

Color, Context, and Cognitive Style: Variations in Color Knowledge Retrieval as a Function of Task and Subject Variables

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Abstract

■ Neuroimaging tests of sensorimotor theories of semantic memory hinge on the extent to which similar activation patterns are observed during perception and retrieval of objects or object properties. The present study was motivated by the hypothesis that some of the seeming discrepancies across studies reflect flexibility in the systems responsible for conceptual and perceptual processing of color. Specifically, we test the hypothesis that retrieval of color knowledge can be influenced by both context (a task variable) and individual differences in cognitive style (a subject variable). In Experiment 1, we provide fMRI evidence for differential activity during color knowledge retrieval by having subjects perform a verbal task, in which context encouraged subjects

to retrieve more or less detailed information about the colors of named common objects in a blocked experimental design. In the left fusiform, we found more activity during retrieval of more versus less detailed color knowledge. We also assessed preference for verbal or visual cognitive style, finding that brain activity in the left lingual gyrus significantly correlated with preference for a visual cognitive style. We replicated many of these effects in Experiment 2, in which stimuli were presented more quickly, in a random order, and in the auditory modality. This illustration of some of the factors that can influence color knowledge retrieval leads to the conclusion that tests of conceptual and perceptual overlap must consider variation in both of these processes. ■

INTRODUCTION

Sensorimotor theories of semantic memory posit that object knowledge is organized in a distributed, modality-specific fashion and that object knowledge is stored in or near the brain regions that subserve perception of and action with objects (Barsalou, 1999; Warrington & McCarthy, 1987; Allport, 1985). A large body of behavioral, neuroimaging, and neurophysiological research has provided evidence for these theories (for a review, see Martin, 2007 or Thompson-Schill, 2003). In particular, neuroimaging studies have demonstrated that retrieving knowledge of object features draws on similar neural substrates as perception in the same modality, as shown through vision (e.g., Simmons et al., 2007; Chao & Martin, 1999; Kosslyn, Thompson, Kim, & Alpert, 1995; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995), hearing (e.g., Kraemer, Macrae, Green, & Kelley, 2005; Hughes et al., 2001; Yoo, Lee, & Choi, 2001; Wheeler, Petersen, & Buckner, 2000), and action (e.g., Yee, Drucker, & Thompson-Schill, 2010; Oliver, Geiger, Lewandowski, & Thompson-Schill, 2009; Hauk, Johnsrude, & Pulvermüller, 2004; Kellenbach, Brett, & Patterson, 2003; Chao & Martin, 2000).

The sensory modality in question in the current investigation is vision and, in particular, color vision, which is of interest for a number of reasons: Crucial to object identification, it is often the feature used to distinguish between two otherwise similar objects (e.g., lemons and limes). Additionally, color can be characterized by both continuous values along multiple dimensions (such as hue, saturation, and luminance) or more coarsely in a categorical fashion. Moreover, unlike other features of object appearance, such as shape or size, color is a feature that is only perceived through visual modality.

The procedures for—and the results of—prior investigations of color perception and color retrieval are varied. Brain regions sensitive to color perception have been identified through the use of passively viewed colored versus grayscale Mondrians (Chao & Martin, 1999; Howard et al., 1998) or while making luminance judgments on visual stimuli (Simmons et al., 2007; Beauchamp, Haxby, Jennings, & DeYoe, 1999). Although active brain regions tend to include lateralized or bilateral fusiform and lingual gyri, there is certainly no overwhelming consensus on the brain areas involved in color perception. Tasks used to identify brain regions involved in color knowledge retrieval have included a similarity task of two named objects in the same color family (Howard et al., 1998), naming colors of objects presented as achromatic line drawings (Chao & Martin, 1999;

Martin et al., 1995) or verifying colors of objects (Simmons et al., 2007; Kellenbach, Brett, & Patterson, 2001). In addition to lateralized or bilateral fusiform and lingual gyri being active, a posterior inferior temporal network can also be activated during retrieval (Kellenbach et al., 2001). Although these findings largely have been interpreted as evidence for sensorimotor theories of semantic memory, there are discrepancies among studies that threaten this conclusion; for example, the absence of evidence for overlapping responses to color perception and color retrieval (Chao & Martin, 1999) was contradicted by the finding of direct overlap between the two (albeit only in the left fusiform gyrus) (Simmons et al., 2007).

Past work on this topic has tended to investigate this overlap between conceptual and perceptual color processing by posing the question: “Does color knowledge retrieval activate *the* color perception area?” Instead, we propose reframing the question as, “What factors influence color knowledge retrieval, and under what circumstances do these factors influence the extent of overlap between color knowledge retrieval and color perception?” We propose that differences in the literature may also be explained by two factors that influence color knowledge retrieval: task factors and individual factors.

To motivate the relevance of task or context factors for color retrieval, consider the following two contexts: First, imagine that you are trying to avoid eating strawberries as you pick through a fruit salad comprising blueberries, blackberries, and strawberries. As you plan your search of the bowl of fruit, you will need to know that the strawberries are the red bits in the bowl. Now instead, imagine that you are trying to avoid eating the strawberries in a fruit salad that also includes raspberries, watermelon, and cherries. Dodging the red pieces will no longer help you; instead, you need to recall the specific shade of red of the strawberry. In other words, the context (created by the other fruits in the bowl) changes the type of color information you retrieve about the fruits. This is the contextual difference we tried to capture with our task manipulation.

Turning to individual factors, differences in cognitive style may play a role in the representation that is retrieved by a given individual. A cognitive style is a psychological dimension that represents consistencies in how an individual acquires and processes information (Kozhevnikov, Kosslyn, & Shephard, 2005). Different individuals process certain types of information differently (e.g., learning through pictures or through words), and this idea has been part of many theories in various avenues of psychological research (Kraemer, Rosenberg, & Thompson-Schill, 2009; for a review, see Kozhevnikov, 2007). In this pair of studies, we use the Verbalizer–Visualizer Questionnaire (VVQ) developed by Kirby, Moore, and Schofield (1988) to identify propensities for visual or verbal cognition. A key difference between task factors and individual factors is that the latter, such as visualizing preferences, are described as being stable over time, whereas the former can vary on a

trial-to-trial basis. Both of these types of factors may affect components of the color knowledge retrieval process, suggesting it to be more dynamic and complicated than previously thought.

In the current investigation, we examined the effects of task factors and individual factors on color retrieval by implicitly varying the retrieval context and by assessing individual preferences for cognitive style. In Experiment 1, subjects performed a verbal task in which they judged the color similarity of three named objects. The composition of the object groups encouraged retrieval of either object colors from the same color category (i.e., three red items) or from different color categories (i.e., two red items and a yellow item). These object groups were, thus, meant to encourage retrieval of more or less detailed color knowledge. Using fMRI, we measured brain activity during retrieval, controlling for difficulty by covarying out RT. We observed effects of both task factors and individual factors, although in different regions: We found that activity in the left fusiform gyrus was significantly greater when retrieving and discriminating object colors from the same versus different color category. The lingual gyrus was responsive to the task (compared with baseline), but there was no significant difference in activity between conditions. However, activity in this region (and task performance) significantly correlated with visual cognitive style preference, as measured by the self-report VVQ (Kirby et al., 1988).

To replicate and extend the results of Experiment 1, we conducted a second experiment that varied detail of color knowledge, with several key procedural changes. In Experiment 2, we used auditory rather than visual stimuli to ensure that any effects were because of the retrieval of visual knowledge and not some modulation of the response to the visually presented words. Second, we used a randomized rather than blocked manipulation of the color task to minimize the contribution of state effects on the retrieval process. Even with these changes, Experiment 2 replicated many of the findings of Experiment 1 with activation in the left fusiform gyrus. Additionally, there was a significant positive correlation of the VVQ and task performance. Our findings support the notion that retrieval of color knowledge representations relies on similar neural substrates as color perception and that the degree to which these systems overlap can be influenced both by context and by cognitive style (Figures 1 and 2).

METHODS: EXPERIMENT 1

Participants

For Experiment 1, 12 healthy subjects (six men, average age = 22.8 years, range = 19–30 years) participated. All subjects (in both experiments) provided written informed consent to participate and received monetary compensation in return for their participation. The human subjects review board at the University of Pennsylvania approved all experimental procedures.

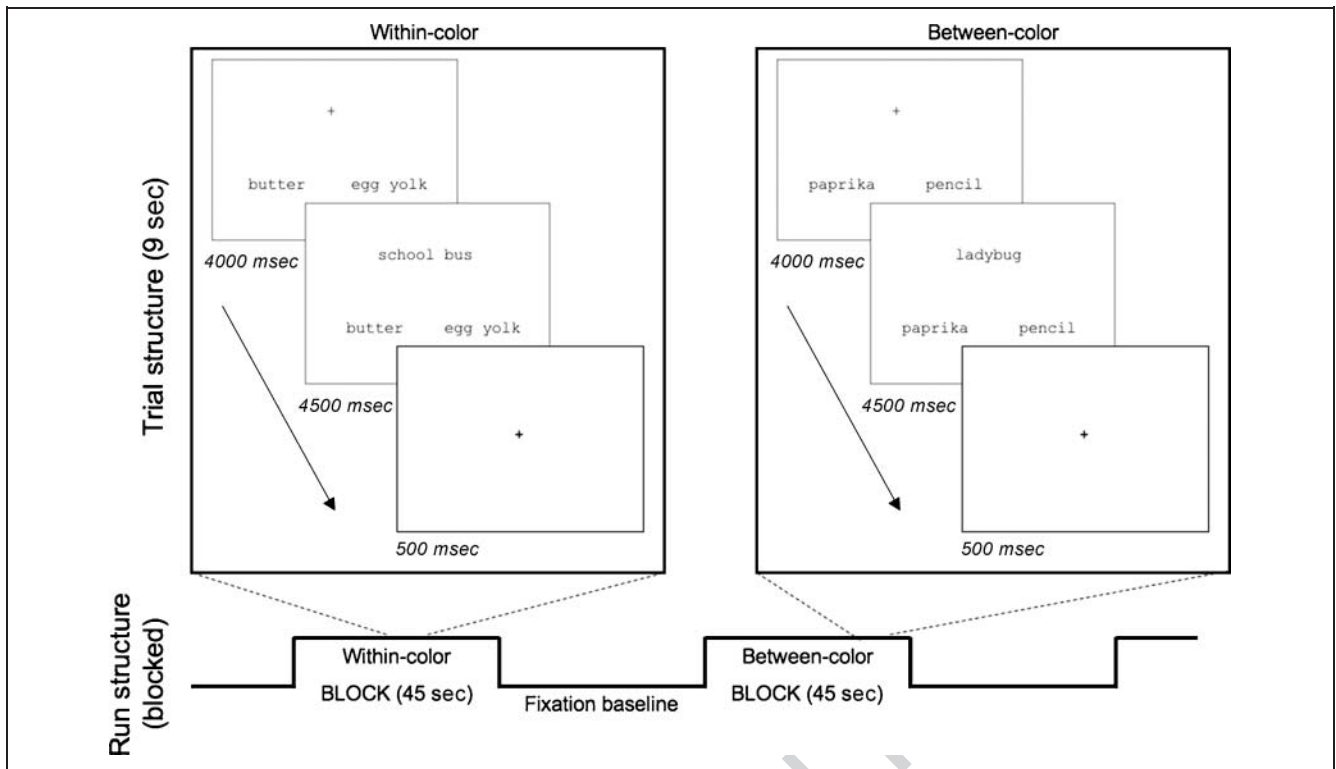


Figure 1. Design of Experiment 1.

Materials

For each trial, subjects judged the similarity of three named objects, indicating which of the two objects was more similar to the third object in terms of color. The conditions of

interest differed such that, to arrive at a correct answer, varying levels of detailed color information were required. Thus, we manipulated the level of detail of color knowledge by having subjects compare either objects drawn from different color categories or between-color categories

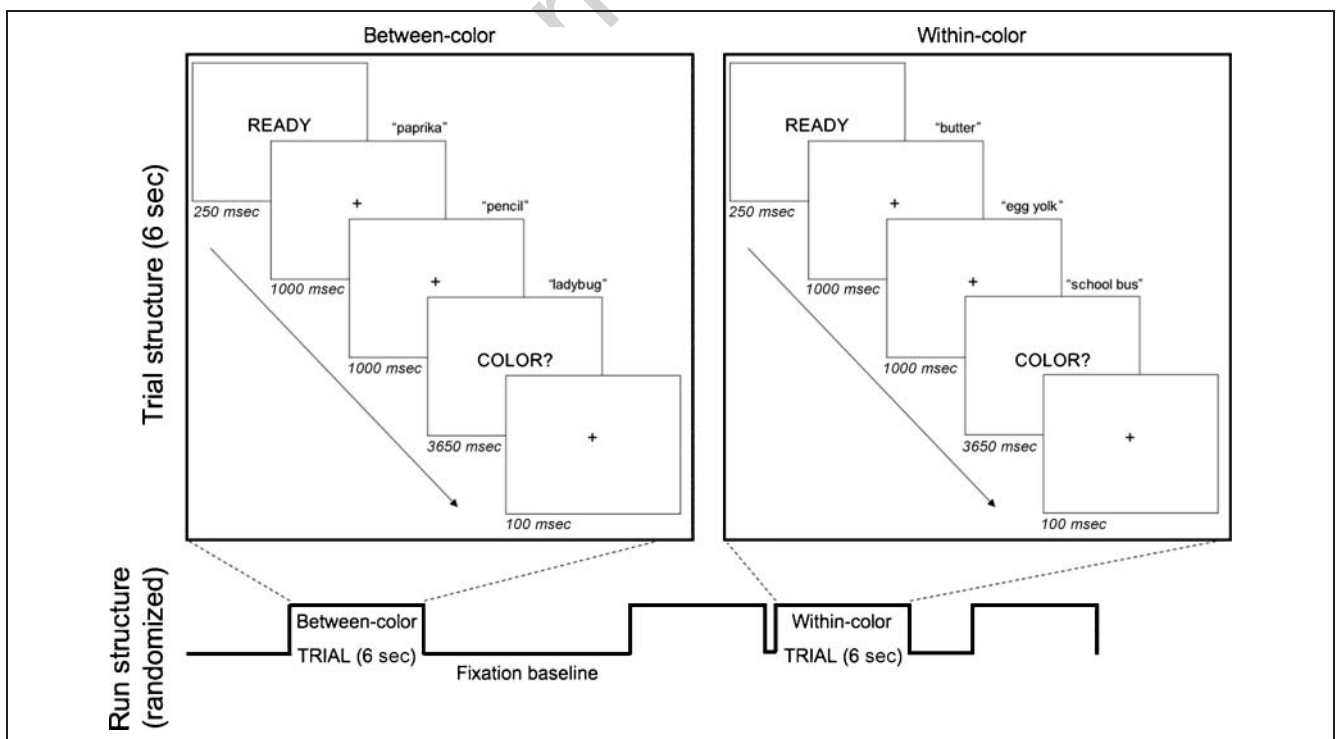


Figure 2. Design of Experiment 2.

(BCC) (e.g., comparing paprika and pencil to *ladybug*, wherein less detailed color information would suffice) or objects drawn from the same color category, or within-color category (WCC) (e.g., comparing butter and egg yolk to *school bus*, wherein more detailed color information becomes necessary).

The 300 objects used in the experiments were rated for color agreement (>66%) by an independent group of 50 subjects, drawn from the same population as the study sample. Furthermore, to alleviate ambiguity in WCC trials and to create WCC trials with agreement for the correct answer, these 50 subjects performed an additional rating task. For this task, they rated the color similarity of pairs of all objects within a color category, and WCC trials were created by pairing two objects (rated for high color similarity) with a third object (rated for low color similarity). Once created, the trials in both conditions of interest were normed in an independent group of 25 subjects for accuracy and RT differences.

Because a substantial portion of the objects used in these experiments did not have listings in the MRC Psycholinguistic Database (Wilson, 1987), as prioritizing for high-color agreement constrained our object names list, we felt that the conditions could not be accurately matched in terms of familiarity and lexical frequency. Thus, we used a lexical decision task (in which all of the words referred to concrete objects) as a proxy measure of familiarity and frequency, which has been used previously (Goldberg, Perfetti, & Schneider, 2006). A separate set of 25 subjects drawn from the same population as the study sample completed the lexical decision task, during which they verified whether each presented word referred to a real world object or not. Each of the 300 words used in the neuroimaging experiments was randomly presented individually and intermixed with 300 pronounceable pseudowords (Rastle, Harrington, & Coltheart, 2002) that were matched with the 300 real words for letter length and number of syllables. RT and accuracy measures were collected, which did not differ across the two conditions of interest. In summary, in Experiment 1, the conditions were matched for lexical frequency and familiarity (as measured by lexical decision RTs) and number of letters, number of phonemes, number of syllables, and color agreement.

No more than 1 week before the scanning session, subjects came to the laboratory to fill out relevant paperwork, provide informed consent, and become acquainted with the tasks by performing practice versions. Additionally, they were administered the VVQ developed by Kirby et al. (1988) in a manner identical to that reported previously (Kraemer et al., 2009).

Procedure: Experiment 1

At the beginning of each trial, two words appeared at the bottom of the screen for 4000 msec, and then a third word replaced a fixation cross at the top of the screen (see Fig-

ure 1). At this point, the subjects' task was to decide which of the two bottom words was more similar in real world color to the top word. Subjects indicated their response with a button press within a 4500-msec response window during which time all three words were visible. We collected response latencies to include as a covariate in all fMRI analyses to control for differences in time on task across conditions. At the end of the trial, a fixation cross appeared in the center of the screen for 500 msec, before the onset of the next trial, for a total trial duration of 9000 msec.

Trials from the WCC and BCC conditions were blocked in Experiment 1 as follows: we presented five trials of one condition (45 sec) followed by 45 sec of fixation ("baseline") and then five trials of the other condition followed by 45 sec of fixation, and so on. In each of two functional scans (or runs), subjects completed five WCC blocks and five BCC blocks, for a total of 50 trials per condition across the two scans, with an equivalent amount of fixation time. To reduce variability across subjects associated with task order, trials were presented in the same order for all subjects, beginning with a WCC block. Before scanning, subjects completed five practice trials of each condition. We used E-Prime software (Psychology Software Tools, Inc., Sharpsburg, PA) to present stimuli and collect response data.

After subjects completed both color retrieval scans, we administered a "functional localizer" to identify brain regions involved in color perception, so that we could compare regions that are affected by task or subject factors during color retrieval to regions that respond to color perception in the same group of subjects. Participants saw blocks of the Farnsworth–Munsell 100-hue stimuli, in which they judged whether chromatic or achromatic color wheels were sequentially ordered from lightest to darkest. The methods and stimuli for this task were identical to those that were used previously by Simmons and colleagues (Simmons et al., 2007) and have previously been used to identify brain regions involved in color perception (e.g., Beauchamp et al., 1999).

Image Acquisition

We acquired imaging data using a 3T Siemens Trio system with an eight-channel head coil and foam padding to secure the head in position. After we acquired T1-weighted anatomical images (TR = 1620 msec, TE = 3 msec, TI = 950 msec, voxel size = 0.9766 mm × 0.9766 mm × 1.000 mm), each subject performed the color knowledge retrieval task, followed by the color perception task, while undergoing BOLD imaging (Ogawa et al., 1993). We collected 912 sets of 44 slices using interleaved, gradient-echo, EPI (TR = 3000 msec, TE = 30 msec, field of view = 19.2 cm × 19.2 cm, voxel size = 3.0 mm × 3.0 mm × 3.0 mm). At least 9 sec of "dummy" gradient and radio-frequency pulses preceded each functional scan to allow for steady-state magnetization; no stimuli were presented, and no fMRI data were collected during this initial period.

Neuroimaging Data Analysis

We analyzed the data off-line using VoxBo (www.voxbo.org) and SPM2 (www.fil.ion.ucl.ac.uk). Anatomical data for each subject were processed using the FMRIB Software Library toolkit (www.fmrib.ox.ac.uk/fsl) to correct for spatial inhomogeneities and to perform nonlinear noise reduction. Functional data were sinc interpolated in time to correct for the slice acquisition sequence, motion-corrected with a six-parameter, least squares, rigid body realignment routine using the first functional image as a reference, and normalized in SPM2 to a standard template in Montreal Neurological Institute space. The fMRI data were smoothed using a 9-mm FWHM Gaussian smoothing kernel. Following preprocessing for each subject, a power spectrum for one functional run was fit with a 1/frequency function; we used this model to estimate the intrinsic temporal autocorrelation of the functional data (Zarahn, Aguirre, & D'Esposito, 1997).

We fit a modified general linear model (Worsley & Friston, 1995) to each subject's data, in which the conditions of interest were modeled as a block and convolved with a standard hemodynamic response function. Several covariates of no interest (global signal, scan effects, and movement spikes) were included in the model. The response latency for each trial was also included as a covariate of no interest to address any confounds of difficulty or "time on task"; in other words, effects of condition reported below describe differences between conditions that cannot be explained by response time differences alone. From this model, we computed parameter estimates for each condition (compared with baseline) at each voxel. These parameter estimates were included in the group-level random effects analyses described below.

To establish functionally defined ROIs (fROIs) in which, to assess the effects of task and individual factors on color retrieval, we first performed a group-level random effects analysis, in which we compared brain activity for both conditions of interest to the fixation baseline. Note that, defined this way, these fROIs are unbiased with regard to the test of interest, namely whether there are differences in activation between the two conditions. Next, from the set of fROIs that emerged from this analysis, we identified the peak cluster of voxels from lingual and fusiform gyri, as these two regions have been implicated in color perception and color knowledge retrieval (Martin, 2007; Simmons et al., 2007; Beauchamp et al., 1999; Chao & Martin, 1999). To create fROIs of comparable size across regions, we did not use a predetermined threshold, but rather we adjusted the threshold that yielded approximately 100 maximally responsive voxels in each of these regions. (For the remaining fROIs about which we did not have a priori hypotheses, we assessed effects using an approach better suited for exploratory analyses, which we discuss in Exploratory, Whole-Brain Analyses.) Finally, within each of these fROIs, we calculated parameter estimates for each subject, for each condition, on the spatially averaged time series (across

the 100 voxels in the fROI), and we used these parameter estimates to assess the effects of task and individual factors on color retrieval (see Figure 4). Task effects were assessed using a paired *t* test of the difference between the WCC parameter and the BCC parameter, and subject effects were assessed using a Pearson's correlation between these values and the difference scores on the VVQ.

RESULTS: EXPERIMENT 1

Behavioral Results

Each dimension of the VVQ ranges from -20 to 20 . Although scores for each dimension were generally positive, we measured preference for a visual or verbal cognitive style as the difference, calculated by subtracting verbal from visual scores. This difference score will be reported throughout the article as "Vis-Verb." Difference scores ranged from -5 to 15 ($M = 4.3$, $SD = 7.15$).

The average RT (in msec) for correct trials in both experimental conditions was 1485.08 ($SD = 678.66$). As expected, the inherent difference in difficulty between the two experimental conditions resulted in notable RT differences (BCC: $M = 1332.25$, $SD = 651.91$; WCC: $M = 1720.17$, $SD = 669.27$; $t(11) = 4.74$, $p < .001$). Vis-Verb scores were not correlated with RT ($r = -.38$, $p = .20$). Accuracy across conditions was fairly high (84%) but lower for the more difficult WCC condition (BCC: 95%; WCC: 74%; $t(11) = 13.40$, $p < .001$). As seen in Figure 3A, accuracy difference scores (calculated by subtracting accuracy on the BCC trials from the WCC trials) significantly correlated with Vis-Verb scores ($r = .58$, $p < .05$). This result suggests that subjects who prefer the visual cognitive style tended to perform better on trials in which object representations of higher detail were retrieved.

Imaging Results

Results are shown in Figure 4A. In the left fusiform region (100 voxels; $t = 6.96$, Talairach coordinates: $-36 -47 -13$, BA 37), activation was significantly greater during WCC blocks (mean percent signal change = 0.53% , $SD = 0.208\%$) than during BCC blocks (mean percent signal change = 0.40% , $SD = 0.14\%$; $t(11) = 4.02$, $p = .002$). A weak but nonsignificant positive correlation also existed between the magnitude of the condition effect (calculated as the difference in signal change between the two conditions) and Vis-Verb scores ($r = .35$, $p = .13$). The finding of task-dependent levels of activity in the left fusiform region during color retrieval support our hypothesis that context can influence the color knowledge retrieval process.

In the left lingual region (119 voxels; $t = 5.5$, Talairach coordinates: $-15 -85 -3$, BA 18), there was significant activation in both conditions but no difference between conditions (WCC: mean = 0.28% , $SD = 0.16\%$; BCC: mean = 0.29% , $SD = 0.14\%$; $t(11) = -0.28$, $p = .83$). Although there was not a reliable main effect of condition,

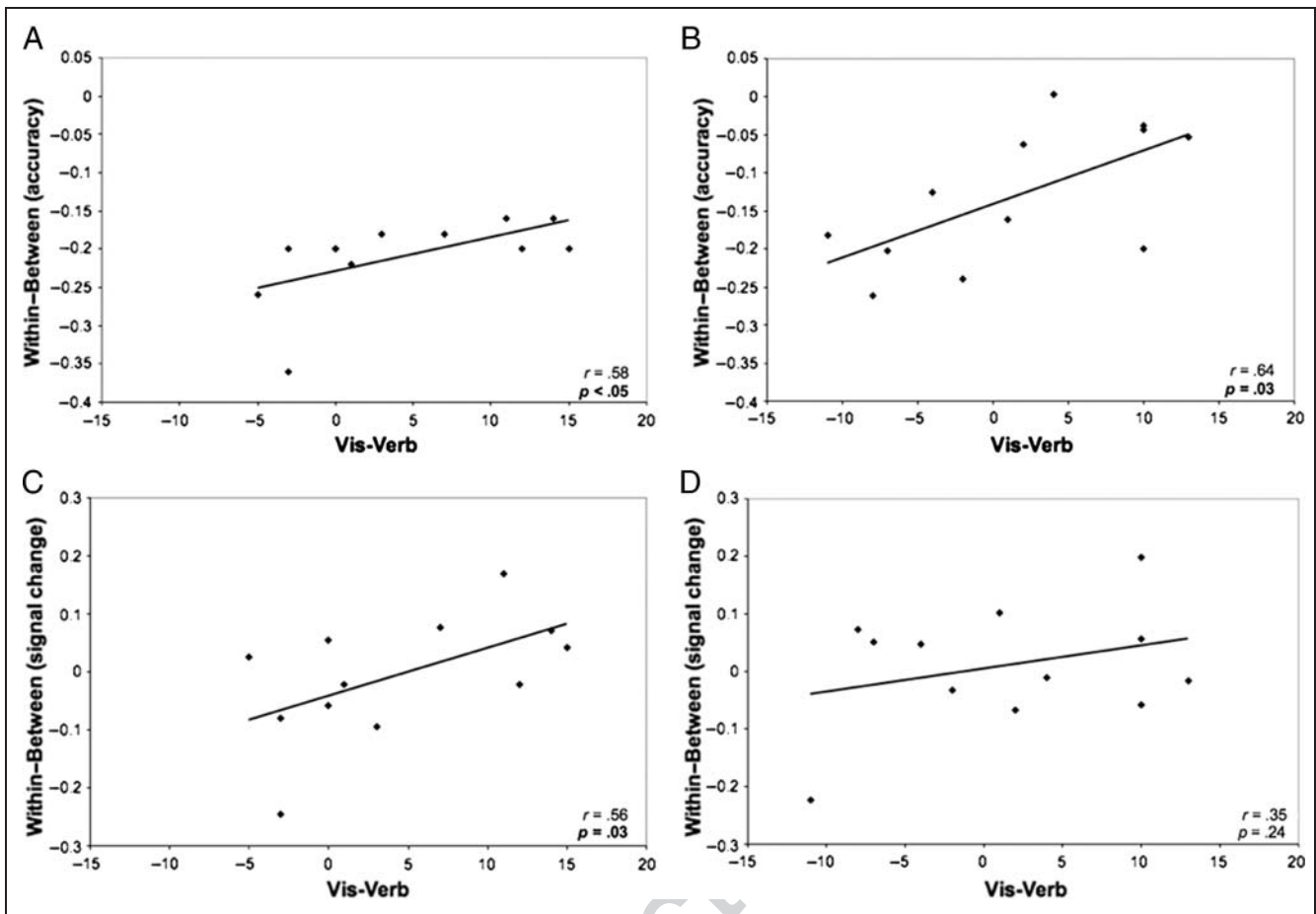


Figure 3. Task accuracy and left lingual gyrus activity correlate with cognitive style preference. Pearson correlations (r) of self-reported cognitive style with task accuracy (A, B) and signal change in left lingual region (C, D) for Experiment 1 (A, C) and Experiment 2 (B, D).

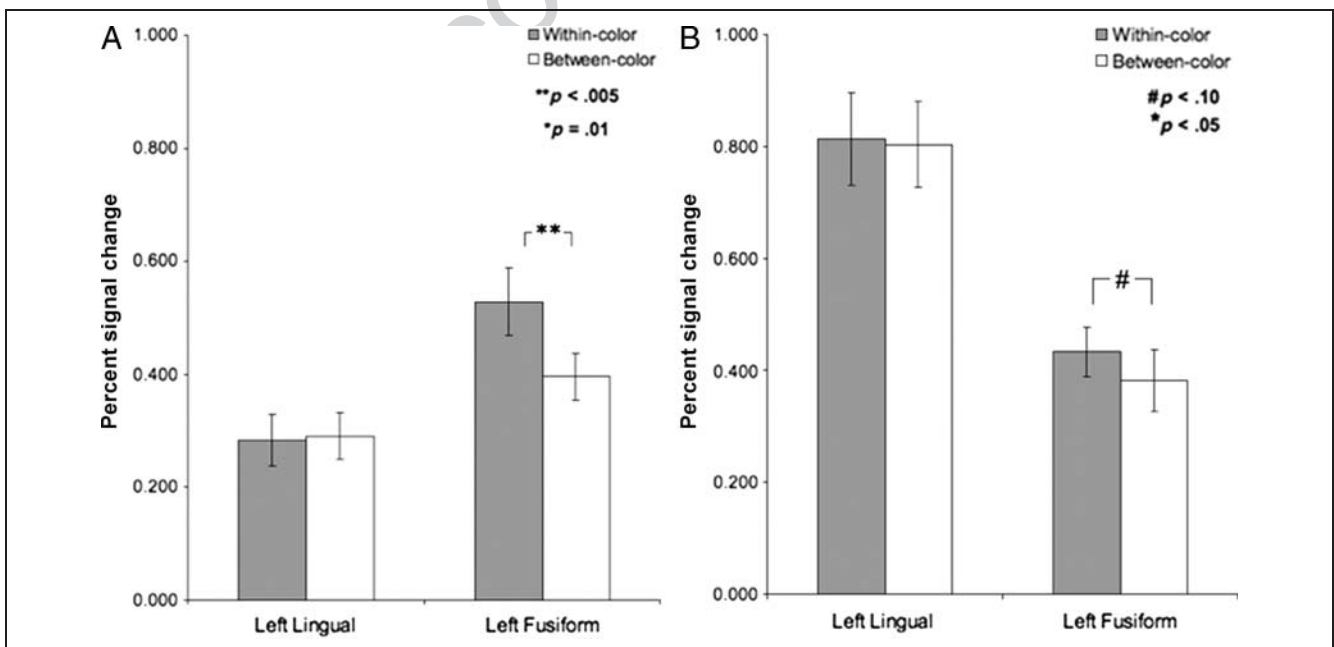


Figure 4. Areas of visual cortex show differences in activity when retrieving color knowledge at differing levels of detail. fROI analysis of left lingual and left fusiform for Experiment 1 (visual stimuli, A) and Experiment 2 (auditory stimuli, B). Error bars indicate ± 1 SE.

there was a significant positive correlation (see Figure 3C; $r = .56, p = .03$) between the magnitude of the main effect and the Vis-Verb scores: Participants who preferred the visual cognitive style had more activation in the left lingual region during trials requiring retrieval of more detailed color information. The finding that activity in the left lingual region is correlated with an individual's cognitive style supports our hypothesis that individual factors can influence retrieval of color knowledge representations.

Additional Analyses

Comparing color retrieval with color perception. A separate analysis investigated the overlap between color perception and color knowledge retrieval by identifying ROIs of approximately 100 active voxels during the color perception localizer in the same manner described for the color retrieval fROIs. This method yielded two ROIs in the left fusiform ($t = 5.05, 102$ voxels) and the left lingual gyrus ($t = 6.5, 110$ voxels). We then assessed the extent to which the regions involved in color perception were also involved in the color knowledge task by overlaying the color perception ROIs with the color knowledge ROIs described above. Here, we found that voxels involved in both color perception and color knowledge retrieval overlapped in both left fusiform gyrus (10 voxels; Figure 5A) and left lingual gyrus (2 voxels; Figure 5B). When we repeated our analyses of task and subject effects in the regions functionally defined to be involved in color *perception*, there was a marginally significant increase for WCC versus BCC trials ($t[11] = 2.20, p = .084$), although the correlation between Vis-Verb scores and brain activity was not statistically significant.

Exploratory, whole-brain analyses. In a group-level random effects analysis, we identified all clusters that surpassed a $p < .001$ (uncorrected) threshold for the task–baseline contrast (for clusters greater than 100 voxels, we picked approximately the peak 100 voxels to be consistent with our approach above). This analysis revealed 13 additional fROIs; within each of these fROIs, we then tested significance of the WCC–BCC contrast as well as the correlation of brain activity with Vis-Verb scores. These regions are reported in Table 1. As can be seen, several other regions activated during color retrieval—beyond those selected for their involvement in color perception—were also modulated by task and subject factors.

DISCUSSION: EXPERIMENT 1

The results of Experiment 1 provide evidence that task factors (context) and individual factors (here, cognitive style) influence conceptual processing of color. Activation during the color retrieval task was observed in two regions—the left fusiform gyrus and the left lingual gyrus—that have been reported in prior research on color perception and memory and that overlapped with regions

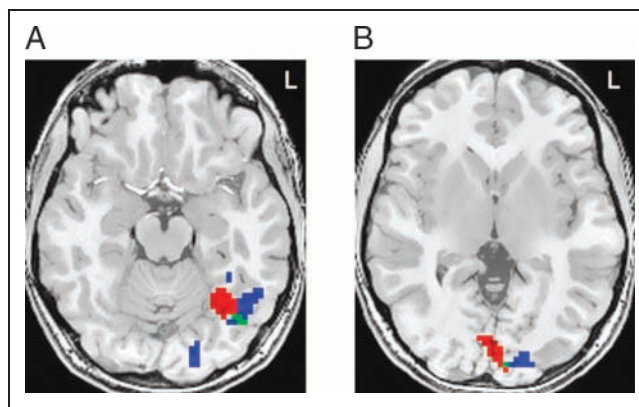


Figure 5. Color perception and color knowledge retrieval activate overlapping brain regions. Overlap of Experiment 1 fROIs for color perception (red) and color knowledge (blue) in left fusiform (A) and left lingual (B) regions. Overlapping voxels are shown in green.

activated by our color perception localizer in the same group of subjects. In these two regions, we found evidence of effects of both task factors and individual factors. Specifically, in the left fusiform region, we observed greater activation when color knowledge was retrieved in a context that requires detailed or specific color information (i.e., WCC blocks) than in one that does not (i.e., BCC blocks). And in the left lingual region, the magnitude of this effect was correlated with the degree to which subjects preferred the visual cognitive style.

These findings paint a picture of color retrieval as a dynamic process that varies as a function of both state and trait factors. The overlap between our two ROIs with voxels that respond to color perception (Figure 5) raises the possibility that one aspect of color retrieval that varies is the extent to which early perceptual processes are recruited during memory retrieval. Furthermore, the finding that subjects who report a visual cognitive style did better on WCC trials than those who did not demonstrates that there can be behavioral consequences of these variations in color retrieval processes. Lastly and more generally, these findings illustrate the utility of using both group and individual analyses, a point to which we return in the General Discussion.

Early visual cortex has been shown to be recruited when retrieving high-resolution details of object surface geometry (Kosslyn & Thompson, 2003). However, to our knowledge, this is the first demonstration that retrieval of color knowledge representations can differentially activate areas of visual cortex that are also involved in color perception. However, there is an alternative explanation of our findings that arises from our choice to present verbal stimuli in the visual modality in Experiment 1: The differences we observed between the WCC and BCC conditions could be explained by a low-level, perceptual explanation unrelated to our hypothesis, if subjects scanned the visually presented words differently during the two conditions (e.g., multiple fixations on each word in the WCC condition). In other words, although we statistically controlled for response time differences (in our general linear model),

Table 1. Clusters Identified in Exploratory, Whole-Brain Analysis

ROI	BA	Peak Location			Peak <i>t</i> Value	Voxels	WCC-BCC <i>t</i> Statistics	Vis-Verb <i>r</i>
		<i>x</i>	<i>y</i>	<i>z</i>				
<i>Experiment 1</i>								
L thalamus/putamen	–	–36	–27	–6	12.12	115	5.69***	–0.09
L intraparietal sulcus	7	–30	–57	44	11.95	92	2.79*	0.11
R inferior frontal gyrus	44/45	51	34	20	9.48	101	3.17**	0.2
L fusiform gyrus	19	–36	–47	–13	9.26	100	4.02**	0.35
L lingual gyrus	18	–15	–85	–3	8.57	116	–0.20	0.56
B anterior cingulate	32	0	26	37	8.42	100	5.36***	–0.14
R angular gyrus/superior parietal lobule	39	33	–48	41	8.11	85	7.55****	–0.05
L inferior frontal gyrus (pars triangularis)	45	–45	30	15	7.74	99	4.20**	–0.08
L inferior frontal gyrus (pars opercularis)	44	–39	11	33	7.67	81	3.12**	0.34
R inferior frontal gyrus (pars triangularis)	45	57	39	4	7.39	23	5.96****	–0.51
L angular gyrus/superior parietal lobule	39	–42	–44	55	7.11	22	4.15**	0.14
R middle frontal gyrus	8/9	42	18	49	6.70	35	4.34**	–0.05
R thalamus/caudate	–	9	5	22	6.10	100	3.22**	0.16
<i>Experiment 2</i>								
L cingulate gyrus	32	–3	11	42	16.75	100	2.34*	0.04
L middle frontal gyrus	6	–39	–1	48	16.75	104	0.90	0.03
L superior temporal gyrus	42	–68	–26	6	11.96	105	–1.01	0.39
L insula	13	–33	15	4	11.86	71	1.20	0.23
L thalamus	–	–18	–26	–1	11.81	112	0.13	0.06
R cuneus	30	9	–69	11	11.09	106	1.91	0.00
L lingual gyrus	18	–18	–82	–6	9.67	101	–0.55	0.19
R superior temporal gyrus	22	42	–26	1	9.37	107	0.03	0.03
R insula	13	30	17	–1	9.23	92	1.83	–0.05
L inferior parietal lobule	40	–39	–39	45	8.65	62	1.25	0.01
L inferior frontal gyrus	9	–45	16	24	7.74	42	2.56*	0.46
R inferior frontal gyrus	9	59	10	30	7.47	43	3.02*	0.08
L fusiform gyrus	37	–42	–53	–12	6.85	116	–0.24	–0.16

These clusters were identified as those surpassing a $p < .001$ (uncorrected) threshold. For clusters larger than 100 voxels, approximately the 100 most active voxels were identified. Bolded *t* statistics surpass Bonferroni-corrected significance threshold ($p < .004$). Other *t* statistics noted for significance ($*p < .05$, $**p < .01$, $***p < .001$, $****p < .0001$). L = left; R = right.

we cannot be certain that the same amount of visual processing occurred per unit time. Experiment 2 addressed this concern by presenting auditory rather than visual stimuli, so we could be certain that activation in visual

areas did not reflect processing of the words per se but instead of the objects to which the words refer.

In Experiment 2, in addition to replicating our initial findings in the auditory modality, we also wanted to address

the time course of dynamic changes in knowledge retrieval. In Experiment 1, subjects were presented with 45-sec blocks that alternated between retrieval of more- or less-detailed color knowledge representations. Thus, the results of Experiment 1 could reflect an anticipatory strategy sustained across an entire block. In Experiment 2, we randomized the order of conditions on a trial-by-trial basis. In this way, subjects were unable to predict the type of knowledge that would be required before each trial. We also reduced each trial's duration to reduce the potential impact of postdecision processes. Therefore, unlike in Experiment 1, where condition differences could have been present even in the intertrial interval of each block, in Experiment 2 any observed differences in activation between conditions would have to reflect the response to each individual set of stimuli.

METHODS: EXPERIMENT 2

Participants

For Experiment 2, 12 healthy subjects (six men, average age = 22.9 years, range = 19–27 years) participated. No subjects participated in both experiments.

Materials

We selected 25 trials from each condition of Experiment 1 for use in Experiment 2. The items in the two conditions were matched for lexical frequency and familiarity (as measured by lexical decision RTs), number of phonemes, and color agreement. Auditory stimuli were recorded using Audacity (version 1.2.5) and were filtered for noise. Because of the inherent difficulty of hearing intelligible words above scanner noise made while acquiring functional images, we modified sound files with a Matlab tool that boosts sound frequencies normally masked by fMRI noise. Behavioral piloting of both file types revealed that the modified sound files were more intelligible than the original sound files. To further facilitate word recognition in the scanner, subjects listened to all of the words before scanning (once each, in a random order) and were told they would hear these words again during the scan. They also generated the typical colors of these objects, and naming latencies (as a proxy of familiarity for the scanned subjects) were compared across the conditions of interest. There were no significant differences in naming latencies across these conditions.

Procedure: Experiment 2

On each trial, subjects heard three words and were instructed to decide which of the first two named objects (spoken in a female voice) was more similar in color to the third named object (spoken in a male voice). The trial structure, illustrated in Figure 2, was as follows: At the beginning of each trial, a "READY?" prompt appeared on the screen for 250 msec. Subjects then heard the names

of three objects (the words' onsets were 1000 msec apart). Simultaneously with the onset of the third word, a visual prompt of "COLOR?" appeared, and subjects had 3650 msec to respond with a button press. Subjects were also told to press a third button if the words in a given triad were unintelligible because of scanner noise so we could eliminate those trials from our analyses. The intertrial interval was 100 msec.

Each subject completed three scanning runs of the color retrieval task (6–7 min each) with eight to nine trials of each condition per run. We presented a unique trial order to each subject using Optseq2 (surfer.nmr.mgh.harvard.edu/optseq) to generate optimized pseudorandom stimulus presentation sequences. For each trial, the entire 6 sec (this includes auditory word presentation and time to respond) was analyzed and reported. Experimental trials were intermixed with jittered fixation periods averaging 6 sec in length. (These trials were also intermixed with filler trials on which subjects made judgments unrelated to object color, which were not further analyzed.)

Additionally, the list of 300 objects contained four homophones (JEANS, PEA, THYME, DOE) that when heard rather than seen, could potentially result in ambiguity irrelevant for the task of interest. Thus, for Experiment 2, during acquisition of anatomical images (and before functional imaging), each of the 300 words was visually presented on the screen for 1000 msec. The words were randomly presented across subjects, but the homophones always came first. Subjects were told that these words were being presented to refresh their memories of the objects that would come up during the task, and they were instructed to read each word silently to themselves.

The "functional localizer" to identify brain regions involved in color perception was administered after the color knowledge task, exactly as in Experiment 1. All image acquisition parameters were as in Experiment 1, although fewer volumes were collected (693) and the overall duration of the experiment was shorter. Behavioral and functional data were analyzed as in Experiment 1, with the exception that we modeled each trial as a separate event with a 6-sec duration.

RESULTS: EXPERIMENT 2

Behavioral Results

Vis-Verb scores ranged from –11 to 13 ($M = 1.5$, $SD = 8.07$) and did not differ from Experiment 1 scores ($p = .37$). The pattern of performance on the WCC and BCC trials resembled that of Experiment 1: There was a small but still reliable difference between conditions in RTs to correct trials (BCC: $M = 1898.42$, $SD = 246.10$; WCC: $M = 2109.38$, $SD = 322.78$; $t(11) = 3.96$, $p = .002$). Vis-Verb scores were not correlated with RT ($p = .97$). Accuracy was high across conditions (81%) and varied between conditions (BCC: 86%; WCC: 73%; $t(11) = 5.09$, $p < .001$). Accuracy differences significantly correlated with Vis-Verb

scores ($r = .64, p = .03$), as seen in Experiment 1 (and shown in Figure 3B).

Imaging Results

Functional ROIs were identified in the same manner as in Experiment 1. There was substantial overlap between the fROIs obtained in Experiment 1 and those obtained in Experiment 2, despite the many methodological variations (see Figure 6).

Results are shown in Figure 4B. In the left fusiform region (66 voxels, $t = 5.5$, Talairach coordinates: $-42 -65 -12$, BA 19), activation was marginally greater during WCC trials (mean = 0.43%, $SD = 0.15\%$) than during BCC trials (mean = 0.38%, $SD = 0.19\%$; $t(11) = 2.169, p = .053$); this effect was not reliably different in magnitude from that observed in Experiment 1, $p = .15$. We also observed a marginally significant positive correlation between the magnitude of the main effect and Vis-Verb scores ($r = .46, p = .07$). These results establish that the effect of context on activation in left fusiform cortex during color retrieval is insensitive to the procedural variations between the two experiments.

In the left lingual region (91 voxels, $t = 5.0$, Talairach coordinates: $-12 -87 -1$, BA 17), there was no significant difference in activation between WCC trials (mean = 0.81%, $SD = 0.29\%$) and BCC trials (mean = 0.80%, $SD = 0.27\%$; $p = .75$). As shown in Figure 3D, we observed a weak, positive correlation between the magnitude of the main

effect and Vis-Verb scores that did not differ in magnitude from the correlation observed in Experiment 1 ($p = .57$) but which also did not reach significance here ($p = .24$).

Additional Analyses

An exploratory, whole-brain analysis revealed several other voxel clusters that surpassed a $p < .001$ (uncorrected) threshold at the whole-brain level for the task–baseline contrast. Identified in the same manner as in Experiment 1, within each of these fROIs, we then tested significance of the WCC–BCC contrast as well as the correlation between brain activity and Vis-Verb scores. These data are now reported in Table 1. Unlike Experiment 1, there were no reliable effects (of either task or subject variables) in any of these regions. Interestingly, a fusiform region that emerged during the exploratory analysis (that was more posterior to the fusiform region identified in our primary analyses and closer to the lingual region identified earlier) did not show the condition effect.

DISCUSSION: EXPERIMENT 2

Experiment 2 replicated many of the results of Experiment 1, despite a number of methodological changes: In Experiment 2, we (i) arranged stimuli in a randomized order, preventing subjects from anticipating the trial condition, (ii) reduced the trial duration from 9 to 6 sec, and (iii) presented auditory rather than visual stimuli during

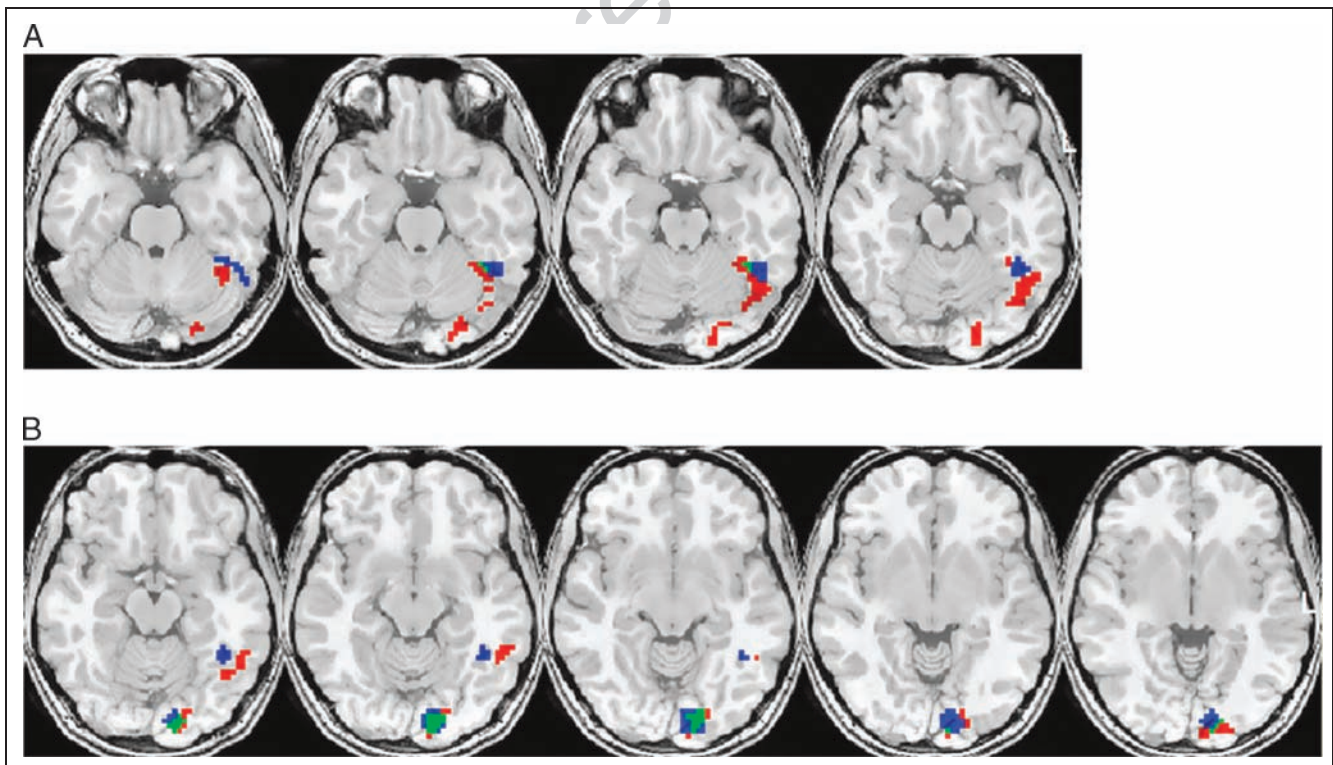


Figure 6. Color knowledge retrieval recruits overlapping brain regions in both Experiment 1 and Experiment 2. fROI overlap in left fusiform (A) and left lingual (B). fROIs are indicated for Experiment 1 (red), Experiment 2 (blue), and their overlap (green).

color knowledge retrieval. Even with these changes, the main effects followed the same pattern as seen in Experiment 1. Specifically, in both experiments, context (i.e., WCC versus BCC) affected the magnitude of activation in the left fusiform region during color knowledge retrieval. In the left lingual region, there was no difference in activity between conditions, although weak to moderate correlations were observed between the condition effect and cognitive style preference. And in both experiments, task accuracy positively correlated with visual-preferred cognitive style.

Although there was substantial replication between the two experiments, there were a few differences. First, slightly different parts of the lingual region were activated during the color retrieval task (the lingual region activated in Experiment 2 was more bilateral and anterior to that activated in Experiment 1, despite some overlap). Although we have no compelling explanation for this difference, the anterior activation is interesting, as it has been suggested that anterior color perception regions involved in color knowledge retrieval can be recruited on the basis of task demand (Simmons et al., 2007; Beauchamp et al., 1999). Perhaps because of this localization difference or perhaps because of one of the methodological changes between the two experiments, the percent signal change in the lingual region was much greater (in both conditions) in Experiment 2 than in Experiment 1, as seen in Figure 4. If anything, one might have predicted *less* activation under auditory presentation conditions.

A second difference between the experiments concerns the correlation between effect size and Vis-Verb scores in the lingual region. Although the correlation in Experiment 2 replicated that of Experiment 1 in pattern, it was a weaker correlation that did not approach significance. Although these correlations did not differ from each other, there are both methodological and theoretical reasons to expect the correlation to be greater in Experiment 1 than in Experiment 2. First, there is less statistical power in a randomized than a blocked design (D'Esposito, 2006); under this account, a more reliable correlation might have emerged with a greater number of trials with which to estimate the condition effect in each subject. Second, if the consequence of having a more visual cognitive style is an increased likelihood of deploying a visual strategy, then the correlation with cognitive style should be greater under conditions that favor the use of anticipatory strategies. In Experiment 2, we switched from a procedure that encouraged such strategies (slow trials in a predictable, blocked sequence) to one that did not (fast trials in a randomly ordered sequence). Under this account, the correlation with cognitive style should be lower in Experiment 2 than in Experiment 1.

GENERAL DISCUSSION

In this pair of studies, we explored factors that influence the retrieval of color knowledge from memory. Specifically, we hypothesized that a task variable (context) and a subject

variable (here, cognitive style) might affect the process of color retrieval, which may in fact be more dynamic and flexible than previously assumed. The results of Experiment 1 supported this hypothesis in two ways: We saw the effects of a task variable in the left fusiform gyrus, where there was significantly greater activity during WCC trials than during BCC trials. In the left lingual gyrus, we saw the effects of a subject variable, in that the magnitude of the condition effect on an individual subject level positively correlated with subjects' preference for a visual cognitive style, as measured by Vis-Verb scores. In Experiment 2, despite numerous methodological changes, we replicated many of the results from Experiment 1.

The Nature of Factors that Influence Conceptual Processing of Color

In both experiments, task accuracy positively correlated with the degree of visual cognitive style preference. Although all (but one) subjects were more accurate on the BCC trials than the WCC trials, subjects with the strongest visual style preference performed with almost equal accuracy whereas subjects with the strongest verbal style preference had differences in accuracy approaching 30% (see Figure 3A and B). Considering the methodological differences between the two experiments, this replication demonstrates an influence of cognitive style on task performance that is not dependent on state effects within a task block (i.e., predicting task condition) or on the modality in which the information is presented (auditory or visual).

In both experiments, we saw more brain activity in the left fusiform during WCC than during BCC trials, and these differences could not be explained by RT differences alone. This replication indicates that color retrieval processes can vary on a trial-to-trial basis, driven by the immediate context. There may also be more sustained changes in color retrieval strategies that emerge when the context is predictable and ongoing (as in Experiment 1), but the findings in Experiment 2 indicate that color retrieval is a dynamically changing collection of processes.

The ability to alter color retrieval processes in contextually appropriate ways might be thought of as a skill that varies across individuals. In accordance with this idea, the positive correlation between signal change and Vis-Verb scores in the lingual gyrus (robust in Experiment 1, weaker in Experiment 2) suggests an influence of cognitive style on knowledge retrieval in an early color perception region (Simmons et al., 2007; Beauchamp et al., 1999; Chao & Martin, 1999). For high visualizers (i.e., those with a higher Vis-Verb score), imagining object colors more closely resembles perception than for low visualizers, and perhaps as a result, these subjects perform better under conditions that require more detailed color information (i.e., WCC trials). Moreover, this result complements some recent findings that modality-specific cortical activity may underlie processing related to visual and verbal cognitive styles (Kraemer et al., 2009).

More generally, one might ask why the fusiform gyrus shows the task effect, whereas the lingual gyrus shows effects of the subject variable. Rather than ascribe functional descriptions to these two regions, we hope that our findings—that both task and subject variables influence the color knowledge retrieval process—point to the utility of using multiple approaches to understand the connections between brain and behavior. Here, we have used average tendencies in a traditional ROI data analysis to demonstrate differential activation based on discrimination of objects from the same or differing color category. Additionally, we have found that the variability in these average tendencies is also meaningful with regard to cognitive styles, highlighting the informativeness of an individual differences approach. By using both types of analyses, our findings help to inform a richer understanding of the factors influencing color knowledge retrieval. Indeed, the conjunction of these approaches has been used in previous researches (see Epstein, Higgins, & Thompson-Schill, 2005; Omura, Aron, & Canli, 2005).

Reconciling Extant Findings and Representations that Vary in “Resolution”

As we reviewed in the Introduction, numerous neuroimaging studies have examined the extent of overlap between regions activated by perception and memory of object properties—including color—to evaluate claims of sensorimotor theories of semantic memory. But the results of such studies have been mixed. For example, an early experiment failed to detect overlap between voxels activated by passive viewing of Mondrian-like displays (color perception) and voxels activated by color naming of achromatically presented object drawings (color knowledge) (Chao & Martin, 1999). However, another study found direct overlap in the left fusiform, using active hue sequencing (color perception) and property verification (color knowledge) (Simmons et al., 2007). In the current study, we observed overlap between color perception and color retrieval in the fusiform gyrus (as in Simmons et al., 2007) and also in the lingual gyrus (direct overlap was *not* found in Simmons et al., 2007); however, we also found that the magnitude of activation in these regions varied across subjects and across contexts. This variability may explain some of the inconsistencies in the literature.

Given these results, we propose that differences in results across studies reflect the existence of multiple types of color representations that vary in resolution. Here, the term “resolution” is used to describe a representation in color space, where a high-resolution color representation is one that contains fine detail (e.g., distinguishing two shades of red), whereas a low-resolution representation contains coarse detail (e.g., red versus yellow). We designed our WCC and BCC trials to tap into these two types of representations, respectively. Just as responses to visual stimuli can be described as varying in abstraction over low-level properties of the stimulus such as orientation, size, and

so on, it may be useful to describe color knowledge at varying levels of abstraction. In this way, the idea of multiple color representations is compatible with sensorimotor theory: retrieval of color knowledge at different levels of resolution would recruit perceptual representations with varying levels of abstraction. According to this view, overlap between color perception and color knowledge retrieval would depend on the “match” in the abstractness of the information represented in each case. It then follows that the tasks implemented in previous neuroimaging studies tapped representations at varying levels of resolution, resulting in slight differences in activation.

Although our results might suggest the existence of multiple color knowledge representations within a sensorimotor framework of semantic memory, we found no areas in which there was greater activity for low- versus high-resolution trials. There are two accounts for the structure in which these putative representations exist. Given a linguistic input (either written or heard words), these representations might be of a serial nature—retrieval of the high-resolution representation is dependent on (or occurs after) retrieval of the low-resolution representation. Or, the representations could be parallel in nature—both representations can be accessed separately in theory, but a serial strategy is applied for this task. That is, one representation is used first to try to solve the current task; if unsuccessful, the other type of representation is used instead. Investigation of these accounts warrants further study, as our data cannot distinguish between the two.

There is also an alternative explanation of our data based on the idea that both trial types involved retrieval of a single representation, but that, in the high-resolution condition, this representation was more difficult to retrieve. Consistent with this explanation, RTs in both experiments were longer for high- versus low-resolution trials, and there was differential activation in the fusiform gyrus. However, this difficulty explanation is unlikely for the following reasons. First, RT was a covariate in all fMRI data analysis, so that the differences in activation we reported for each experiment cannot be attributed to RT differences. Indeed, this type of hierarchical regression model will tend to *underestimate* the effect of task on activation. Second, in both experiments, the lingual gyrus was activated equally for both retrieval conditions, so the specificity of our effects is not well explained by a task difficulty explanation. Third, we found a positive correlation of Vis-Verb scores with brain activity in the lingual gyrus for Experiment 1a as well as with improved task accuracy. Under a difficulty account, task accuracy should negatively correlate with lingual activity; however, we do not find this to be the case.

Conclusions

Taken together, this pair of studies demonstrates the first neuroimaging evidence that context (a task factor) and cognitive style (an individual factor) can influence color knowledge retrieval, and it may be that these factors also

influence the degree to which color knowledge retrieval and color perception share a common neural substrate. We have proposed that these factors affect the resolution of the color information that is retrieved, and we suggest that the degree of overlap between color retrieval and color perception depends on the match between the resolution of the information required of each. More generally, these findings illustrate that color retrieval is a more dynamic and variable process than previously described and necessitate some modifications to current sensorimotor theories of semantic memory.

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