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A common neural substrate for perceiving and knowing about color

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Abstract

Functional neuroimaging research has demonstrated that retrieving information about object-associated colors activates the left fusiform gyrus in posterior temporal cortex. Although regions near the fusiform have previously been implicated in color perception, it remains unclear whether color knowledge retrieval actually activates the color perception system. Evidence to this effect would be particularly strong if color perception cortex was activated by color knowledge retrieval triggered strictly with linguistic stimuli. To address this question, subjects performed two tasks while undergoing fMRI. First, subjects performed a property verification task using only words to assess conceptual knowledge. On each trial, subjects verified whether a named color or motor property was true of a named object (e.g., TAXI-yellow, HAIR-combed). Next, subjects performed a color perception task. A region of the left fusiform gyrus that was highly responsive during color perception also showed greater activity for retrieving color than motor property knowledge. These data provide the first evidence for a direct overlap in the neural bases of color perception and stored information about object-associated color, and they significantly add to accumulating evidence that conceptual knowledge is grounded in the brain's modality-specific systems.

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1. Introduction

Recent decades have witnessed a renewal of the centuries-old debate concerning the format of human knowledge (Barsalou, 1999, 2008; Paivio, 1986). On one side of the debate are accounts asserting that mental representations about entities in the world bear only an arbitrary relationship to perceptual representations of those entities—in short, that knowledge representation is fundamentally amodal (Fodor, 1975; Kintsch, 1998; Pylyshyn, 1984). On the other side are accounts assert-

ing that knowledge representations are grounded in the neural mechanisms for perceiving and acting on entities' real-world referents (Allport, 1985; Barsalou, Simmons, Barbey, & Wilson, 2003; Damasio, 1989; Martin, 2001; Pulvermüller, 1999, 2005; Thompson-Schill, 2003). This latter position – often described by various names such as “embodied cognition,” “sensory-motor theory” and “simulation theory” – has gained support from growing behavioral, neuropsychological, and neuroimaging results demonstrating that knowledge representation is grounded in the brain's modality-specific systems.

In behavioral research, one basic strategy has been to demonstrate that well-established sensory-motor variables (e.g., such as the time cost associated with switching attention between perceptual modalities) are also observed in subjects' performance on conceptual tasks. For example, Pecher, Zeelenberg, and Barsalou (2003, 2004), using only linguistic stimuli, found

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that modality switching costs are observed when subjects verify that a tiger has stripes (a visual property) immediately after verifying that a tea pot whistles (an auditory property). For a review of similar behavioral evidence, see Barsalou (2003b); for reviews of related neuropsychological phenomena, see Cree and McRae (2003) and Simmons and Barsalou (2003).

Functional neuroimaging studies also provide evidence that knowledge is grounded in the brain's modality-specific systems. In particular, much of this work demonstrates that retrieving knowledge about objects activates a distributed circuit of property representations in and around the brain's systems for perception, action, and interoception (Martin, 2001, 2007). Processing tool concepts, for example, activates middle temporal gyrus and premotor areas associated with the perception of nonbiological motion and the execution of motor action (Beauchamp, Lee, Haxby, & Martin, 2002, 2003; Chao & Martin, 2000). Similarly, processing food concepts activates the insula/operculum and left orbitofrontal cortex, regions previously implicated in the representation of taste and food reward properties (Simmons, Martin, & Barsalou, 2005). Particularly noteworthy are findings from Hauk, Johnsrude, and Pulvermüller (2004), who found direct topographic overlap in areas along the motor cortex activated for physical action and the meanings of words that describe actions.

Theories that ground knowledge in the brain's modality-specific systems hold as a central tenet that retrieving conceptual knowledge activates cortical areas used in perception and action. However, Hauk et al.'s (2004) finding of direct overlap in the neural bases of actions and conceptual representations is perhaps the only case where this has been demonstrated clearly. Researchers rarely map within individuals the brain regions involved in perception of a particular property, and then test if those same regions are active during conceptual processing of that property. Because of this, with the exception of the domain of action knowledge, there is scant functional neuroimaging evidence demonstrating direct overlap in the neural bases of perceptual and conceptual representations.

As a case in point, consider the representation of color knowledge. Electrophysiological, neuropsychological, and functional neuroimaging evidence all indicate that color perception depends on a network of brain regions centered in the ventral occipitotemporal cortex, and also branching up into dorso-medial occipital and parietal cortices (Bartels & Zeki, 2000). Neuropsychological and functional neuroimaging evidence similarly implicates the ventral occipitotemporal cortex in the representation of color knowledge. For example, lesions to ventral temporal cortex can result in color agnosia (Farah, Levin, & Calvino, 1988; Luzzatti & Davidoff, 1994). Analogously, in PET and fMRI studies, researchers have observed activations in ventral temporal cortex when subjects either name objects' canonical colors or verify the color properties of objects (Chao & Martin, 1999; Goldberg, Perfetti, & Schneider, 2006; Kellenbach, Brett, & Patterson, 2001; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Oliver & Thompson-Schill, 2003; Wiggs, Weisberg, & Martin, 1999).

The lesion literature also demonstrates another point of potential significance: representations of color perception and

color knowledge in the ventral occipitotemporal cortex are at least somewhat dissociable. Whereas lesions to lingual gyrus often result in achromatopsia in the presence of spared color knowledge (Bouvier & Engel, 2006), lesions to ventral temporal cortex result in color agnosia with spared color vision (Miceli et al., 2001). Neuropsychological evidence for a dissociation between color knowledge and color perception does not necessarily implicate a system in which the two abilities are completely independent. Although color knowledge and color perception differ somewhat in their neural bases, they could still rely on some common mechanisms. Nevertheless, there has been no evidence to date that color knowledge relies on *any* of the neural substrate for color perception.

In the only study to map activity associated with both color perception and color knowledge retrieval in the same subjects, Chao and Martin (1999) observed that generating color names for achromatic objects activated portions of the fusiform gyrus anterior to the occipital activations in the lingual gyrus associated with passively viewing color stimuli. Although the finding that activation for color knowledge was *near* a color perception region may support sensory-motor accounts of knowledge representation, by no means must it be interpreted in this manner. Rather, proponents of amodal knowledge representation could argue that the failure to find areas common to the two processes actually supports their view, with color knowledge regions perhaps storing amodal descriptions of information represented in adjacent color perception cortex.

Theories that ground knowledge in the brain's modality-specific systems would receive much stronger support if evidence demonstrating a direct overlap in the neural bases of color perception and color knowledge could be obtained. To this end, we scanned subjects while they verified color and motor properties of objects. Subjects were not presented with pictures of the objects or properties, but only received words that described them (e.g., GRASS – green, SCREWDRIVER – turned). On each trial in a fast event-related fMRI design, subjects received the name of an object for 2 s (GRASS), followed by the name of a property for 2 s (green), with random inter-stimulus intervals between trials. We also included catch trials containing concepts that were not followed by properties, so that we could deconvolve the BOLD responses for the concepts and properties, given that they always occurred in a fixed temporal sequence (Ollinger, Shulman, & Corbetta, 2001). Analyses of the property verification task focused on activations for the properties, deconvolved from activations for the concepts. The critical test of modality-specific accounts was whether activations for the color properties overlapped with activations for color perception, as assessed by a functional localizer task for color perception.

Subjects performed the color perception functional localizer after completing the property verification task. We used a common clinical test of color perception (the Farnsworth-Munsell 100 Hue Test) adapted for fMRI by Beauchamp, Haxby, Jennings, and DeYoe (1999). Fig. 1 illustrates this task in detail. In our analyses, we first used the color localizer to identify areas important for color perception. We then assessed whether any of these areas were also involved in representing the color prop-

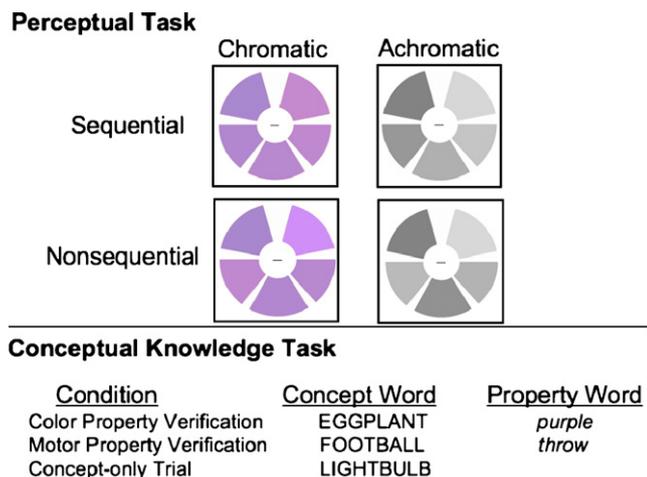


Fig. 1. Examples of stimuli used in the perceptual and conceptual knowledge tasks. The top half of the figure displays example stimuli from the color perception functional localizer task. Subjects viewed 21-s blocks of chromatic and achromatic stimuli and determined if the wedges in each stimulus wheel formed an orderly clockwise hue sequence. The bottom half of the figure depicts stimuli from the event-related property verification task. In concept-property trials, subjects were presented a concept word for two seconds, followed by a property word, also for two seconds. Their task was to indicate whether the property could be true of the concept. Property words could indicate either colors or motor actions. On a subset of trials, subjects saw concept words that were not followed by properties. These trials were included to allow deconvolution of the response to concept words from the response to the property words.

erties verified during the property verification task. Specifically, we assessed whether color properties activated any of these areas more than did the motor properties.

2. Methods

2.1. Subjects

Ten right-handed, native English-speaking volunteers from the Emory University community participated in the scanning study for pay (six female and four male; age range, 19–44 years). All subjects completed health questionnaires prior to scanning, and none indicated a history of head injury or other neurological problems. In accordance with the prescribed protocols of Emory University's Institutional Review Board, all subjects read and signed an informed consent form describing the procedures and possible risks.

2.2. Experimental design

Subjects performed two tasks while undergoing fMRI: an event-related property verification task in which subjects retrieved knowledge about common objects' color and motor properties, followed by a block design version of the Farnsworth-Munsell 100 Hue Task, adapted from [Beauchamp et al. \(1999\)](#).

2.2.1. Property verification task

In the property verification task, subjects received two kinds of randomly inter-mixed events: concept-property events, and concept-only events. In concept-property events, a concept word that named a physical object (animate or inanimate) appeared for 2 s (e.g., BANANA, SCREWDRIVER), followed immediately by either a word for a color or motor property, also presented for 2 s (e.g., yellow, turned). On reading the property word, subjects determined whether the property could possibly be true of the concept and indicated their decision by making a binary response with the fingers of their dominant hand on a button box. Verification latencies were measured from the onset of the property name. Decision latencies shorter than 200 ms or longer than 2600 ms were excluded from analyses of the behavioral data. On the concept-only events,

only a concept word was presented for 2 s. Interspersed among the two event types were variable duration interstimulus intervals during which a centrally located fixation mark was present on the screen (average duration = 6.7 s, range 2–24 s).

During the 112 concept-only events, the same concept words from the concept-property trials were presented but without a subsequent property word. These concept-only events were included in the design to allow the hemodynamic response for the property words to be mathematically deconvolved from the response for the concept words ([Ollinger et al., 2001](#)). Concept-only events were then modeled within the same column of the design matrix as concepts in the concept-property events. As a result, concept words occurred frequently enough in the absence of property words to allow us to uniquely estimate the hemodynamic responses to concepts and properties separately, even though in concept-property trials the property words always followed the onset of concept words at a short fixed interval (2 s). Simulations run in AFNI (<http://afni.nimh.nih.gov/afni>) prior to the study demonstrated that the concept and property events were not collinear and that the concept and property events could be deconvolved reliably. For more information on this innovative technique for separating events with fixed temporal sequences in fast event-related designs, see [Ollinger et al. \(2001\)](#).

At the start of any given trial, subjects did not know whether they would see a concept-only or concept-property event. Subjects were instructed to read all concept words and prepare to respond to a property, should one be forthcoming. Because no property words were presented during concept-only events, however, subjects did not make a response. They were instructed that if a property did not appear, they should instead prepare for the next concept word. From the subjects' perspective, the task was identical during the concept period of both the concept-only and concept-property trials. For each concept-property trial, the property named either a color (112 trials) or a motor action (56 trials). As described earlier, the motor property trials served as a contrast condition for the color property trials.¹

Seven optimized pseudo-random stimulus presentation sequences for the property verification trials were created in optseq2 (<http://surfer.nmr.mgh.harvard.edu/optseq/>). Trial sequences for these seven optimized runs were then counterbalanced across participants. To control for stimulus repetition effects, concept word presentations were balanced across runs. Approximately half of the concept words appeared in a concept-only trial before appearing in a concept-property trial; the other half appeared afterwards.

Among the color items, 18 different color words appeared across the trials. Some color properties were repeated multiple times: 12 color words were presented 4 times, 2 color words were presented 8 times, and 4 color words were presented 12 times.

2.2.2. Color perception functional localizer task

To functionally localize brain regions underlying color perception, subjects performed a version of the Farnsworth-Munsell 100 Hue Task adapted for fMRI.

¹ Prior to conducting the study, we considered, as an alternative research design, comparing BOLD responses to concept words having strong implicit color associates with those having weak implicit color associates. We decided against this approach because concepts that do not have strong color associates may still nonetheless have associated color information. In the strong color associate condition, subjects would reliably retrieve a particular color property for a particular concept (e.g., BANANA – yellow). In the weak color associate condition, subjects might still retrieve color properties, but the particular properties might be more idiosyncratic (e.g., CAR – blue or red or black or green). Because both conditions would thus involve retrieving color information, comparing the two would yield a null effect, when in fact color property retrieval was critical for the task. The only solution to this problem would be to compare concepts with and without associated color information. Unfortunately, it is difficult to identify concepts that do not have any associated colors. Fortunately, this is not the case for other types of property information. In particular, it is relatively easy to generate lists of concepts without associated motor information (e.g., CLOUD, ELEPHANT). For this reason, we chose to compare activity observed when subjects verified concept's color properties with the activity when they verified motor properties.

Subjects saw five wedges encircling a central fixation mark (Fig. 1). The wedges located at the 2 o'clock and 10 o'clock positions were either the lightest or darkest hues in the wheel, with the hues of the remaining three wedges being free to vary. Subjects were instructed to maintain fixation on the centrally located fixation mark, and to judge whether the five color or grayscale wedges were uniformly ordered from lightest to darkest hue. In each 21-s block, subjects saw seven color or grayscale wheels presented for 2.5 s, each separated by a 500 ms interstimulus interval. Across each MR scanning run, subjects saw three grayscale wheel blocks, and three color wheel blocks, with all six blocks separated by 15-s fixation periods.

Block orders in the color perception task were counterbalanced across both subjects and runs. Subjects were instructed to press one button indicating whether the hues in each wheel formed a monotonically increasing sequence, or another button if the hues did not. Color and grayscale wheels formed increasing hue sequences on half of the trials. Among the wheels arranged in orderly sequences, the wedges were equally likely to move from darkest to lightest clockwise and counter-clockwise. Subjects performed the functional localizer task in four scanning runs immediately following completion of the seven property verification task runs.

2.3. Imaging details

Stimuli were back-projected onto a screen located at the head of the scanner and viewed through a mirror mounted on the head coil. Stimulus presentation and response collection were controlled using Eprime (www.psnet.com). Subjects indicated their responses to stimuli by using the right thumb to press one of two buttons on a button box held in the right hand.

In each of the seven scanning runs for the property verification task, 208 echoplanar MR volumes depicting BOLD contrast were collected with a 3 T Siemens Trio scanner. Each volume consisted of 30 contiguous 3-mm slices in the axial plane (TE = 30 ms, TR = 2000 ms, flip angle = 90°, voxel size = 3 mm × 3 mm × 3 mm). In each of the four scanning runs for the color perception task, 72 echoplanar MR volumes were collected. Each volume consisted of 30 contiguous 3-mm slices in the axial plane (TE = 30 ms, TR = 3000 ms, flip angle = 90°, voxel size = 3 mm × 3 mm × 3 mm). Given the TR and slice thickness, it was not possible to image the entire brain. For each subject, the inferior slice was aligned a few millimeters inferior to the ventral temporal cortex. After completing the 11 functional runs, a high resolution MPRAGE scan was collected (TE = 6 ms, TR = 25 ms, flip angle = 15°, voxel size = 1 mm × 1 mm × 1 mm).

Prior to statistical analyses, image preprocessing was conducted in AFNI. To attenuate motion-related signal changes, each subject's scans were coregistered to the 20th volume of the first EPI scan, and smoothed in the axial plane using an isotropic 6 mm full width at half max Gaussian kernel. After applying a slice time correction to each volume, the signal intensity at each time point was divided by the mean signal value for that run, and the result multiplied by 100, after which the subject's data reflected the percent signal change from the run mean.

2.4. Statistical analyses

To identify color-responsive regions in the color perception localizer task, multiple regression was used to detect changes in MR signal between color and grayscale stimulus blocks within each subject. The regression model included two regressors of interest representing the color and grayscale stimulus blocks, and regressors of no interest to account for slow changes in the MR signal within each run (signal mean, linear trend, second-order polynomial). Six regressors were also included to account for residual motion-related signal changes after volume registration. The two regressors indexing color and grayscale stimulus blocks were constructed by convolving a boxcar function of width 21-s corresponding to presentation of each stimulus condition with a gamma-variate function, thus adjusting the predictor variables to account for the overall delay and shape of the BOLD response. Individual subjects' data were then warped to Talairach space using a linear transformation. Finally, a general linear test comparing the response to color and grayscale stimulus blocks yielded *t*-maps that were then input into a second-level random effects analysis across subjects. Because a large body of literature implicates fusiform and lingual gyri in color perception (see Sections 1 and 4), we applied a small-volume correc-

tion to these regions, accepting clusters with a volume threshold of at least 135 mm³ and a *p*-threshold < 0.0001. Based on Monte Carlo simulations run in AlphaSim (<http://afni.nimh.nih.gov/afni>), the probability of observing a cluster this size and *p*-threshold in the combined volume of these two brain regions is less than 0.05 corrected for multiple comparisons. Outside the fusiform and lingual gyri, no areas of activity were observed after correction for multiple comparisons.

Analyses of property verification runs assessed activations for properties deconvolved from concepts, as described earlier (i.e., activations for concepts were removed). The data were analyzed using a finite-impulse-response function model, with stick functions indicating the event onsets of the four trial types: concept words (both concept-only and concept-property events), motor property words, true color property words, and false color property words. Regressors of no interest were also included to account for low frequency changes in the MR signal within each run (signal mean, linear trend, second-order polynomial), as well as six regressors output from the volume registration software to account for residual motion-related signal changes. Peristimulus time courses were estimated for each condition to depict activity from stimulus onset to 14-s post-stimulus with a 2-s resolution. Prior to the group analyses, the subjects' brains were transformed into Talairach standard space.

Because our primary goal was to determine if color knowledge retrieval engaged color perception brain regions, we defined each color-perception cluster significant in the activation of the localizer data as a separate functional region of interest (ROI). We then used a repeated measures random effects ANOVA to compare the response amplitude between 4 and 8 s post-stimulus onset for true color and motor trials, averaged across all voxels in each ROI. Equal numbers of true color and motor property trials were included in this test (56 concept-property trials in each condition).

To examine activity outside the ROIs, the individual subjects' data were analyzed collectively in a two-way mixed effects ANOVA (property type × subject), comparing the response amplitude between 4 and 8 s post-stimulus onset for true color and motor trials. We applied a cluster size threshold correction to the data, accepting clusters with a volume threshold of at least 297 mm³ and a *p*-threshold < 0.0001. Using Monte Carlo simulations run in AlphaSim, we ascertained that the probability of observing a cluster this size and *p*-threshold within a whole-brain volume, after masking out the ventricles and most white matter, is less than 0.05 corrected for multiple comparisons.

3. Results

3.1. Color perception localizer task

3.1.1. Behavioral results

Decision latency for color and grayscale judgments did not differ significantly (color: *M* = 1456 ms, S.D. = 176 ms; grayscale: *M* = 1395 ms, S.D. = 179 ms), *t*(20) = 0.81, *p* = 0.43. There was, however, a trend toward lower accuracy in color judgments (color: *M* = 68%, S.D. = 6%; grayscale: *M* = 74%, S.D. = 10%), *t*(20) = 1.86, *p* = 0.08.

3.1.2. Brain activity

As reported in Table 1, two regions responded more strongly to color stimuli than to grayscale stimuli: the right lingual gyrus (volume = 147 mm³, anterior/posterior *Y*-coordinates = -69/-76), and left fusiform gyrus (volume = 142 mm³, anterior/posterior *Y*-coordinates = -33/-38). Of these regions, the most color-responsive voxels (i.e., those with the highest *t*-values) were found in the left fusiform gyrus. Nowhere in the brain was the response to grayscale stimuli reliably greater than the response to color stimuli.

Table 1
Regions showing differential responses following corrections for multiple comparisons

	Coordinates			Peak <i>t</i>	<i>p</i>
	X	Y	Z		
Regions showing differential responses to color and grayscale perception					
Color wheels > grayscale wheels					
Left fusiform gyrus	−33	−36	−16	13.66	<0.000001
Right lingual gyrus	12	−74	−5	9.43	<0.000006
Grayscale wheels > color wheels					
None					
Regions showing differential responses to color and motor property verification					
Color property verification > motor property verification					
None					
Motor property verification > color property verification					
Left middle temporal gyrus	−57	−53	7	11.15	<0.000002

Note. Coordinates are listed in Talairach space.

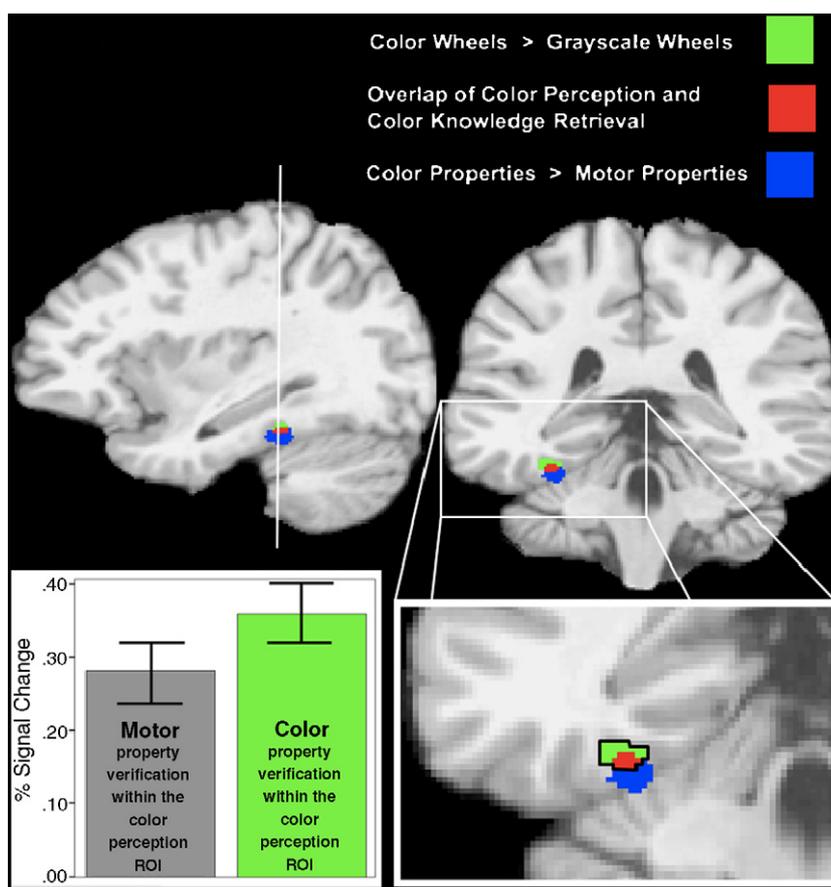


Fig. 2. Overlap in perceptual and conceptual color processing. On top, the figure depicts sagittal and coronal sections from the N27 template brain warped to Talairach space (template available in AFNI, <http://afni.nimh.nih.gov/afni/>). The functional overlays represent Talairach-normalized group data from the random effects analysis. Green patches indicate regions where activity was greater for processing color than grayscale wheels in the color perception task ($p < 0.0001$). Blue patches indicate regions where activity was greater for verifying color properties than motor properties in the knowledge retrieval task ($p < 0.01$ with a cluster size of at least 108 mm^3). The red patch stretching from $Y = -33$ to -38 in the left fusiform gyrus indicates the region of overlap between the two tasks. The inset bar graph demonstrates that within the left fusiform ROI where color perception produced a greater response than grayscale perception (in other words, within the union of the green and red patches), the average BOLD response to color property words in the property verification task was greater than the response for motor property words ($p = 0.006$). The y-axis indicates percent signal change relative to signal baseline, with error bars representing ± 1 standard error of the subject means.

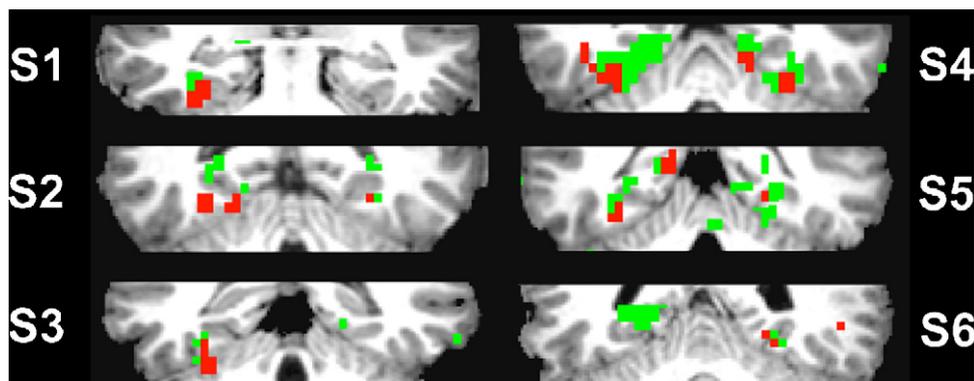


Fig. 3. Overlap in the neural bases of color perception and color knowledge retrieval in six individual subjects (S1–S6). Each coronal image demonstrates ventral temporal cortex in a different subject (between $Y = -30$ and -45). Green regions indicate voxels that were more active for color perception than grayscale perception in the functional localizer task ($p < 0.01$). Red regions indicate voxels within the subset of color-perception voxels that were also more active for color property verification than motor property verification ($p < 0.05$).

3.2. Property verification task

3.2.1. Behavioral results

No response accuracy differences were observed between color and motor property verifications (color: $M = 88\%$ correct, $S.D. = 12\%$; motor: $M = 92\%$ correct, $S.D. = 4\%$), $F(1,48) = 1.16$, $p = 0.29$. Similarly, verification latency for the two property types did not differ significantly (color: $M = 1279$ ms, $S.D. = 267$ ms; motor: $M = 1198$ ms, $S.D. = 219$ ms), $F(1,48) = 1.15$, $p = 0.29$.

3.2.2. Neural correlates of color knowledge versus motor knowledge retrieval

Having mapped the regions underlying color perception in the functional localizer task, we next examined whether either of these regions were also active during color property verification. To do so, random effects ROI analyses comparing color and motor property verification were conducted within each of the clusters identified by the color perception localizer task. Significantly, the left fusiform gyrus cluster shown in Fig. 2 exhibited stronger activation during the color property trials than during the motor property trials (percent signal change color $M = 0.36$, $S.D. = 0.16$; motor $M = 0.28$, $S.D. = 0.16$), $F(1, 9) = 12.48$, $p = 0.006$ (see inset line graph in Fig. 2, also see Fig. 3). In contrast, no difference was observed between color and motor property verification trials in the right lingual gyrus cluster (percent signal change color $M = 0.10$, $S.D. = 0.12$; motor $M = 0.13$, $S.D. = 0.25$, $F(1, 9) = 0.34$, $p = 0.58$). Outside the color perception ROIs, motor properties, when compared to color properties, activated a region extending from the left posterior middle temporal gyrus up into superior temporal sulcus (volume = 299 mm^3 , anterior/posterior Y -coordinates = $-50/-63$).

4. Discussion

Using an fMRI adaptation of a common clinical measure of color perception, we mapped regions in visual cortex more responsive to color than to grayscale stimuli. The most intensely activated color perception region, located in the left fusiform gyrus, also exhibited greater activity when subjects verified color

properties than when they verified motor properties. Similar to how Hauk et al. (2004) demonstrated that motor cortex is activated by reading motor property words (e.g., “lick”, “kick”, etc.), we have shown that color perception cortex is activated by processing color property words (e.g., “purple”, “yellow”, etc.). By revealing a direct overlap in the brain regions underlying color perception and color property retrieval, this finding extends a growing body of literature demonstrating commonalities in the neural bases of perception, action, and knowledge (Barsalou, 2008; Barsalou et al., 2003; Martin, 2007; Martin & Chao, 2001; Pulvermüller, 2005).

Proponents of amodal accounts might offer several alternative explanations of the present results, as well as those of earlier studies demonstrating that knowledge is grounded in modality-specific systems (e.g., Hauk et al., 2004; Simmons et al., 2005). It could be argued that the activations in modality-specific areas for color and action reflect explicit generation of mental images associated with the property word (e.g., “yellow”, “lick”). We cannot absolutely rule-out the possibility that some subjects used color and motor imagery to perform the property verification task. The neural bases of color perception and explicit color imagery share many commonalities, and were we to ask subjects to explicitly imagine colors, we would expect to see areas of activation similar to those reported here. This expectation follows naturally from a theoretical stance that perceptual information is used in many areas of cognition, including imagery and memory. The goal of the present study, however, was to determine whether retrieving color property knowledge in the property verification task activates color perception cortex. Indeed, according to our findings, it does. Importantly, at no point were subjects instructed to use imagery to perform the property verification task, nor from the amodal perspective, should imagery even be necessary. In fact, most amodal accounts would posit that property information is stored propositionally with the relevant concept information. This being the case, it would seem extremely odd for a proponent of amodal accounts to argue that the task cannot be performed using the amodal representations central to amodal theories, but instead must be performed using additional, ancillary, effortful processes. In other words, if color or motor knowledge is amodal, then why activate color or motor cortex to per-

form the task? If property information is amodal, then why would one need to “imagine” the property? Yet subjects do activate modality-specific cortex when accessing property knowledge.

If the activations in color regions are not due to explicit imagery of the color property words, then what is left for the amodal account to argue? One possibility is that the left fusiform area activated by color properties and color perception contains amodal symbols that stand symbolically for color information, rather than implementing color perception *per se*.

This explanation is unlikely for two reasons. First, evidence that the left fusiform gyrus represents color perceptual information, not amodal color descriptions, comes from functional neuroimaging studies of word-color synesthetes who experience vivid color images on hearing *non-color* words (Nunn et al., 2002; Paulesu et al., 1995). Both PET and fMRI studies demonstrated that these individuals' synesthetic color experiences were associated with activity in left fusiform gyrus near the area reported here, as well as in more posterior fusiform cortex. Specifically, Nunn et al. observed that color word synesthetic experiences were associated with activity in color region V4 α near to the left fusiform color ROI reported here. This was not the case, however, for non-synesthetic control subjects. Interestingly, Nunn et al. also observed that color word synesthetic experiences activated a more posterior region in V4/V8, overlapping with activations observed when their subjects viewed color Mondrian stimuli passively. As will be discussed later, these two regions likely serve different purposes. Whereas the more posterior region underlies low-level sensory experiences of color, the more anterior fusiform region underlies higher-level perceptual representations of color. Taken together, the functional neuroimaging findings with color word synesthetes suggest that the left fusiform gyrus activity observed in the present study is related to experiencing color, rather than amodal representations of color information.

There is a second and even more compelling reason that the overlapping activations for color perception and color property verification do not simply reflect amodal symbols for color. A recent neuroimaging study with monkeys – who presumably do not have amodal symbols – exhibits remarkable correspondence with the findings reported here, and also with those of Nunn et al. (Tootell, Nelissen, Vanduffel, & Orban, 2004). Tootell et al. observed that the most color-responsive brain regions in rhesus monkeys were located in areas TEO and TE, possible homologues of human fusiform gyrus. We observed in humans that a similar fusiform region also contained the most color-responsive voxels during both the perception and conception of color. In principle, it is unclear why humans, in the course of color perception, would transduce color perceptual information into a symbolic, amodal format, and then represent that information within the visual system. It is even less clear why monkeys would do the same.

4.1. Relations with previous findings on brain activation during color perception

As Table 1 illustrates, two regions were more active when subjects made hue order judgments while judging color ver-

sus grayscale stimuli: the right lingual gyrus, and the fusiform gyrus. These findings are consistent with many previous functional neuroimaging studies observing posterior ventral occipital cortex activity, particularly in the lingual gyrus, in comparisons of passively viewed color and grayscale stimuli (Chao & Martin, 1999; Clark et al., 1997; Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; Kleinschmidt, Lee, Requardt, & Frahm, 1996; Zeki et al., 1991). The ubiquity of this finding in passive color viewing tasks suggests that this region is important for representing the experience of color sensation. In contrast, more anterior activity in the left fusiform is typically only observed in imaging studies requiring more effortful color stimulus processing, such as attention to detailed color information during the sequencing of hues (Beauchamp et al., 1999; Beauchamp, Haxby, Rosen & DeYoe, 2000). In the present study, we observed activity in both regions: a posterior cluster in the right lingual gyrus, and a second, more anterior cluster, located approximately 1 cm anterior to the anterior fusiform cluster observed by Beauchamp and colleagues.

4.2. Relations with lesion patients

Neuropsychological findings shed light on the specific information processing that these two areas perform. A recent meta-analysis of lesion loci associated with achromatopsia found that nearly all reviewed cases had damage in right ventral occipital cortex, with the maximum lesion overlap located approximately 1 cm lateral to the right lingual gyrus activity observed in the present study (Bouvier & Engel, 2006). In other words, damage to more posterior ventral occipital color-selective areas is associated with failures in color vision. Interestingly, however, achromats' color knowledge often remains intact. Although they cannot *see* that a banana is yellow, achromats *know* that bananas are yellow.

In contrast, color agnosia is the failure to retrieve color knowledge about objects (e.g., not knowing that bananas are yellow), which may or may not be attended by achromatopsia. Cases of object color agnosia in the presence of spared color vision have resulted from lesions to the left temporal lobe (Farah et al., 1988; Luzzatti & Davidoff, 1994; Miceli et al., 2001). Particularly noteworthy is case IOC who, following damage to left ventral temporal cortex (including the fusiform gyrus), had spared color vision and intact knowledge of object form and function, but was severely impaired on tests of object color knowledge (Miceli et al., 2001). Patient IOC, and other object color agnosics with intact color vision, suffer from damage to left cortical regions anterior to the areas that support color vision.

4.3. Levels of color representation

The neuropsychological findings, together with the imaging finding that color-selective activity in left fusiform is only observed when color perception tasks require fine-grained attention to color information, suggests the following conclusion. Posterior color-selective regions in occipital cortex support *passive* color sensation by representing the lower-level color qualia of stimuli. Anterior color-selective regions in ventral temporal

cortex, by contrast, become engaged when subjects *actively* process color information so as to extract and encode meaningful, high-level color perceptual representations.

Theories of object perception and categorization often propose that learning the properties of objects requires using selective attention to extract meaningful higher-order representations from low-level sensory-motor features (Schyns, Goldstone, & Thibaut, 1998; Schyns & Rodet, 1997). Building on these accounts, theories that ground knowledge representation in perceptual mechanisms argue that these higher-order representations are themselves inherently perceptual, rather than amodal. Furthermore, in the absence of the entity itself, reenactments of these high-level perceptual representations form the backbone of knowledge about the entity, such as object-color associations (Barsalou, 1999, 2003a). If high-level perceptual representations of color properties are extracted and stored in the left fusiform gyrus, then sensory-motor accounts would predict that this region should be particularly active when subjects retrieve information about objects' color properties. Indeed, this prediction is borne out both by the findings of the present study, and also by those of Kellenbach et al. (2001), who observed that color knowledge retrieval activated the left fusiform gyrus only 4.5 mm from the activation peak observed in the present study's color perception task.

4.4. Responses to motor properties

In contrast to color property verification, verifying motor properties activated the left middle temporal gyrus. Activation of the left middle temporal gyrus/STS for motor trials is significant because this region becomes active when individuals perceive both biological and non-biological motion (Beauchamp et al., 2002, 2003; Grossman & Blake, 2002; Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005; Puce & Perrett, 2003). Thus, it is likely that this region was representing how the physical motions associated with the motor properties would appear visually, for both the actions of animate agents (e.g., HOSTAGE – tied) and manipulated objects (e.g., AXE – sharpened).

The scan parameters in the present study were chosen to optimize measurement of ventral temporal color perception cortex, and not activity in widely distributed motor regions associated with the motor property control task. As such, we were unable to image dorsal brain regions, and so cannot report whether the motor cortex was activated in the motor property control condition. For findings demonstrating involvement of motor cortex in conceptual processing, see Hauk et al. (2004).

4.5. Conclusion

By having subjects perform both color perception and color knowledge retrieval tasks, we addressed a hypothesis that is central to the claim that conceptual knowledge is grounded in modality-specific simulations, namely, that retrieving property knowledge shares the neural substrate underlying property perception. Previous studies have provided evidence that support this hypothesis indirectly by inferring overlap based on findings reported elsewhere in the literature. In contrast, the present

study is the first to show, within the same group of subjects, that retrieving conceptual knowledge about object-color properties modulates activity in a region active when colors are perceived.

Taken together, these findings inform both cognitive and neurobiological accounts of perception and knowledge representation. The overlap between perceptual and conceptual color representation favors accounts that ground conceptual knowledge in the brain's modality-specific mechanisms. Clearly, however, disjunctions exist in the neural bases of these two cognitive abilities. Perception and knowledge representation are not the same phenomena, and many questions remain regarding the relationship between the two. For example, we have shown that color knowledge retrieval modulates activity in a high-level color perception region. It remains unclear whether a different, perhaps more demanding, color knowledge retrieval task might modulate activity in lower-level color perception regions, such as the right lingual gyrus cluster found in our color localizer task, and also found in color perception studies that used passive viewing paradigms (Chao & Martin, 1999; Zeki et al., 1991). More generally, it will be important for future research to articulate the commonalities and boundaries between perception and knowledge, if we are to develop satisfactory process-level accounts of these fundamental cognitive abilities.

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