Visual Neuroscience (2006), **23**, 357–364. Printed in the USA.

DOI: 10.1017/S0952523806233200

Global integration of local color differences in transparency perception: An fMRI study

MICHEL DOJAT,[1] LOŸS PIETTRE,[1] CHANTAL DELON-MARTIN,[1]
MATHILDE PACHOT-CLOUARD,[1] CHRISTOPH SEGEBARTH,[1] AND KENNETH KNOBLAUCH[2]

[1]Unité mixte Inserm/UJF U594, Neuroimagerie Fonctionnelle et Métabolique, LRC CEA 30V, Grenoble, France
[2]Inserm, U371, Cerveau et Vision, Department of Cognitive Neurosciences, Bron, France
[3]Université Claude Bernard Lyon 1, Lyon, France

(RECEIVED December 21, 2005; ACCEPTED December 28, 2005)

Abstract

In normal viewing, the visual system effortlessly assigns approximately constant attributes of color and shape to perceived objects. A fundamental component of this process is the compensation for illuminant variations and intervening media to recover reflectance properties of natural surfaces. We exploited the phenomenon of transparency perception to explore the cortical regions implicated in such processes, using fMRI. By manipulating the coherence of local color differences around a region in an image, we interfered with their global perceptual integration and thereby modified whether the region appeared transparent or not. We found the major cortical activation due to global integration of local color differences to be in the anterior part of the parahippocampal gyrus. Regions differentially activated by chromatic *versus* achromatic geometric patterns showed no significant differential response related to the coherence/incoherence of local color differences. The results link the integration of local color differences in the extraction of a transparent layer with sites activated by object-related properties of an image.

Keywords: Color vision, Transparency, Color scission, fMRI, Human vision

Introduction

Discounting an intervening medium to recover attributes of the world is a general and powerful ability of the visual system that renders it particularly robust in surface perception and object recognition in a way that current machine vision systems are not (Adelson, 2000). Numerous examples can be cited, such as seeing through shadow or illuminant changes (D'Zmura et al., 2000) and gradients and seeing objects through screens or turgid and noisy media, such as fog, a dirty window or a poor video image (Hagedorn & D'Zmura, 2000). Little is actually known about the mechanisms and the sites in the brain that perform these tasks. The phenomenon of transparency provides an interesting model for studying such processes.

While several stimulus cues can evoke a transparent percept, for example arising from motion (Adelson & Movshon, 1982; Wallach, 1976) or lightness relations across junctions at surface boundaries (Adelson, 1993; Anderson, 1997; Kersten, 1991; Metelli, 1974), it has recently been demonstrated that local changes in color across a region that follow certain rules of coherence suffice to produce the appearance of color transparency (D'Zmura et al., 1997; Faul & Ekroll, 2002; Khang & Zaidi, 2002). For example, Fig. 1a shows an image of 33 rectangles which, appear to be composed of 23 rectangles with a square transparent overlay partially covering the 10 rectangles in the center. The figure was generated in two steps. First, random tristimulus values were assigned to the 23 rectangles of a base image. Then, in the square region in the center of the image, a constant vector was added to the tristimulus values of each pixel. This translation of tristimulus values results in the central region appearing as a transparent overlay. The changes in tristimulus values between the outer and inner fields bordering the overlay region are indicated as vectors in Fig. 1b in a cone modulation space.

Not all translations appear as transparent, however, (Chen & D'Zmura, 1998; Faul & Ekroll, 2002) nor does transparency arise only from translations (D'Zmura et al., 1997; Faul & Ekroll, 2002). Convergences also typically appear transparent. Some other systematic color changes do not lead to the appearance of transparency. Fig. 1c was generated by reversing the direction of the translation for alternate surfaces. Half of the surfaces from the interior of the overlay region of Fig. 1a are distributed in the exterior and *vice versa*. Now the central overlap does not look transparent. The changes in tristimulus values between the outer and inner fields bordering the overlay region are indicated in Fig. 1d and are like a shear.

Address corresponding and reprint requests to: Kenneth Knoblauch, Inserm Unité 371, Cerveau et Vision, 18 avenue du Doyen Lépine, 69500 Bron, France. E-mail: knoblauch@lyon.inserm.fr

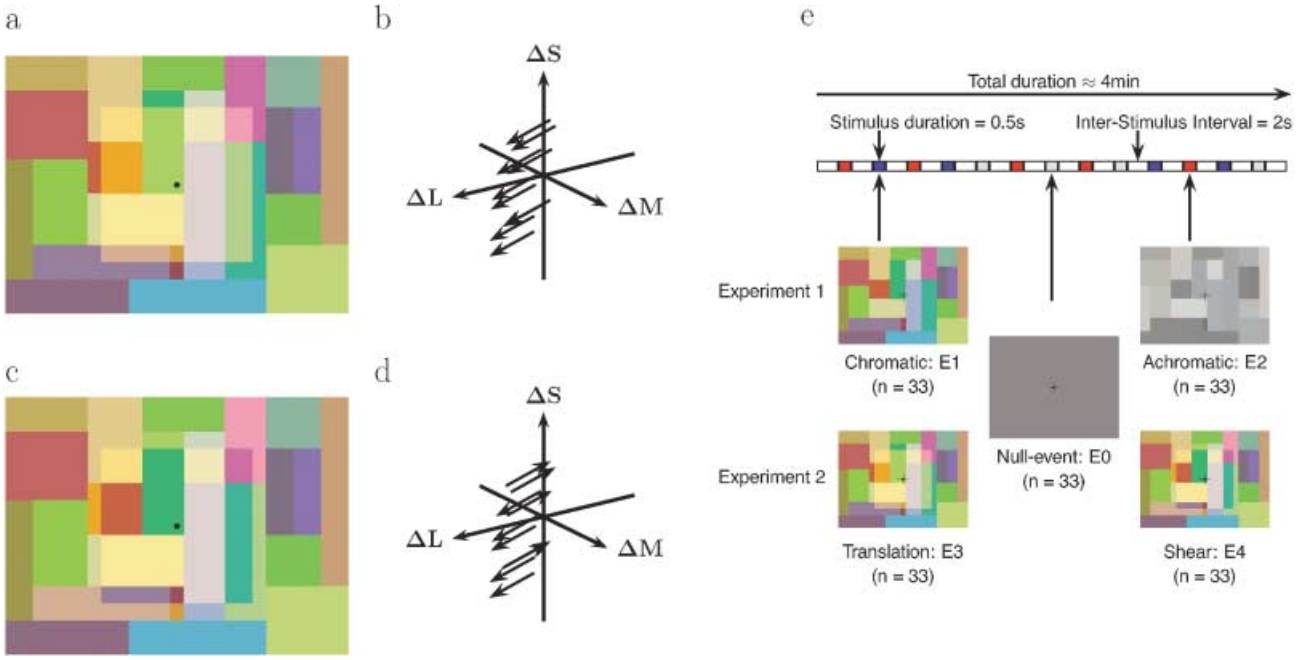

Fig. 1. (**a**) A square transparent overlay of uniform color appears to be placed over the region of a field of randomly colored rectangles. In fact, this effect was obtained by added a constant vector (translation) to the tristimulus values in the square region. (**b**) The vector field shows the change in the mixture between adjacent surfaces at the border of the overlay in the figure to the left. The mixture at the tail of each vector corresponds to the surface exterior to the overlay and the head to the surface that appears to be the extension of the first under the overlay. Around the transparent layer, all the surfaces undergo the same translatory modification. (**c**) An example of a shear-like change applied to the tristimulus values in the central square region. The square central region does not appear as a uniform transparent overlay. (**d**) Half of the changes in part c correspond to the same translation as in part a and half a translation in the opposite sense. Since the endpoints of the vectors are the same in this and the preceding figure, the reversal of direction means that the interior and exterior surfaces have been exchanged. Thus, the color differences between the interior and exterior regions around the square overlay are the same. Only their global coherence has been altered. (**e**) Paradigm. The three event types occurring in Experiment 1 are labeled E0, E1, and E2 while those occurring in Experiment 2 are labeled E0, E3, and E4. E0 is a "null-event" for which the image presented was a fixation cross. During the inter-stimulus intervals (2 s), this fixation cross was presented, rotated by 45°. Each event was displayed 0.5 s. Ninety-nine events were displayed per fMRI scan. For the achromatic/chromatic comparisons, the three coordinates in color space of the rectangles within the central square overlay were set equal to those of the adjacent surfaces outside of the overlay region, thus, reducing the total number of rectangles to 23.

The difference between the translation and shear of Figs. 1a and 1c is simply the global coherence of the vector field of color differences applied to the checkerboard surfaces to generate the colors of the fields within the overlay region. In the case of translation, the colors of the overlay are all described by $v_i + t$, where vi is the vector of tristimulus values of the surfaces beneath the overlay and t is a constant vector. In Fig. 1b, all vectors point in the same direction. In Fig. 1d, half of the vectors point in the opposite direction or, in other words, half of the vectors correspond to $v_i - t$. The color changes around the overlay are directly visible to the observer. In both images, they are of the same magnitude and fall along the same color axis; only their global coherence is different. In the first instance, the visual system is able to integrate local color differences, such as these, and interprets them as an intervening color transparent layer, thus allowing the observer to interpret the forms and the colors of the underlying surfaces as well as the global color of the intervening layer. The process of separating an image into transparent layers is sometimes called scission to differentiate it from segmentation that simply segregates different regions or objects in an image. In the second instance, the discontinuity in the vector field of color differences interferes with this percept.

The distribution of activity among neurons coding local color differences would be quite similar in the two images where translation and shear are applied. On the other hand, neurons that integrate over the coherence of local color changes in a scene would be expected to respond differently to the two images. Thus, by manipulating the coherence of local color differences, it is possible to modify and interfere with their global perceptual integration—as evidenced by the visibility of transparency in an image—while at the same time maintaining similar local color contrasts. We would expect such integrative processes to occur in extrastriate visual areas containing neurons with large enough receptive fields to respond over a large region of the visual field. This type of stimulus manipulation has been successfully used in the domains of orientation (Ramsden et al., 2001) and motion (Orban, 2001) to differentiate first and second order processes. In this study, we exploited this possibility in an effort to identify the cortical regions involved in higher order perceptual integration of color differences using fMRI. We also test whether the cortical

areas involved in integrating local color differences are the same areas activated differentially by chromatic stimuli.

Materials and methods

Subjects

Nine subjects (4 men, 5 women, mean age = 28 ± 6 years) with normal color vision were examined. Four of the observers had previously participated in several fMRI experiments and could be considered accustomed to the procedures. All subjects gave informed consent to participate in the study, which was approved by our institutional review board.

Experiments

All subjects participated in two experiments. Experiment 1 was aimed at localizing the functional responses produced by the introduction of chromatic contrast, Experiment 2 at identifying functional responses related to color scission. Each observer also participated in preliminary tests to estimate individual conditions yielding equiluminance, based on a minimum motion task (Anstis & Cavanagh, 1983) performed in the scanner.

Paradigms

For each of Experiments 1 and 2, four event-related fMRI scans were performed. During each of these scans, three different types of events (33 of each type) were programmed, in a pseudo-random fashion, at 2.5 sec intervals. We used a stationary, stochastic experimental design with a constant occurrence probability for each type of event equal to 1/3 (see Fig. 1e). The sequence of the events was designed so as to optimize the efficiencies of the estimation both of the main and of the differential effects (Friston et al., 1999). Each event consisted in the presentation of an image, during 0.5 seconds. The three event types occurring in Experiment 1 are labeled E0, E1, and E2 whereas those occurring in Experiment 2 are labeled E0, E3, and E4. E0 is a "null-event" for which the image presented was just a fixation cross. During the inter-stimulus intervals (2 s), a fixation cross was also presented but rotated by 45°.

Prior to the experiment, we verified that the stimulus manipulations (translation and shear) did differentially affect the perception of transparency. Observers classified images with translatory and shearing transformations of the tristimulus coordinates across a central square region as to whether the region appeared transparent or not. The overall accuracy was at 95% correct. Examples that were misclassified by observers were excluded from the stimulus set used in the rest of the experiment.

Visual stimulation

Visual stimuli were created with Matlab (Mathworks, Inc., Natick, MA) and controlled during the experiment by a PC, running Windows 98 with the software Presentation (Neurobehavioral Systems Inc). The stimuli were presented to the observers using a video-projector (Epson 7250M, Epson Inc., Long Beach, CA), a back-projection screen, and a mirror system. Viewing distance was 160 cm. The projected image spanned 13 by 10°. Spectral and luminance calibrations of the display were performed with a Minolta CS-1000 spectroradiometer. The spectral radiance measures were used to calculate the coordinates of all stimuli in terms of Judd's modification of the 1931 CIE 2° observer (Judd, 1951).

The test stimulus for all experiments was a rectangular field (11 by 8°) on a gray background Bg (luminance: 383 cd/m^2, Judd CIE xy = [0.31, 0.38]). The rectangular field was divided into either 23 or 33 rectangles of various sizes (see Figs. 1a, 1c, and 1e). During the "null-event" and the inter-stimuli intervals, the fixation cross was presented on a uniform gray screen equal to the Bg.

For Experiment 1, the rectangles of the test stimulus were either assigned random chromaticities at equiluminance (E1, "chromatic event") or random luminances (E2, "achromatic event"). The only constraints on the choice of chromaticities and luminances of the patches of E1 and E2 were that the mean chromaticity and luminance for each set is to be equal to those of the background Bg.

For Experiment 2, the chromaticity coordinates of 10 central rectangles were modified to induce the perception of a central transparent square of 5° (E3, "translation event," see Fig. 1a). Transparency was obtained by adding a constant vector (translation) to the coordinates in color space of each rectangle. The direction and length of the translation in the color space were randomly chosen for each image. Images were customized with respect to the luminosity of each observer. Only translations that induced a strong perception of transparency were retained. For the second set of stimuli, the direction of the translation was reversed for half of the surfaces (E4, "shear event," see Fig. 1c). Practically, this means that the positions of the adjacent surfaces interior and exterior to the central square overlay are exchanged. Because the chromaticity coordinates across the border have not changed, the chromatic contrasts around the square overlay are the same for translation and shear. Only the coherence (or phase) of the chromatic contrasts has been changed between translation and shear conditions.

Attentional and behavioral tasks

Observers were instructed to fixate the central fixation cross during the presentation of the stimuli. Eye movements were not monitored over the course of the experiment. In order to maintain and control observers' attention, additional tasks were built into the paradigm for both experiments. Subjects were instructed to report, by means of a three button mouse press, the occurrence of chromatic, achromatic, or null events in Experiment 1 and whether the image included a transparent region or not, or a null event in Experiment 2.

MR acquisition

Subjects were examined at 1.5 T on a clinical MR scanner (Philips ACS II, Best, Eindhoven, The Netherlands). The body coil was used for excitation. A head coil was used for detection. Head motion was restricted by means of sand bags placed on each side of the head. Positioning of the volume of interest was performed on scout images acquired in the sagittal plane. Both experiments were performed during the same session with the following sequencing: acquisition of 4 functional runs (Experiment 1), an anatomic run (T1-weighted), and then four functional runs (Experiment 2). The functional volume of interest was composed of adjacent transverse 5-mm thick slices and oriented parallel to the bicommissural plane. A conventional gradient-recalled echo (GRE) MR EPI sequence was used with the following major parameters: TR/TE/flip = 2.5s/45ms/70°, FOV = 256 × 256 mm^2, acquisition matrix = 64∗64. The total acquisition duration per functional scan was about 4 min.

Data processing

Data analysis relied on the General Linear Model, as implemented in the statistical parametric mapping (SPM99) software package (Friston et al., 1995) and in the SnPM toolbox (Nichols & Holmes, 2002).

Preprocessing

Functional data were successively corrected in time to take into account the inter-slice delay caused by multiple single slice image acquisition, realigned to the functional scan closest to the anatomical one, normalized for group study using the template provided by the Montreal Neurological Institute (MNI), and finally spatially smoothed with a Gaussian kernel of $8 \times 8 \times 10$ voxels FWHM, to conform to the assumptions underlying random Gaussian field theory used in SPM. Coordinates of statistically significant voxels initially expressed in the MNI space were converted for reference to the Talairach space.

Statistical analysis

For each experiment, the analysis was performed in a two-stage procedure. In the first stage, at the individual level, the response for each event type was modeled with the canonical Hemodynamic Response Function and then convolved with a train of delta functions, corresponding to each stimulus onset, and a constant term for each functional run (session effect), to create corresponding covariates in a general linear model. From voxel time courses, parameter estimates for each covariate were computed. Contrasts were designed to assess the main effect of each event type and the differential effect between two event types (chromatic *vs* achromatic or translation *vs* shear events).

In a second stage, the "differential effect" images were used for a statistical non-parametric group analysis (random effects analysis). This was performed using the SnPM toolbox (Nichols & Holmes, 2002). Similarly to SPM99, SnPM relies on the General Linear Model. Based on minimal assumptions, (i.e., independence of the subjects and a smooth variance structure) this approach is well-suited for variance estimation in the presence of a limited number of degrees of freedom, when high variance images lead to noisy statistical images and when the assumption that data are normally distributed is not viable. To overcome these difficulties, weighted locally pooled variance estimates are obtained by smoothing the raw variance images. Then, permutation tests performed on the data allow the computation of the corresponding null sampling distribution. Pseudo t-statistic images are formed with smoothed variance estimators, which are assessed for significance using a standard, non-parametric, multiple comparisons procedure based on permutation testing. The smoothed variance t-statistic via the pseudo t-statistic improves sensitivity relative to the standard t-statistic (Nichols & Holmes, 2002). With a parametric voxel-based statistic, the null distribution is generally used to specify a threshold by using a t-table. With a non-parametric voxel-based statistic, the null-distribution is not known *a priori*. Based on a parametric voxel-based statistical analysis of the data from Experiment 1 (which was less noisy, perhaps owing to the greater robustness of the perceptual differences than in Experiment 2) statistically significant activated clusters were established at a pseudo-t >4 and region size >8 voxels.

In order to assess the possible involvement of color sensitive areas in color transparency processing, a region of interest- (ROI) based analysis was additionally performed as follows. First, the two most active regions found in Experiment 1 were used as functional individual ROIs. The MarsBar toolbox was used for individual ROI extraction (Brett et al., 2002), (http://marsbar.sourceforge.net). Second, within these ROIs, the mean parameter estimates were computed separately for each main covariate of Experiment 2 (corresponding to translation and shear events) for each subject. Third, a paired *t*-test was performed to evaluate the statistical significance of the differences between the mean parameter estimates for the two covariates.

Results

Experiment 1: cortical areas involved in chromatic processing

In the first experiment cortical activity evoked by "chromatic" and "achromatic" events was compared to determine the cortical sites involved in chromatic processing.

Group analysis

The statistical group analysis for "chromatic" *versus* "achromatic" events showed bilateral activation within the posterior fusiform gyri (see Fig. 2a). In the left hemisphere, the large activation cluster is composed of two overlapping smaller clusters positioned along the antero-posterior direction, and that could correspond to the activations denoted as areas V4 and V4α by Bartels & Zeki (2000). Activation was also found in the superior parietal gyrus. The coordinates of the major peak activations are listed in Table 1. No significant clusters were found in areas V1/V2. In Table 2, the Talairach coordinates of the color sensitive posterior region detected here are listed along with those from the literature. The "achromatic" events did not activate any significant areas in comparison with "chromatic" events.

Experiment 2: cortical areas involved in color scission

The second experiment was designed to determine the cortical areas involved in the perception of color scission.

Group analysis

The group analysis for the [translation-shear] contrast reveals an activation within the left parahippocampal gyrus (Fig. 2b). Talairach coordinates, z-score, and cluster size of this activation

Table 1. *Experiment 1. Talairach coordinates of the voxels most strongly activated for the [chromatic–achromatic] contrast. In the left hemisphere, the major cluster can be split into two regions along the antero-posterior direction. The size (expressed in terms of voxels) is given for the entire cluster. (9 subjects, non-parametric statistical analysis, pseudo-t $>$ 4 and cluster size $>$ 8 voxels).*

Region	Hemisphere	x	y	z	size	Pseudo-t
FusG	R	28	−70	−9	10	4.88
FusG	L	−28	−71	−13	34	5.6
FusG	L	−32	−55	−10	34	5.66
P1	L	−12	−55	58	12	5.13

FusG = fusiform gyrus; P1 = superior parietal gyrus.

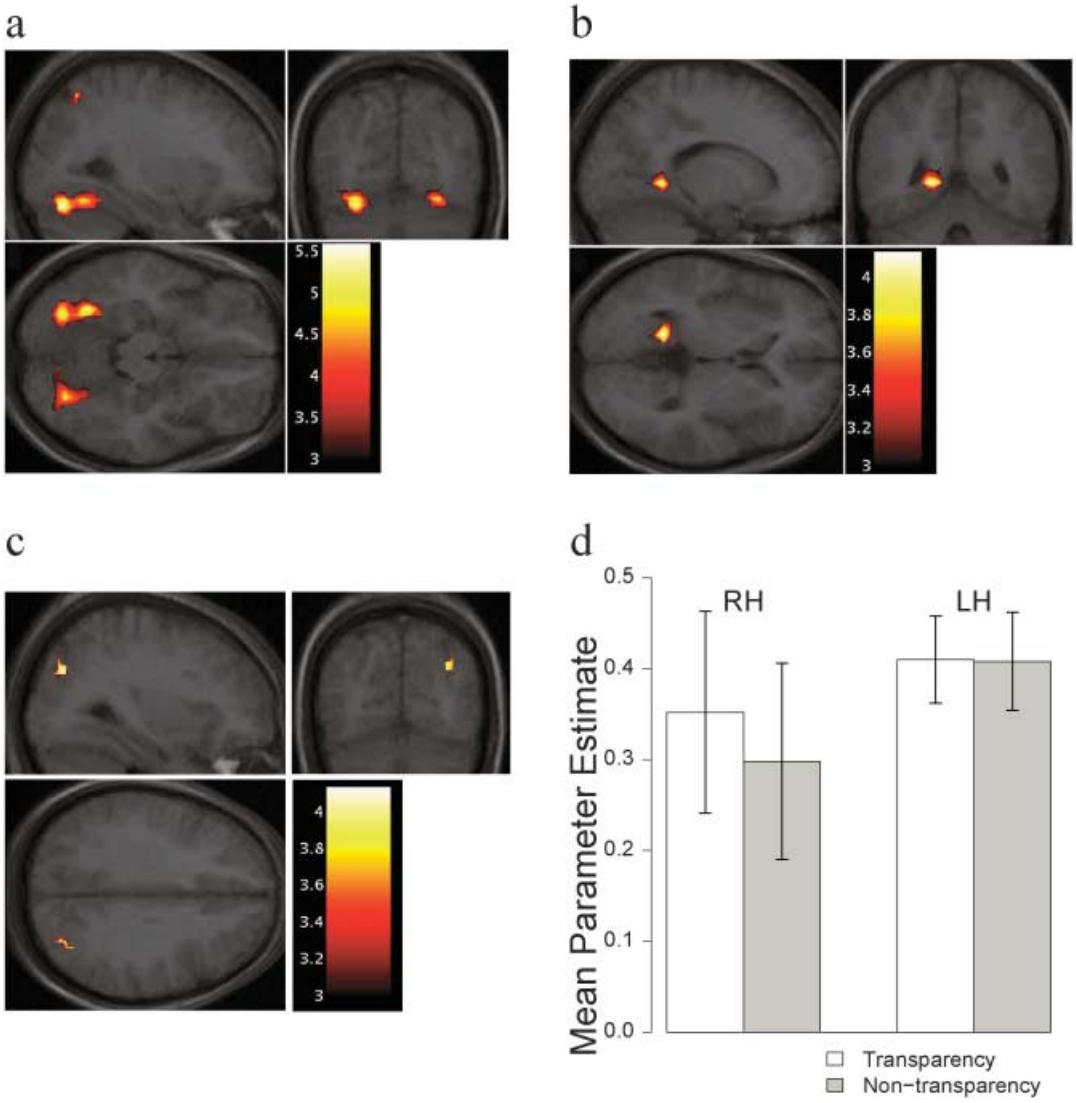

Fig. 2. (**a**) Differential activation corresponding to Experiment 1, chromatic versus achromatic (Non-parametric statistical analysis), appears at two large clusters located in the ventral occipital region, (sagittal: X = −28, coronal: Y = −70, transverse: Z = −9). Note that some clusters with a size less than eight voxels are displayed on the figure but are not reported in Table 1. (**b**) Differential activation corresponding to Experiment 2, translation *versus* shear (Non-parametric statistical analysis) appears in the left Parahippocampal Gyrus (sagital: X = −16, coronal: Y = −46, transverse: Z = 2). (**c**) Regions preferentially activated by non-transparency events (non-parametric analysis) were in the-Posterior Parietal Gyrus (sagital: X = 33, coronal: Y = −72, transverse: Z = 31). (**d**) A ROI analysis was performed in the area defined by the Chromatic/Achromatic experiment. The mean parameter estimates were computed separately for each main covariate, corresponding to translation and shear events, in the left and right regions of each subject, delineated on the basis of the Chromatic/Achromatic experiment (Experiment 1). The data are averaged across subjects. Error bars represent ±SEM. No significant difference was found in either condition.

are presented in Table 3. This activation is distinct from that induced by the (chromatic–achromatic) contrast in Experiment 1. No activation was detected in area V1/V2, either for the (translation–shear) contrast or for the reverse. The (shear translation) contrast revealed activation within the superior part of the right posterior parietal gyrus (see Fig. 2c and Table 3).

For both experiments, subjects were instructed to press one of three buttons for occurrences of chromatic, achromatic or null events or of transparency, and non-transparency or null events in Experiments 1 and 2, respectively. The activations during the null events served as a baseline to control for the button-pressing behavior. The behavioral task was not found to modify expected activations in Experiment 1, and the results are in excellent agreement with those already published in the literature (see Table 2). Similarly, for Experiment 2, it is highly unlikely that the activations obtained were caused by pressing a specific key.

ROI analysis

The mean parameter estimates for each main covariate, corresponding to translation and shear events, computed in the left and right ventral areas differentially activated by chromatic contrast of each subject as previously delineated on the basis of the results of Experiment 1, are displayed in Fig. 2d. Both regions were sensitive to the events, but as already shown in Fig. 2b, no significant

Table 2. *Talairach coordinates for the posterior region activated for the (chromatic–achromatic) constrast in Experiment 1. Comparison with data from the literature.*

	x	y	z
Zeki et al. (1991) (PET)			
left	−26	−68	−8
right	20	−66	−4
Sakai et al. (1995) (fMRI)			
left	−18	−63	−10
right	20	−63	−10
McKeefry Zeki (1997) (fMRI)			
left	−29	−68	−14
right	30	−75	−19
Clark et al.(1997) (fMRI)			
right	19	−69	−7
Hadjikhani et al. (1998) (fMRI)			
left & right	±33	−65	−14
Howard et al. (1998) (fMRI)			
left	−12	−78	−13
right	26	−78	−13
Bartels & Zeki (2000) (fMRI)			
left	−34	−68	−18
	−22	−76	−16
right	34	−74	−14
Nunn et al. (2002) (fMRI)			
left	−32	−73	−13
right	28	−56	−13
This study (fMRI)			
left	−28	−71	−13
right	28	−70	−9

difference was found between either event (RH: Translation: 0.35 ± 0.04, Shear: 0.30 ± 0.04; LH: Translation: 0.41 ± 0.02, Shear: 0.408 ± 0.02). Our data do not provide evidence for a differential involvement of the "color specific" regions in color scission. A ROI analysis performed in the left parahippocampal gyrus revealed no differential activation for chromatic *versus* achromatic events.

Discussion

We identified cortical areas that are differentially activated by the manipulation of the coherence of local color differences so as to modulate the perception of a transparent overlay. Transparency is not a particularly exotic phenomenon because it frequently occurs in natural contexts. In fact, the underlying neuronal mechanisms may be common to color induction phenomena such as neon spreading (Anderson, 1997) and more general compensatory mechanisms, such as color (D'Zmura et al., 1997; Khang & Zaidi, 2002; Koffka, 1935; Ripamonti & Westland, 2003) and lightness constancy (Gilchrist, 2005; Schirillo & Shevell, 1997). Thus, transparency perception presents a potentially rich model for exploring the neural substrate of these fundamental visual processes. We found the major cortical activation, caused by color scission, to be located in the anterior part of the parahippocampal gyrus. In previous studies of color, parts of the parahippocampal gyrus have been reported to be activated by tasks requiring the retrieval of object color or color imagery (Howard et al., 1998), color knowledge (Martin et al., 1995), or the perception of naturally colored objects (Zeki & Marini, 1998). Thus, color scission seems to be implicated in a stage of processing at which object properties are associated with the chromatic information coded from an image.

The association of transparency with object perception raises a question as to whether the responses that we measured were because of the perception of a square object in the image or the coherent color change, as we propose. This alternative suggestion would be valid if the square test region was less salient during the shear trials. In fact, as the examples in Fig. 1a and c demonstrate, the square region is equally visible whether the chromatic change is coherent or not. During the experiment, the observers' attention was directed to this region on every trial to decide if it appeared transparent or not. Thus, it seems unlikely that the salience of the square or attention to it could explain our results.

The extraction of surface characteristics in the presence of global illuminant changes has been attributed to V4 and associated areas (Bartels & Zeki, 2000). Bartels and Zeki (2000) reported that area V4 can be dissociated into 2 sub-areas: posterior V4 and anterior V4. Retinotopy is clearly revealed in the former, whereas it is not evident in the latter. Natural object colors also activate sites beyond this V4-complex (Bartels & Zeki, 2000; Zeki & Marini, 1998). The parahippocampal activation suggests that the global integration of local color differences is not restricted to the V4 area proposed as a color center (Bartels & Zeki, 2000). Rather, our results support the view of a complex network for color processing and are consistent with studies on macaque monkeys (Tootell et al., 2004), on human observers with normal vision (Brewer et al., 2005), on achromatopsic patients (Cowey et al., 2001; Huxlin et al., 2000) displaying color deficits following cortical lesions anterior and ventral to area V4 as well as studies that indicate that inactivation of area V4 through cooling (Girard et al., 2002) or lesions (Walsh et al., 1993) does not alter simple hue discriminations. The parahippocampal activation could be relayed through pathways arising from V4 and more rostral temporal regions as have been shown to exist in the macaque (Suzuki & Amaral, 1994). The left activation found here does not exclude the possible involvement of the right hemisphere, the activations of which might be below threshold in this study.

The possible implication of ventral regions differentially activated by chromatic contrast was explicitly addressed using an ROI

Table 3. *Experiment 2. Talairach coordinates of the voxels most strongly activated for the [translation-shear] and [shear-translation] contrasts. (9 subjects, non-parametric statistical analysis, pseudo-t > 4 and cluster size > 8 voxels).*

Percept	Region	Hemisphere	x	y	z	size	Pseudo-t
Transparent	Parahippocampal Gyrus	Left	−16	−48	2	11	4.14
Non-transparent	Posterior Parietal Gyrus	Right	32	−68	31	14	4.08

based analysis, which offers an increased sensitivity to task-related effects compared to standard voxel-based statistical analysis. For this purpose, the goal of the first experiment was to define, on an individual basis, cortical areas that are differentially activated by the comparison of chromatic and achromatic stimuli. These areas were found in the ventral part of the occipital cortex, and the coordinates in the Talairach space were compatible with those from previous studies (Table 2). Although these areas respond to transparency and non-transparency conditions, no differential activity could be demonstrated there. Our data provide no evidence that color scission is processed in regions differentially activated by chromatic versus achromatic geometric patterns. Negative evidence, of course, does not prove the absence of such processing. Integrative mechanisms could operate on a finer scale than our apparatus was able to discriminate. Nevertheless, such integrative mechanisms, if they are present in these areas, do not seem to generate a sufficient increment in metabolic activity to be discerned from the overall activity caused by the processing of local color differences.

The participation of area V1 in high-level vision is currently a matter of debate. In color perception, it has been attributed functions ranging from simple spectral encoding (Zeki & Marini, 1998) to color constancy (Hurlbert, 2003). In Experiment 2, we detected no differential activation in V1 between stimulus conditions that produce color transparent and non-transparent layers using a non-parametric analysis of the group data. However, for a few subjects, V1 was activated and, thus, we cannot exclude a role for V1 cells in the global processes required for transparency perception. The demonstration of their participation will require the use of a more sensitive imaging acquisition technique than we were able to use in this study.

Posterior parietal areas have been closely linked to visual spatial relations and localization. The dorsal activity evoked in the absence of transparency may perhaps have been related to an implicit visual search engaged when a transparent region did not "pop-out." Interestingly, although LO cortex has been reported to have a possible role for the detection of a salient region that "pops-out" (Stanley & Rubin, 2003), no activation was found in this region for color scission. We cannot exclude an alternative possibility that the observers are making involuntary saccades to the target edge. These would have to be selective for one type of image, or their activations would not appear in the statistical analysis. Observers were instructed to fixate the central cross. If such involuntary eye movements did occur, the impression of the authors who served as observers is that they did not do so systematically.

We did not test conditions that evoke transparency based on lightness cues in the present study, primarily to limit the number of functional scans (in our case, eight in one session) in order to minimize potential effects due to fatigue and the time spent in the scanner. This condition will be of interest to resolve whether the region that we have identified is activated specifically with respect to color transparency or is involved more generally in the processing of lightness transparency, as well.

In conclusion, the neural areas activated by transparency are separable from those areas differentially activated when subjects view color patterns *versus* the same achromatic patterns. Thus, our study suggests that the integration of local color differences to signal a transparent layer in an image involves a stage at which coding of the stimulus is being transformed into a representation of an object. Processes involved in transparency perception may be exemplary of general mechanisms that the brain employs in surface perception to differentiate illuminant from material object changes such as in color and lightness constancy, although such an association remains to be demonstrated.

Acknowledgments

L. Piettre was supported by a doctoral grant from the French Ministry of Research and Technology. Financial support from the Action Concertée Incitative "Cognitique" (1999) is gratefully acknowledged.

References

Adelson, E.H. (1993). Perceptual organization and the judgment of brightness. *Science* **262**, 2042–2044.

Adelson, E.H. (2000). Lightness perception and lightness illusions. In *The New Cognitive Neurosciences*, ed. Gazzaniga, M., pp. 339–351. Cambridge, MA: MIT Press.

Adelson, E.H. & Movshon, J.A. (1982). Phenomenal coherence of moving visual patterns. *Nature* **300**, 523–525.

Anderson, B.L. (1997). A theory of illusory lightness and transparency in monocular and binocular images: The role of contour and junctions. *Perception* **26**, 419–454.

Anstis, S. & Cavanagh, P. (1983). A minimum motion technique for judging equiluminance. In *Colour Vision: Physiology & Psychophysics*, eds. Mollon, J.D. & Sharpe, L.T., pp. 155–166. London: Academic Press.

Bartels, A. & Zeki, S.M. (2000). The architecture of the colour centre in the human visual brain: New results and a review. *European Journal of Neuroscience* **12**, 172–193.

Brett, M., Anton, J., Valabregue, R. & Poline, J. (2002). Region of interest analysis using an SPM toolbox, in 8th International Conference on Functional Mapping of the Human Brain, volume 16, June 2–6, 2002, Sendai, Japan: available on CD-ROM in *NeuroImage* **16**, 497.

Brewer, A.A., Liu, J., Wade, A.R. & Wandell, B.A. (2005). Visual field maps and stimulus selectivity in human ventral occipital cortex. *Nature Neuroscience* **8**, 1102–1109.

Chen, V.J. & D'Zmura, M. (1998). Test of a convergence model for color transparency perception. *Perception* **27**, 595–608.

Cowey, A., Heywood, C. & Irving-Bell, L. (2001). The regional cortical basis of achromatopsia: A study on macaque monkeys and an achromatopsic patient. *European Journal of Neuroscience* **14**, 1555–1555.

D'Zmura, M., Colantoni, P., Knoblauch, K. & Laget, B. (1997). Color transparency. *Perception* **26**, 471–492.

D'Zmura, M., Rinner, O. & Gegenfurtner, K.R. (2000). The colors seen behind transparent filters. *Perception* **29**, 911–926.

Faul, F. & Ekroll, V. (2002). Psychophysical model of chromatic perceptual transparency based on subtractive color mixture. *Journal of the Optical Society of America A* **19**, 1084–1095.

Friston, K., Zarahn, E., Josephs, O., Henson, R. & Dale, A. (1999). Stochastic designs in event-related fMRI. *NeuroImage* **10**, 607–19.

Friston, K.J., Holmes, A.P., Poline, J.B., Frith, C.D. & Frackowiak, R.S.J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping* **2**, 189–210.

Gilchrist, A.L. (2005). Lightness perception: Seeing one color through another. *Current Biology* **15**, 330–332.

Girard, P., Lomber, S.G. & Bullier, J. (2002). Shape discrimination deficits during reversible deactivation of area V4 in the macaque monkey. *Cerebral Cortex* **12**, 1146–1156.

Hagedorn, J. & D'Zmura, M. (2000). Color appearance of surfaces viewed through fog. *Perception* **29**, 1169–1184.

Howard, R.J., Fytche, D.H., Barnes, J., McKeefry, D., Ha, Y., Woodruff, P.W., Bullmore, E.T., Simmons, A., Williams, S.C., David, A.S. & Brammer, M. (1998). The functional anatomy of imagining and perceiving colour. *Neuro Report* **9**, 1019–1023.

Hurlbert, A. (2003). Colour vision: primary visual cortex shows its influence. *Current Biology* **13**, 270–272.

Huxlin, K.R., Saunders, R.C., Marchionini, D., Pham, H.A. & Merigan, W.H. (2000). Perceptual deficits after lesions of inferotemporal cortex in macaques. *Cerebral Cortex* **10**, 671–683.

Judd, D.B. (1951). Report of the U.S. Secretariat Committee on Colorimetry and Artificial Daylight, in *CIE Proceedings*, Vol. 1, Part 7, (Stockholm): Paris: Bureau Central CIE, p. 11.

Kersten, D. (1991). Transparency and the cooperative computation of scene attributes. In *Computational Models of Visual Processing*, eds. Landy, M.S. & Movshon, M.S., pp. 209–228. Cambridge, MA: MIT Press.

Khang, B.G. & Zaidi, Q. (2002). Cues and strategies for color constancy: Perceptual scission, image junctions and transformational color matching. *Vision Research*, **42**, 211–226.

Koffka, K. (1935). Principles of Gestalt psychology, New York: Harcourt, Brace and Company.

Martin, A., Haxby, J., Lalonde, F., Wigg,s C. & Ungerleider, L. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* **270**, 102–105.

Metelli, F. (1974). The perception of transparency. *Scientific American* **230**, 47–54.

Nichols, T. & Holmes, A. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping* **15**, 1–25.

Orban, G.A. (2001). Imaging image processing in the human brain. *Current Opinion in Neurology* **14**, 47–54.

Ramsden, B.M., Hung, C.P. & Roe, A.W. (2001). Real and illusory contour processing in Area V1 of the primate—A cortical balancing act. *Cerebral Cortex* **11**, 648–665.

Ripamonti, C. & Westland, S. (2003). Prediction of transparency perception based on cone-excitation ratios. *Journal of the Optical Society of America A* **20**, 1673–1680.

Schirillo, J.A. & Shevell, S.K. (1997). An account of brightness in complex scenes based on inferred illumination. *Perception* **26**, 507–518.

Stanley, D. & Rubin, N. (2003). fMRI activation in response to illusory contours and salient regions in the human lateral occipital complex. *Neuron* **37**, 323–31.

Suzuki, W.A. & Amaral, D.G. (1994). Perirhinal and parahippocampal cortices of the macaque monkey: Cortical afferents. *Journal of Comparative Neurology* **350**, 497–533.

Tootell, R.B.H., Nelissen, K., Vanduffel, W. & Orban, G.A. (2004). Search for color center(s) in macaque visual cortex. *Cerebral Cortex* **14**, 353–363.

Wallach, H. (1976). *On Perception*. New York: Quadrangle.

Walsh, V., Carden, D., Butler, S.R. & Kulikowski, J.J. (1993). The effects of V4 lesions on the visual abilities of macaques: hue discrimination and colour constancy. *Behavioral Brain Research* **53**, 51–62.

Zeki, S.M. & Marini, L. (1998). Three cortical stages of colour processing in the human brain. *Brain* **121**, 1669–1685.