater increase in their subjective strength than did those rated as having lower strength.

JC's subjective reports were relatively consistent, despite the considerable delay between testing sessions. An overall ANOVA for the ratings (pooled over all letters and contrasts) showed a trend towards lower ratings from the first to the third session [F (2, 1580) = 2.85, p = .058]. However, further analyses of this trend showed that it was probably driven by some inconsistency in the use of the rating scale at the lowest contrasts (perhaps due to a shift in criterion). Ratings for contrasts of 2%-5% decreased significantly from the first to the third session [all Fs (2, 141) > 4.5, p < .05]. At the 5% contrast level, five out of six letters showed a significantly lower rating or a trend in this direction. At 2% and 3% contrast, only one data point showed a significant effect of session (J and H, respectively) and at 4%, two points showed non-significant trends towards lower contrast (E and O). On the other hand, an ANOVA run on the rating data with these lowest contrasts

excluded finds no effect of session [F (2, 860) = .69, p > .45]. For contrasts between 10% and 100%, only one data point shows a significant effect of session [20% O, F (2, 21) = 5.50, p < .05]. These data suggest that, despite some variability at the very lowest contrasts, JC consistently reported the same color strengths across sessions.

On 252 catch trials over three sessions, JC reported experiencing a color (of strength 1) on only one trial. Similarly, he reported experiencing colors on 0 out of 76 trials at 1% contrast and 2 out of 76 trials (both of strength 1) at −1% contrast suggesting that JC was veridically reporting his experience of not experiencing colors at very low contrast. The fact that the reported strength of the experience increases with contrast, both for black and white text on a gray background also argues against the possibility that JC was confabulating. Black text on a gray background was rated as eliciting stronger color experiences at maximum contrast that white text on a gray background, despite the fact that 100% white text was higher contrast than 100% black text (Weber contrast 3.89 for white, −1.00 for black).

Overall, these data suggest that JC is veridically reporting a decline in the subjective strength of his synesthetic colors with contrast. We therefore turned to the question of whether these subjective effects could be quantified behaviorally.

EXPERIMENT 2

Contrast Embedded Figures

To more precisely quantify the dependence of synesthetic colors on contrast, we modified our previous embedded figures task (Ramachandran and Hubbard, 2001a) to present displays at varying contrasts. In this task, subjects were presented with displays containing a large number of randomly placed graphemes. Embedded among these randomly placed graphemes were a number of other graphemes (e.g., 5 sec among 2 sec), which made up an embedded figure, such as a square or triangle. Because of the visual similarity between the graphemes, non-synesthetic subjects found it difficult to identify the embedded figure. On the other hand, synesthetes, who experienced the 5 sec and 2 sec as different colors were better able to detect the embedded figure (Ramachandran and Hubbard, 2001a; see also Hubbard et al., 2005).

We used a modified version of this experiment, using three contrasts (3%, 10% and 100% black on a neutral gray background). Because his reported color experiences were strong at 100% and nearly non-existent at 3% contrast, we predicted that JC would show better performance than controls at high contrast, but not at low contrast. Because JC rated his color experience at 10% contrast to be weaker, but still present, we predicted a moderate

behavioral advantage for JC compared to controls at this contrast. In pilot testing, we found that overall performance was reduced to chance at black levels of 1-2%. We therefore chose 3% as the lowest contrast yielding better than chance performance.

Methods

Subjects

We tested 20 naïve UC San Diego undergraduate subjects and JC. All subjects had normal or corrected-to-normal vision. This project was approved by the Institutional Review Board of UC San Diego, and all subjects gave informed consent prior to participating in this study.

Apparatus

For Experiments 2 and 3, we used a 16" Sony VisionMaster E773 Monitor. This monitor generated slightly lower luminance values (0 to 65.3 cd/m^2) than that used for Experiment 1, but because the luminance of the neutral gray was also lower (7.8 cd/m^2 compared to 18.4 cd/m^2) overall Weber contrasts were higher, ranging from -1.00 to 7.37.

Stimuli

Subjects were presented with displays containing 44-48 letters for one second. Embedded in these displays was one of four shapes (square, rectangle, diamond or triangle) composed of 6-8 letters. The embedded shape could appear in one of eight locations randomly. Subjects were presented with 4 blocks of 96 trials each, for a total of 384 trials. Within a block, the same letter always made up the target shape. For a given display two of the non-target letters were distracters. The identity of the distracters varied within blocks.

Displays were presented at three levels of contrast (nominally, 3%, 10% and 100% black; Weber contrast $-.10$, $-.32$ and -1.00 respectively) on a neutral gray (7.8 cd/m^2) background. All three contrasts were randomly presented within the same block. For control subjects, block order was counterbalanced using a Latin-square design. Synesthete JC participated in only one order. Subjects were told to indicate which target shape they saw via button press ('s', 'd', 'r' or 't'), and if they were uncertain as to the identity of the target shape, they should guess.

Analysis and Results

Results are plotted in Figure 3. As ANOVA is not appropriate for comparing a single subject against controls when using percent correct data (the variance of the synesthete group is by definition 0) we used a modified version of the
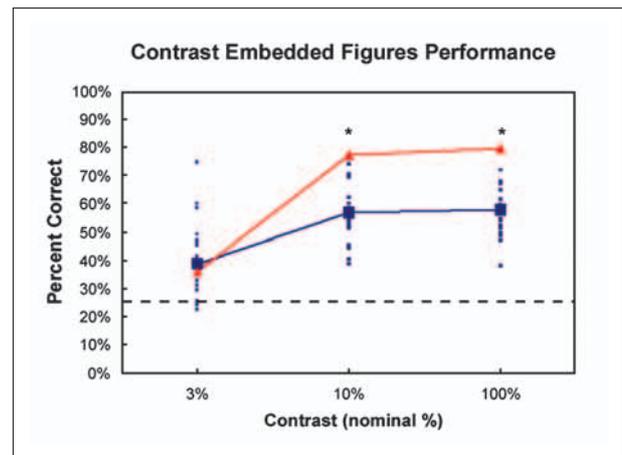

Fig. 3 – *Performance as a function of contrast for synesthete JC and controls on the embedded figures task. Percentage correct as a function of contrast is indicated for our synesthete JC and 20 control subjects. Synesthetic subject JC is indicated by large red triangles, individual control subjects are indicated by small blue squares and the mean of the controls by large blue squares. Chance performance is indicated by the dashed line at 25% correct.*

standard t-test, which is preferable for the comparison of single subjects against small samples (Crawford and Howell, 1998). Due to the small sample size, we first computed Shapiro-Wilke Ws (Shapiro and Wilke, 1965), which assess deviations from normality in a sample. At all contrasts, the control subjects' performance was normally distributed (all Ws > .85, all ps > .05). A second potential concern is that the variance of synesthetes may be greater than the variance of controls, as this might yield artificially high Type I error rates (Mycroft et al., 2002). Although we cannot rule this out with the current data, analyses of other data obtained from high-contrast versions of the tasks used here give no evidence that synesthetes are more variable in their performance than controls (see Hubbard et al., 2005).

We computed the modified t-tests for each contrast level independently. Using this modified t-test, we find that JC is significantly better than control subjects at 100% contrast [t(19) = 2.33, p < .05 two-tailed] and shows a trend towards better performance than control subjects at 10% contrast [t(19) = 1.65, p = .06 one-tailed], but was no different from controls at 3% contrast [t(19) = $-$.20, p > .30 one-tailed]. Finally, inspection of individual subject data (Figure 3) shows that JC performed better than any of the twenty control subjects in both the 100% and 10% contrast conditions[2]. Finally, we note that both the control subjects and JC performed significantly better than

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[2]These data suggest that the modified t-test we have used here may be somewhat conservative since the probability of obtaining this result by chance alone is p < .05 (by definition). That is, out of 21 randomly chosen observations from the same population each value would have the same chance of being the top score. The chance of any individual sampling event producing the top score must be 1/21 = 4.76%. So on a random basis, with 20 controls and 1 synesthete, there would be a less than 5% chance of JC being the top scorer by chance alone.

chance (38.87% and 35.94% correct, respectively) in the 3% contrast condition, arguing against the possibility that this effect is simply due to floor effects in the 3% contrast condition.

The fact that JC performed better than control subjects at high contrast, but not at low contrast, where he reports that his synesthetic colors were not experienced, demonstrates a tight coupling between the subjective measures of color strength in Experiment 1 and the objective data obtained here in Experiment 2. These results suggest, at least for JC, that the presence or absence of synesthetic colors can be modulated by contrast and that these effects mediate behavioral performance on the embedded figures task.

EXPERIMENT 3

Contrast Crowding

In our third experiment, we examined the effect of contrast on behavioral performance in our crowding task (Ramachandran and Hubbard, 2001b). Briefly, crowding occurs when a single target item is surrounded by other flanking items, such as when a target letter is surrounded by other flanking letters in reading (Bouma, 1970). This effect is relatively small in the fovea, but increases dramatically in the periphery, far more quickly than peripheral factors such as optics, retinal sampling, or cortical magnification in V1 can account for (Strasburger et al., 1991), leading some to suggest that the mechanisms of peripheral and foveal crowding are different (compare Levi et al., 2002a, 2002b).

A large body of research has examined the effects of contrast and similarity on detection of letters in the periphery, and the magnitude of the crowding effect. For example, Strasburger et al. (1991) examined the effects of contrast, target size and crowding on number identification at various eccentricities. Overall, at greater eccentricities, numbers had to be larger and higher contrast to be accurately identified (67% threshold, 10-AFC). These two factors traded off, so that with larger size stimuli (for a given eccentricity) the contrast required to identify the number was reduced. In the presence of flankers, the contrast threshold was slightly increased for the smallest size stimuli, but not for larger stimuli. Under the conditions used in our experiment (a 1.2° tall letter presented at about 8° eccentricity) the presence of crowders had no impact on the contrast threshold to identify the number. Similarly, Chung et al. (2001), using spatially filtered letters showed that contrast has only a marginal effect on threshold elevation in the crowded condition compared to the uncrowded condition.

Crucially for our experiments, it has been shown that the magnitude of the crowding effect significantly modulated by target-flanker similarity (Kooi et al., 1994). Subjects were better able to report the orientation of the target (the letter 'T') when the flankers were presented in either opposite achromatic contrast polarity (black *vs.* white) or different colors. For example, if a red target is surrounded by green flankers, the magnitude of crowding is reduced relative to if both the target and flanker were red. In addition, Chung et al. (2001) have provided data showing that as the ratio of the contrast between the flankers and targets increases, the effect of crowding (measured as threshold elevation) increases. This suggests that the Kooi et al. (1994) results are not simply due to low-level grouping by contrast, but instead may be due to higher-level interactions.

In our earlier experiments, we have demonstrated that synesthetic colors lead to a similar reduction in the magnitude of the crowding effect (Ramachandran and Hubbard, 2001b). JC reported that he experienced his colors, despite not being able to actually identify the target letter, and that he inferred the identity of the target letter based on his synesthetic colors. One way to make sense of these results is in terms of attentional theories of crowding (He et al., 1996; Strasburger et al., 1991), which suggest that spatial uncertainty may make it difficult to integrate stimulus features into a coherent whole. These attentional limitations may have decreased JC's ability to appropriately bind features, thereby leading to his inability to recognize the grapheme despite substantial processing. However, this processing may have been sufficient to elicit a synesthetic color, and since chromatic differences do not depend on attention or spatial position information, crowding would have left color pop-out unaffected.

In the current experiment, we predicted that because JC reports experiencing colors when presented with high-contrast letters, he should show a behavioral advantage on this crowding task compared to control subjects, replicating our previous findings with black letters on a white background (Ramachandran and Hubbard, 2001b). However, because JC no longer experiences synesthetic colors when presented with low-contrast letters his behavioral advantage would be reduced or eliminated at low contrasts. We should make clear that our prediction here is not that an interaction between crowding and contrast will eliminate synesthetic colors. As we have already demonstrated, synesthetic colors can be eliminated even in free foveal viewing with no flankers (Experiment 1). Rather, we predict that since JC experiences colors at high contrast, he should perform better than controls due a synesthetically induced contrast between the target and the flankers. In the absence of those colors at low contrast, this behavioral advantage should be eliminated. In order to better compare psychophysical performance with JC's phenomenological reports, we tested a wider

range of contrasts, from −100% contrast (white on gray) to 100% contrast (black on gray).

Methods

Subjects

Subjects were 12 naïve UC San Diego undergraduates and synesthete JC. All subjects had normal or corrected-to-normal vision. This project was approved by the Institutional Review Board of UC San Diego, and all subjects gave informed consent prior to participating in this study.

Apparatus

All stimuli were generated by a PC running a Java program and were displayed on a 16" ViewSonic E773 monitor (1024-768 pixels, refresh rate 70 Hz). Stimuli were presented in a dimly lit room at a viewing distance of 60 cm (24"). The display area of the screen measured 320 × 243 mm, corresponding to 30 × 22 degrees. The appearance of stimuli was timed to an accuracy of ± 7 ms.

Stimuli

Subjects initiated each trial with a button press, after which a central fixation cross appeared for 1000 msec. They were then presented with one of four different target letters (E, F, H or O, which elicit strong experiences of red, yellow, green and blue respectively for JC) flanked on all four sides (above, below and to the left and right) by one of the four letters for 100 msec, after which the screen was blanked for 250 msec to avoid any masking effects. Subjects were then prompted to respond by making a 4-alternative forced choice response by key press on the computer keyboard. Subjects were not given feedback.

Target and crowder letters varied in a full 4 × 4 factorial design (that is, the target letter and crowder letters varied independently on any given trial for a total of 16 possible combinations), so that the identity of the crowders presented no information about the identity of the target letter. The letters were in presented Arial font and subtended a visual angle of 1.2-1.6 degrees. The central stimulus letter appeared at an eccentricity of 7.1 degrees. The spacing from the edge of one letter to the next was .2 degrees, and center-to-center spacing of the letters averaged 1.4 degrees. Chung et al. (2001) have shown that at 5° eccentricity, crowding is maximal within a critical letter spacing of approximately 2°, irrespective of spatial frequency. Given that our stimuli were presented more peripherally, we would expect this window to be even larger for our stimuli, so we can be relatively certain the target grapheme was strongly crowded.

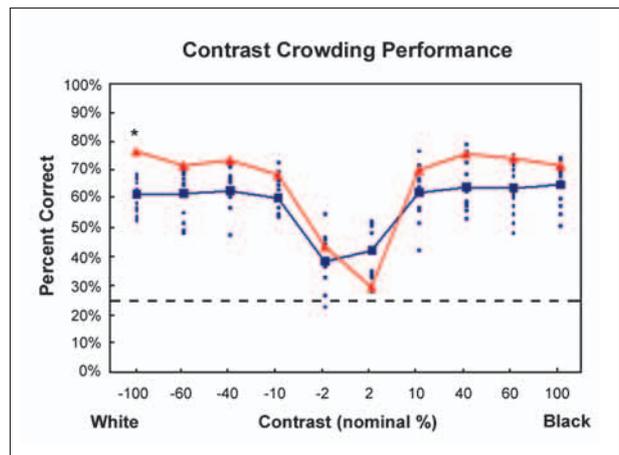These 16 combinations were presented randomly to the left or right of fixation, at five

Fig. 4 – *Performance as a function of contrast for synesthete JC and controls on the crowding task. Percentage correct as a function of contrast is indicated for our synesthete JC and 12 control subjects. Synesthetic subject JC is indicated in red and controls in blue. Chance performance is indicated by the dashed line at 25% correct.*

levels of contrast (nominally 100%, 60%, 40%, 10%, 2%) in two colors (black and white) for a total of 320 displays (16 × 5 × 2 × 2). Subjects were presented with 8 blocks of 160 trials (the trial list was shuffled and a break inserted midway through the 320 trials), in random order, totaling 1280 trials. Background screen luminance was 7.8 cd/m^2 and Weber contrast ranged from − 1 to + 7.37. All the shades of gray had CIE chromaticity coordinates x = .27-.30, y = .30.

Analysis and Results

As shown in Figure 4, performance varied as a function of contrast for both synesthetes and controls, with the worst performance being observed at the lowest contrasts. Additionally, Figure 4 shows that JC performed better than controls at high contrast, but not at low-contrast. To compare performance between JC and control subjects, we again used the modified t-test used for the embedded figures task, and tested the same assumptions of normality in controls, and homogeneity of variance between synesthetes and controls. Control subjects' performance was normally distributed at all three contrast levels (all Ws > .90, all ps > .05). There was a trend towards positive skew at the 3% contrast level (W = .91, p = .06) suggesting that performance was approaching floor. However, the median performance (37.5%) and range of the sample (23%-75%) suggest that performance was not limited by chance performance. Additionally, analysis of data from a high-contrast version of this task, again suggests that there is no difference in the variability of synesthetes and controls (Hubbard et al., 2005).

When we compute the modified t-statistic, we find that JC's performance exceeds that of controls at only 100% white [t(11) = 2.437, p < .05 two-

tailed], replicating our previous finding of a behavioral advantage in the crowding task for JC at high contrast. However, given that the sample size is relatively small, an examination of the individual subjects data may be more informative. Examination of the individual subject data at each contrast shows that JC performs better than any of the controls at 40%, 60% and 100% contrast (white), and better than all but two controls at 10% and −10%, −40%, −60% and −100% (black) contrast. However, there is no single control subject that consistently performed better than JC. Instead, several subjects consistently performed well, sometimes better than JC, and sometimes worse than JC.

Interestingly, at the lowest contrast JC's performance was markedly impaired (29.7%), consistent with his introspective report that when he did not experience his colors, he "didn't know what to do." In our previous study using high-contrast targets and crowders JC had reported that he often was unable to identify the target letter, but experienced his colors, and was able to infer the identity of the target letter on the basis of the correspondence between his colors and the identify of the graphemes (Ramachandran and Hubbard, 2001b). It seems that, in the absence of this strategy, JC was unable to infer the identity of the target letter and therefore had to resort to more traditional routes of letter recognition in the crowded condition.

Discussion

A growing body of evidence suggests, at least for some synesthetes, that their synesthetic concurrents are real and that they have verifiable perceptual consequences (Palmeri et al., 2002; Ramachandran and Hubbard, 2001a; Smilek et al., 2001). Imaging studies further suggest that synesthetes' brains respond differently than non-synesthetes brains when hearing words (Nunn et al., 2002; Paulesu et al., 1995) or when viewing graphemes (Hubbard et al., 2005). The finding that the subjective strength of synesthetic colors (and to a lesser extent, the behavioral advantage seen in our embedded figures and crowding paradigms) decreases with contrast suggests that, not only are synesthetic *concurrents* perceptual, but so too are synesthetic *inducers*. Specifically, our results suggest that it is the *percept*, rather than the abstract concept of the grapheme, or any associated higher level processing, that elicits synesthetic colors in subject JC, consistent with our prior observations that clusters of dots and Roman numerals were ineffective in eliciting synesthetic colors (Ramachandran and Hubbard, 2001b).

An examination of the known properties of synesthetic experience and the known properties of fusiform responses to letters and other classes of object stimuli suggests that this region may be the neural level at which synesthetic experience is elicited. Numerous imaging studies have identified a region of the fusiform gyrus (especially in the left hemisphere) that responds more strongly to visually presented letters and words than to false fonts with equivalent visual complexity (Petersen et al., 1988, 1990) dubbed the visual word form area (VWFA) (Cohen et al., 2000, 2002; for a review see Cohen and Dehaene, 2004). Previous studies using visually presented numbers have also found activation in roughly this same region (Pesenti et al., 2000; Rickard et al., 2000). Recordings from cortical surface electrodes find distinct populations that respond to letters and numbers (Allison et al., 1994), suggesting an extremely fine-grained organization (perhaps too fine to be observed with functional imaging). Finally, the VWFA responds only to written, but not spoken words (Dehaene et al., 2002) and damage to this area results in a severe impairment in word identification, pure alexia, which is restricted to the visual modality (Leff et al., 2001). Both of these results suggest that the VWFA that is specialized for the *visual perceptual* identification of these stimuli, rather than representing higher order conceptual processes.

One prediction we would therefore make is that responses in the VWFA should be modulated by contrast, as are the strength of synesthetic colors. Mechelli et al. (2000) measured rCBF in six subjects while they viewed either short or long words (3, 6 or 9 letters) at either high or low contrast. They find that (1) responses in the both the fusiform and lingual gyri are larger for long words than short words (2) increased contrast leads to an increased response in the fusiform gyrus, but a decreased response in the lingual gyrus and (3) contrast linearly shifts the rCBF upward or downward in these regions (i.e., there is no interaction between word length and contrast). Avidan et al. (2002) measured contrast responses along the ventral visual pathway from V1 to inferior temporal regions LOC and pFs using fMRI. They found that although contrast dependency decreased at higher levels of the visual pathway, even object selective regions in the inferior temporal lobe were still substantially modulated by contrast. Intriguingly, measured fMRI responses in LOC and pFs increase from 0% to 10%, and then level off between 10 and 100% contrast, mirroring the pattern of behavioral performance we observed here (Figures 3 and 4). Together, these results suggest that similar modulations of neural responses in the VWFA underlie the modulations in the strength of the synesthetic colors that we observe here.

Additional comparisons between what is known about the response properties of the VWFA and what is known about synesthesia further suggests that this area is the neural substrate of the

synesthetic inducer. This region is activated by letters that are defined both by standard luminance edges and by motion defined edges (Noguchi et al., 2004), suggesting a certain degree of invariance over the specific features used to define the letter (for converging single unit data with other classes of objects, see Kovács et al., 2003). Palmeri et al. (2002), report that their synesthete WO experiences synesthetic colors for luminance defined, disparity defined and motion defined letters, and we find that presentation of letters defined by illusory contours and amodally completed forms elicits the usual colors, although the exact quality of these colors is mildly affected (Ramachandran and Hubbard, 2003). This suggests that the activation of same letter selective neurons in the VWFA is occurring independent of whether the letter is defined by traditional luminance boundaries, motion boundaries or illusory contours.

The proposal that the VWFA is the neural correlate of the synesthetic inducer is also consistent with phenomenological observations we have previously reported indicating that variations of font affect the exact strength of the synesthetic colors (Ramachandran and Hubbard, 2003). We suggest that the letter and number selective neurons in the VWFA may respond most strongly to prototypical examples of these graphemes, and that when they are presented in less typical fonts, the amount of activation should change, too, in the same way manipulating a face will cause the firing properties of face selective neurons to change. This would then lead to a different pattern of cross-activation between the VWFA and hV4. Consequently, the exact nature of the synesthetic colors should vary depending on low-level perceptual factors such as contrast and font, but might be invariant over the lower-level visual features used to define these letters.

Numerous studies have demonstrated that the VWFA responds in a case and location invariant manner, consistent with the common observation that synesthetic colors are the same for letters irrespective of case (e.g., 'a' and 'A' are both experienced as red) and that they are experienced as having the same color no matter where in the visual field the letter is presented. Polk and Farah (2002) report that responses do not differ depending on whether a word is presented in a mixed case (such as hOuSe) or in one consistent case. Dehaene et al. (2001, 2004) report that the VWFA shows reduced responses when the same word is presented in a different case (e.g., RAGE followed by rage) even if the visual features of the letters are highly dissimilar (e.g., 'A' and 'a'). These neuroimaging findings are consistent with previous behavioral reports of case-invariant priming on letter and word naming tasks (Arguin and Bub, 1995; Bowers et al., 1998; Humphreys et al., 1990) and suggest that the VWFA is the neural locus of these effects. More detailed analysis of the

VWFA repetition suppression demonstrates that there may be two distinct regions, a posterior region, which shows no repetition suppression when letters are presented in different locations, and an anterior region, which shows positionally invariant repetition suppression (Dehaene et al., 2004; c.f., Ito et al., 1995).

Based on the observation that synesthetic colors can be affected by context and meaning, Merikle and colleagues have argued that synesthetic colors may be mediated by feedback between conceptual representations in the anterior inferior temporal (AIT) and color selective regions, rather than the direct cross-activation between adjacent VWFA and hV4 (Myles et al., 2003; Dixon et al., 2004). However, the presence of contextual modulations does not rule out the possibility of direct cross-activation between the VWFA and hV4 in synesthesia. Instead, neurons in the VWFA may be modulated by top-down influences from AIT. If different populations of neurons in the VWFA were active due to this modulatory influence, this would lead to cross-activation of different color selective neurons in hV4. Given the coarse resolution of both psychophysical and functional neuroimaging, the resolution of these debates will probably depend on the use of techniques that permit more fine-grained temporal resolution, such as EEG or MEG.

Finally, it has been suggested that the visual grapheme does not need to be physically presented, but that a conceptual representation may be sufficient for the experience of synesthetic colors (Dixon et al., 2000; Smilek et al., 2002). Dixon et al. presented their synesthetic subject, C, with addition problems by presenting a digit, an operator, second digit and a color patch (e.g., 5 + 2, green). C was required to report the color of the patch and then the solution to the addition problem. Reaction times were slower when the color patch was incongruent with the color that C experienced for the solution of the addition problem. In this example, if the addition problem was followed by a green color patch (C experiences 7 sec as yellow) then reaction time was longer than if a yellow color patch was presented.

However, these results do not provide unambiguous proof for the conclusion that C was using only a conceptual representation of the number. If C were to have imagined the graphemes, she would have activated category selective regions in the fusiform gyrus (e.g., O'Craven and Kanwisher, 2000), leading to the activation of the synesthetic color. Although Smilek et al. (2002) recognize that imagery might be a factor, they suggest that, "for C, digits qualify as higher level concepts" (p. 573). We instead suggest top-down activation of the VWFA through mental imagery as an alternative explanation of their results, although behavioral data cannot distinguish between these two accounts.

Finally, it should be noted that whether the synesthetic color is elicited at a perceptual or conceptual stage might vary significantly between synesthetes. We have previously suggested that grapheme-color synesthesia may be composed of (at least) two subtypes, which we refer to as "higher" and "lower" synesthetes (Ramachandran and Hubbard, 2001b; for similar distinctions see Dixon et al., 2004; Grossenbacher and Lovelace, 2001; Smilek and Dixon, 2002). One piece of evidence for this heterogeneity comes from our recent behavioral and neuroimaging studies of synesthetic concurrents (Hubbard et al., 2005). We tested six grapheme-color synesthetes, who all reported seeing colors for letters and numbers, on our embedded figures task (Ramachandran and Hubbard, 2001a) and our crowding task (Ramachandran and Hubbard, 2001b). We find that overall, synesthetes perform better than controls on the embedded figures task, replicating our previous finding. However, in the crowding task, only three of our synesthetes perform better than their respective control populations. Analysis of individual subject's data, however, shows that those synesthetes who showed the best behavioral performance in the embedded figures task also showed the best performance in the crowding task.

Subsequent fMRI studies of hV4 activation in these same subjects showed that hV4 was more active in synesthetes than controls. Crucially, we also find that the magnitude of the activation correlates with psychophysical performance on the crowding task. Those synesthetes who showed the greatest behavioral advantage on the crowding task also showed the greatest about amount of fMRI activation in hV4. We suggest that these differences at individual level indicate that, although group level studies can uncover significant differences between synesthetes and non-synesthetes, that there may also be important differences between individual synesthetes.

Future studies of grapheme-color synesthesia will have to carefully evaluate the level of processing at which both the synesthetic inducer and concurrent are elicited. If we are correct in our hypothesis about higher and lower synesthetes, we would predict that those synesthetes who experience the strongest concurrents would have perceptual level inducers, while those who experience weaker concurrents would have conceptual level inducers.

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