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Report

Decoding the Yellow of a Gray Banana

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Summary

Some everyday objects are associated with a particular color, such as bananas, which are typically yellow. Behavioral studies show that perception of these so-called color-diagnostic objects is influenced by our knowledge of their typical color, referred to as memory color [1, 2]. However, neural representations of memory colors are unknown. Here we investigated whether memory color can be decoded from visual cortex activity when color-diagnostic objects are viewed as grayscale images. We trained linear classifiers to distinguish patterns of fMRI responses to four different hues. We found that activity in V1 allowed predicting the memory color of color-diagnostic objects presented in grayscale in naive participants performing a motion task. The results imply that higher areas feed back memory-color signals to V1. When classifiers were trained on neural responses to some exemplars of color-diagnostic objects and tested on others, areas V4 and LOC also predicted memory colors. Representational similarity analysis showed that memory-color representations in V1 were correlated specifically with patterns in V4 but not LOC. Our findings suggest that prior knowledge is projected from midlevel visual regions onto primary visual cortex, consistent with predictive coding theory [3].

Results

Hering [4] postulated that memory color exerts a significant influence on the perception of object color. This prediction is supported by recent psychophysical studies showing that the color appearance of color-diagnostic objects is biased toward their corresponding typical colors even when they are presented achromatically [1, 2]. However, the implementation of these cognitive influences in the neural architecture of color processing has remained unknown.

We hypothesized that somewhere in the color-processing pathway of the visual system, bottom-up signals representing sensory chromatic input share a common neural representation with top-down color signals based on object knowledge. We used human functional magnetic resonance imaging (fMRI) in combination with pattern classification to test our hypothesis.

In the first four runs of our fMRI experiment, 18 naive participants (eight females) with normal color vision viewed achromatic images of eight color-diagnostic objects (Figure 1) representing four different memory colors (red, green, blue, and yellow, with two objects per category). Each object was presented in a separate miniblock. We used grayscale photos of real objects (instead of line drawings, for instance) because previous psychophysical research had indicated that the impact of object knowledge on color appearance depends critically on the stimuli appearing natural [2]. In the last six runs, participants were shown real chromatic ring-shaped stimuli from four different hue categories (red, green, blue, and yellow), each at two luminance levels (in separate mini-blocks) to maximize subsequent classifier generalization (Figure 1). We asked participants to perform a motion discrimination task at all times in order to ensure naivety with regard to the purpose of the experiment, to maintain balanced attention across all trials, and to direct attention to an attribute different than color or objects.

Memory-Color Decoding: Searchlight Analysis

We first performed a whole-brain searchlight analysis (4-voxel radius) to find out where in the brain local fMRI patterns of blood oxygen level-dependent (BOLD) responses to real color were also predictive of memory color [5]. Four-way color classifiers were trained on all local activity patterns elicited by the chromatic ring stimuli to distinguish between the four color categories across both luminance levels. These classifiers were then tested on the local fMRI responses to each of the eight object images, with each object image being labeled by its memory color. In this way, we obtained a whole-brain map of decoding accuracies (chance level = 25%) for every participant. These maps indicated where object colors could be predicted based on real-color training. We found the largest significant cluster of informative voxels within visual cortex bilaterally near the calcarine sulcus (Figure 2A) ($t_{17} > 2.57$, $p_{voxel} < 0.01$, cluster size ≥ 68, $p_{cluster} < 0.001$). Additional significant clusters were found in the left hemisphere along the occipital and temporal lobes, near the left supramarginal gyrus, as well as the postcentral gyri and the posterior portion of the frontal lobe bilaterally.

Memory-Color Decoding: ROI Analysis

To verify the anatomical location of memory-color encoding, we repeated the above analysis for functionally defined regions of interest (ROIs) of visual areas V1–V3 and V4+ (union of areas hV4 and VO-1; see the Experimental Procedures) and object-responsive lateral occipital cortex (LOC), identified independently in nine of our participants. We used recursive feature elimination (RFE) for voxel selection and permutation tests for statistical inference (see the Experimental Procedures). As shown in Figure 2B, activity patterns in V1 allowed prediction of object colors above chance (34%, one-tailed permutation tests, p = 0.0005, Bonferroni corrected for five ROIs), but not V3 (27%, p = 0.22, uncorrected), V4+ (23%, p = 0.89, uncorrected), or LOC (28%, p = 0.048, uncorrected). A trend toward significant decoding was observed in V2 as well, although it marginally failed to reach significance (30%, p = 0.052, Bonferroni corrected). These results were replicated in the independent group of nine subjects for whom retinotopic mapping data were unavailable and anatomical masks were used instead (Figure 2C): the prediction of memory color based on real-color decoders worked only in V1 (30%, p = 0.012, Bonferroni corrected for three ROIs) and not in V2 (23%, p = 0.80, uncorrected) or fusiform gyrus (25%, p = 0.47, uncorrected).

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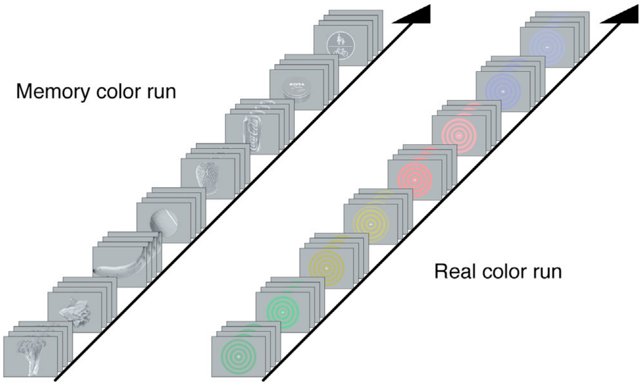

Figure 1. Experimental Design

Left: in the first four runs, participants viewed grayscale images of eight different color-diagnostic objects (broccoli, lettuce, banana, tennis ball, strawberry, coke can, Nivea tin, and blue traffic sign) in miniblocks of four stimuli (stimulus duration = 2 s, interstimulus interval [ISI] = 1 s). Objects rotated by 3°/s, and participants indicated the motion direction (clockwise or counterclockwise). Right: in the last six runs, participants viewed real-color stimuli of four different hues (red, green, blue, and yellow) at two luminance levels. See also Table S1 available online.

Real-Color Decoding: Searchlight and ROI-Based Analyses

As the prediction of memory color was restricted to early visual cortex with no successful decoding in higher regions such as V4+ and LOC, it appeared to be worthwhile to investigate whether this result was specific to memory-color decoding or whether it reflected classification accuracies for real-color stimuli. We therefore trained and tested color decoders on the data from the six "real-color runs" using an $n - 1$ cross-validation technique, leaving out a different run on every iteration that was then used for testing. A corresponding searchlight analysis showed that the whole occipital cortex, including the fusiform region, encoded real colors (Figure 2D). Accordingly, all ROIs encoded real colors. For functionally localized ROIs, decoding accuracies were as follows: V1 = 40%, V2 = 38%, V3 = 34%, V4+ = 37%, and LOC = 31%. Each ROI achieved $p = 0.005$ in one-tailed permutation tests, Bonferroni corrected for five ROIs (see Figure 2E). For anatomically defined ROIs, decoding accuracies were as follows: V1 = 39%, V2 = 40%, and fusiform gyrus = 35%. Each ROI achieved $p = 0.003$ in one-tailed permutation tests, Bonferroni corrected for three ROIs (see Figure 2F). Therefore, as real color could be decoded successfully from every ROI, including V4+, the absence of information predictive of memory color in extrastriate areas cannot be explained simply by the potential poor signal quality that has been shown to be a problem with measurements of the V4+ region in some individuals [6].

Feedback from Extrastriate Visual Areas to V1

The fact that V1 encoded memory colors of objects shown in grayscale strongly suggests that feedback from higher visual areas was involved (see the Discussion). V4+ and LOC are potential candidates for such feedback, as the former is involved in high-level color perception (e.g., [7]) and the latter in shape and object processing (e.g., [8]). We conducted two additional analyses to examine whether the data provide support for both regions being potential candidates as sources for feedback to V1.

First, we tested the possibility that memory color may be represented in V4+ and LOC, yet in a way that differs from the representation of real color. We trained classifiers to discriminate between colors on one half of the objects that represented four memory colors (e.g., strawberry, banana, lettuce, and Nivea tin) and tested them on the remaining half (e.g., coke can, tennis ball, broccoli, and traffic sign). We averaged the results over all 16 possible partitions into training and test set. The assumption was that generalization would only work if the classifier relied on memory color of objects. This analysis showed that memory color could be decoded significantly better than chance in V4+ (37%, $p = 0.002$, one-tailed permutation tests, Bonferroni corrected for two ROIs) and LOC (30%, $p = 0.002$) (see Figure 3A).

The alternative account for these results would be that classifiers relied on low-level or shape features that could have been by chance more similar among exemplars of the same memory color. In order to test for this alternative, we performed the same classification analysis using simulated data instead of fMRI data. We used a physiologically plausible computational feed-forward model of object recognition to calculate feature vectors (corresponding to C2 layer responses in HMAX [9]) for our stimuli in a way that mimics the filtering processes thought to be carried out by V4+ and IT circuitry. The classification based on the modeled data (see the Experimental Procedures) was not significant (28%, $p = 0.216$, one-tailed permutation test, same correction as used for V4+ and LOC). This analysis suggests that shape-related information is unlikely to account for the across-object decoding in V4+ and LOC, which in turn suggests that both regions encode memory color, yet differently than V1. However, as this validation relies on a computational model, it cannot fully rule out the alternative interpretation.

Second, we therefore sought to identify an additional way in which memory-color representations in V1 may be related to activity in V4+ and LOC. We used representational similarity analysis (RSA) [10] to probe whether the representational structure between real colors and memory colors was similar in V1 and in the extrastriate regions. To this end, we calculated the correlation coefficients between every activity pattern related to each of the real colors and to each memory color, yielding one representational dissimilarity matrix (RDM) for each ROI. We then examined which ROIs achieved highest similarity of the obtained matrix with that obtained for V1. We found that the average correlation between RDMs was significant only between V1 and V4+ ($r = 0.53$, $t_8 = 3.79$, $p = 0.005$, one-tailed t test, Bonferroni corrected for two ROIs), and not between V1 and LOC ($r = 0.17$, $t_8 = 1.188$, $p = 0.135$, one-tailed t test, uncorrected), with the former being significantly higher (one-tailed paired t test, $t_8 = 5.37$, $p < 0.001$). These results show that V1 and V4+ resemble each other significantly in terms of the similarity relationships between patterns encoding memory and real colors, respectively.

Discussion

In the present study, we addressed a fundamental question in color vision, namely the effect of prior knowledge on color processing. Our results show that color decoders could predict, from fMRI activity in V1, the true color of eight color-diagnostic objects, representing four different color categories, in the complete absence of chromatic stimulation. The results were found in naive observers carrying out a motion task and therefore appear to be the result of an automatically occurring process during object vision rather than of active imagery. A potential source of the memory-color signal in V1 may be

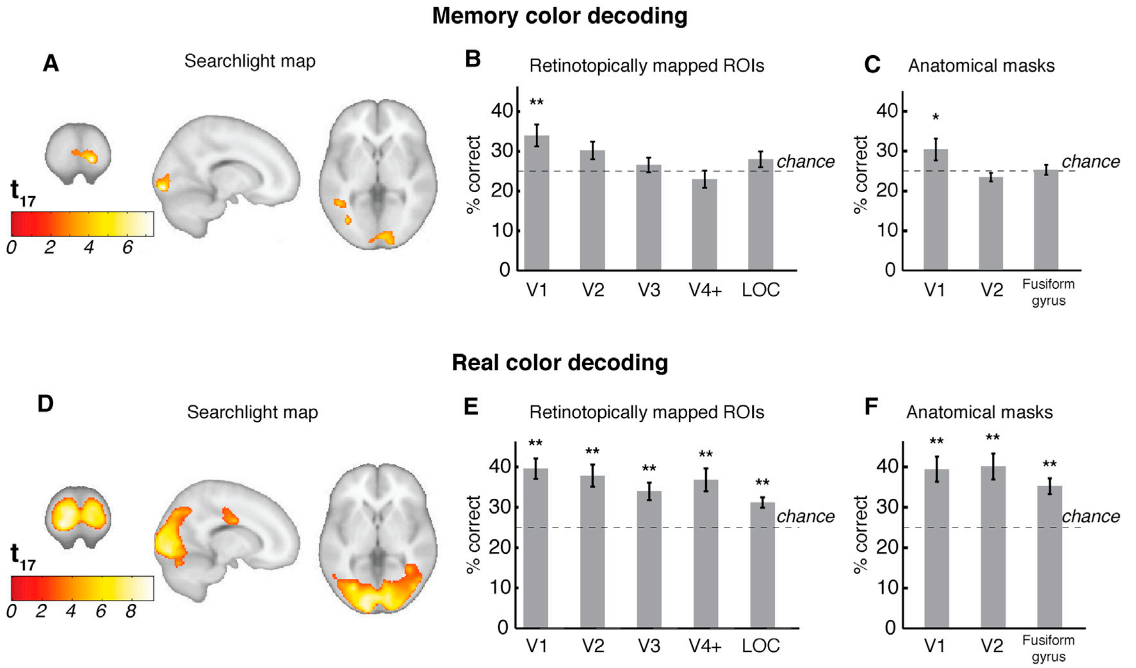

Figure 2. Multivoxel Pattern Analysis Results

(A) Whole-brain searchlight analysis across all 18 subjects. Prediction of the memory colors of the grayscale object images based on training on the real-color runs using local fMRI activity patterns was significantly above chance in early visual cortex. Brain sections are centered on position x = 14, y = −94, z = 0 in MNI space. Searchlight maps are cluster-size-corrected at $p_{voxel} < 0.01$, $p_{cluster} < 0.001$.

(B) Among functionally localized ROIs in nine subjects, prediction of memory color based on real-color training was successful only in area V1.

(C) In anatomically defined ROIs of the remaining nine subjects, prediction of memory color based on real-color training was successful only in area V1.

(D) Searchlight analysis. Prediction of real colors based on real-color training was significantly above chance in the entire occipital cortex. The same conventions as those in (A) are used.

(E) Among functionally localized ROIs, prediction of real colors was significantly above chance in all visual areas and in LOC.

(F) In anatomically defined ROIs, real-color prediction based on real-color training worked in each of the three ROIs.

Bar plots depict mean decoding accuracies. Error bars represent the SEM. $^{*}p < 0.05$, $^{**}p < 0.01$ (one-tailed permutation tests, Bonferroni corrected). See the Supplemental Experimental Procedures for further analyses. See also Figure S1.

V4+, as they shared a strong correlation in the structure of memory-color representations. Some authors interpret such similarity as "representational connectivity" between brain regions [10], which in this case fits well with our interpretation of the results that information is projected from higher-level visual regions onto primary visual cortex. The neural substrates revealed in the present findings may underlie several perceptual effects having to do with top-down influences of prior knowledge involving color [1, 2, 11–13]. To our knowledge, the present results are the first to demonstrate that memory color influences neural activity at the earliest levels of cortical processing, in the primary visual cortex.

The results are consistent with numerous experiments showing that, instead of encoding a veridical representation of the physical environment, V1 activity is in fact strongly modulated by top-down feedback, which can be readily detected with fMRI [14]. V1 activity has been shown to represent perceived lightness rather than physical stimulus intensity [15], to represent perceived rather than the physical size of stimuli [16, 17], to encode context-dependent feedback in the visual field [18], and to signal high-level grouping effects of global Gestalt cues [19].

Our own and the discussed results are consistent with predictive coding theory [3]. In the context of the present study, the assumption is that higher visual areas send predictions of expected object colors to V1, where they are compared to bottom-up information. Predictive coding is efficient in that it can enhance weak sensory input through prior knowledge and at the same time boost neural processing of unexpected (as opposed to predictable) aspects of the environment [20]. Thus, the omission of an expected visual stimulus can, for instance, even lead to stronger fMRI responses in V1 than its presence [21].

In this context, the BOLD signal in V1 represented either the mismatch between expected and incoming color signals or the predictive signal fed back to early visual cortex. Interestingly, this prediction-related activity resembled the expected signal driven by real-color input. Similarly, the agreement between representational structures in V1 and V4+ suggest that V4+ may be both receiver and source of color signals in V1 during sensory color stimulation and object viewing, respectively.

Based on previous imaging studies (e.g., [7, 22]), it may seem surprising that significant decoding was observed in V1 only but not in color-sensitive V4+. Several reasons may have contributed to this. Color signaling in V4+ could have been weakened due to vascular artifacts [6] and due to the attentional focus on motion rather than on color [23, 24]. Slotnick [25], for instance, does find upmodulation of V4+ in a memory task when subjects actively remembered that an abstract figure had previously been presented in color in the study phase. However, these reasons cannot fully account for the lack of decoding in V4+ as decoding of real colors was well above chance in V4+. Perhaps one reason lies in

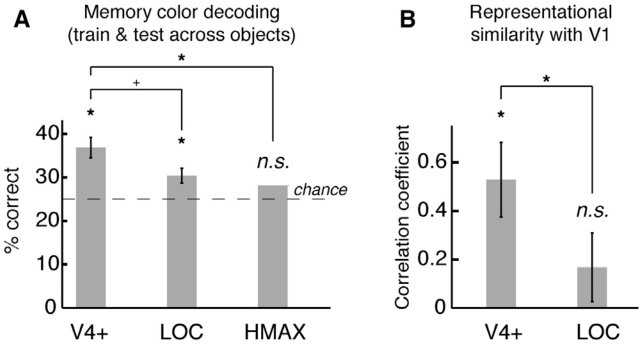

Figure 3. Color Generalization across Objects and Representational Similarity with V1

(A) Classifiers trained on responses to one set of color-diagnostic objects and tested on the other (with no overlap of object identities in the two sets) correctly predicted the memory color of objects in the test set in V4+ and LOC, with an advantage for V4+ [V4+ versus HMAX: $t(8) = 3.69$, $p = 0.009$, Bonferroni corrected for three comparisons; V4+ versus LOC: $t(8) = 2.33$, $p = 0.024$, uncorrected]. In contrast, classifiers failed to predict low-level and shape features between objects of the training and test sets. Features were extracted using the physiologically plausible HMAX algorithm.

(B) Representational similarity with V1 was found in V4+ but not LOC. This shows that the similarity relationships between patterns encoding memory and real colors were significantly correlated between V1 and V4+.

Error bars represent the SEM. $^*p < 0.01$ (Bonferroni corrected) $^+p < 0.05$ (uncorrected). One-tailed paired t tests ($df = 8$) were used for pairwise comparisons.

the categorical perception of grayscale rather than colored objects.

Also, classification accuracy may in principle be related to differences in the spatial inhomogeneity of feature-selective neuronal assemblies across voxels [26], which has recently also been suggested in context of color encoding along cardinal color axes [27]. Accordingly, our analyses cannot exclude the possibility that memory color may also be present in high-level regions (as is indeed suggested by our across-object classification).

Our data provide, to our knowledge, the first evidence for encoding of color in V1 in the absence of any chromatic input. The present results therefore add one more dimension, color, to a growing body of literature showing that V1 activity is heavily influenced by feedback from higher-level regions, encoding perceived rather than purely physical stimulus properties even if they are absent from bottom-up input. The present results offer a neural account for previously observed perceptual effects of memory color and provide additional evidence for a role of V1 as convergence zone between bottom-up input and top-down predictive signals. The present findings have implications beyond color vision, as they show how object knowledge can serve as a prior to constrain the inferences the visual system makes at earliest processing stages about the appearance of complex natural scenes.

Experimental Procedures

Participants

Eighteen volunteers (mean age 27.2 years, SD 4.1 years, eight female) with normal color vision, as assessed using Ishihara plates, participated in the main experiment. All provided written informed consent, and the ethics committee of the University Hospital Tübingen approved the experiment. Participants were naive with respect to the purpose of the study. Instead, they were told that its aim was to investigate motion using object and color stimuli. Nine participants (mean age 28.4, SD 5.1 years, four female) took part in a retinotopic mapping experiment.

Behavioral Tasks and Imaging Paradigm

In the first four fMRI runs, participants were required to view slowly rotating grayscale images of objects and to indicate for each stimulus by button press whether rotation occurred in a clockwise (right button) or counterclockwise (left button) direction. The images were isoluminant grayscale photos of eight different color-diagnostic objects, two for each color category: a strawberry and coke can for red, broccoli and lettuce for green, a traffic sign and Nivea tin for blue, and a tennis ball and banana for yellow (see the Supplemental Experimental Procedures for details). Every image was presented for 2 s, and the ISI was 1 s. Object images were presented in miniblocks of four trials containing the same object but with random rotation direction on each presentation (see Figure 1). Each run contained 32 miniblocks. The sequence of objects was pseudorandomized such that every object was preceded equally often by all objects.

In the last six runs, participants viewed chromatic stimuli consisting of abstract color rings similar to those used by Brouwer and Heeger [7] (see the Supplemental Experimental Procedures for details). Each ring was defined by its color (red, green, blue, or yellow) and brightness (high or low: ±10% around the object's luminance), yielding eight stimuli that were presented in separate miniblocks (see Table S1 for chromaticity coordinates). In each trial within a miniblock, rings randomly either expanded or contracted. The design was identical to that of the object runs. Participants performed a one-back matching task that amounted to a motion task in the majority of trials since hue and luminance were constant within miniblocks.

fMRI Scan Parameters and Preprocessing

Data were collected on a 3T fMRI system with a resolution of 3 mm isotropic voxel size across 33 slices and preprocessed with SPM5 (http://www.fil.ion.ucl.ac.uk/spm/). Neural responses to objects and color rings were estimated with a separate general linear model for each run and with separate boxcar regressors for each miniblock (see the Supplemental Experimental Procedures for details).

Retinotopic Mapping and Anatomical Masks

In nine subjects, polar angle maps were obtained using standard methods. Areas hV4 and VO-1 are reported as joint ROI "V4+" since segregated analyses yielded same results as for the joint ROI. To confirm memory-color decoding in V1 for the remaining nine participants, we used the automatic cortical parcellation provided by Freesurfer to obtain ROI masks of V1, V2, and fusiform gyrus (see the Supplemental Experimental Procedures and Figure S1).

Multivoxel Pattern Analysis

We analyzed our data with in-house Matlab code based on the Princeton multivoxel pattern analysis toolbox (http://www.pni.princeton.edu/mvpa/). For all analyses, we applied linear discriminant analysis for pattern classification using shrinkage estimation to make sure that covariance matrices were nonsingular [28, 29]. We obtained a whole-brain map of decoding accuracies for every participant. After smoothing with a 6 mm Gaussian kernel, group statistics were calculated using one-sample t tests. Results were corrected for multiple comparisons using a cluster size threshold determined on the basis of Monte-Carlo simulations [30]. For ROI-based decoding of memory color based on real-color training, we first used a feature selection algorithm (RFE) to identify those voxels that contributed most strongly to the discrimination of real colors (see the Supplemental Experimental Procedures). We used the more accurate approach of permutation tests for statistical inference in the ROI-based classification analyses [28]. This involved permuting the labels of the training data repeatedly to bootstrap a null distribution for every statistic (see the Supplemental Experimental Procedures).

Reported p values represent the fraction of permutations yielding classification accuracies that were at least as high as the observed one.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, one figure, and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.09.016.

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