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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 significantly add to accumulating evidence that conceptual knowledge is grounded in the brain's modality-specific systems.

February 21, 2007

Dr. Andrew Mayes
Editor
Neuropsychologia

Dear Dr. Mayes,

My colleagues and I would like to resubmit a manuscript that you last handled on September 17th for *Neuropsychologia* (NSY-D-06-00408). The title of the manuscript was, "A Common Neural Substrate for Perceiving and Knowing About Color." We apologize for being somewhat slow on returning this revision, but as I described in my email to you on 12/05/06 requesting an extension of the resubmission deadline, responding satisfactorily to the reviewers' comments required significant revisions. We have continually tried to refine our manuscript and to incorporate the reviewers' comments and suggestions, and we believe that this manuscript represents a significant improvement over the previous submission.

We are most grateful to you and the reviewers for your excellent suggestions. The comments offered by the reviewers were very different. Reviewers #1 and #2 offered very positive comments on the manuscript and requested only minor revisions, whereas Reviewer #3 expressed many theoretical and methodological concerns. In your decision letter, you invited us to resubmit our manuscript if we were able to address the concerns, particularly those expressed by Reviewer #3. We have thought about all the reviewers' comments at length, and as you will see they have had considerable impact on our revision. We believe the manuscript is much better for the suggestions and criticisms offered in the previous review cycle. We are grateful for the careful reading that you and your reviewers gave our manuscript.

We particularly wish to draw your attention to two significant revisions to our manuscript. You may recall that participants in our study performed two tasks: a property verification task with both color and motor properties, followed by a color perception localizer. The central finding of the article was that a region in the left fusiform gyrus identified in the color perception task was more active for color than motor property verifications. In our previous submission, the analyses demonstrating this effect did not deconvolve the activations for concept word presentations from the activations to property word presentations. Reviewer #3 expressed concerns about this, and so we now report the results of a reanalysis that deconvolves the response functions for concept and property words. All of the property verification results reported in this revision pertain to the responses to properties after removing the concept responses. Importantly, the left fusiform color perception region is still modulated by color properties, relative to motor properties.

The second significant revision pertains to the dominance manipulation described in the earlier submission. The previous reviews expressed concerns about this manipulation and the theoretical bases for our explanations of the dominance results. In the course of

reanalyzing the data to deconvolve concepts and properties, we found that the results of the dominance manipulation became difficult to interpret. Because the dominance findings were secondary to the important finding that color perception and color knowledge share neural substrates, we have decided not to report on the dominance manipulation. We believe that the results of the analyses comparing color and motor properties are now more compelling than ever, and the organization of the manuscript, without discussion of the dominance effects, draws this central finding into sharper focus.

The following points summarize the reviewers' comments (in italics) and the changes we have made. We have ordered the comments and our responses by our estimations of their significance for the article.

1. Reviewer #3 had many questions pertaining to the catch-trial design of the study. For example, the reviewer stated: *“The 2 words in each concept-property pair were each presented for 2 secs, with no delay between them. The concept-only trials consisted of a single 2 sec stimulus. The possible effect of this timing difference (4 sec vs 2 sec) is never discussed. Also, the authors never comment on the potential consequences of the fact that subjects were carrying out different tasks in the concept+property and concept-only trials. In the former they were making a property verification judgement and in the latter they were preparing for a response which they did not make.”* Reviewer #2 had a related question, *“My concern is that concept word was presented for 2 sec, immediately followed by the color property word, and hence regressors of interest may not be orthogonal.”*

We are particularly grateful for this feedback, given that it revealed that we did not do a good enough job explaining the rationale for this somewhat complex and unusual design. We presented two types of events: concept-property events, and concept-only events that served as catch-trials. Often in fast event-related fMRI, when researchers want to estimate the BOLD response to two different types of events that occur close together in time, they separate these events with jittered interstimulus intervals so that the resultant BOLD responses can be mathematically deconvolved. But how does one deconvolve the responses to stimulus events that occur close in time together at fixed intervals? In many cognitive experiments, it is often necessary to present two stimuli separated by a fixed interval, such as a concept and a property on a verification trial.

Ollinger, Shulman, and Corbetta (2001) developed an ingenious method for separating stimulus events within the same trial separated by fixed duration. This method relies on the inclusion of catch-trials that present only part of the multi-stimulus events that occur on regular trials. As mentioned in the previous version of our manuscript (although not as clearly as it should have been), we implemented exactly the type of design that Ollinger and his colleagues developed. On most trials of our experiment, participants received a concept followed by a property, each for 2 seconds, such that the temporal interval between them was fixed. On some trials of our experiment, however, we presented concepts that were not followed by property words (i.e., catch trials). From the subjects' perspective, they could not tell if a trial was going to be a regular trial or a catch

trial. As Ollinger et al. note, not being able to anticipate which kind of trial will occur is an important requirement of using their deconvolution method.

In our previous submission, we reported two types of analyses. First, we reported analyses comparing color and motor trials that did not deconvolve concepts from properties. After presenting those results, we then reported analyses that did deconvolve concepts and properties, but only for the color items. This was done to examine whether dominant color properties produced less activation than non-dominant color properties. We have now re-analyzed the data, with all concepts being deconvolved from properties. Here's how we did it.

First, following Ollinger et al, we constructed the deconvolution matrix with a single vector indicating both the onsets of the concepts in the concept-property trials AND the onsets of the concepts in the concept-only events. In other words, both types of concepts were modeled together. This is justified because, from the subject's perspective, all concept trials were the same. Subjects didn't know whether a property would follow or not. A second vector then indicated the onsets to the properties, which only occurred on concept-property trials. According to Ollinger et al., as long as the catch trials are psychologically identical to one of the events in the multi-event trials, and as long as catch trials occur with at least 40% of the frequency of multi-event trials, then it is possible to reliably deconvolve the response to the two events. Both of these conditions are met in our experiment.

Reviewer 3 was concerned that the concept-only and concept-property events had timing differences (2 vs 4 seconds). Were we to compare the two events directly, this would indeed be a problem. It was never our goal, however, to compare the two event types, nor did we ever do this. Instead, what we did do was to combine the concept-only trials (2-seconds) with the concepts in concept-property trials (2-seconds), providing us with activations for the concepts deconvolved from activation for the properties. This further allowed us to measure activations of the properties (2-seconds) independently of the concepts. The central analyses of our experiment only report activations for the properties deconvolved from activations for the concepts. They never include activations from the concepts, and at no point do we compare events that have timing differences.

With respect to Reviewer 3's concern that the subjects were doing different tasks in the concept-only and concept-property events, again, let us be clear. At no point do we compare the two event types. As such, this is not a problem for the design. In fact, the task was designed so that, from the subjects' perspective, the concept periods of the two events are identical. In both the concept-only and concept-property events the subject thinks that they are about to receive a property word. If the trial turns out to be a catch-trial, then they don't receive a property, but the subject doesn't know this until a property doesn't appear. This does, however, create a difference between the concepts and properties, namely that properties are associated with responses, whereas concepts are not. This is one of the reasons we do not directly compare the responses to the concept and property words. Because of the catch-trial design, however, in the comparisons we

do make, there are absolutely no differences between conditions in timing, frequency, or response method.

We apologize for the considerable confusion that occurred surrounding our design in the original review cycle. Again, we are grateful to Reviewer 3 for bringing this matter to our attention. For this reason, we have added a paragraph in the Methods section 2.2.1 that better explicates the design. Also, prior to the study, we performed simulations in AFNI to ensure that the design of the property verification task did not suffer from multicollinearity between the concept and property columns of the deconvolution matrix. As such, we believe that we were able to independently model the concepts and properties. We have added a paragraph in the Methods section 2.2.1 better explicating the design, and noting the simulations in AFNI to ensure that the concept and property events were not collinear and that the events could be reliably deconvolved. In addition, we have included several sentences later in the Methods section making it clear that, from the subjects' perspective, the task was identical during the concept periods of both event types.

2. Both Reviewers #1 and #3 and the Editor asked related questions about our interpretation of the property word activations. For example, Reviewer # 1 wrote, *“The authors may want to consider another argument that could be put forward by a wily supporter of the amodal account. Activity in perceptual color processing regions may simply reflect color word processing (having nothing to do with color knowledge).”* Similarly, Reviewer #3 wrote, *“Simmons et al ... ask whether concept- color property pairs activate the same regions as are activated by colors..... Testing the ETC by presenting subjects with concept-property pairs raises the possibility that the property name itself (eg purple) generates the activity in color regions.”* A very similar point was noted by the Editor in his communication to us of his interim decision: *“To what extent does your task differentiate between the neural bases of conceptual knowledge of certain kinds and this knowledge's triggering of certain kinds of visual imagery? Or, in different words, what are you asking beyond whether the perceptual regions that mediate colour perception overlap with the areas activated by imagining particular colours when triggered by verbal stimuli?”*

At no point were subjects instructed to use imagery to perform the task. Thus, it is unlikely that they adopted it intentionally. Furthermore, from the amodal perspective, imagery definitely should not be necessary to perform the task. If color and motor knowledge is amodal, then why should subjects activate color and motor cortex to perform 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. We believe this is a very important point to address in the article, as well as in all studies testing embodied cognition effects. For example, this exact criticism could be leveled at Pulvermüller and colleagues' study in which subjects read motor property words. In that study, which was a significant motivator of our work, it could be similarly argued that the motor activations observed didn't reflect semantic knowledge about the words but was just associated imagery. As such, we have included a new paragraph as the second paragraph in the Discussion section defending both our

article, and more generally other embodied cognition findings (e.g., Hauk, Johnsrude, & Pulvermüller, 2004) from the criticism that these effects represent mental imagery, rather than conceptual processing.

Additionally, with respect to the Editor's question in particular, we expect there should be much overlap in the neural bases of color perception and explicit color imagery. This expectation follows naturally from our theoretical stance, namely that perceptual information is used in many areas of cognition, including imagery and memory. Were we to explicitly instruct subjects to imagine colors indicated by verbal stimuli, we believe we would see areas of activation in ventral temporal cortex similar to those reported in our manuscript. 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.

3. Reviewer # 3 expressed concern about the repetition of concept and property words. As you will see in our response, this point is very much related to #1 above. Reviewer #3 stated, "*The fact that same concepts were repeated in the concept+property condition and the concept-only condition raises another set of issues about the consequences of repeated presentation... Was the order of presentation of each concept counterbalanced to take this into account? I assume that this was a fully randomised design (except for the color hue block), but the authors do not explicitly say so.*" In a related comment the reviewer asked about the repetition of the property words.

According to Ollinger, Shulman, and Corbetta (2001), catch-trial events need to be psychologically identical to, and occur with at least 40% of the frequency of, the portion of the multi-trial event they are intended to separate. As such, we decided that the most reasonable thing to do was to use the same concept words in both event types. If we held to their recommended 40% frequency, however, how would we choose which concepts to repeat? We decided that the best course was to repeat all of the concepts. It is quite possible that there were repetition suppression effects to the repeated concept words. This is not a problem, however, because concept word presentations were balanced across the runs, with approximately half of the concept words appearing in a concept-only trial before appearing in a concept-property trial, and the other half appearing after presentation in a concept-property trial. We have included several sentences in the Methods section to make this clear. In addition, we used optseq2 to develop randomized trial sequences for each scanning run. Furthermore, all runs were counterbalanced across subjects, such that any differences associated with particular trial sequences were controlled over time. We have also noted this in the Methods section.

With respect to repetitions of the property words, 12 color words were presented 4 times, 2 color words were presented 8 times, and 4 color words were presented 12 times. Analogous to the concepts, presentations of the property words were also controlled temporally. We have included several sentences in the Methods section stating the relative frequency of the repeated colors, as well as making clear that we controlled for the presentation of the color property words.

4. In a related comment, Reviewer # 3 questioned our focus on the property words presented in our design, as opposed to the concept words. The reviewer stated, *“The most direct test of the (embodied theory of cognition –ETC) claim is to follow the Pulvermüller approach. In his studies, subjects are presented with words which have intrinsic motor properties - eg kick, lick, pick - to determine whether they activate the same regions as involved in the motor actions themselves. Surely, to test the claim of embodied cognition, the authors need to establish that the concept itself activates color (or motor) properties? That would mean showing that seeing the word aubergine, for example, activates color regions. This would be predicted on the grounds that the word aubergine consists of a set of properties, among which is the color purple. A critical claim of the embodied cognition account is that these properties will be activated when the word aubergine is seen and they should engage those neural regions involved in the relevant sensory systems. This would be evidence that the same regions are involved in perceptual processing and "conceptual processing of that property" (p4).”* In a related comment, Reviewer #3 states that *“surely a critical piece of evidence in favour of the ETC would be to find that the concept-only stimuli activate regions involved in color processing (this would be analogous to the Chao & Martin, 1999 paper)?”*

We appreciate the reviewer’s concerns here, and agree that it would be good to demonstrate that concept words, independent of property words, activate modality-specific regions. The most immediate problem in demonstrating this is that you must have an appropriate condition with which to contrast the activity associated with processing concepts. We believe it is very likely that, as the reviewer suggests, reading the word “aubergine” activates color regions representing an aubergine’s ‘purple-ness’. But then virtually all objects have associated colors, so what object would one use in the contrast condition? As a result, simply comparing the activation between any two groups of objects, both of which have their own object-associated colors, will result in a null effect. Another approach is the one used both in our article and by Pulvermüller and colleagues, in which activity associated with reading different kinds of property words is compared. In our study, we presented subjects with concept-property pairs and compared activity for properties on different modalities (again, our design allowed us to deconvolve property activations for both property types from concept activations). In Pulvermüller and colleagues’ study, subjects were presented with motor property words (e.g., “lick,” “kick,” and “pick”). In both studies, activation was observed in the relevant property’s perceptual areas.

With respect to the second half of Reviewer #3’s comment, we believe it is very likely that, as the reviewer suggests, reading concept words activates color regions representing those concepts’ color properties. Because virtually all objects have associated colors, it is difficult to know what object one would use in the contrast condition. As a result, simply comparing the activation between any two groups of objects, both of which have their own object-associated colors, will result in a null effect. Chao and Martin (1999) did not compare the response among object words or between pictures of objects that do and do not have highly associated colors. There is no analogous finding in the literature showing a response in color perception regions for concepts, most likely because of the difficulty in identifying an appropriate contrast condition.

5. Reviewer #3 did not understand why the motor condition was included in the study, and on several occasions asked for clarifications about how analyses with the motor condition were implemented. For example, the reviewer stated, *“It is not completely clear why the motor condition (hair-combed) was included... Perhaps the differences in numbers of items in the color vs motor conditions contributes to the differences they find in activation strength...”* Later, Reviewer #3 asked further questions about why the motor condition was contrasted with the color condition, and requested *“more detail about this effect - detail of the peak voxel and extents, for example.”*

Motor property trials were included in the study as a contrast condition for the color trials. It was important to demonstrate that the response in the color perception region was not due to a general stimulus effect, but rather was specific to color knowledge trials. For example, it would not be enough to show that color property verification trials activated color perception regions relative to a low-level baseline task or fixation. In demonstrating that the color perception region was more active for color property verification events, we compared the response amplitude for true color and motor properties. We have now made this clearer in the article.

Importantly, this test is based on equal numbers of color and motor property trials (56 property presentations in each condition), so that the signal strength associated with each mean is comparable. We have included several sentences in the section 2.2.1 (“Property verification task”) and in section 2.4 (“Statistical Analyses”) explicating why the motor condition was included and stating that the analyses were based on equal numbers of events. Also, in Table 1 we have included information about the middle temporal gyrus cluster that was more responsive to motor than color properties (e.g., peak voxel, t-value) and in the text we describe its volume and extent along the y-axis.

6. Both Reviewers #1 and #3 commented on the location of the color perception region identified in the functional localizer task. Reviewer # 1 stated, *“The left fusiform gyrus is anterior to the well-known color perception system, even anterior to V4alpha/V8 which is regarded as higher color center... Although authors attributed this to effortful color processing, further explanation is necessary.”* Reviewer #3 made a similar point, *“The fusiform activations for color stimuli are unusually anterior (peak -33 -36 -16). They are more anterior than previously reported activations (e.g., Chao & Martin, 1999; Beauchamp et al, 1999). It would be helpful to have details about the extents of the activations, and not just their peaks. The fusiform activation may be very large.”*

The peak voxel for the left fusiform color perception cluster observed in our study was located approximately 1 cm anterior to the to the anterior fusiform cluster observed by Beauchamp and colleagues. This distance is measured from peak-to-peak, and may not represent the true overlap in the two clusters. Nevertheless, it is interesting that these clusters were observed in somewhat different locations, given that the studies used nearly identical stimuli and the same task. We can only speculate that the functional organization of ventral temporal cortex may be relatively more idiosyncratic than other brain regions, and thus this approximately 1 cm difference may be due to subject

differences between the two studies. To alert the reader to this difference, we have included a sentence at the end of Discussion section 4.1 noting that the fusiform color perception cluster in the our study was located anteriorly to the fusiform cluster reported by Beauchamp and colleagues. To respond specifically to Reviewer #3's concern, in the Results section 3.1.2 ("Brain Activity" for the localizer) we have included volumetric information about the size of the active clusters and their extents in the y-dimension, the direction most relevant for localizing activity in the fusiform gyrus.

7. Reviewer #2 asked us to comment on the activation of the left fusiform gyrus in the color perception localizer task relative to the findings of Nunn et al. (2002) with synesthetes: "*Word-color synesthetes reported by Nunn et al. (2002) showed the activation of the V8 (or equivalent V4alpha) on the left by the word presentation. The Talairach's coordinates was (-35, -64, -13). More anterior fusiform areas were activated by words presentation, but not by color task. The activated cluster is at (-33, -36, -16), far anterior to the V4/V8. This needs discussion.*"

We have now devoted the fourth paragraph in the Discussion section to the Nunn et al. findings. As noted by Reviewer #2, Nunn and colleagues report a cluster that was active for words associated with color synesthetic experiences in the left "anterior fusiform" (see Table 1 of Nunn et al.). This cluster, which they label as V4 α , was located 7 mm posterior to the cluster we observed in our study. This would appear to be even further evidence that the fusiform cluster we report represents color information. Nunn and colleagues also report that color-word synesthetic experiences also activated a more posterior region in V4/V8, a cluster that overlapped with activations associated with passively viewing color mondrian stimuli. We believe this is consistent with the account offered in our Discussion section whereby the more posterior color region subserves low-level color sensory experience, and the more anterior fusiform region underlies higher-level perceptual representations of color. We would also like to draw the Reviewers' attention to the findings of Tootell, Nelissen, Vanduffel, and Orban, 2004, who observed that the most color-selective regions in the macaque were located in areas TEO and TE, possible homologues of the human fusiform gyrus. Taken together with the findings of Nunn et al., we believe this makes a strong case that the fusiform region identified in our functional localizer task is directly involved in high-level color perception.

8. Reviewer #1 noted that "*it is now standard in fMRI analysis to formally correct for multiple comparisons using some method (e.g., false discover rate, cluster extent threshold)*". Reviewer #1 also requested that we include a companion table of activations.

We have gone back through the article and implemented corrections for multiple comparisons in all analyses. For the comparison of color versus grayscale perception in the functional localizer data, we used Monte Carlo simulations run in AlphaSim (<http://afni.nimh.nih.gov/afni>) to estimate the probability of observing clusters of at least 135 mm³ with a *p*-threshold < .0001 in the volume of the lingual and fusiform gyri, regions that we predicted *a priori* to be involved in this task. The probability of observing a cluster this size and *p*-threshold was estimated to be less than .05 corrected for multiple comparisons. At this threshold, we observed two clusters, one in the left fusiform, and

another in the right lingual gyrus. In the property verification dataset, we once again used AlphaSim to implement a cluster extent threshold. The results of these Monte Carlo simulations demonstrated that the probability of observing clusters of at least 297 mm³ with a p -threshold $< .0001$ within a whole-brain volume, after masking out the ventricles and most white matter, is less than .05 corrected for multiple comparisons. At this p -value and extent threshold, we observed one cluster located in the left middle temporal gyrus. We have clarified the statistical thresholds used in the study, and explained the corrections for multiple comparisons, in Methods section 2.4 (“Statistical Analyses”). In addition, per Reviewer #1’s request, we have summarized these areas of activation in Table 1.

9. Reviewer #3 asked about the logic of sampling across all voxels in an ROI. With respect to the results of the property verification task, the Reviewer states, “*Given what is reported in the Figure caption, I assume that this is a VOI in the fusiform region identified in the color localisation task. This is probably a huge cluster, so it is not clear what the value is of sampling across it. Also, why did they not use, as a VOI, the fusiform region which was more active for color vs motor properties?*”

With respect to the first part of the Reviewer’s comment, this is indeed a ROI/VOI analysis within the voxels identified as being color-selective in the perception task. Also, at 142 mm³, this is not a “huge cluster,” and there is no *a priori* reason why we should not sample across it, given that our aim was to test whether color perception cortex was responsive to color knowledge retrieval. We used a statistical threshold corrected for multiple comparisons in the functional localizer task to identify regions that were truly color-selective, so that if we found an effect in the knowledge task, we could have confidence that the activated region was representing color information.

With respect to the second part of the Reviewer’s comment, it would be dangerously circular to identify a region that was responsive for color property verification, and then use the same data in a subsequent VOI analysis. Rather, it makes for a much more impressive finding that we identified color perception selective cortex in one dataset, and then observed effects in this region in a color knowledge retrieval task measured in a completely independent dataset.

10. Reviewer #3 asked for greater clarity in exactly which statistical analyses were performed: “*A significance value of $p < .05$ is reported. What is the statistical analysis that was performed?*”

In Methods section 2.4 (Statistical Analyses), we have included two new sentences clarifying the statistical analyses. For the ROI analysis of the color perception ROI, the manuscript now states that we used a repeated measures random effects ANOVA to compare the response amplitude between 4 and 8 seconds post-stimulus onset for true color and motor trials to determine if color knowledge retrieval engaged the color perception ROIs. For the comparison of color and motor property verification in the whole-brain analyses, the manuscript states that we used a two-way mixed effects

ANOVA (property type X subject), comparing the response amplitude between 4 and 8 seconds post-stimulus onset for true color and motor trials.

11. *“Did any of the other ROIs show any similar effects which were just below the threshold? In general more Tables of results are necessary.” (Reviewer #3)*

After correcting the activation maps for multiple comparisons, besides the left fusiform gyrus, only the right lingual gyrus exhibited greater activity while viewing color wheels than grayscale wheels. In Results section 3.2.2, we have included a sentence stating that “no difference was observed between color and motor property verification trials in the right lingual gyrus cluster (percent signal change color $M = .10$, $SD = .12$; motor $M = .13$, $SD = .25$), $F(1, 9) = 0.34$, $p = 0.58$.” Outside the color perception ROIs, the only cluster to survive correction for multiple comparisons was in the left middle temporal gyrus. Thus, the results are now constrained to the two color perception clusters in the right lingual gyrus and left fusiform gyrus, and the motor-responsive cluster in the MTG in the property verification task. As such, we feel that Table 1 and the cluster extent information included in the text is all that is necessary to convey the relevant information about these three regions.

12. *“When the authors talk about overlap between their activations and those reported in other studies, it would be helpful if they could be more precise, especially since they report large and poorly-described regions of activity (eg bottom of page 18; p19 where Tootell's results are described; p21 discussion of patients).” (Reviewer #3)*

In the discussion section we describe the relationship between areas activated in our study and those implicated in several neuropsychological cases of color deficits, as well the interesting findings of Tootell et al. in the macaque. Unfortunately, it is often the case that lesions are diffuse and impossible to characterize with the same specificity that one can describe functional neuroimaging findings. This is the case with virtually all the reported cases of color agnosia that we cite. When possible, however, we have included more specific descriptions of the anatomical relationships between our findings and those reported in the literature. For example, we note that our area of activity in the right lingual gyrus is “located approximately one centimeter lateral” to the achromatopsia center reported by Bouvier and Engel (2006). With respect to the comparisons between our left fusiform cluster and the color center reported by Tootell and colleagues, we would like to note that we are making an inter-species comparison, and that it is very difficult to make claims about the relationship between these regions beyond those already included in the manuscript.

13. Reviewer #3 stated that the Discussion section was “*too wordy*” and that it “*could be cut by at least 1/3.*” Reviewer #3 also took issue with our citation of a paper by Hoenig et al. that is currently unpublished, though under review.

The Reviewer’s request to shorten the Discussion section played a role in our decision to cut the dominance manipulation from the article. After removing the description of the dominance manipulation findings, the Reviewer will be pleased to note that the

Discussion section is much shorter. In addition, per Review # 3's request, we have also removed our discussion of the Hoenig et al. findings.

14. *"The authors relate their findings to Barsalou's interesting claims about re-enactment, and yet some of the co-authors (Martin) was author on a paper on objects and color processing (Chao & Martin, JOCN 1999) in which they conclude "these results indicate that retrieving previously acquired information about an object's typical color does not require reactivation of brain regions that subserve color perception". Some comment reconciling these views, and the basis of these claims, would be useful."* (Reviewer #3)

It is true that Chao and Martin (1999) found somewhat different activations for conception and perception. There is an important difference, however, between the methods of the present study and those used by Choa and Martin (1999). Choa and Martin (1999) identified color perception regions by comparing activity measured while subjects *passively* viewed color mondrians. As demonstrated by Beauchamp et al. (1999), passive viewing tasks do not activate the full extent of the color perception cortex in the ventral temporal lobes. In contrast, our study used a more active color perception task (an adaptation of the Farnsworth Munsell color perception test), and replicated Beauchamp et al.'s findings in the fusiform gyrus. The observed overlap in color perception and color knowledge retrieval was found in this more anterior region.

Increasingly, there is a growing body of evidence demonstrating overlaps in conception and perception and action. For example, Pulvermüller and his colleagues have found such overlap, and in an article we recently published on the perception vs. conception of taste we found yet further evidence that this is the case. We have continued finding such overlap in our subsequent work, including our paper here. Thus, we now believe that there is good reason to assert that shared areas underlie perception/action and conception to some extent (certainly not all areas are overlapping). We do not discuss this at length in the in the manuscript, given that we wanted to reduce Discussion. If the Editor and Reviewers believe that is an important point, however, we'd be glad to include it.

15. *Figure 2 and Table 1 showed discrepancies in terms of the color perception related clusters... Probably transaxial section of the normalized high resolution MR images would be better for this purpose rather than the inflated brain. (Reviewer #2)*

In the original figure, we showed activations at different statistical thresholds than activations mentioned in the text. This was intended to provide the reader with surplus information about the system of regions in ventral temporal cortex representing color information. We chose to use an inflated surface because it was easier to see all the areas of interest without the folded cortical structure. We now see that this can be confusing to the reader, and have changed the figure in two ways. First, Figure 2 now depicts sagittal and coronal slices of a standard Talairach normalized volume. Second, the map now only shows the fusiform clusters reported in the text for the color perception task, and the activity in the property verification task surviving a p -threshold < 0.01 with a cluster

extent threshold of at least 108 mm³. We have also explained these thresholds in greater detail in the figure caption.

16. Reviewer #2 asked that we alter the bar graph in Figure 4 to “*to clearly indicate that the response of the left fusiform gyrus is color specific (in terms of perception and knowledge), the %signal change during motor condition should be added.*”

The % signal change bar graph showing the responses for color and motor property verification is now located in the lower left-hand corner of Figure 2.

17. Reviewer #3 felt that it is “*odd to report ROI analyses before whole brain analyses.*”

In the Results, we first report the regions identified by the color perception functional localizer. Given that the central hypothesis of this project was that color perception regions should be modulated by color knowledge retrieval, it makes sense to then immediately report whether the color perception ROIs are modulated in the property verification task. The whole-brain analysis of the property verification data is superfluous to this task. Our observation of greater activation in the middle temporal gyrus for motor property verification in the whole-brain analysis simply strengthens the study overall. It is not, however, the central message of the article, and so we believe that it should not take precedence over the ROI analyses in the Results section. Thus, we believe that it is in the best interests of the reader to maintain the ROI analyses of the color perception regions in their current place in the text.

18. Reviewer #1 noted that “*EPI volumes consisting of 30 contiguous 3-mm axial slices (as was used) will not provide whole brain coverage (at this thickness, ~45 slices are required)...This is fine given that the ventral cortex contained the regions of interest, but this issue should be mentioned.*”

We have noted this in Methods section 2.3 (“Imaging Details”) by including the following statement: “Given the TR and slice thickness, it was not possible to image the entire brain. As such, for each subject the inferior slice was aligned a few millimeters inferior to the ventral temporal cortex.”

19. Reviewer #3 asked whether we were “*surprised that there was no increase of activation in motor regions (following Pullvermuller's findings) for the concept-motor property compared to the concept-color property conditions?*”

Indeed, this finding surprised us. We have two ideas as to why we did not observe activity in motor regions for the motor property verification trials. First, if the effect size of the motor region activations is somewhat weaker than in ventral temporal cortex, which typically exhibits robust responses, then it is quite possible to observe color region activations without observing the corresponding effects in motor regions. Second, there were significant signal processing differences between our study and the earlier study by Pullvermuller and colleagues. For example, Hauk, Johnsrude, & Pulvermüller smoothed their data with a 12 mm Gaussian kernel, whereas we smoothed with a 6 mm kernel. In

addition, as noted in our response to #18, given the scan parameters we were not able to image the more superior parts of the brain, which limited our ability to detect activations in some parts of the motor cortex. The inability to image these sections does not, however, bear directly on the central focus of the article, namely that ventral color perception cortex is involved in color knowledge retrieval. Individually, or collectively, these factors could explain the lack of motor region effects observed in our study.

20. Reviewer # 1 noted that *“it should be stated whether slice-time correction was applied... It should also be mentioned whether warping into Talairach space was a linear or non-linear transformation.”*

Yes, slice-time correction was applied, and we have now indicated this in section 2.3 (“Imaging Details”). Also, AFNI uses a linear transformation of the data to convert the subjects’ anatomical scans to Talairach space. We have thus noted this in section 2.3 (“Statistical Analyses”).

21. Reviewer #3 asked whether *“the MTG activity overlap with that found in previous studies?”*

Indeed, the MTG activity in response to motor property verification is co-located with activity observed in previous studies of both biological and non-biological motion. In section 4.4 of the Discussion section we describe these findings and suggest that this region represents the physical motions associated with the motor properties, which applied to both animate agent and manipulable object concepts (e.g., HOSTAGE- tied, AXE – sharpened).

22. *“Hadjikhani, Liu, Dale, Cavanagh, & Tootell (1998, Nature Neuroscience) should be referenced.” (Reviewer #1)*

Thank you for bringing this reference to our attention. It was an oversight on our part, and we have now referenced it in the Discussion section.

23. *“Where were verification times measured from? The onset of the concept-property pair or the property?” (Reviewer #3)*

As indicated in Methods section 2.2.1, “Verification latencies were measured from the onset of the property name.”

24. *P4L1--"Functions neuroimaging" is to be read as "Functional neuroimaging." (Reviewer #2)*

We have corrected this. Thank you.

We hope that we have done justice to the comments, concerns, and suggestions made by you and the reviewers. We believe that feedback from the first review cycle has improved this version of the manuscript considerably. Please let us know if you need

anything else from us at this time. Thank you for considering our manuscript for publication in *Neuropsychologia*.

Sincerely,

Kyle Simmons
Vimal Ramjee
Michael Beauchamp
Ken McRae
Alex Martin
Lawrence Barsalou

Running head: COMMON SUBSTRATE FOR PERCEIVING AND KNOWING COLOR

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 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

1. INTRODUCTION

Recent decades have witnessed a renewal of the centuries-old debate concerning the format of human knowledge (Barsalou, 1999; 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 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). 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, 1996), 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 is *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 sec (GRASS), followed by the name of a property for 2 sec (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 is 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). Figure 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 properties verified during the property verification task. Specifically, we assessed whether color properties activated any of these areas more than did the motor properties.

INSERT FIGURE 1 ABOUT HERE

2. METHODS

2.1 Subjects

Ten right-handed, native English-speaking volunteers from the Emory University community participated in the scanning study for pay (6 female and 4 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 Institutional Review Board's, 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 sec (e.g., BANANA, SCREWDRIVER), followed immediately by either a word for a color or motor property, also presented for 2 sec (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 sec. 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 sec, range 2 – 24 sec).

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 sec). 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.

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. Subjects saw five wedges encircling a central fixation mark (Figure 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-second block, subjects saw 7 color or grayscale wheels presented for 2.5 seconds, each separated by a 500 ms interstimulus interval. Across each MR scanning run, subjects saw 3 grayscale wheel blocks, and 3 color wheel blocks, with all 6 blocks separated by 15-second 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.pstnet.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 7 scanning runs for the property verification task, 208 echoplanar MR volumes depicting BOLD contrast were collected with a 3 Tesla 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 X 3 X 3 mm). In each of the 4 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 = 3000ms, flip angle = 90°, voxel size = 3 X 3 X 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 X 1 X 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 twentieth 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 mean signal value for each run was then subtracted from every time point in 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-seconds corresponding to presentation of each stimulus condition with a γ -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 Introduction and Discussion), we applied a small-volume correction 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 .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-seconds post-stimulus with a 2-second 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 seconds 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 X subject), comparing the response amplitude between 4 and 8 seconds 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 .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, $SD = 176$ ms; grayscale: $M = 1395$ ms, $SD = 179$ ms), $t(20) = 0.81$, $p = 0.43$. There was, however, a trend toward lower accuracy in color judgments (color: $M = 68\%$, $SD = 6\%$; grayscale: $M = 74\%$, $SD = 10\%$), $t(20) = 1.86$, $p = 0.08$.

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.

INSERT TABLE 1 ABOUT HERE

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, $SD = 12\%$; motor: $M = 92\%$ correct, $SD = 4\%$), $F(1, 48) = 1.16, p = 0.29$. Similarly, verification latency for the two property types did not differ significantly (color: $M = 1279$ ms, $SD = 267$ ms; motor: $M = 1198$ ms, $SD = 219$ 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 Figure 2 exhibited stronger activation during the color property trials than during the motor property trials (percent signal change color $M = .36, SD = .16$; motor $M = .28, SD = .16$), $F(1, 9) = 12.48, p = 0.006$ (see inset line graph on Figure 2, also see Figure 3). In contrast, no difference was observed between color and motor property verification trials in the right lingual gyrus cluster (percent signal change color $M = .10, SD = .12$; motor $M = .13, SD = .25$), $F(1, 9) = 0.34, p = 0.58$. 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).

INSERT FIGURE 2 AND FIGURE 3 ABOUT HERE

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 et al., 2003; 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”). The neural bases of color perception and 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. At no point, however, 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 perform 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 and colleagues 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 versus 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 et al., 1996; Zeki, Watson, Lueck, Friston, Kennard, & Frackowiak, 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 centimeter 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 one centimeter 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, Levin, & Calvino, 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, Brett, and Patterson (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/STS for motor trials is significant because this region becomes active when individuals perceive both biological and non-biological motion (Beauchamp, Lee, Haxby, & Martin, 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).

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, Watson, Lueck, Friston, Kennard, & Frackowiak, 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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Table 1.

Regions showing differential responses following corrections for multiple comparisons.

Contrast	Side / Location	<u>Coordinates</u>			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
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Note. Coordinates are listed in Talairach space.

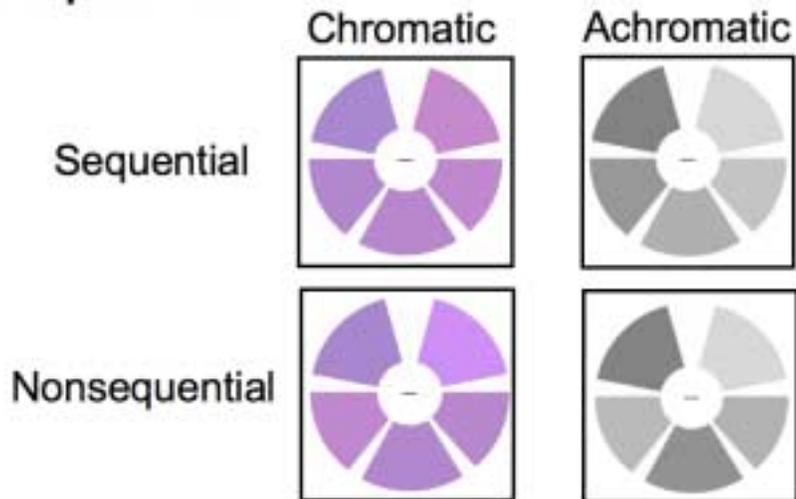
Figure Captions

Figure 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-second 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.

Figure 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 $Y = -38$ 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.

Figure 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 $Y = -45$). 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 ($p < 0.05$).

Perceptual Task



Conceptual Knowledge Task

<u>Condition</u>	<u>Concept Word</u>	<u>Property Word</u>
Color Property Verification	EGGPLANT	<i>purple</i>
Motor Property Verification	FOOTBALL	<i>throw</i>
Concept-only Trial	LIGHTBULB	

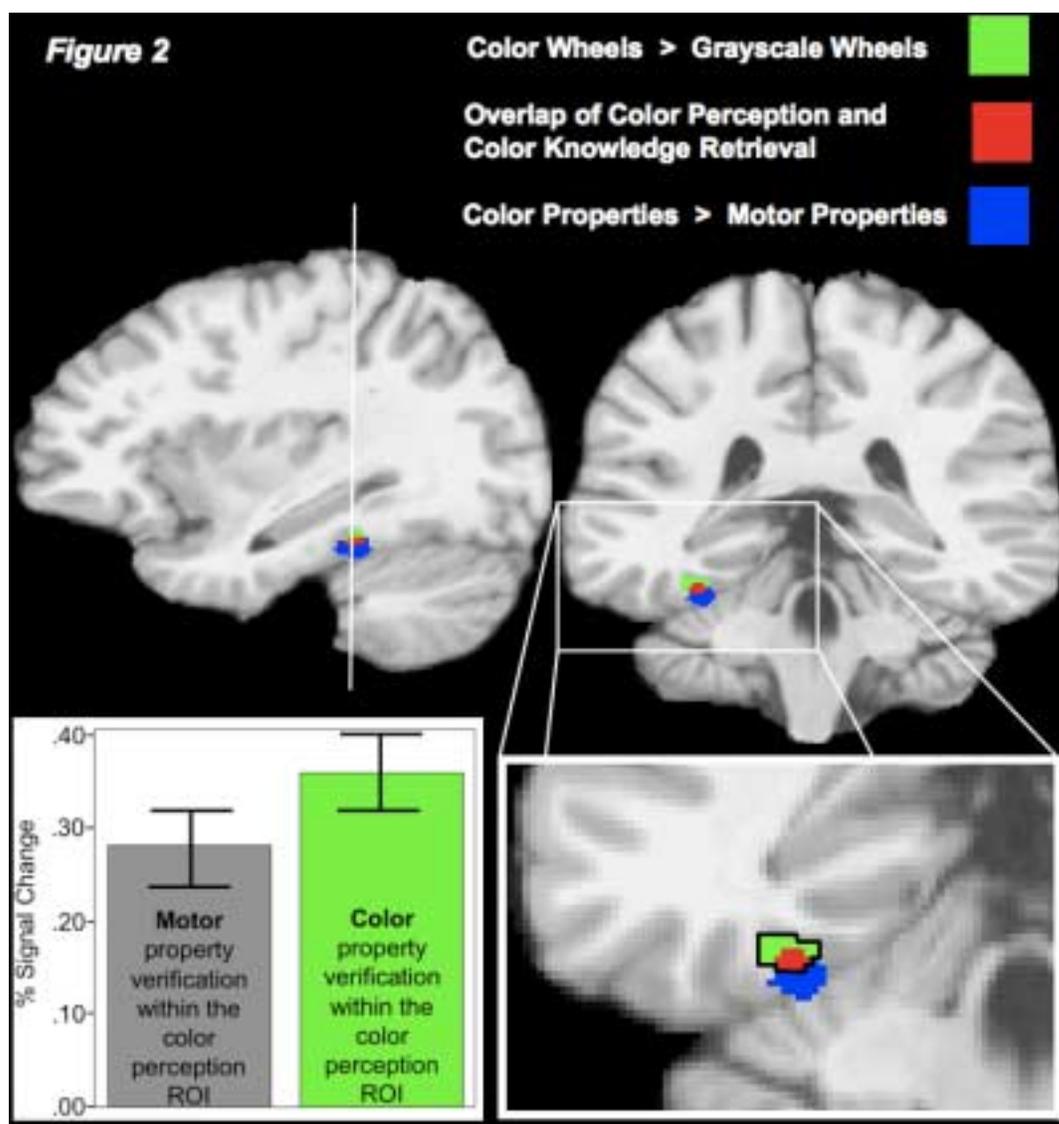
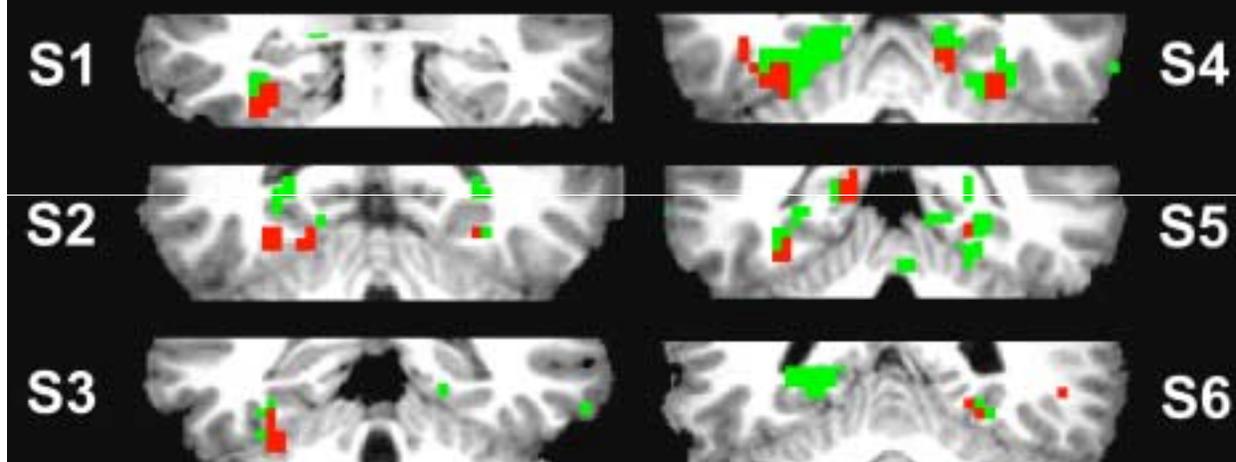
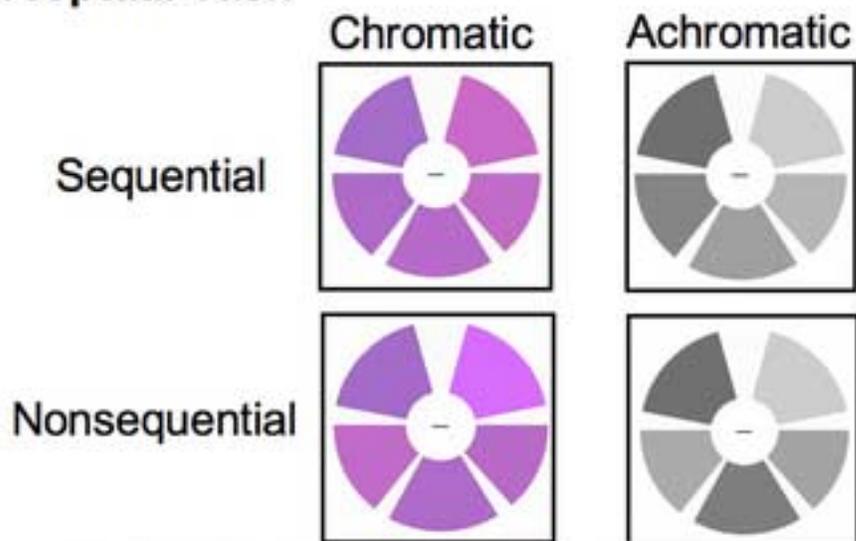


Figure 3

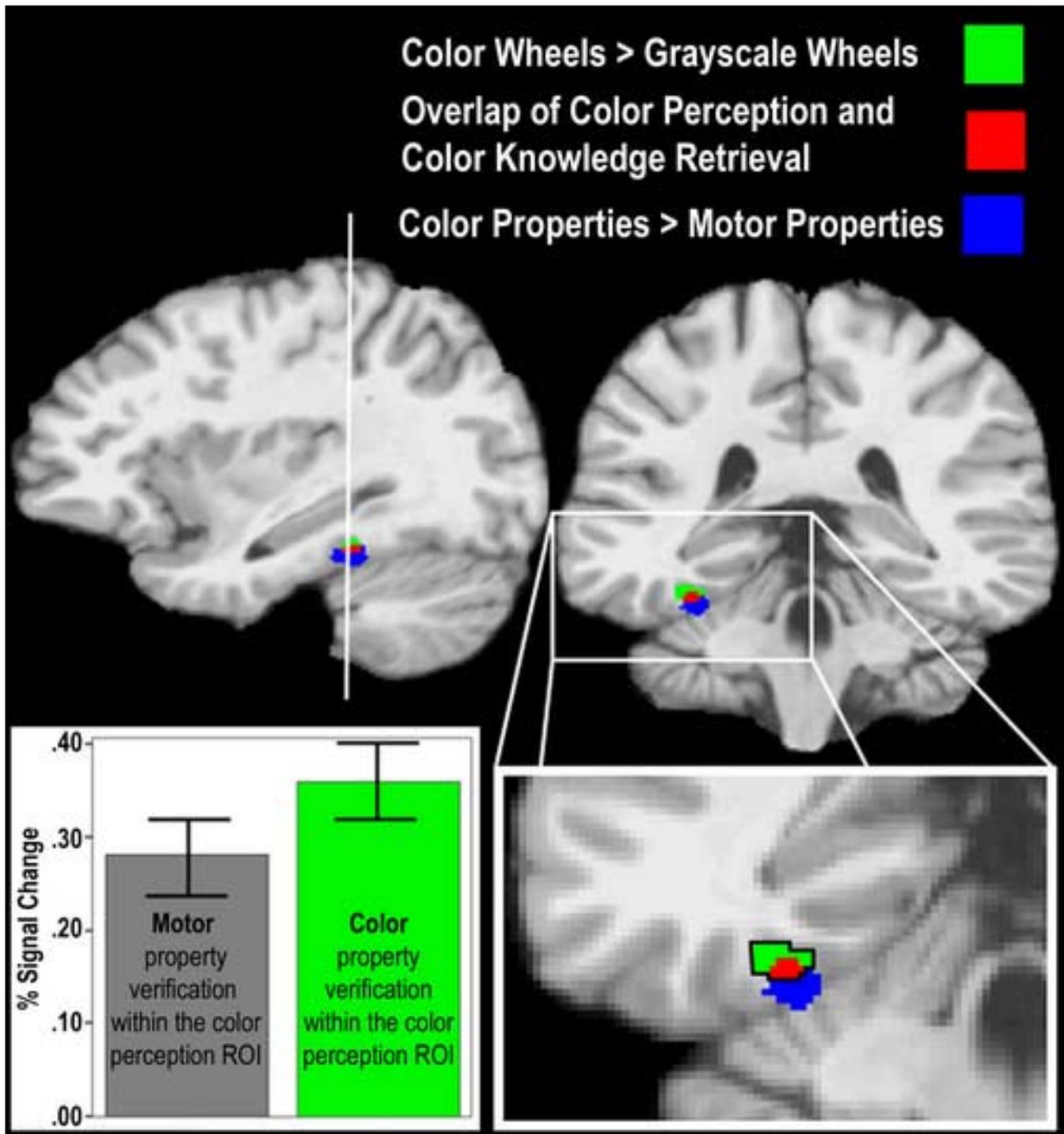
Perceptual Task



Conceptual Knowledge Task

<u>Condition</u>	<u>Concept Word</u>	<u>Property Word</u>
Color Property Verification	EGGPLANT	<i>purple</i>
Motor Property Verification	FOOTBALL	<i>throw</i>
Concept-only Trial	LIGHTBULB	

Figure_2
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Figure_3

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