A Conceptual Lemon: Theta Burst Stimulation to the Left Anterior Temporal Lobe Untangles Object Representation and Its Canonical Color

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Abstract

■ Object recognition benefits greatly from our knowledge of typical color (e.g., a lemon is usually yellow). Most research on object color knowledge focuses on whether both knowledge and perception of object color recruit the well-established neural substrates of color vision (the V4 complex). Compared with the intensive investigation of the V4 complex, we know little about where and how neural mechanisms beyond V4 contribute to color knowledge. The anterior temporal lobe (ATL) is thought to act as a "hub" that supports semantic memory by integrating different modality-specific contents into a meaningful entity at a supramodal conceptual level, making it a good candidate zone for mediating the mappings between object attributes. Here, we explore whether the ATL is critical for integrating typical color with other object attributes (object shape and name), akin to its role in combining nonperceptual seman-

tic representations. In separate experimental sessions, we applied TMS to disrupt neural processing in the left ATL and a control site (the occipital pole). Participants performed an object naming task that probes color knowledge and elicits a reliable color congruency effect as well as a control quantity naming task that also elicits a cognitive congruency effect but involves no conceptual integration. Critically, ATL stimulation eliminated the otherwise robust color congruency effect but had no impact on the numerical congruency effect, indicating a selective disruption of object color knowledge. Neither color nor numerical congruency effects were affected by stimulation at the control occipital site, ruling out nonspecific effects of cortical stimulation. Our findings suggest that the ATL is involved in the representation of object concepts that include their canonical colors. ■

INTRODUCTION

Conceptual knowledge refers to a crucial aspect of human cognition that enables us to assign meaning to different entities (words, objects, etc.) and further construct an abstract web representing relationships between factual information (e.g., "lemon" denotes an edible fruit with distinct aroma and flavor). Despite decades of research, there is still debate regarding the mechanisms whereby the human brain represents conceptual knowledge. The divergent opinions on this issue can be generally classified into two prominent camps. On one side of the debate are accounts asserting that concepts require mental simulation of bodily experiences and rely upon neural activity occurring in the perceptual and motoric system (Barsalou, 2008; Martin, 2007). This view, often termed "embodied cognition," rejects the idea that concepts can be built upon amodal symbols and propositions. Instead, it posits that concepts are represented by a distributed network of sensorimotor regions, rather than localized to a module acting as the core neural substrate. For instance, the con-

cept of a lemon would involve a constellation of cortical regions processing its yellow color, round shape, and sour taste. On the other side of the debate are accounts proposing that the central component of conceptual knowledge is a representational "hub" that synthesizes various perceptually based fragments (underpinned by sensorimotor regions, which form "spokes") into a meaningful entity (Lambon Ralph & Patterson, 2008; Patterson, Nestor, & Rogers, 2007). This latter position, generally termed the "hub-and-spoke" theory, suggests that the anterior temporal lobes (ATLs) subserve this integrative processing of the "hub." According to this view, a "conceptual lemon" would entail modality-specific areas (spokes) coding sensory attributes and the ATLs (the hub) constructing a supramodal representation that incorporates these features.

Most research addressing the neural basis of conceptual knowledge has focused on the "spokes" that contribute to modality-related content; the function and neural locus of the "hub" remains a matter of speculation (for discussion, see Binder & Desai, 2011). One approach, frequently adopted by proponents of embodied cognition, is to demonstrate using fMRI that the brain areas that underpin perception or action also mediate the neural representation of conceptual knowledge. For example, there has

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been extensive research into whether retrieving color knowledge (e.g., knowing a lemon is yellow) recruits a cortical region primarily responsible for color perception (the V4 complex, which encompasses the fusiform and lingual gyri; see Bartels & Zeki, 2000).

In a seminal neuroimaging study examining the neural correlates for knowing about and perceiving color, Chao and Martin (1999) probed color knowledge by asking participants to generate canonical color names for gray-scale objects. The area sensitive to chromatic information was localized using the typical protocol of passively viewing color Mondrians (square patches containing multiple colors). The color knowledge task activated portions of the left lingual gyrus that were 2 cm lateral to but did not overlap with the activation of the left fusiform triggered by color perception. The authors therefore concluded that the neural basis for knowing about color is distinct from that for perceiving color. By contrast, Simmons et al. (2007) reported that a task requiring retrieval of object color knowledge activated a left fusiform region that was also highly responsive to color perception. They interpreted this as a commonality in neural architecture. It is noteworthy, however, that, when identifying the area sensitive to color perception, Simmons et al. used stimuli of the Farnsworth–Munsell hue test (Farnsworth, 1957), a challenging task requiring detection of subtle differences in hue. This task evoked more extensive regional activity in the ventral occipitotemporal cortex than passive viewing of Mondrians, which could increase the likelihood of an overlap in cortical activity.

In more recent research, a number of factors have been suggested to determine whether percepts and concepts of color recruit the same brain regions. For instance, the V4 complex tends to show greater activity when participants retrieve fine- rather than coarse-grained color memories and also when they have a propensity to process information using visualization rather than verbal skills (Hsu, Kraemer, Oliver, Schlichting, & Thompson-Schill, 2011). This implies that the V4 activity observed in conceptual tasks may be driven by both contextual factors (a difficult task prompting mental imagery) and cognitive factors (a tendency to use color imagery), particularly given that color imagery alone can activate V4 (Rich et al., 2006). Such findings together lend some support to the embodied hypothesis by showing that color knowledge activates some ventral occipitotemporal areas in the vicinity of V4. However, "near" is not "same"—whether the core representation of color knowledge shares any common neural mechanisms with color perception remains a matter of debate (Rugg & Thompson-Schill, 2013).

Considerably less is known about whether brain regions lying beyond the V4 complex contribute to color knowledge and what cognitive operations these areas may underpin. The "hub-and-spoke" theory predicts that, apart from V4 (or its adjacent areas) encoding specifically the chromatic aspect of objects, there is also a hub that unifies color with other sensory attributes and linguistic labels into a supramodal concept (Patterson et al., 2007). Patient research provides hints that the ATL would be a good candidate zone coding supramodal representation. Atrophy of the ATL causes loss of knowledge across various constituent features of an object in the presence of intact ability to perceive those features (Rogers, Patterson, & Graham, 2007; Adlam et al., 2006; Miceli et al., 2001). For instance, Miceli et al. (2001) reported that two patients exhibited severe deficits in object color knowledge but normal color perception. One patient, with damage to the left lingual gyrus but intact ATL, showed a selective loss of object color concept but preserved knowledge for other perceptual and functional properties. The authors argued that lesion of V4 selectively compromised color knowledge. Crucially, the other patient with extensive lesions in bilateral ATLs but spared lingual gyri exhibited widespread deficits in the knowledge for all attributes (color, shape, function, etc.) linked to an object, implicating the ATL "hub" in the conceptual amalgamation of object attributes.

Despite some patient research suggesting a role for the ATL in color knowledge, the picture is not yet clear. In these studies, the damage is not perfectly circumscribed to the ATL. Moreover, fMRI studies have rarely observed ATL activity in response to retrieval of the chromatic memory of objects. This has led to its possible contribution in neurocognitive models of color knowledge being given short shrift. The "failure" to find ATL activation in fMRI research could result from multiple methodological limitations: First, images of the ATL are usually distorted because of field inhomogeneity around the air-filled cavities near the ATL (Devlin et al., 2000). Second, some studies have limited coverage of the temporal lobe because of a restricted field of view during data acquisition. According to a meta-analysis, the inferior section of the ATL tends to get excluded when the researchers use imaging parameters that have a field of view narrower than 15 cm (Visser, Jefferies, & Lambon Ralph, 2010). Third, because the primary aim is often to test whether color knowledge engages the same neural basis of color perception, many studies employ a ROI approach, focusing on the V4 complex (e.g., Hsu, Frankland, & Thompson-Schill, 2011; Hsu, Kraemer, et al., 2011; Simmons et al., 2007). As a consequence, areas outside of the scope of V4, including the ATL, are often not included as ROIs. Thus, it remains unclear whether representing the chromatic aspect of objects at a conceptual level involves the ATL.

The aim of this study was to explore the role of the ATL in the neural representation of color knowledge, contributing to our understanding about how the brain represents a "conceptual object" in general. We used TMS to temporarily disrupt neural processing within the left ATL. TMS allows us to test the causal relationship between a cognitive function and a targeted cortical region in healthy individuals. As most of the patients with ATL lesions have extensive and often bilateral lesions outside the anatomical territory of the ATL (e.g., Adlam et al., 2006; Mummery et al., 2000), TMS in healthy participants

provides a more constrained approach than research of patients (although note that there can be propagation beyond the area stimulated directly). Access to object color knowledge was probed using a naming task in which target objects were presented in their typical or atypical color. Specifically, this task required verbal naming in response to objects with highly diagnostic colors. Object images were presented in either their respective congruent/typical color (e.g., a yellow lemon) or an incongruent/atypical color (e.g., a red lemon). This induced a highly reliable color congruency effect that canonically colored objects are identified faster than atypically colored objects. This task has been used in previous studies of both patients (Miceli et al., 2001) and healthy participants (Bramao, Reis, Petersson, & Faisca, 2011) as an objective measure of object color knowledge.

We applied stimulation targeting the left ATL, which we hypothesize acts as a hub linking object identity with its characteristic color, and a control site, the occipital pole (OP, which is not involved in conceptual knowledge; see Pobric, Jefferies, & Lambon Ralph, 2010b) in separate sessions. Participants performed two tasks: An object naming task that probes color knowledge and elicits a robust color congruency effect (Bramao et al., 2011) and a control numerical task that also results in a reliable congruency effect but involves no conceptual integration (Bush, Whalen, Shin, & Rauch, 2006). The control quantity task required verbal naming of the quantity of an array of Arabic digits. The identity of the digit could be either congruent (e.g., "3 3 3") or incongruent (e.g., "5 5 5") with the required response ("3" in this example). Whereas the color congruency effect was triggered by the conceptual link between objects and colors, the numerical congruency effect was caused by potential conflicts between lexical retrieval of the element versus total number (MacLeod, 1991).

By including both a control site and a control task, we ensured that any effect of ATL stimulation was because of disruption of color knowledge specifically, rather than alternative explanations of nonspecific effects. With the control site, we tested whether disruption to color knowledge resulted solely from ATL stimulation or was potentially a corollary of stimulation at any cortical site. Additionally, with the control task, we tested whether only color congruency would be affected or whether stimulating the ATL would similarly disrupt any type of cognitive congruency or verbal naming response. We adopted off-line continuous theta burst stimulation (cTBS), which uses repetitive magnetic pulses at high frequency and produces a more pronounced and longer-lasting effect than conventional low-frequency stimulation (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). The longer-lasting impact of cTBS, compared with the relatively brief effect of low-frequency protocols, gave us a better opportunity to assess whether the ATL would be a critical brain region for integrating color with other integral constituents of an object concept.

METHODS

Participants

Eight native speakers of English (three women; mean age = 28 ± 4.5) gave informed consent and participated in the study for monetary compensation. All reported right-handedness and normal color vision and completed safety screening for TMS and MRI before the experiment. None reported any history of neurological disease or mental illness. No participant was on medication or had a history brain injury. This study was reviewed and approved by the Human Research Ethics Committee of Macquarie University.

Design

We used a 2 × 2 × 2 within-participant factorial design, with Stimulation Site (ATL vs. OP), Task (object naming vs. quantity naming), and Congruency (congruent vs. incongruent) as the three repeated-measure factors. In separate sessions, we stimulated one of the two sites, and participants performed both tasks in each session. The order of stimulation sites, as well as that of tasks, was fully counterbalanced across participants. We adopted an off-line stimulation paradigm (i.e., participants received cTBS before the tasks, and performance was probed immediately following stimulation), as this design avoided nonspecific interference on performance because of discomfort, noise, muscle twitches, and so on, relative to on-line paradigms (i.e., applying concomitant stimulation during task execution). This design had two additional advantages over low-frequency (1 Hz) stimulation. First, whereas 1-Hz TMS takes at least 10 min to complete, cTBS requires only 40 sec and hence minimizes possible discomfort during stimulation. Second, compared with the short-lasting effect of 1-Hz TMS (which usually dissipates in 10 min; Sandrini, Umilta, & Rusconi, 2012), cTBS might be able to produce greater inhibitory impact in terms of magnitude and longevity (although note previous demonstrations of the long-lasting effect were based on motor cortex stimulation eliciting motor-evoked potential; see Huang et al., 2005).

Behavioral Tasks

Participants completed two tasks in each experimental session. Each session contained two practice blocks of 12 trials (one block of each task), followed by four experimental blocks of 48 trials (two blocks of each task).

In the object task, participants had to name the object shown in a colored image (Figure 1A). We selected images of 12 objects with strongly associated canonical colors (blueberry, carrot, celery, cherry, corn, eggplant, garlic, kiwifruit, lemon, mushroom, pumpkin, and strawberry). We manipulated the congruency between the display color of each object and its canonical color such that, on congruent trials, objects were presented in the color they

Figure 1. The sequence and time frame of trial events in the (A) object task and (B) quantity task. Target images shown here are example stimuli in both of the congruency conditions. Participants named the object and the amount of digits in the object and quantity task, respectively.
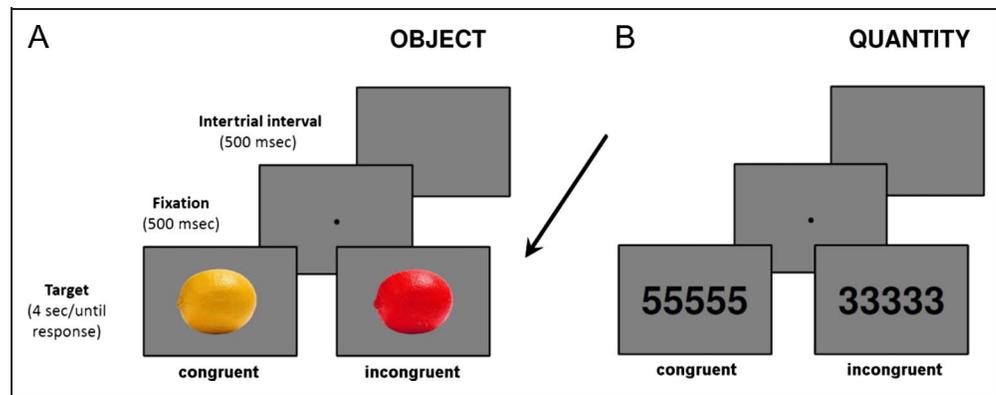
were normally associated with (e.g., a yellow lemon). On incongruent trials, we modified the images using Photoshop so that objects were presented in an atypical color for the object (e.g., a red lemon). The incongruent color was selected from another object's canonical color, avoiding similar or potentially possible colors (e.g., the incongruent color for the lemon was not green; incongruent color for the strawberry was not the cherry red). Thus, each color and object was equally probable in the congruent and incongruent conditions.

In the quantity task (Figure 1B), participants saw an array of Arabic digits (arranged either horizontally or vertically; all elements in a given array were identical) and had to name the quantity of digits. The numbers ranged from one to six. On congruent trials, the identity of the element digit matched the amount of digits in the array. On incongruent trials, the elements and total amount mismatched. The numbers at the amount and element levels as well as the orientation in which they were presented were equiprobable in congruent and incongruent conditions.

For both tasks, each block had equal number of trials in each congruency condition, giving 48 trials per condition, and the two congruency conditions were randomly intermingled within each block.

Each trial began with a black fixation dot on a gray background (RGB triplet = (128, 128, 128); 500 msec), followed by the target image (either an object or a digit array in different blocks) presented for 4 sec or until a response was detected. There was a 500-msec intertrial interval. Participants were asked to name the object (in the object task) or the amount of digits (in the quantity task) into a microphone that registered vocal responses. We asked them to respond as quickly and accurately as possible. In the object task, we emphasized ignoring the color of the object and focusing on its shape/contour/texture to make a response. In the quantity task, we stressed ignoring the constituent digits and concentrating on the quantity of elements. Erroneous responses were recorded manually. A Pentium III computer was used for stimulus presentation and response collection, and the stimuli were displayed on a 17-in. CRT monitor. The experiment was controlled by

MATLAB 7.5 with Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

TMS Procedure

Before the TMS experiments, we obtained high-resolution anatomical T1-weighted MR brain scan for each participant using a Siemens 3T system (Macquarie Medical Imaging, Macquarie University Hospital, Sydney). The individual structural images and the coregistration of cerebral with scalp locations were used to guide the localization of the ATL.

Because of the strong lateralization of language functions to the left hemisphere (Binder, Desai, Graves, & Conant, 2009), we selected the left ATL as the stimulation site and localized its anatomical position on the basis of individual neuroanatomy. In accordance with previous research (Ishibashi, Lambon Ralph, Saito, & Pobric, 2011; Pobric et al., 2010b; Pobric, Lambon Ralph, & Jefferies, 2009; Pobric, Jefferies, & Ralph, 2007), we defined the ATL using anatomical landmarks for each participant: the site 10–15 mm posterior to the temporal pole, along the middle temporal gyrus. The average coordinates of this ATL site in standard space was [−61, −1, −30] across participants, derived using SPM8 (Wellcome Department of Imaging Neuroscience, London, United Kingdom) to normalize each participant's ATL in individual brain into the point in the Montreal Neurological Institute (MNI) template (Figure 2). Note that this was performed for comparison with other studies after we completed the experiment and was not used to identify the cortical site or guide the positioning of the TMS coil. After the location of the ATL was pinpointed on each individual's structural scan, the scalp spot directly above this site was identified and marked during the coregistration procedure. Specifically, we used a magnetic tracking system (MiniBird 500, Ascension Tech) and an MRI coregistration software (MRIreg; McCausland Center for Brain Imaging, USA) to identify the scalp location that corresponds the cortical coordinate of the ATL. The control site, OP, was defined as the location of electrode Oz on the international 10–20 system of scalp electrodes. This site fell on a posterior

point on the approximate midline of the occipital cortex and was also marked on the scalp to guide subsequent stimulation, consistent with previous research (e.g., Ishibashi et al., 2011).

cTBS was administered using a Magstim Rapid2 system and a 70-mm figure-of-eight induction coil. We used cTBS in repeating trains of 200 bursts (three magnetic pulses per burst; 50 Hz) with an intertrain interval of 200 msec (5 Hz); the stimulation was applied for 40 sec, with a total number of 600 magnetic pulses (Huang et al., 2005). The stimulation was set at 80% of resting motor threshold (RMT; the minimum stimulation intensity on the motor cortex that causes a visible finger twitch), resulting in an average stimulator output of 38% (range: 34–40%). Before stimulation, we set the experimental stimulus presentation program to standby so that, immediately after the 40-sec cTBS, participants pressed a button to commence the first trial of the behavioral task.

Different lines of inquiry have documented that the scalp-to-cortex distance of the ATL is greater than that of other cortical regions, such as the motor cortex (e.g., Pobric et al., 2007; Stokes et al., 2005). This leads to the possibility that TMS could have less impact at the ATL site because of its distance from the scalp, relative to other areas. As it has been repeatedly demonstrated that RMT is reliably higher than active motor threshold (the minimum intensity that triggers a motor-evoked potential; see Chen et al., 1998; Hess, Mills, & Murray, 1987), we used RMT rather than active motor threshold to circumvent the potential attenuation issue. When testing RMT for each individual, we applied single pulse stimulation to the left primary motor cortex hotspot; the value was defined as the minimum intensity capable of eliciting a visible twitch
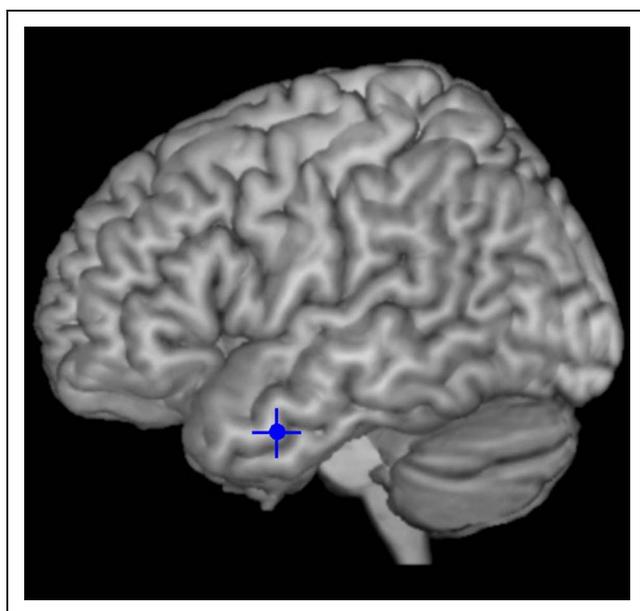
in the right abductor pollicis muscle on 6 of 10 contiguous trials.

It has been shown that the behavioral impact of TMS at ATL does not vary with different coil orientations (Pobric, Jefferies, & Lambon Ralph, 2010a; Lambon Ralph, Pobric, & Jefferies, 2009). Thus, we manipulated coil positions to find an angle that minimized facial muscle twitches in each individual. For the ATL, the coil was placed tangentially to the scalp with the handle pointing posteriorly (parallel to the rostral-caudal axis) for six participants and upward (perpendicular to the axis) for the remaining two. For the OP, the coil was always held with the handle pointing upward. The order of stimulation sites was counterbalanced across participants, and the two sessions were separated by at least 72 hr.

RESULTS

After excluding errors (2.6%) and RT outliers (RTs < 100 msec: 1.8%; RTs > 2500 msec: 0.1%) for eight participants, we analyzed the mean RTs of each condition (Figure 3A) with a repeated-measures ANOVA, with the within-participant factors of Site (ATL vs. OP), Task (object vs. quantity), and Congruency (congruent vs. incongruent). The analyses revealed significant main effects of Task, $F(1, 7) = 10.41, p = .01, \eta^2 = .59$, and Congruency, $F(1, 7) = 64.95, p < .001, \eta^2 = .90$, and a Task × Congruency interaction, $F(1, 7) = 7.82, p = .02, \eta^2 = .52$. Importantly, there was a significant three-way interaction between Site, Task, and Congruency, $F(1, 7) = 6.34, p = .04, \eta^2 = .47$. To identify the source of the three-way interaction, we conducted post hoc pairwise comparisons, testing whether there was a significant congruency effect (incongruent vs. congruent RTs) in each condition. As evident in Figure 3B, stimulation of the control OP site did not affect either the significant color ($p = .003$) or the significant numerical ($p < .001$) congruency effects. Crucially, the numerical effect remained robust after ATL stimulation ($p < .001$), but we no longer see a significant color effect ($p = .13$, ns). Although a lack of statistical significance does not necessarily mean "no effect exists," the change from a large significant effect to the substantially smaller and no longer significant difference suggests the key role of ATL in color knowledge.

Furthermore, we then directly tested whether the magnitude of the congruency effect was significantly reduced after ATL stimulation relative to the control OP stimulation. We first derived the difference scores (incongruent minus congruent, indexing the size of the effect) for each condition and participant. These data were then analyzed using repeated-measures ANOVA with within-participant variables of Site (ATL vs. OP) and Task (object vs. quantity). Results showed a significant main effect of Task, $F(1, 7) = 8.15, p = .02, \eta^2 = .53$, and, pertaining to our main interest, a significant Task × Site interaction, $F(1, 7) = 6.58, p = .03, \eta^2 = .48$. On the basis of the significant interaction, we performed post hoc tests by Task. Results showed that,

Figure 2. The location of the left ATL on a standardized brain template with the average MNI coordinates [−61, −1, −30].

Figure 3. Performance of eight participants on the object and quantity naming tasks. (A) RT as a function of Stimulation Site (ATL vs. OP), Task (object vs. number), and Congruency (congruent vs. incongruent), with the mean error rate (%) of each condition in parentheses. (B) The magnitude of the congruency effects (incongruent − congruent RT) for each task and stimulation site. Error bars represent one repeated-measure *SEM*. An asterisk represents a statistically significant difference in the post hoc comparison. Abbreviations: ATL = anterior temporal lobe stimulation site; OP = occipital pole control site; cong. = congruent; incong. = incongruent.
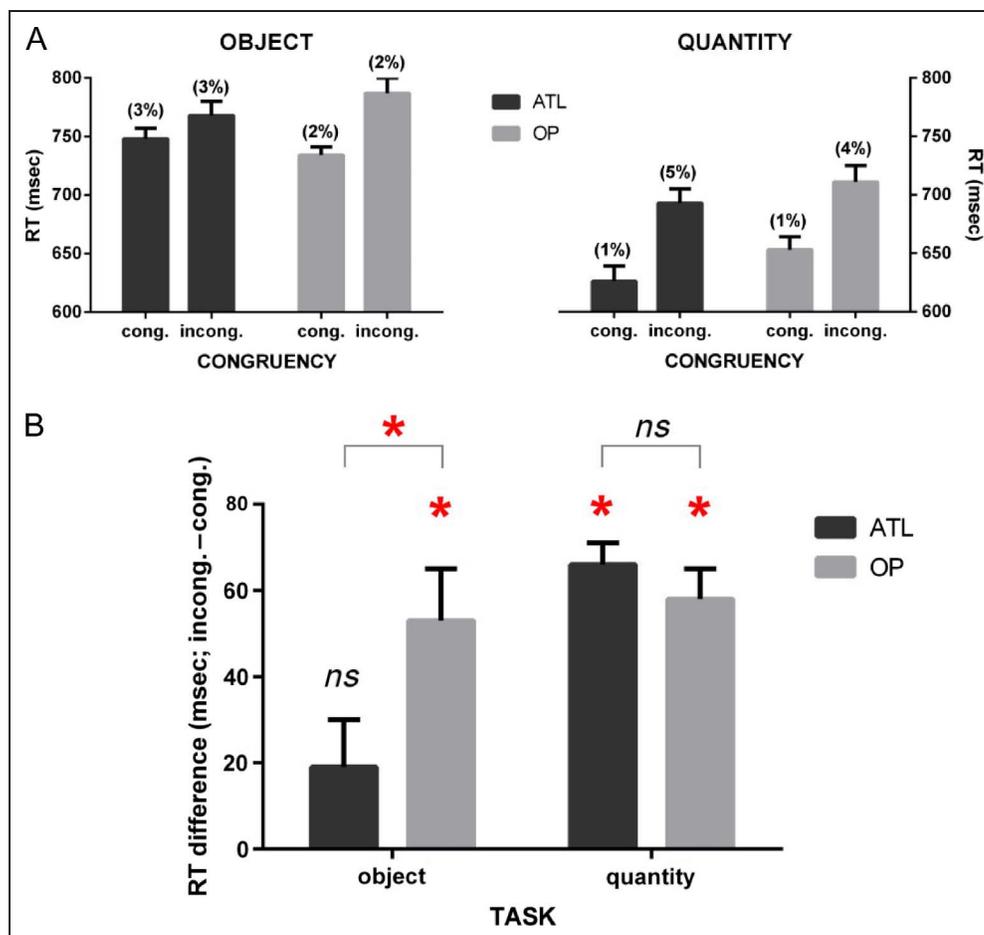
in the critical object naming task, there was a significant difference in the magnitude of the color effect between the ATL and OP conditions ($p = .03$, comparing the leftmost two bars in Figure 3B), with the effect being ~2.7 times smaller in the ATL condition (19 msec) than in the OP condition (53 msec). In contrast, there was no difference in the magnitude of the effect on the quantity naming task between the ATL and OP conditions ($p = .32$, *ns*, the rightmost two bars in Figure 3B). Together, the results demonstrate that ATL stimulation selectively reduced the impact of color knowledge on object recognition and naming.

The analyses on the mean error rates (Figure 3A) only revealed an effect of Congruency, $F(1, 7) = 5.27$, $p = .05$, $\eta^2 = .43$. This is consistent with previous suggestions (e.g., Pobric et al., 2007) that the effect of TMS to the ATL manifests in RTs rather than in errors (as seen in patient research) because the impact of a TMS-elicited "virtual lesion" is more subtle than real brain lesions.

DISCUSSION

The neural basis of object color knowledge is a topic under intensive exploration because it provides important clues as to how the human brain generally integrates sensory information with more abstract knowledge. Most

research examines whether color knowledge depends on the V4 complex, a ventral occipitotemporal region specialized for color perception. The status of V4 as the sole neural substrate for representing color is challenged by the observation that some patients with atrophy of the ATL but intact V4 (hence normal color vision) nonetheless exhibit impairments in color knowledge, implying that the neural representation of color knowledge engages areas beyond V4. However, the scope of the atrophy usually extends to areas outside the realm of the ATL, rendering the inference of its neurocognitive function difficult. In this study, we employed cTBS to explore whether the ATL plays a pivotal role in object color knowledge, synthesizing canonical color with other object attributes at a conceptual level. Our results revealed that disrupting the neural processing of the ATL using cTBS eliminated the otherwise robust congruency effect of color knowledge on object naming. By contrast, stimulating the ATL had no impact on the numerical congruency effect in the quantity naming task. This suggests that ATL stimulation did not yield domain-general interference with any congruency-type effect or with giving verbal responses, but instead specifically disrupted conceptual knowledge. Both color and numerical congruency effects remained robust after we stimulated the control OP site, ruling out the possibility that cortical stimulation of any site could

generate nonspecific influences eliminating the color effect. Our findings corroborate previous patient research regarding the potential contribution of the ATL in representing object attributes, mimicking the pattern of cognitive deficits in patients with a mild extent of ATL atrophy (Hoffman, Jones, & Lambon Ralph, 2012). The TMS evidence complements patient and neuroimaging research by directing a virtual lesion at the ATL to enable inference about causality. Taken together, we suggest that the neural processing of color knowledge goes beyond the perceptual analysis of the V4 complex. More importantly, the ATL is engaged in representing object color knowledge, integrating the perceptual and conceptual components of an object to allow successful identification.

As with all TMS studies, we need to add the caveat that our results may be because of disruption of an area connected to the ATL, rather than the ATL itself. With the widespread interconnection of the brain, the impact of neurostimulation does not necessarily stay within the targeted site but may well propagate to other regions with which that area is connected, modulating the neural activity of remote areas (e.g., van Schouwenburg, O'Shea, Mars, Rushworth, & Cools, 2012). Therefore, one possible interpretation of our finding is that the ATL or an unspecified connected area is critical for color knowledge. Given the established role of the V4 complex in color-related processing, could stimulating the ATL interfere with neural processing of V4, thereby abolishing the color effect? If this were the case, we would expect that stimulation of the OP (V1 of the visual cortex) would similarly abolish the color effect, as it is anatomically closer to V4 than is the ATL and hosts multiple color-sensitive subregions that send signals to V4 for further processing (Goddard, Mannion, McDonald, Solomon, & Clifford, 2011; Shapley & Hawken, 2011). Contrary to this possibility, however, our results showed that the color congruency effect remained robust after the stimulation of the OP, making this an unlikely explanation. Moreover, the fact that stimulating the ATL did not affect the control numerical effect is also helpful in showing that cTBS only affects only certain domains of cognitive processing rather than having an "across-the-board" effect. Given the improbability of color knowledge being mediated solely by a single cortical subregion, we favor the view that the ATL is one critical component within a wide network that converts percepts into concepts. To further elucidate the properties of this network, future work could combine TMS and neuroimaging to examine the effects of ATL stimulation on neural activity in remote structures.

Relevant to the discussion laid above, the embodied cognition theory is skeptical of the supramodal hub and postulates instead that object knowledge is represented in a widely distributed manner across modality-based cortices (Martin, 2007). With regard to the neurocognitive function of the ATL, the embodied view suggests that the ATL underlies some abstract concepts devoid of perceptual referents, such as knowledge about social relations

(Simmons, Reddish, Bellgowan, & Martin, 2010; Simmons & Martin, 2009). By establishing a causal link between the ATL and the effects of color congruency on object naming, we demonstrate the importance of this area even when the concept pertains to a perceptual aspect of tangible objects. Our results are thus consistent with the "hub-and-spoke" theory (Lambon Ralph & Patterson, 2008; Patterson et al., 2007), which predicts a division of labor between the ATL and modality-specific regions for the neural architecture of color knowledge. The V4 complex ("spoke") specifically contributes to chromatic dimension of object representation (Chao & Martin, 1999). The ATL, as the "hub," fuses different object attributes together to form a supramodal concept that transcends different senses. Thus, when the neural processing of ATL is disrupted, by either disease or TMS, the cognitive capacity to associate typical color with object identity would be severely weakened, despite the patients/participants having intact color perception.

The possibility for impaired color knowledge with intact color perception leads us to speculate that the essence of conceptual knowledge does not rely on embodied experiences alone. This is not to say that the building blocks of concepts are entirely symbolic and propositional. Rather, it seems that sensorimotor representations play a key role especially when a context requires an "instantiation" of bodily experience for retrieval of conceptual pieces (e.g., a question asking whether a cherry is darker in color than a raspberry—answering this question necessitates mental simulation of memorized colors and activates V4; see Rich et al., 2006). In addition to perceptual experiences that provide "raw materials" for concept formation, the conceptual system requires a supramodal representation, possibly coded in a region that receives multimodal inputs like the ATL, to permit coherent "feature-to-concept" mapping. With this supramodal "hub," the operation of the cognitive system is able to transcend constituent perceptual features and extract meaning at a more abstract level (e.g., knowing that candy floss resembles clouds in appearance but is conceptually similar to lollipops, despite it being perceptually distinct). Our interpretation of the contemporary literature and our own finding is consistent with the behavioral deficits observed when the hypothesized supramodal representation breaks down because of a lesion of the ATL (e.g., Hoffman et al., 2012; Lambon Ralph, Sage, Jones, & Mayberry, 2010). For instance, patients with atrophied ATLs but intact perception have been observed to ignore the conceptual relationship between objects and base their judgments heavily on perceptual similarity (Lambon Ralph et al., 2010).

It is worth noting that color knowledge is not the sole object feature that the ATL underpins. A recent neuroimaging study by Peelen and Caramazza (2012) found that, whereas perceptual features of object images were represented by the occipitotemporal regions, locative and motoric properties of objects at conceptual level (e.g., corkscrews are usually found in the kitchen and used

with a rotating action) were coded in the ATL. In line with our finding, the ATL appears to distill information from every sensorimotor channel and to synthesize different properties into a supramodal concept of objects.

Although we used visual stimuli, there is other evidence showing that ATL contributes to conceptual processing whether the input stimuli are presented as images (Pobric et al., 2010a), words (Holland & Lambon Ralph, 2010), ambient sounds (Visser & Lambon Ralph, 2011), or even odors and flavors (Piwnica-Worms, Omar, Hailstone, & Warren, 2010; Luzzi et al., 2007). The modality-independent nature suggests that the "ciphers" coded by ATL for conceptual knowledge are supramodal in nature (although note that it has been suggested that the brain preferentially codes verbal and pictorial knowledge in the left and right ATL, respectively; see Gainotti, 2012).

In conclusion, there has been considerable debate over how the brain represents color knowledge, with most research focusing on the V4 complex. We show, for the first time, that knowing how objects and colors are typically coupled together requires a representational hub mediated by the ATL. We interpret the results in favor of the hub-and-spoke theory where conceptual knowledge can be envisioned as a neural network containing a hub that mediates conceptual integration at an abstract level and multiple spokes that process modality-specific contents.

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