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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.

Keywords: Conceptual knowledge; Fusiform gyrus; fMRI; Color perception; Property verification

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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 asserting 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 dorsomedial 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 interstimulus 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-