The quality of perception without attention

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Prior knowledge about the world determines neural color representation in human visual cortex.

CHAPTER 7

Abstract

To create subjective experience, our brain must translate physical stimulus input by incorporating prior knowledge and expectations. For example, we perceive color and not wavelength, and this in part depends on our past experience with colored objects (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006; Mitterer & De Ruiter, 2008). Here, we investigated the influence of object knowledge on the neural substrates underlying subjective color vision. In a functional Magnetic Resonance Imaging (fMRI) experiment, human subjects viewed typical red (e.g. tomato), typical green (e.g. clover), and semantically meaningless (nonsense) objects in an ambiguous color that lay midway between red and green. Using decoding techniques, we could predict whether subjects viewed ambiguously colored typical red objects or ambiguously colored typical green objects based on the neural response of veridical red and veridical green. This shift of neural response for the ambiguous color did not occur for nonsense objects. The modulation of neural responses was observed in visual areas (V3, V3A, V4, VO1, lateral occipital cortex) involved in color and object processing, as well as frontal areas associated with memory processing. This demonstrates that object memory influences wavelength information relatively early in the human visual system to produce subjective color vision.

Introduction

As the brain processes incoming information, visual representations become detached from the low-level properties of stimulus input: the visual world is interpreted to match our beliefs and expectations, and these processes seem to occur instantly. Color constancy - the phenomenon that a color is perceived differently depending on its context - is one of the most telling examples of this process (Foster, 2003; Land, 1959). For example, when we see an apple under artificial light or under sunlight, the color of the apple seems unchanged. The color information that enters our eyes in these two situations, however, is very different, perhaps being dominated by yellow in the first situation and by blue in the second situation.

One of the mechanisms driving color constancy is expectancy (Hansen et al., 2006; Mitterer & De Ruiter, 2008): we expect bananas to be yellow, and carrots to be orange. Which neural substrates underlie the incorporation of object knowledge to obtain color constancy, however, remains unknown. Previous research has shown that striate and extrastriate areas V1 and V2 are color selective, however, cells in these areas are primarily color-opponent and luminance dependent and are therefore suggested to specifically process wavelength (Brouwer & Heeger, 2009; Shapley & Hawken, 2011; Zeki, 1983). Area V4 and visual areas anterior to V4 (VO1), on the other hand, have been shown to be involved in color constancy (Heywood & Kentridge, 2003; Zeki & Marini, 1998); but for critical reviews see (Gegenfurtner & Kiper, 2003; Shapley & Hawken, 2011) and are suggested to respond according to perceptual color space rather than to low-level color properties (Brouwer & Heeger, 2009). Possibly, mid- and higher-level areas beyond V4 serve to combine color perception with memory for objects, thereby influencing neural responses to color in lower-level areas and creating subjective color experience (Shapley & Hawken, 2011).

In this study, we investigated which neural substrates underlie the effect that object knowledge has on our subjective color experience by using the phenomenon of color constancy. Using functional magnetic resonance imaging (fMRI) decoding techniques (Brouwer & Heeger, 2009; Seymour, Clifford, Logothetis, & Bartels, 2009), we determined whether the representation of a color that lies midway between red and green (ambiguous) can be shifted towards red when presented on typical red objects (typical-red: tomato, strawberry, rose, cherry) and towards green when presented on typical green objects (typical-green: pine tree, clover, pear, zucchini (Fig. 7.1, top). Specifically, we examined whether early visual areas (V1, V2, V3, V4) that are involved in processing color merely represent physical and perceptual color attributes or whether they are influenced by our prior knowledge. In addition to investigating our

predefined ROIs, we performed a searchlight analysis on the whole brain of every individual subject to investigate which higher level areas might be engaged in a shift in color perception.
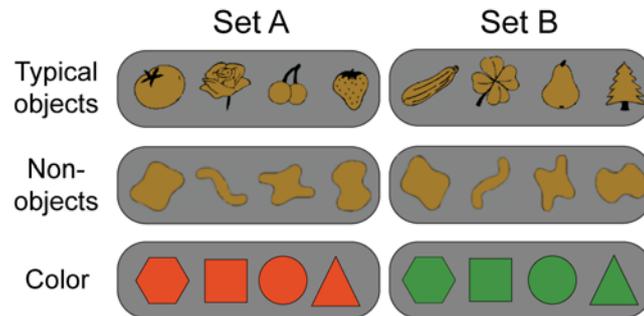

Figure 7.1. Stimuli. *Stimuli used for the typical object runs, nonsense object (non-objects) runs and color runs.*

Methods

fMRI acquisition

Ten subjects (1 male, Mean age = 23.5, SD = 4.5) participated in this experiment voluntarily or for monetary reward. All subjects had normal or corrected-to-normal vision and were tested on color vision using the Ishihara color blindness test. The study was approved by the local Ethics Committee of the University of Amsterdam and subjects were screened on risk factors precluding participation from MRI experiments.

Scanning was performed on a 3T Philips TX Achieva MRI scanner at the Spinoza Center in Amsterdam. A high-resolution T1-weighted anatomical image (TR, 8.17 ms; TE, 3.74 ms; FOV, 240 x 220 × 188) was recorded for each subject. Functional MRI was recorded using a sagittally oriented gradient-echo, echo-planar pulse sequence (TR, 2000 ms; TE, 27.63 ms; FA, 76°; 37 slices with interleaved acquisition; voxel size, 2.5 x 2.5 x 3 mm; 80 x 80 matrix; FOV, 200 x 200 x 122). Stimuli were back-projected on a 61 x 36 cm LCD screen using Presentation software (Neurobehavioral Systems, Inc., Albany, CA) and viewed through a mirror attached to the head coil.

Stimuli

To map the green and red responses for each subject, 16 geometrical shapes (4 squares, 4 triangles, 4 circles, 4 hexagons; Fig. 7.1, bottom) were presented surrounding a white fixation cross. (Mean object size = 1.3° x 1.3°, SD = 0.1° x 0.1°). To optimize the level of activity in lower visual areas, objects rotated around the white fixation cross during a 12 second presentation (4).

The objects were placed on three circles (radius: 2.9°, 4.7° and 6.9°; movement speed: 1.5°/s, -2.5°/s, 3.6°/s) containing 4, 6 and 6 objects. Red and green were selected to be isoluminant (red: CIE L*= 55, a* = 60, b* = 54; green: CIE L*= 55, a* = -40, b* = 38; both 65 cd/m^2) with respect to a gray background (CIE L*= 55, a* = 0, b* = 0; 65 cd/m^2) based on their CIE L*a*b color values. To map the responses for the ambiguous color in a specific object-color association, 16 typically green objects (typical-green: 4 pine trees, 4 clovers, 4 pears, 4 zucchini; M obj. size = 1.3° x 1.3°, SD = 0.2° x 0.1°) and 16 typically red objects (typical-red: 4 tomatoes, 4 strawberries, 4 roses, 4 cherries; M obj. size = 1.2° x 1.4°, SD = 0.2° x 0.2°) were filled in with the ambiguous color (CIE L*= 55, a* = 10, b* = 46; 65 cd/m^2) (Fig. 7.1, top). These objects were line drawings taken from various sources on the internet, which we modified such that the typical-green and typical-red object sets had the same amount of colored and black pixels. As a control, 16 nonsense objects (4 different figures computed in Matlab using sine/cosine transforms; M obj. size = 1.4° x 1.4°, SD = 0.2° x 0.2°) were filled in with the ambiguous color and presented in 2 conditions, with the figures in the one condition (set A) rotated 90˚ compared to the other condition (set B) (Fig. 7.1, middle).

Procedure

In each fMRI run, two conditions (red vs. green, or typical-red vs. typical-green, or nonsense objects set A vs. set B) were presented in 10 separate blocks (20 blocks per run). One block lasted 16 seconds containing a 4 second rest period. Each run started with a 16 second rest period and ended with a 20 second rest period (total run time 356 seconds, 178 TR). Blocks were presented pseudo-randomly per run, and block presentation was counterbalanced between runs. During the whole run, subjects had to fixate on the fixation cross and press a button when the cross turned into a circle (3 times per 12 second presentation period, timed randomly). We used eyetracking (Eyelink-1000, SR Research) to make sure that subjects properly fixated throughout each run.

Subjects performed 12-16 runs depending on whether they performed one or two scanning sessions. Four subjects underwent 1 scanning session in which 4 typical object runs, 4 nonsense object runs and 4 color runs were recorded. Two subjects started with the typical object runs and two subjects started with the nonsense object runs. All subjects ended with the 4 color runs to make sure that there was no effect of seeing veridical red or veridical green on the perception of the ambiguous color (for example by inducing a bias in a shift towards either red or green). Six subjects underwent 2 scanning sessions of 8 runs. In the first session, 4 typical object runs and 4 color runs were recorded and in the second session, 4 nonsense object runs

and 4 color runs were recorded. The color runs were recorded again in the second session to reduce variance that could be caused by imperfect registration or different BOLD dynamics between sessions.

On a different day after the scanning session(s), subjects performed a behavioral task in which they rated colors on a 7-scale continuum as either red or green to investigate the perceptual shift for the ambiguously colored stimuli. The seven colors (ranging from CIE L*= 55, a* = 25, b = *52 to CIE L* = 55, a = *-10, b = *40 in steps of a* = 5 and b* = 2) were presented on the objects used in the fMRI runs. Each stimulus was presented once a block and there were five blocks (560 trials total). A randomly colored noise mask was presented in between each presentation to prevent spillover effects of the previous trial.

Region of Interest localization

To define 5 visual Regions of Interest (ROIs: V1, V2, V3, V4 and these regions combined), each subject completed 1 – 4 polar mappings and 1-2 eccentricity mappings. For polar angle mapping, a checkerboard (red-green, flickering at 8 Hz) wedge rotated around fixation (clockwise or counterclockwise; complete revolution in 32s; 8 repetitions) and for eccentricity mapping, a checkerboard ring (red-green, flickering at 8 Hz) expanded from center to periphery (or vice versa; complete revolution in 32s; 8 repetitions). During runs, subjects fixated at the center while detecting blue squares presented in the red-green checkerboard stimuli to keep their attention with the stimuli and maximize the visual response.

Multi-Voxel Pattern Analyses (MVPA)

Data were analyzed using Brainvoyager 2.2 (Brain Innovation, Maastricht, The Netherlands; Goebel et al., 2006) and Matlab 2010 (MathWorks Inc). Functional scans were slice-time corrected, motion corrected, spatially smoothed with a Gaussian of 2 mm FWHM and high-pass filtered at 0.01 Hz. All functional scans were aligned to the functional scan that was recorded closest in time to the T1-weighted anatomical image. This functional scan was then coregistered to the anatomical image. Structural images were transformed to Talairach space using an ACPC transform (Talairach & Tournoux, 1988). Each run was z-transformed and for each stimulus block, the 4 volumes (8 seconds) that corresponded to the peak of the BOLD-response were averaged (the peak of the BOLD-response was calculated for each subject separately by cross-correlating the z-transformed data of the training runs for the combined ROI (com) with a Gaussian (alpha 2.5)). This created a specific voxel pattern for each subject and each stimulus presentation, separately for each ROI.

We used the Princeton MVPA toolbox (http://code.google.com/p/princeton-mvpa-toolbox) in combination with a Support Vector Machine (SVM) from the Bioinformatics toolbox to train the classifiers. To test the usability of MVPA on our dataset, we first tried to predict the presentation of red vs. green, typical-red vs. typical-green, and nonsense object set A vs. set B using a leave-1-out procedure. In these analyses, three runs were used for training and the fourth run was used to test whether the presentations in this run could be correctly classified as red or green. All combinations of runs were once used for training and each run was tested. Data for these 4 iterations were averaged and this yielded a classification score (proportion correct) for each subject and each ROI. The three averaged classifications were tested against chance (0.50) using two-sided paired t-tests.

To test whether the ambiguous color shifted towards a red or green color representation depending on object-color association, the classifier was trained on either the 4 color runs or on the 4 typical object runs. The 4 runs belonging to the non-trained condition were tested as such that a correct classification corresponded to the typical-red condition being classified as the color red or the color red being classified as the typical-red condition (depending on whether training was performed on the color runs or on the typical object runs). Data for the two iterations (color to prototype and prototype to color) were averaged and tested against chance (0.50) using two-sided paired t-tests. To verify that the effect was due to typical object-color associations, we used the same procedure on the nonsense object condition. To obtain a classification score for the nonsense objects, one set of stimuli was arbitrarily chosen to represent the association with red (set A) and the other set was chosen to represent the association with green (set B).

We further investigated whether there were brain areas that we did not specifically test using our predefined ROIs, but were involved in the object-color association, by using a searchlight procedure to test patches of voxels throughout the entire brain (excluding the cerebellum and brainstem). To test all voxels, each voxel served as center of a voxel kernel with a radius of 4 voxels (no smoothing applied, 257 voxels were weighted equally). Again, the classifier was trained on one condition (color or typical/nonsense objects) and tested on the other condition, and the outcomes of these two iterations were averaged. The searchlight procedure yielded a classification score for each voxel, and data for all subjects were tested against chance (0.50) using two-sided paired t-tests. Single voxels were thresholded at a p-value of 0.01 (corresponding to a T-value of 3.25). To apply a cluster threshold, we used a boxplot (Frigge, Hoaglin, & Iglewicz, 1989) to identify clusters that deviated from our sample based on the interquartile range of cluster sizes (see Fig. 7.3A).

Results

ROI decoding results

To test the usability of MVPA on our dataset, we first determined whether we were able to correctly predict the presentation of color (red vs green), typical objects (typical-green vs. typical-red) and nonsense objects (set A vs. set B) by themselves. Classification performance averaged over subjects is shown in Figure 7.2A. Red and green could be predicted for all 4 ROIs and when combining these ROIs (com), classification performance increased (all t(9) > 5.7, all p < .001). The two sets of real objects could be predicted from all visual areas as well (all t(9) > 3.1, all p < .014). The two types of nonsense objects could not be classified (V4: t(9) = 1.9, p = .090, V1-V3 and com: t(9) < 1.0), indicating that there was not enough difference in spatial information to distinguish the two nonsense objects sets (that were identical except for a rotation of each object) in lower level visual areas. Color categorization was superior to object categorization, in line with the idea that these low level areas represent elementary features rather than full objects (Brewer, Liu, Wade, & Wandell, 2005; Wandell & Winawer, 2011).

To investigate whether the representation of the ambiguous color shifted towards either red or green in the different object sets, we performed two between-category classifications. In these classifications, the classifier is trained on all the runs of one category (e.g. color) and tested on all the runs of the other category (e.g. objects). Data for the two iterations averaged (color to typical objects and typical objects to color) are shown in Figure 7.2B. Classification of the ambiguously colored typical objects as their typical color was significantly above chance for area V3 (t(9) = 4.3, p = .002), V4 (t(9) = 2.8), p = .021) and for the 4 ROIs combined (t(9) = 2.9, p = .017). This suggests that for the typical objects, the representation of the ambiguous color in V3 and V4 shifted towards either red or green, depending on the color associated with the specific object set.

To verify that the effect was due to typical object-color associations, we used the same procedure on the nonsense object condition. To obtain a classification score for the nonsense objects, one set of stimuli was arbitrarily chosen to represent the association with red (set A) and the other set was chosen to represent the association with green (set B). In contrast to the typical objects, the classification between ambiguously colored nonsense objects and color was at chance performance (V1: t(9) = 1.6, p = .144, V2-V4 and All: t(9) < .9, p > .42). As the ambiguous color was chosen to lie midway between red and green in CIE L*a*b color space, it was equally often classified as either red or green in both sets.

Together, these findings show that the representation underlying the ambiguous color in itself did not resemble either red or green, but object knowledge influenced its neural representation in V3 and V4 such that it shifted towards the expected color.
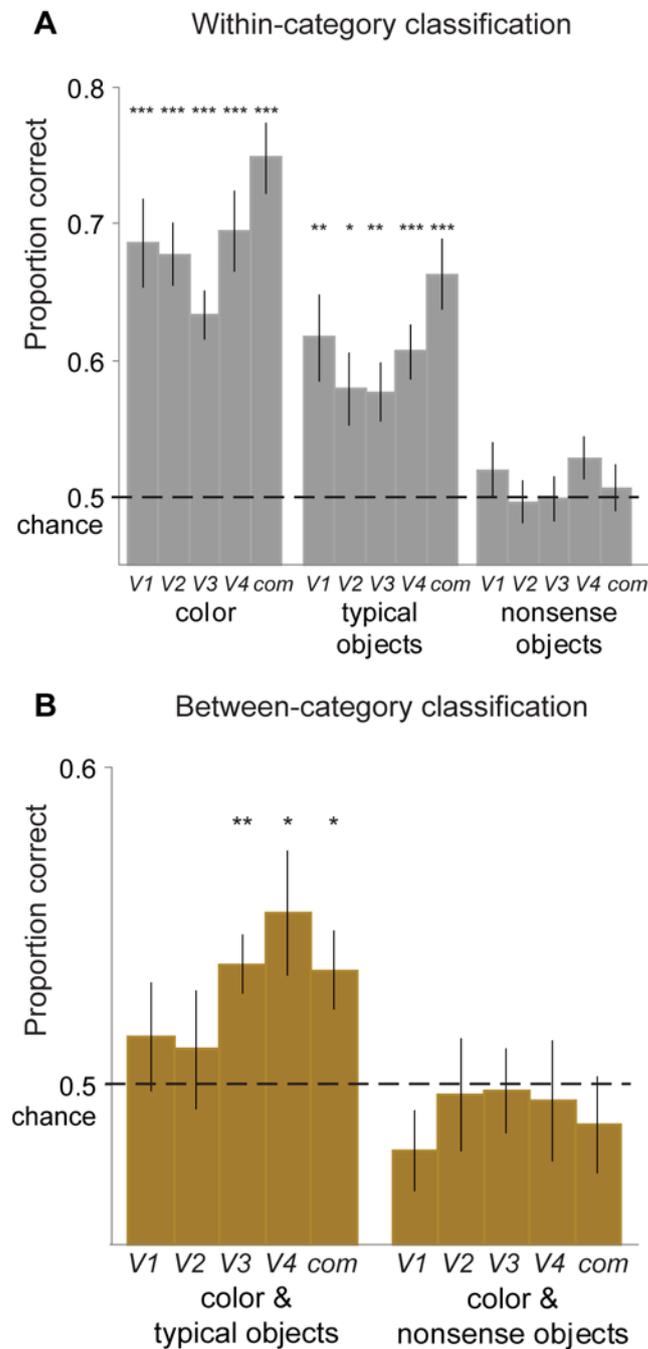

Figure 7.2. ROI analyses. *A) Within category classification using a leave-1-run-out procedure for red and green (color), typical-red and typical-green objects (typical objects) and nonsense objects set A and B (nonsense objects) averaged over subjects. Classification of color and typical objects was significantly above chance (dotted line) for each ROI (V1-V4) and for all ROIs combined (com).*

Classification of nonsense objects did not significantly exceed chance. B) Classification between color and typical objects and between color and nonsense objects averaged over subjects and over training sets (see Text). The between-category classification for color and typical objects was significantly above chance in V3, V4 and when all ROIs were combined (com). The between-category classification for color and nonsense objects did not deviate from chance. Error bars denote within-group standard errors.*p < .05, ** p < .01, *** p < .001

Searchlight decoding results

To investigate which mid- and higher-level regions were involved in the shift in color perception, we performed a searchlight analysis on both the typical objects and nonsense objects. We found 3 clusters for which the classification between colors and typical objects was significantly above chance (Fig. 7.3B; no clusters survived the threshold for the nonsense object sets; Fig. 7.3C): one right-lateralized visual dorsal cluster, one left-lateralized visual ventral cluster and one left-lateralized prefrontal cluster. The visual dorsal cluster overlapped with area V2 and V3, and the visual ventral cluster overlapped with V4, thereby confirming the findings on V3 and V4 of our ROI analyses. Possibly, the patch of voxels that was involved in V2 was not large enough to yield a correct classification when all voxels in V2 were taken into the analysis. In addition to significant classification in our predefined ROIs, we found that the ventral cluster covering V4 also covered voxels anterior to V4, probably encompassing VO1 (Wandell & Winawer, 2011), which is known to be involved in perceptual color processing just as V4 (Bartels & Zeki, 2008; Brewer et al., 2005; Brouwer & Heeger, 2009), and voxels in the left lateral occipital cortex (LOC), which is involved in object processing (Grill-Spector, 2003; Malach et al., 2002). The visual dorsal region also encompassed the region adjacent to V3 (probably V3A; Wandell & Winawer, 2011). In addition to the involvement of visual areas, we found significant classification in left superior and middle frontal areas in the vicinity of the Dorsolateral Prefrontal Cortex (DLPFC).
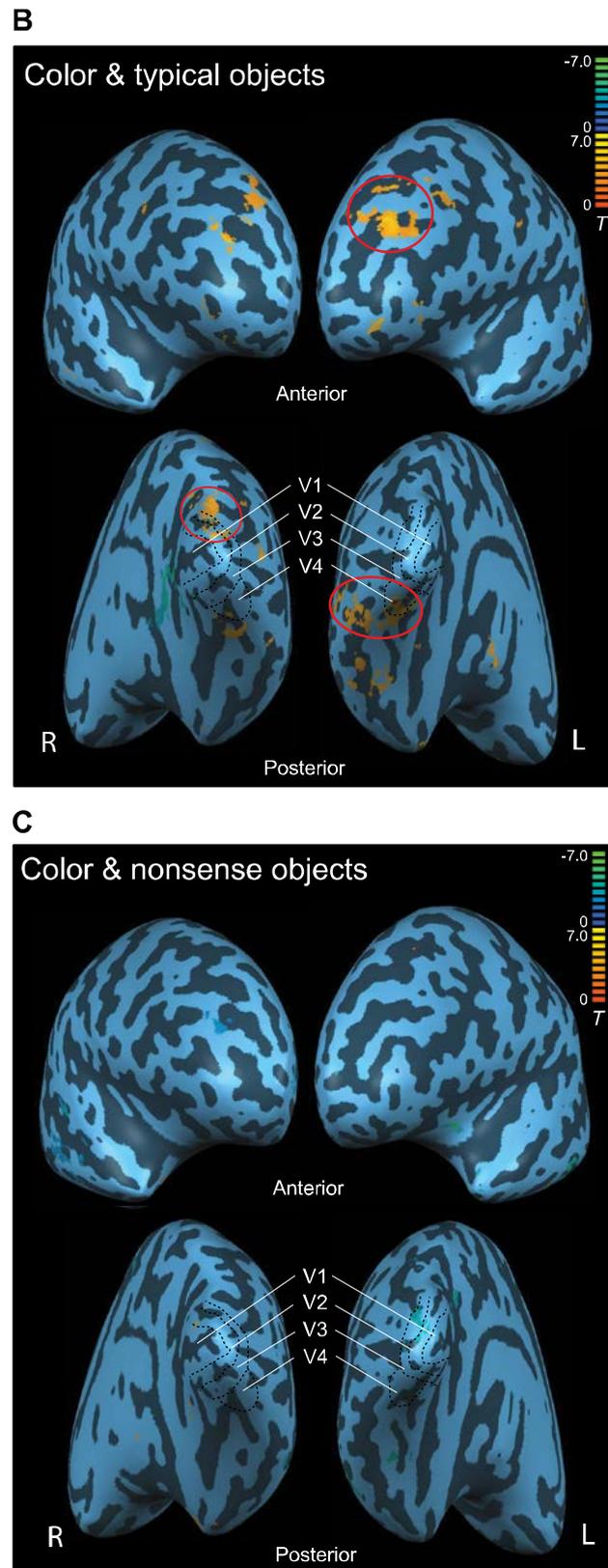
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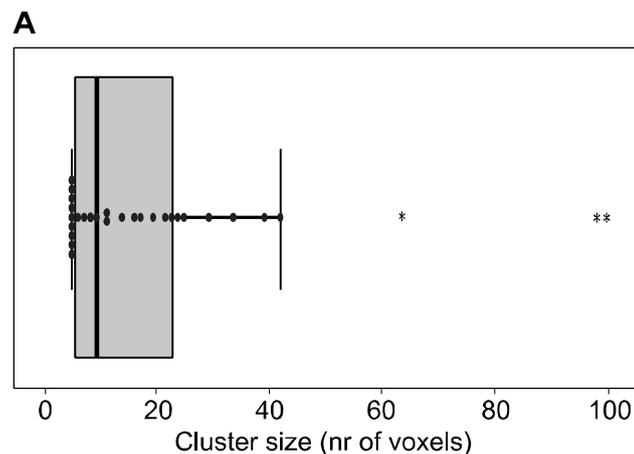
Figure 7.3. Searchlight analyses. *A) Cluster correction method used for the between-category (color & typical objects and color & nonsense objects together) searchlight analyses. As the data were not normally distributed, we used a boxplot to identify clusters that deviated from the*

sample (using only clusters that had a voxelsize > 5). The advantage of using this method is that a boxplot is non-parametric, and thus does not make any assumptions about the underlying statistical distribution. The box indicates the interquartile range (IQR; left side = 1st quartile, right side is 3rd quartile), and the whiskers show the lowest and highest datum still in the 1.5*IQR range. The thick line indicates the mean of the data. Three clusters exceeded the cluster threshold (stars), and these three clusters belonged to the color & typical objects condition. B) The three significant clusters for the typical-objects and color classification (circled in red, colors depict voxel T-values) were located in the right dorsal visual region, left ventral visual region and left medial prefrontal region. (C) No clusters for the color & nonsense objects condition exceeded the cluster threshold.

Behavioral results

To determine whether the typical objects evoked a behavioral change in perception that coincided with the neural findings, after scanning subjects performed a task in which they had to indicate whether they perceived a color (from a 7-scale continuum) presented on an object as either red or green. Figure 7.4A shows the amount of 'red'-responses for each of the seven hues on the four object sets, together with a fit of the data based on a binomial regression (logit transformed). For these 10 subjects, there was a trend towards giving more 'red'-responses for the typical-red objects than for the typical-green objects when presented in hue 4, which was the color that was used in the fMRI experiment (t(9) = 2.1, p = .067). The two nonsense object sets were labeled 'red' more often than both the typical-green and the typical-red objects. This suggests that the perception of color on these objects leans towards red, possibly because there is less contrast in the nonsense objects than in the typical objects. We then investigated whether the behavioral effect on the color that was presented in the fMRI experiment correlated with our neural measure. We found that classification scores for the left visual ventral cluster (encompassing V4/VO1/LO) correlated positively with the behavioral effect (Pearson's R = .66, p = .037; Fig. 7.4B), supporting the hypothesis that these areas are involved in subjective color perception by combining memory for colors with incoming color information (Shapley & Hawken, 2011). No significant correlations were found for the nonsense object set.
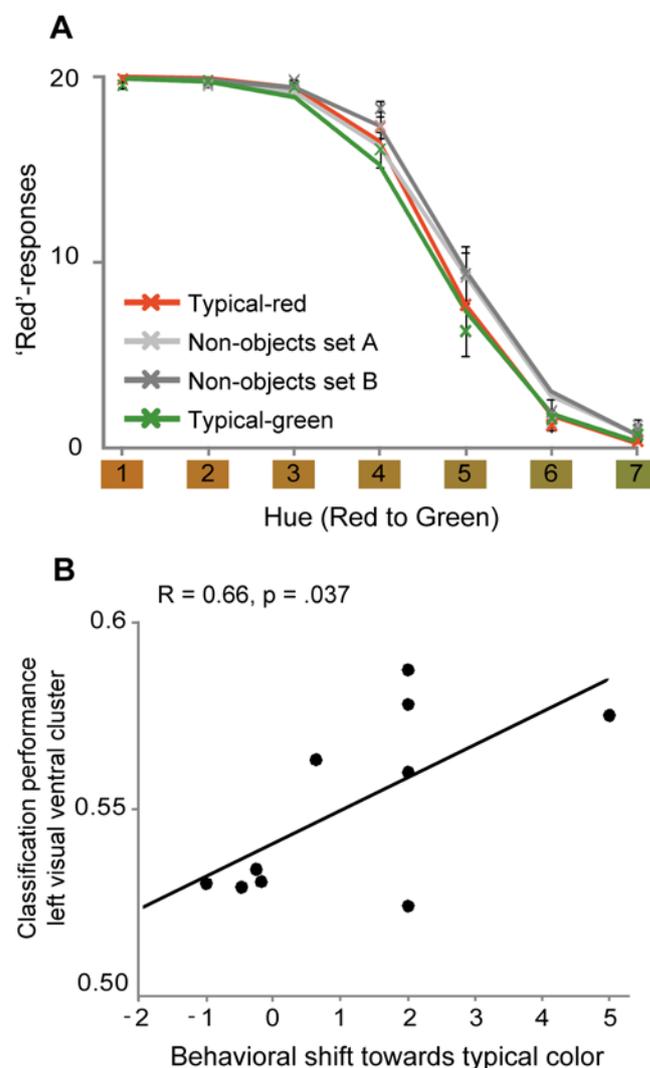
Figure 7.4. Behavioral results. *A) Number of 'red'-responses for each hue in each object set. Crosses indicate the response averaged over all subjects. Solid lines represent the fit of the data using a binomial regression (logit transformed). Subjects gave more 'red'-responses to typical-red objects than to typical-green objects. The nonsense object sets (Non-objects set A & B)were labeled red more often than both the typical object sets. Hue 4 is the ambiguous color that was used in the fMRI experiment. Error bars denote within-group standard error for the unfitted data (crosses). B) Correlation between the behavioral effect and classification performance for the left visual ventral cluster (V4/VO1/LO). The behavioral shift was calculated as the difference in 'red'-responses for hue 4.*

Discussion

In this study we investigated which brain regions are influenced by prior knowledge about objects, thereby shaping our subjective color experience. Using Multi Voxel Pattern Analysis, we

were able to classify the response to an ambiguous color as red when presented on typical-red objects, while that same color was classified as green when presented on typical-green objects. In contrast, when the ambiguous color was presented on two sets of nonsense objects that did not have any color associations, the color could not be classified as either red or green. The areas we found to be involved in this transformation were located in lower-level visual areas such as V3 and V4. This shows that subjective experience at least partly overrides the representation of physical stimulus properties at relatively low-level visual areas. In addition, occipitotemporal and frontal regions were involved in the shift in color perception. This suggests that subjective color experience is mediated by object-color knowledge through involvement of higher-level visual and frontal areas.

The neural correlates found in this study coincide with previous work showing that responses to color in V4 and VO1 (and somewhat in V3) progress through perceptual color space and not physical color space (Brouwer & Heeger, 2009). In V1 and V2 on the other hand, responses to color can be easily decoded, but do not progress through color space in the same manner as in V4. This suggests that V4 represents perceptual color rather than physical color input, whereas responses in V1 might be mainly driven by physical color input. In the present study, we found that object information shifted the representation of a single color towards either red or green in V3 and V4, showing that the representations in these areas are not only dominated by perceptual color, but are modulated by object-color knowledge. In addition, the shift in experience occurred instantly, as the same ambiguous color was presented on typical-red and typical-green objects within one experiment. In V1 and V2, on the other hand, veridical red and green representations were decodable, but the representation of the ambiguous color did not shift according to object-color associations. Possibly, representations in V1 and V2 are dominated by physical color input, but are not influenced by object information. This might also explain why combining all ROIs improved classification performance for within-category classification (red vs green), but did not improve between-category classification (colors with objects); in the latter case, the representations in V1 and V2 diverges from that in V3 and V4 and combining the information represented in these areas does not lead to superior performance.

In addition to investigating predefined ROIs, we performed a searchlight analysis and found that the voxel pattern associated with the ambiguous color also shifted towards red or green in left VO1 and left LOC. VO1 (or V4α/V8) is an area that is known to be involved in color processing as well and has been suggested to be involved in perceptual color representations just as V4 is (Bartels & Zeki, 2008; Brewer et al., 2005; Brouwer & Heeger, 2009). The LOC sits higher up in the visual hierarchy and is known to be involved in object processing (Grill-Spector,

2003; Malach et al., 2002). LOC might be involved in the shift in color perception because the perception of the typical objects is coupled to a specific color, thereby automatically activating the associated object-color representation. Moreover, individual classification scores in this cluster correlated with the behavioral color naming effect, supporting the claim that these areas are involved in the creation of subjective color experience by combining incoming color information with existing object-color memories (Shapley & Hawken, 2011).

Strikingly, in addition to visual cortex, our searchlight analysis revealed significant between-category classification in prefrontal areas including the DLPFC. There are different possible explanations for this finding: one possibility is that visual information is processed by prefrontal cortex in the same manner as it is in visual areas, and any shift in perception will therefore be reflected in these regions as well. However, this is unlikely, since this would be a redundant operation and there is not much evidence showing that frontal cortex is involved in sec visual processing. Alternatively, prefrontal cortex has been shown to be involved in retrieval of associative long-term memory items (Hasegawa, Fukushima, Ihara, & Miyashita, 1998; Ranganath, Cohen, Dam, & D'Esposito, 2004). It could be that when viewing a certain stimulus, associated concepts are activated and therefore, when viewing an ambiguously colored object, the memory for the typical color of that object is activated as well.

The present study shows that object-color associations influence color processing in visual areas representing colors and objects, as well as in frontal areas associated with memory. This suggests that subjects not only categorize a color according to semantic expectations, but actually *perceive* a color differently depending on the object it is presented on. Moreover, this effect occurs instantly, as the same ambiguous color can be represented as green or red within one experiment. Such a process might be supported by predictive signaling from higher level to lower level brain areas (Rao & Ballard, 1999). The current results reveal that the brain shapes our subjective experience by rapidly incorporating world-knowledge, altering neural responses in the cortical areas that are involved in the initial stages of visual processing.

Acknowledgements