Language regions of brain are operative in color perception

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The effect of language on the categorical perception of color is stronger for stimuli in the right visual field (RVF) than in the left visual field, but the neural correlates of the behavioral RVF advantage are unknown. Here we present brain activation maps revealing how language is differentially engaged in the discrimination of colored stimuli presented in either visual hemifield. In a rapid, event-related functional MRI study, we measured subjects' brain activity while they performed a visual search task. Compared with colors from the same lexical category, discrimination of colors from different linguistic categories provoked stronger and faster responses in the left hemisphere language regions, particularly when the colors were presented in the RVF. In addition, activation of visual areas 2/3, responsible for color perception, was much stronger for RVF stimuli from different linguistic categories than for stimuli from the same linguistic category. Notably, the enhanced activity of visual areas 2/3 coincided with the enhanced activity of the left posterior temporoparietal language region, suggesting that this language region may serve as a top-down control source that modulates the activation of the visual cortex. These findings shed light on the brain mechanisms that underlie the hemifield-dependent effect of language on visual perception.

functional magnetic resonance imaging (fMRI) | lateralization

A typically viewed scene permits multiple visual parses, some of which can be readily mapped onto linguistic terms, whereas others cannot. Does linguistic information play a role in visual perception? For more than half a century, this question has provoked controversy. According to the hypothesis proposed by Benjamin Lee Whorf (1), by filtering perception, language affects our apprehension of the world. This hypothesis has received conflicting evidence (2–21); a recent review favors the view that linguistic categories filter some, but not all, perceptual inputs and that perceptual factors influence, but do not exclusively determine, linguistic categories of color (22).

Recent neuropsychological investigations examining visual field asymmetries in the categorical perception (CP) of colors have provided a new perspective on Whorfian effects. In a study using a visual search task (7), adult English speakers were required to detect a single target color among 11 identical distractor colors. Response times for finding the target were faster when target and distractors were from 2 different lexical categories (e.g., a green target among blue distractors) than when target and distractors were from the same lexical category (e.g., a particular green among distractors of a different green), but only when the target was exposed in the right visual field (RVF). Because the RVF projects to the left cerebral hemisphere, the dominant hemisphere for language in most adults, and because the effect was eliminated by a concurrent task occupying verbal processing resources but not by an equally difficult task occupying nonverbal resources, the RVF CP finding suggests that the spontaneous use of lexical codes in the left hemisphere may be the origin of the differential visual hemifield

response to colors. A subsequent study (9) with different tasks extended this result and showed stronger category effects (i.e., faster responses to between-category color pairs than to within-category color pairs) in the RVF than in the left visual field (LVF), although the LVF did show a significant, if weaker, category effect. A third study (12), testing a color term boundary in Korean that does not exist in English, found CP only in the RVF for relatively rapidly responding subjects but CP in both visual fields for slowly responding subjects and no CP at the Korean-only boundary for English-speaking subjects. The authors of that study suggest that LVF color CP in slower-responding adults probably reflects cross-callosal transfer; the same conclusion has been drawn elsewhere (14, 23). Hence it is possible that in normal adults, color CP is restricted to the left hemisphere, with apparent LVF CP an artifact of transcallosal transfer and/or scanning.

Despite growing behavioral evidence for hemifield-dependent category effects, the neural correlates of these effects remain unknown. One previous functional MRI (fMRI) study (24) found that, in comparison with hard-to-name colors, perceptual discrimination of easy-to-name colors evoked stronger activation in the posterior temporoparietal regions responsible for successful word-finding processes, but the study was not designed to look into neural substrates of the behavioral RVF superiority in color perception, and it did not clarify whether linguistic information aids in the activity of brain regions responsible for color vision.

In the current rapid event-related fMRI study, we investigated neural mechanisms underlying hemifield-modulated Whorfian effects in adults. We scanned subjects' brain activity while they performed the visual search task used in the original lateralized Whorf study (7). The search included colors selected from a set of 4 (Fig. 1A). These 4 colors form a graded series from green to blue, with the green−blue boundary falling between G2 and B1. In the visual search task, each stimulus display consisted of a ring of colored squares surrounding a central fixation marker (Fig. 1B). Except the target, all the squares were of the same color. The target and distractor colors were either from within the same lexical category (e.g., a blue target and distractors of a different shade of blue, "within category") or from different lexical categories (e.g., a green target and blue distractors, "between category"). On each trial, participants were asked to indicate whether the target was on the left or right side of the circle by making timed button-press responses with the corresponding hand. In this manner, 2 variables were manipulated:
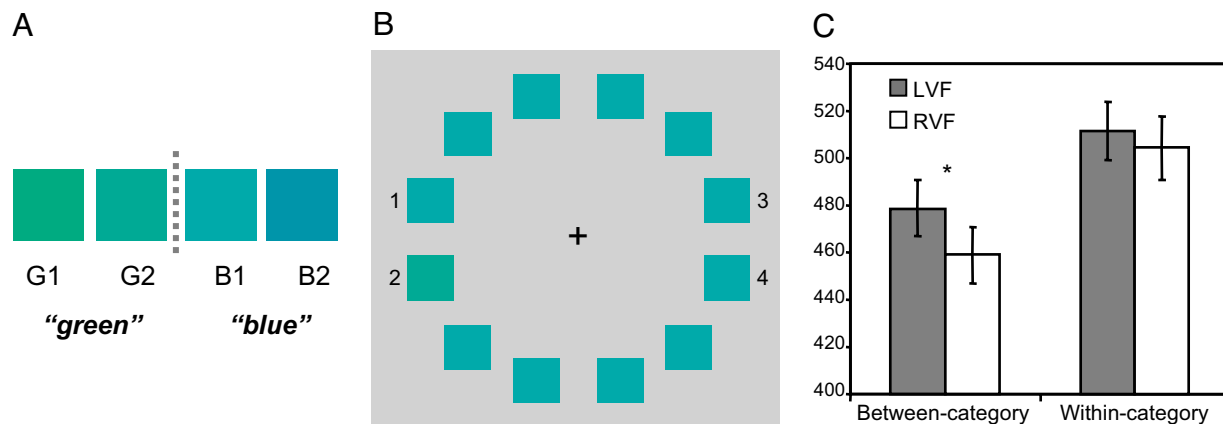
Fig. 1. Experimental materials and behavioral results. (*A*) Printed-rendered versions of the 4 colors used. (*B*) Sample display for the visual search task. The target occupied any of the 4 positions (position 1, 2, 3, or 4). This example shows a between-category, LVF pair. (*C*) Behavioral performance in the 4 conditions. Error bars indicate SEM. *, significant difference in response ($P < 0.05$).

the visual field of the target (LVF vs. RVF) and the categorical relationship between the target and distractor colors (between-category vs. within-category). There were 2 types of target-distractor pairs: 1-step within-category (G1G2 and B1B2) and 1-step between-category (G2,B1).

We tested 2 predictions of the Whorf hypothesis. First, if lexical codes of colors are accessed during visual search, discrimination of colors should evoke activations of cortical regions contributing to language processes, such as left temporoparietal areas and the left inferior prefrontal gyrus. Furthermore, activity levels of these language regions should be stronger for between-category than within-category stimuli, especially in the RVF, as predicted by previous behavioral studies (7, 9, 12). Second, if lexical information enhances the perceptual difference rather than merely being accessed as a byproduct of color identification, activations of brain regions for color perception, such as visual area 2/3 (V2/3) and visual area 4 (V4), should be altered by the activation of linguistic information, particularly in the RVF condition.

Results

Behavior. Trials in which the participant pressed the wrong key or in which the reaction time (RT) was > 2 SD from the grand mean were excluded. Two participants' behavioral data were discarded, 1 because of head motion during the brain scan and the other because button responses were recorded inaccurately. As illustrated in Fig. 1*C*, with regard to main effects, between-category RTs were significantly faster than within-category RTs [468.80 ms vs. 507.89 ms, $F(1, 13) = 27.24$, $P < 0.001$], and RVF RTs were faster than LVF RTs at a level approaching significance [481.6 ms vs. 495.09 ms, $F(1, 13) = 3.41$, $P = 0.088$]. The interaction of the 2 variables also approached significance [$F(1, 13) = 3.62$, $P = 0.079$], with RVF between-category RTs being the shortest. For between-category pairs, RVF RTs were significantly faster than LVF RTs (458.9 ms vs. 478.69 ms, $t = 2.73$, $P < 0.05$). For within-category pairs, LVF RTs were faster by a scant 7 ms, not approaching significance (511.497 ms vs. 504.29 ms, $t = 0.08$, $P = 0.423$). For RVF targets, RTs in the between-category condition were 45 ms faster than in the within-category condition ($t = 5.68$, $P < 0.001$). For LVF targets, RTs in the between-category condition were 33 ms faster than in the within-category condition ($t = 3.914$, $P < 0.005$). In general, this pattern of behavioral data is consistent with previous studies using the same (7) or similar (9, 12) paradigms, suggesting that the color CP effects for normal language users are stronger in the RVF than the LVF (i.e., lateralized Whorf).

fMRI Results. We first calculated an average effect of color perception tasks by collapsing and contrasting all of the color conditions (LVF within-category, LVF between-category, RVF within-category, and RVF between-category) against an implicit baseline available in the fast event-related fMRI design (Fig. 2 and Table 1). Consistent with previous neuroimaging studies of color vision (24–31), subjects showed strong activations in the neural circuitry attributed to color perception, including V2/3 and V4 bilaterally. The left temporoparietal areas known to mediate lexical processes were activated also. Bilateral inferior parietal cortex and motor cortex also showed strong activity, presumably because of motor responses required by the visual search task.

The main effect of categorical relationship (between-category versus within-category pairs) was computed by collapsing the data from the 2 visual fields. As depicted in Fig. 3 (Table 2), several language areas involving the left posterior temporoparietal region [Brodmann areas (BA) 40 and 39], the left middle-superior temporal gyrus (BA 21 and 22), and the left inferior
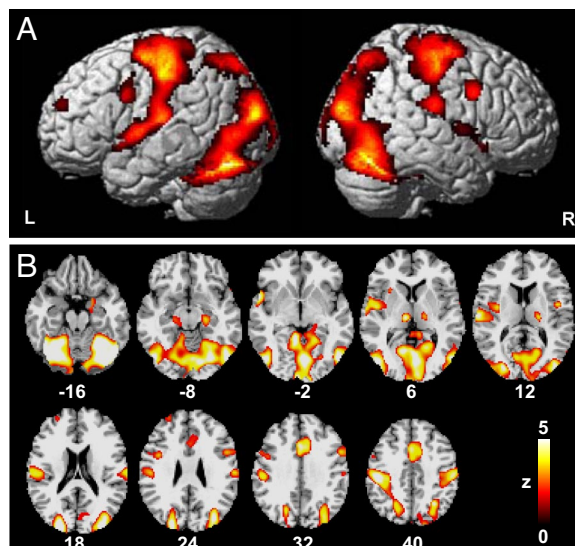

Fig. 2. An average effect map of color discrimination tasks. Data from all of the color conditions (LVF within-category, LVF between-category, RVF within-category, and RVF between-category) were collapsed. (*A*) Lateral view. (*B*) Axial sections. The significance threshold is $P < 0.05$ FDR-corrected. L, left hemisphere; R, right hemisphere.

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Table 1. Coordinates of activation peaks: An average effect of color discrimination tasks

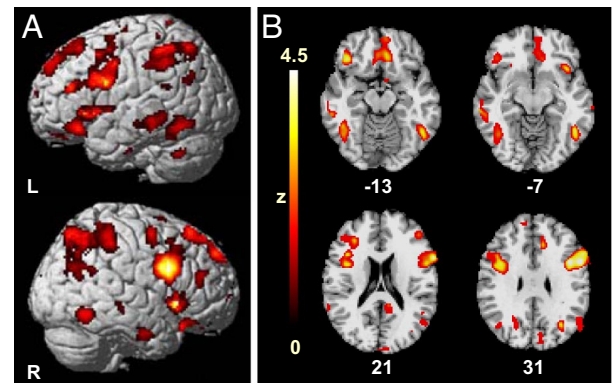| Regions activated	Brodmann area	X	Y	Z	Z-Score
Occipital					
Left V4		−28	−69	−12	5.71
Left V4 alpha		−36	−50	−19	6.60
		−46	−59	−17	6.31
Right V4		26	−69	−13	6.05
Right V4 alpha		46	−59	−19	5.77
V1		4	−72	4	5.78
		0	−72	−1	5.53
V2/3		−28	−84	21	6.60
		28	−86	25	5.84
		−16	−64	9	5.54
Frontal					
Left inferior frontal gyrus	44	−44	5	27	3.88
Left middle frontal gyrus	6	−36	−3	57	5.09
	9	−53	9	33	3.10
	10	−30	53	19	3.65
Left precentral gyrus	4	−51	−13	52	5.16
	6	−32	−18	64	5.16
Left postcentral gyrus	2	−48	−25	44	5.39
Right inferior frontal gyrus	44	48	11	29	4.42
Right precentral gyrus	4	48	−7	57	5.35
	6	40	−3	59	4.93
	4	53	−13	47	4.85
	6	42	−1	11	3.99
Cingulate gyrus	24	−4	2	46	6.13
	32	−2	17	36	4.98
Left insula		−32	16	5	3.28
Parietal					
Left superior parietal lobule	7	−26	−58	51	4.97
Right superior parietal lobule	7	26	−56	45	5.15
Temporal					
Left superior temporal gyrus	22	−57	6	−2	4.99
	42	−61	−17	14	4.98
Right superior temporal gyrus	22	63	0	4	3.71
	38	55	17	−8	3.13
	22	61	10	1	3.05
Subcortical areas					
Thalamus		−12	−19	6	5.18
		16	−17	10	3.94

Fig. 3. A main effect map of categorical relationship (between-category and within-category colors). Data from the 2 visual hemifields were collapsed. (*A*) Lateral view. (*B*) Axial sections. The significance threshold is $P < 0.05$ FDR-corrected. L, left hemisphere; R, right hemisphere.

prefrontal gyrus (BA 47) were strongly activated. These regions had been shown to govern lexical search and semantic retrieval in past lesion and neuroimaging investigations of aphasia and language functions (24, 32–47); their activation in the visual search task indicates that linguistic information of colors is rapidly activated and represented in the brain.

To ascertain whether there is a stronger activation category effect in the RVF than in the LVF, we calculated separate activation maps for each visual field, relating between-category color discrimination to within-category color discrimination, with a significance level for between-condition differences being set at $P < 0.05$ false discovery rate (FDR) corrected for multiple comparisons. For the RVF color stimuli, activation produced by discrimination of colors from different lexical categories minus activation from same-category colors was very strong in the left posterior temporoparietal region (BA 40), the left middle temporal gyrus (BA 21), and the left inferior prefrontal cortex at BA 47 (Fig. 4 *A* and *B*). This pattern of data converges with the aforementioned results from the main effect of categorical relationship. The total activation volume in these 3 regions, as indexed by number of voxels, is 1007 (Fig. 4*D*). Equally impor-

tant is the significant difference in response delay between colors in the same lexical category and colors in differing lexical categories, as illustrated in an averaged response delay difference map (Fig. 4*C*). On a voxelwise basis, hemodynamic responses were slower in all 3 language regions for same-category pairs than for different-category pairs, suggesting that lexical information speeds up the perceptual processing of the RVF colors.

Nonetheless, when the color stimuli were displayed in the LVF, discrimination of colors from different lexical categories minus colors from the same lexical category did not provoke stronger activation of any of language-related regions such as the left posterior temporoparietal network (BA 40) when the significance threshold was set at $P < 0.05$ FDR corrected. When a less stringent threshold of $P < 0.005$ uncorrected was used, the activation of the left posterior temporoparietal regions was seen, with only 92 voxels totally (see Fig. S1). In addition, differences in mean hemodynamic delays were not found in this neural circuitry. These results indicate that differences between the activation of language regions by the LVF between-category stimuli and the LVF within-category stimuli, if any, would be very weak. This finding confirms previous findings that LVF stimuli may activate left-hemisphere language areas by virtue of a longer and "noisier" transcallosal pathway (48, 49).

To determine whether lexical color categories are used to sharpen the perceptual difference through enhanced activation of brain regions for color perception, particularly for RVF color stimuli, we performed a whole-brain, voxel-based analysis of the interaction between visual hemifield and categorical relation. A small set of regions hypothesized a priori to be involved in color perception on the basis of prior results (24) as well as the lexical category effect map of this study were defined to determine the significance of predicted peaks. These regions included the left visual areas (V2/3 and V4) and the left language regions. Peaks that survived the whole-brain analysis thresholded at $P < 0.005$ (uncorrected) and small volume correction with $P < 0.05$ FDR-corrected were considered significant. Relevant regions emerging from this analysis are the left temporoparietal area (BA 40) responsible for language processes and V2/3 crucial for color vision. Fig. 5 depicts averaged activity levels in the 4 conditions. The result shows that activity levels in both V2/3 and BA 40 were significantly enhanced when colors from different lexical categories were exposed in the RVF. Thus, it seems that lexical category information enhances the neuronal response at V2/3 for colors appearing in the RVF.

Table 2. Coordinates of activation peaks: Main effect of categorical relationship

Regions activated	Brodmann area	X	Y	Z	Z score
Frontal					
Left inferior frontal gyrus	47	−32	21	−1	5.97
	47	−44	28	−13	4.33
	44	−42	5	22	5.27
	45	−44	17	19	4.41
Left middle frontal gyrus	8	−38	31	43	3.09
Left superior frontal gyrus	8	−12	33	48	3.74
Left precentral gyrus	6	−38	0	37	4.74
Left insula		−40	2	2	3.38
Right inferior frontal gyrus	47	34	21	−3	6.06
Right middle frontal gyrus	46	42	40	16	3.58
Right superior frontal gyrus	8	12	32	52	4.40
Medial frontal	11	−2	34	−19	4.66
	6	−6	−5	61	3.68
Cingulate gyrus	32	6	23	36	4.62
Parietal					
Left inferior parietal lobule	40	−40	−43	39	4.77
Left precuneus	7	−20	−62	36	5.82
Right inferior parietal lobule	40	44	−35	44	4.00
Right superior parietal lobule	7	28	−56	49	4.44
Right precuneus	7	12	−67	49	3.53
Right supramarginal gyrus	40	46	−49	25	3.38
Temporal					
Left inferior temporal gyrus	20	−51	−13	−30	3.31
Left middle temporal gyrus	21	−67	−29	−7	3.86
Left superior temporal gyrus	22	−65	−46	21	3.26
Left fusiform gyrus	37	−48	−49	−11	3.85
Left angular gyrus	39	−44	−64	31	2.92
Right inferior temporal gyrus	20	53	−9	−25	3.49
Right superior temporal gyrus	38	36	22	−21	4.31
Right fusiform gyrus	37	46	−55	−7	4.47
Right angular gyrus	39	51	−67	29	3.44
Occipital					
V2/3	18	8	−85	13	3.98
	18	4	−72	28	3.61
	18	−8	−83	13	3.13
	19	4	−84	32	2.75
Right superior occipital gyrus	19	32	−69	26	3.71
Limbic lobe					
Posterior cingulate	31	6	−61	14	3.32

Brain Region	BA	Voxel	Talariach coordinates			Z value
			x	y	z	
L inferior frontal gyrus	47	420	-44	28	-15	5.88
L middle temporal gyrus	21	410	-67	-41	2	4.13
L supramarginal gyrus	40	177	-48	-55	30	3.44

Fig. 4. Brain regions with significant activation during the identification of colors from different lexical categories in the right visual field in comparison with colors from the same lexical category in the right visual field. (*A*) Lateral view. (*B*) Language regions in the brain showing stronger activation in the between-category condition than in the within-category condition. (*C*) Language regions in the brain that exhibited significantly slower hemodynamic responses in the within-category color condition than in the cross-category color condition. (*D*) Coordinates of activation peaks in the 3 language areas. The significance threshold is $P < 0.05$ FDR-corrected.

Discussion

We have found brain language regions participating in categorical color perception when subjects performed a visual search task. The activity of the language regions, however, was modulated by the visual field in which the stimulus appeared, as demonstrated by the following findings. First, in the RVF, perception of target and distractor colors from different linguistic categories (contrasted with target and distractor colors from the same linguistic category) activates language areas including the posterior temporoparietal region, the middle temporal gyrus, and the inferior prefrontal cortex in the left cerebral hemisphere, but in the LVF perception of target and distractor colors from different lexical categories is not associated with stronger activity in any language regions. Second, the activation of language regions seems to exhibit a slower hemodynamic response for colors from the same lexical category than for colors from different lexical categories, but only when the colors are presented in the RVF.

These findings therefore extend prior neuropsychological and brain mapping studies (7, 9, 12, 24) and unequivocally demon-
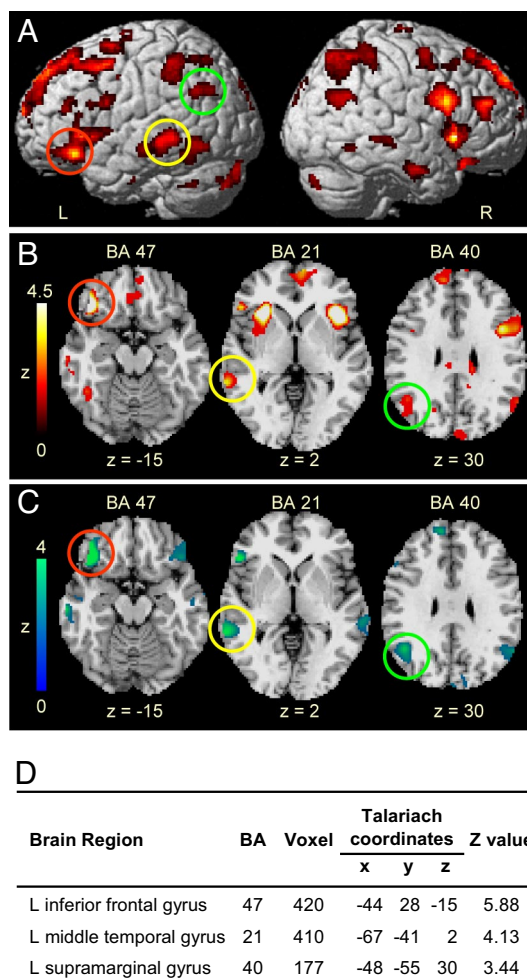
strate hemifield-dependent activations of language regions in a color-discrimination task.

Lexical color information not only was accessed in color discrimination but also enhanced the activation of color region V2/3. When the colors exposed in the RVF were from differing lexical categories, activation of V2/3 was much stronger than with other color conditions. Notably, the increased activity of V2/3 for the RVF between-category colors coincided with the increased activity of the posterior temporoparietal region for language processes, as demonstrated by the significant interaction of visual field and categorical relation, suggesting that CP of color provokes orchestrated cortical activity occurring within subsystems involving the posterior temporoparietal region and V2/3.

We tentatively infer that the posterior temporoparietal cortex serves as a top-down control source that interacts with and modulates the activity of the visual cortex (V2/3) serving data-driven analysis of visual stimuli. Anatomical studies have found multiple reciprocal neural pathways between the parietal cortex and visual processing areas, and these pathways may govern such control (50–53). Our results are consistent with lesion studies of
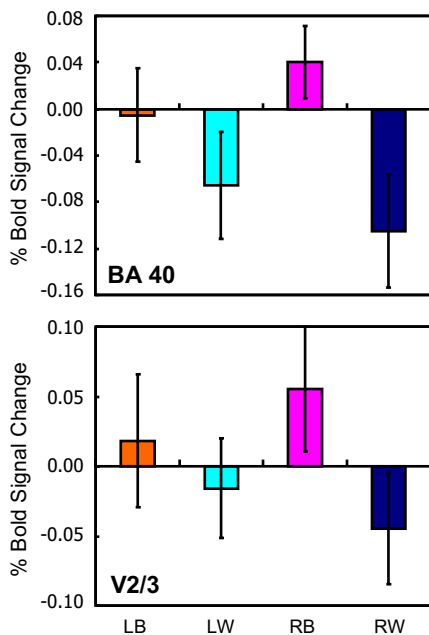
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Fig. 5. Regions of interest that survive small volume correction with $P < 0.05$ FDR-corrected and a whole-brain voxel-based analysis (thresholded at $P < 0.005$ uncorrected for multiple corrections) of the interaction between visual field and categorical relationship. LB, left visual field between-category; LW, left visual field within-category; RB, right visual field between-category; RW, right visual field within-category.

visual attention (54) indicating that the posterior parietal cortex interacts with the response of neurons in the visual areas in ways that may fundamentally influence object representations.

At present a direct functional connection and interaction between the posterior temporoparietal region and the color region(s) in color perception has not been established. Future research may address this question by performing an effective connectivity analysis of fMRI data and/or by providing more refined time-course information with the event-related potential technique. Our study nevertheless has identified the neural correlates of the behavioral RVF advantage in color discrimination and thus shed light on the mechanisms that underlie Whorfian effects. Language, by enhancing the activation level of the visual cortex, differentially influences the discrimination of colors presented in the left and right visual hemifields.

Materials and Methods

Subjects. Beijing college students [8 males and 8 females; mean age, 23.7 years (SD 1.8 years)] participated in the fMRI experiment. The data of 1 subject were discarded because of head motion and a low identification score in the color boundary test. Subjects were paid for their participation and gave informed consent according to guidelines set by the Administrative Panels on Human Subjects in Medical Research of the Beijing MRI Center for Brain Research at the Chinese Academy of Sciences. They were tested with the Ishihara test for color blindness; all subjects had normal color vision and no history of neurological or psychiatric illness. All subjects were strongly right-handed.

Stimuli and Experimental Design. The RGB values of the 4 colors were as follows (see Fig. 1*A*): G1 = 0, 171, 129; G2 = 0, 170, 149; B1 = 0, 170, 170; B2 = 0, 149,

Table 3. CIEL*u*v* values and inter-pair distances

Stimulus	L*	u*	v*	Pair	ΔE
G1	62.263	−52.327	23.044		
G2	62.44	−50.447	6.856	(G1,G2)	16.29776282
B1	63.054	−48.768	−10.53	(G2,B1)	17.47767241
B2	56.483	−41.453	−27.34	(B1,B2)	19.47468526

170. The brightness and saturation values were adjusted to make them equal, based on the independent judgments of 4 observers. The RGB values for the background were 210, 210, and 210. CIEL*u*v* values are given in Table 3. The inter-pair distances are (G1,G2) = 16.3 ΔE, (G2,B1) = 17.48 ΔE, and (B1,B2) = 19.47 ΔE. The mean within-category distance, 17.89 ΔE, slightly exceeds the between-category (G2,B1) distance, 17.48 ΔE .

A rapid event-related design was used. During each trial, a ring of 12 colored squares surrounding the fixation marker was presented simultaneously for 200 ms against a gray background (Fig. 1*B*), followed by a fixation screen against a gray background. Subjects indicated whether the target was on the left or right side of the circle by making button-press responses with the corresponding hand as quickly and as accurately as possible. The duration of the fixation screen varied to jitter the blood oxygen level-dependent (BOLD) responses. Inter-stimulus intervals of 1800, 2800, or 3800 ms were assigned randomly to the trials, resulting in corresponding stimulus onset asynchronies of 2000, 3000, and 4000 ms. There were 6 target–distractor pairs formed by using all 1-step pairwise combinations of the 4 colors (3 pairs: G1G2, B1B2, and G2B1) and having each member of a pair serve once as target and once as distractor. The target occupied any of the 4 positions (position 1, 2, 3, or 4 in Fig. 1*B*), and there were 24 possible stimulus configurations. There were 400 trials in total. In half of the trials, the target was located to the left of center (position 1 or 2), and in the other half of the trials it was located to the right of center (position 3 or 4). In addition, half of the trials presented within-category combinations (G1G2 or B1B2), and the other half presented the between-category combination (G2B1).

The stimuli were presented via a liquid crystal display projector and were back-projected onto a projection screen placed at the end of the scanner bore. Subjects viewed the rear projection screen through a mirror attached to the head coil. The distance from the projection screen to the mirror was 70 cm, and the distance from the mirror to the eyes of the subject was 10 cm. The inner edge of the target color was presented 3.9° to the right or to the left of a centrally presented "+". Hence, the stimuli were separated by a visual angle of 7.8°.

After the fMRI scans, subjects were given a blue–green lexical boundary test. On each trial, a square stimulus (1 of the colors, G1, G2, B1, or B2) was presented centrally on a gray background for 200 ms, followed by an 1800-ms interval. Participants indicated whether the stimulus was green or blue by pressing 1 of 2 keys, corresponding to the Mandarin Chinese words for "green" and "blue," respectively. Each stimulus was presented 10 times in a total of 40 randomized trials. Fifteen subjects identified more than 93% of the presentations of G1 and G2 as "green" and of B1 and B2 as "blue." One subject identified only 53% of the presentations in this way; the data from this subject were discarded.

Image Acquisition and Data Analysis. Details of image acquisition and data analysis are given in the *SI text*.

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