

Neuronal Mechanisms for Illusory Brightness Perception in Humans

Report

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Summary

Biological visual systems are extraordinarily capable of recovering the shape and brightness of objects from sparse and fragmentary information. Using functional magnetic imaging, we show that two associative areas of the dorsal pathway—in the caudal region of the intraparietal sulcus and in the lateral occipital sulcus—respond specifically to the Craik-O'Brien-Cornsweet illusion generated by high-pass filtered edges. Other visual areas, including primary visual cortex, also respond strongly to the retinotopic location of the edge, but these areas respond equally well to a line of matched contrast and detectability, rather than specifically to the brightness illusion. The reconstruction of surface and/or its brightness seems to be achieved by associative areas from the information about visual features provided by the primary visual cortices, even where there is no physical difference in luminance.

Introduction

The human visual system is unable to perceive static low spatial frequency information (Campbell and Robson, 1968). However, it can use sparse and fragmented spatial information from very distant parts of the visual field to derive context-specific information for object segregation, visual field completion (filling-in; Gilbert and Wiesel, 1992; Ramachandran and Gregory, 1991), and brightness computation (for review see Mendola, 2003; von der Heydt et al., 2003). The Cornsweet illusion (COC) (Cornsweet, 1970; Craik, 1966; O'Brien, 1958), illustrated in Figure 1A, is an example where edges, containing only high spatial frequencies and limited in spatial extent, generate the percept of a solid

surface brighter than the surround, even when separated from each other by 30° or more. Occluding the edges abolishes the perception of the lighter surface in the center, demonstrating that the square is indeed illusory. Although the phenomenon has been widely used for centuries in art (such as in Chinese ceramics; Ratliff, 1972) and occurs frequently in real scenes, the neuronal circuitry and its properties are poorly understood, especially in humans. Several explanations of the illusion suggest that local edge contrast spreads over space up to the point of contrary information (Burr, 1987; Campbell et al., 1978). The neuronal mechanisms underlying the computation could either be a diffusion of the activity of neurons responding to the edge to neighboring neurons, usually referred to as the “filling-in” theory (Davey et al., 1998; Gerrits and Vendrik, 1970; Ramachandran and Gregory, 1991), or a more abstract operation, usually referred to as symbolic theory, where the neuronal process attaches a label (brightness) to a region of space, possibly at a later stage of visual processing (Burr, 1987; Kingdom and Moulden, 1992; Mendola, 2003; Morrone and Burr, 1988; Watt and Morgan, 1985; for review see von der Heydt et al., 2003). The basic assumption of the symbolic theory is that, in the absence of contrary information, the default rule applied by the brain is one of minimal variation: edges signal a change of brightness that is consistent with the absence of activity from neurons located in the enclosed area.

To study the neural activity associated with the illusion, we compared BOLD activity of a stimulus that generates strong illusory brightness (Figure 1A) to one where the local 1D edges were changed to lines (Figure 1B) via the Hilbert transform (a transformation that affects the phase spectrum while leaving the local and global power spectra unaffected). These stimuli have the same RMS contrast and generate an impression of a central square surface: the edge stimulus generates the perception of a surface of lighter (or darker) brightness, while the line stimulus generates a surface of the same brightness, but raised in depth. Differences in the BOLD response generated by these stimuli would be interesting and likely to be associated with the neuronal mechanisms mediating the brightness illusion.

Results

In separate block-design sessions, we compared the responses of noise-embedded edge (Figure 1A) and line stimuli (Figure 1B) to noise alone and to each other. In successive ON phases, the stimuli were presented alternatively in the original and in the polarity inverted contrast to be certain that the response was not selective for the sign of the contrast. High-contrast dynamic noise was added to all stimuli to minimize neural and local BOLD adaptation and to obtain a sustained neuronal activity over the entire visual field. The noise was refreshed every 300 ms, helping to direct attention to the whole pattern, minimizing any differences of spatial

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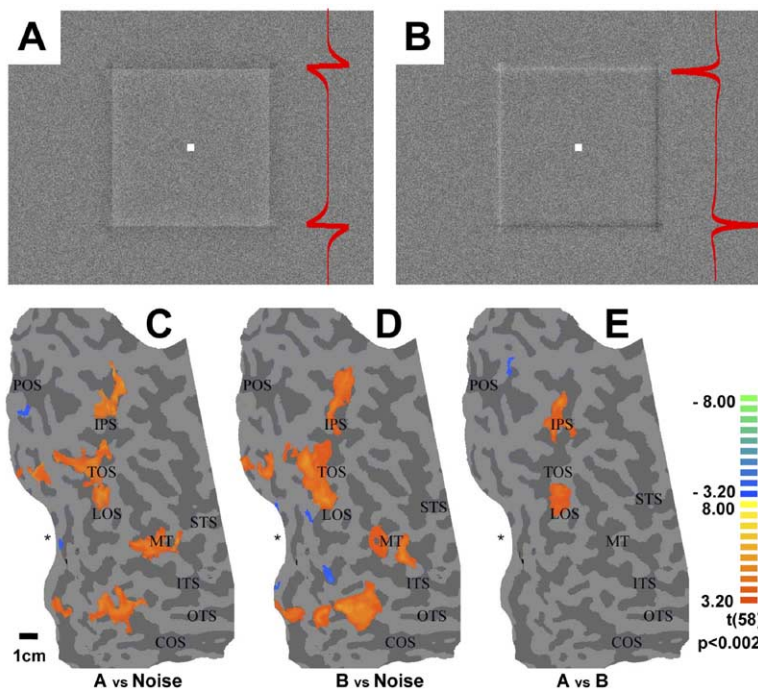


Figure 1. Edge and Line Stimuli, and the Regions of Cortex that Respond to Them

(A and B) Examples of the stimuli used: (A) the COC illusion and (B) the Hilbert transform of the stimulus in (A), where each 1D edge has been transformed into a line. The stimulus appears as a 3D surface (to observe the depth cue inversion, rotate the printed page). The profile in red shows the luminance modulation of the stimuli along a vertical line.

(C–E) Examples of the BOLD activity measured in one subject when the stimulus in (A) was presented against only dynamic noise (C), the stimulus in (B) against noise (D), and the stimulus in (A) against the stimulus in (B) (E). The maps ($p < 0.002$, GLM) were produced by flattening and opening the cortex along the calcarine sulcus. Positive correlated activity is shown in red, negative correlated activity in blue. The color scale gives the t test values associated with suprathreshold activity. The star represents the fovea, with the upper visual field represented below that. TOS, transverse occipital sulcus; LOS, lateral occipital sulcus; IPS, intraparietal sulcus; POS, parieto-occipital sulcus; ITS, inferior temporal sulcus; STS, superior temporal sulcus; COS, collateral sulcus.

attention allocation in the three conditions. The edge and line stimuli had the same local and global energy and were equally detectable (edge r.m.s. contrast threshold = 0.56 ± 0.03 , line = 0.57 ± 0.05) and had the same contrast increment discrimination threshold (0.89 ± 0.03 and 0.84 ± 0.02 , respectively) at the base contrast used in this study, even though the line stimulus had twice the Michelson contrast of the edge.

In all subjects, both edge and line stimuli (Figures 1C and 1D) elicited strong BOLD responses against noise in most visual cortical areas, including V1. In the retinotopic region along the calcarine sulcus (inside BA 17), the positive response overlapped with the activation elicited by a localizer checkerboard stimulus extending between 6.5 to 8.5 deg eccentricity (see Experimental Procedures), demonstrating that both the line and the edge stimuli elicited specific retinotopic responses in these areas. There was also a small negative activation of some regions within the central visual field representation (marked in blue). The negative activation of regions not corresponding to the features is less than that reported previously (Shmuel et al., 2002; Tootell et al., 1998), possibly because of the continuous presence of dynamic noise.

The edge versus line stimuli produced no positive response in primary visual cortex or in most other visual areas (Figure 1E) in all subjects, presumably because the responses were identical and cancelled each other out; the only activity ever observed was a weak hypo-activity in one subject (author M.C.M.) in the region representing the fovea.

However, there was a strong positive response to the line stimuli in two associative areas within the dorsal pathway: one that extends from the caudal region of the intraparietal sulcus (CIP) up to the median portion

of the transversal occipital sulcus without crossing it; the other extends more caudally and laterally, below the transversal occipital sulcus along the lateral occipital sulcus (LO). In all eight subjects, the two positively correlated regions were identified, always anatomically distinct, separated by two or more slices (see example in Figure 3D). The mean Talairach localization of the most active voxels of the two dorsal areas was ± 43 , -79 , 11 (SE: 1.1, 1.0, 1.5) for LO and ± 31 , -82 , 25 (SE: 1.4, 1.3, 1.9) for CIP. In two subjects, such as the example reported in Figure 1E, there was sometimes a small negative response in extrastriate peripheral cortex, but never robust enough over scan repetitions to be studied in detail.

The absence of edge-specific responses in primary visual cortex indicates that the local responses to edges and lines are similar, despite the differences both in Michelson contrast and in the apparent brightness of the surface. To probe for very subtle edge-specific responses in V1 and other areas, we performed a region of interest (ROI) analysis in individual subjects and then pooled the results over all subjects (Figure 3D). For V1, the ROI was defined by the voxels located along the calcarine sulcus that responded to the edge versus noise stimulus, using both a normal ($p < 0.001$) and a highly permissive threshold ($p < 0.05$) (giving similar results). The ROIs for the two associative areas were defined by the selective responses to edge versus line, and these ROIs were then compared with the edge or line response against noise.

The average BOLD responses of the ROIs to the various stimulus combinations are shown in Figure 2. All regions showed a strong average response to edges and lines against noise, both very similar, with a sharp rise time (about as sharp as the hemodynamic rise

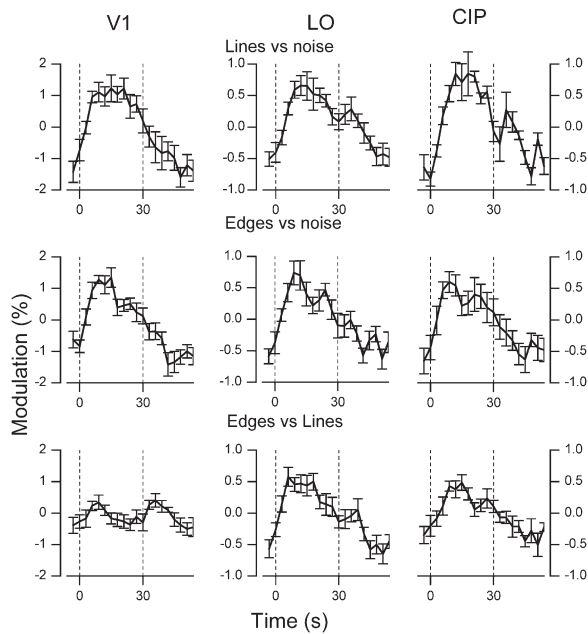


Figure 2. Time Courses of BOLD Responses in Three Visual Areas. Signal modulation for V1, LO, and CIP in response to edge versus noise stimuli (top row), to line versus noise stimuli (middle row), and to edge versus line stimuli (bottom row) averaged across all subjects for one alternation of the stimulus. The bars represent the SE of the mean. The dashed lines show the time of the stimulus transition ($t = 0$).

time; Boynton et al., 1996) and a slower decay time of 10–20 s. In the two associative areas (but not V1), there was a strong positive response to edge versus line stimuli (even though the response to the two stimuli against noise was of similar amplitude). The responses were slightly smaller than the responses to edges or lines versus noise, but far stronger than would be predicted from their difference, indicating the action of nonlinear mechanisms. In V1, the pattern of the average response was quite different: there was a small but significant modulation in response to edge versus line stimulation, but the modulation occurs with each change in stimulus type (second-harmonic modulation), showing no preference for edge over line stimuli.

The difference in the responses of primary and associative visual areas is brought out more clearly in the analysis of the individual subject data. Figure 3 (left column) plots the mean amplitude and phase of the first harmonic of the response to the edge versus line stimulus for each ROI of the cortical areas: 90° phase represents a response phase-locked to the edge stimulus. Each symbol represents a single subject with associated amplitude and phase SEM (calculated from the 2D dispersion of single voxel activity inside the ROIs). There was virtually no modulation of the first harmonic of the responses of V1 (Figure 3A). Each individual response is associated with large error in both amplitude (crossing the zero) and in phase, indicating weak synchronization between voxels. The phases of the responses varied randomly from one subject to the other, with average amplitude less than 0.002. This suggests

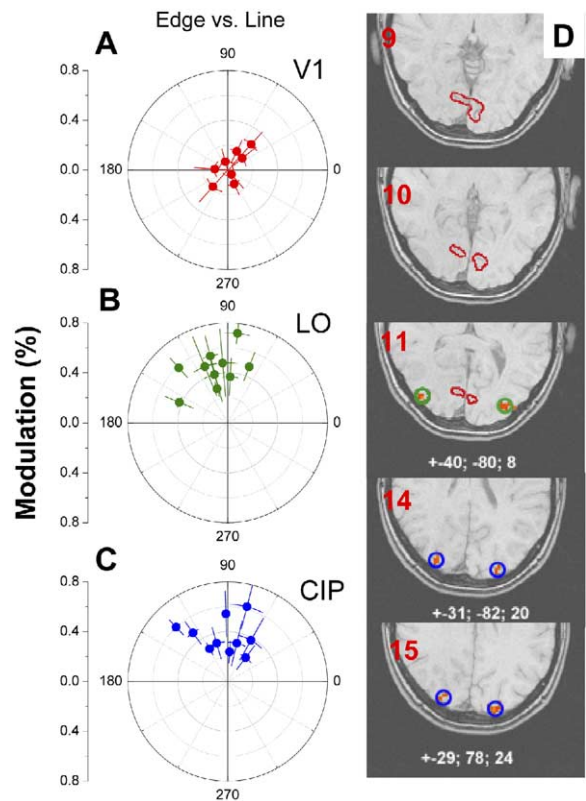


Figure 3. Amplitude and Phase of Individual Observer Responses (A–C) Polar plot of the amplitude and phase of the first harmonic of the response (with associated SEM) of all individual subjects to the edge versus line stimuli in V1 [A]: red symbols), in LO [B]: green symbols), and CIP [C]: blue symbols). (D) An example in one subject illustrating how ROIs were selected. The ROI activity for CIP (blue circles) and the LO (green circles) sulcus areas were selected from the responses to edge versus line. The activity threshold was set to $p < 0.002$ using GLM. The color scale for t test values was the same as in Figure 1 both for positive and negative correlation. However, no hypoactivity was labeled in this subject. The ROI for V1 is shown in slices 9, 10, and 11 with the red contour. No statistically significant active voxels were marked inside these ROIs. The white numbers are the Talairach coordinates of the center of the active voxels. Slice numbers shown in red in each panel

that the second harmonic modulation of the grand average of Figure 2 does not result from some subjects responding preferentially to the line stimulus and others to the edges stimulus. The responses of the two associative cortices LO and CIP (Figures 3B and 3C) were quite different: the responses of those areas to edges alternated with lines were strong (amplitude larger than 0.002) and consistent, with response phases clustering near 90° , the phase reflecting a response to edges.

To test that the responses of the two associative areas were specific to the illusory brightness rather than to the presence of edges in the stimulus, we devised a further control by interchanging the two horizontal edges of the COC stimulus of Figure 1A to produce that of Figure 4A (the “incongruent edges” stimulus). As the horizontal edges now signal a dark central square while the vertical edges signal a bright

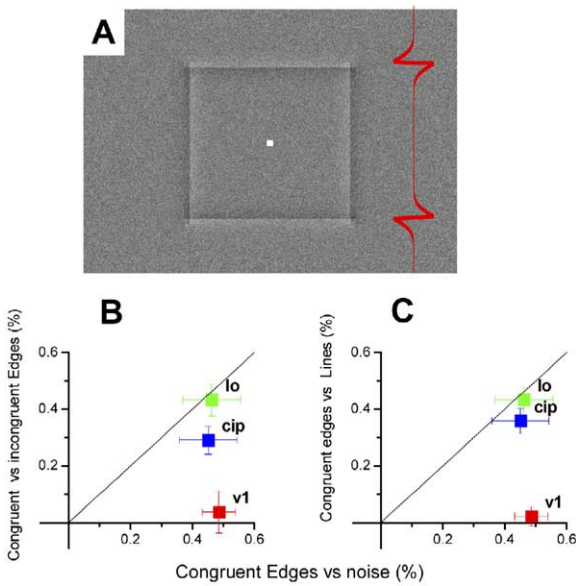


Figure 4. Control Stimulus with No Brightness Illusion, and the Response to It

(A) Control stimulus made from horizontal and vertical edges that have opposite polarity.

(B) Scatter plots of the response of the congruent edge versus incongruent edges stimuli (stimulus in Figure 1A versus stimulus in Figure 4A) against the response to edges versus noise alone for V1 (red symbols), LO (green symbols), and CIP (blue symbols). The abscissa shows the amplitude of the vector average across subjects of the response to edges versus noise alone. The ordinate shows the average of the projected amplitude of the response of each subject along the direction given by the phase of the average response to edge versus noise alone (reported in the abscissa).

(C) Same as for (B), but now the abscissa plots the average projected response to edge versus line stimuli.

central square, the brightness illusion and the subsequent surface perception are effectively annulled. However, the new stimulus has the same local, global energy and Michelson contrast as the original edge stimulus. Figure 4B plots the average projected amplitude of the response (Boynton et al., 1999) to congruent versus incongruent edges stimuli against the average response of edge versus noise alone. Each symbol represents the average across subjects, with both conditions measured in the same scan session. The responses of primary cortex V1 (Figure 4B) are strong for congruent edges versus noise, but are virtually nonexistent for congruent versus incongruent edges stimuli, with amplitude not significantly different from zero. The two associative areas both responded significantly to the alternation with a similar strength as to the alternation of the edge stimulus against noise. Figure 4C plots the results of the same analysis performed for the congruent edge versus line stimulus for comparison. The similarity of the pattern of responses for the two types of stimuli is striking, suggesting that the responses in these areas are neither to edges per se nor to the perception of a surface, but to the illusory change in brightness.

Discussion

This study establishes several facts. First, that the primary visual cortex responds with equal strength to features with the same amplitude spectra and RMS contrast, but with different profiles and different Michelson contrasts. Pooling data over all subjects revealed a small but significant response in V1 to edges versus lines, but this response was in synchrony with the change in stimulus (second harmonic), not with a specific feature, and was equally strong for both stimuli. BOLD imaging sensitivity can predict contrast increment and color discrimination thresholds (Boynton et al., 1999; Engel et al., 1997), effects that are perceptually far more subtle than those generated by the Cornsweet illusion (Burr, 1987), yet here the same technique revealed no selective response for brightness in primary cortex. Furthermore, there was no response (either positive or negative) to the edge versus line stimuli in the retinotopic representation of the central bright square, reinforcing the suggestion that primary visual cortex does not specifically encode the illusory brightness.

This result is consistent with electrophysiological studies showing that luminance filling-in of the Troxler effect is generated by edge and not surface neurons in monkey V1 (von der Heydt et al., 2003) and with the fact that in cat a strong response to the Cornsweet illusion can be recorded in area 18 both with intrinsic signal optical imaging and single-cell activity, but only very limited and barely significant in area 17 ($p = 0.4$) (Hung et al., 2001). However, it is not consistent with other physiological data on cat showing an induction of the V1 neuronal responses by a peripheral modulation of luminance (MacEvoy et al., 1998; Rossi et al., 1996). The discrepancy may reflect a genuine difference between species: in less complex visual systems, primary visual cortex may be able to fulfill complex functions, such as the reconstruction of the perceptual brightness of surfaces that occurs at a higher level in humans. This would be consistent with the small and variable response recorded in cat area 17 to the Cornsweet illusion and with the recent unpublished evidence that a similar brightness induction cannot be revealed in human cortex (Cornelissen et al., 2003). Recently, it has been reported that an abrupt luminance change is able to elicit a BOLD response in human V1 (Haynes et al., 2004), and this has been interpreted as evidence that the raw luminance signal reaches and is processed by V1. However, the response did not vary with temporal exposure, indicating that its origin could be the transient response to the abrupt change rather than the encoding of steady-state luminance levels. Such nonlinear behavior of the response is typical of retinal ganglion cells as well as cortical cells. Interestingly, the present data also show a nonlinearity in the V1 BOLD response (second harmonic modulation of Figure 2), even in our stable steady-state condition where both mean luminance and global contrast do not change. The presence of this strong nonlinear transient response supports the use of stimuli that produce small perturbations that do not modulate automatic neuronal

gain control mechanisms for contrast and luminance, especially when studying subtle effects.

Second, the present data implicate a part of the dorsal pathway (LO and CIP) in the perception of the brightness of a surface. Many dorsal areas are selective to spatial form and in particular to line or edges drawings (Braddick et al., 2000; Denys et al., 2004; Kourtzi and Kanwisher, 2000; Malach et al., 1995). Scrambled versus intact grayscale level images or drawings of objects elicit strong responses in both the dorsal and the ventral part of LO in addition to activity in V3, hV4, and KO (Denys et al., 2004). The line and edge stimuli used here are perceived as different objects, and in principle they could elicit a similarly widespread activation in all the LO complex and other ventral areas. Interestingly, the activation was limited to the dorsal part of LO, suggesting a modular organization of this complex. The selectivity of the response to the illusion is in line with other selectivities of the LO complex for amodal contours, symmetry, and for the preference of rendered rather than two-tone images (Mendola, 2003; Mendola et al., 1999; Sasaki et al., 2005). At first glance it could be seen to be at odds with the known selectivity of LO to 3D volume (Moore and Engel, 2001), given that the nonpreferred line stimulus appears to have more depth. In the present experiment, line stimuli with both positive and negative polarity were used, and these stimuli generate opposite depth cues. It is therefore possible that the selectivity for 3D volume is modulated by the sign of the depth cue, so averaging the response across different ON phases annulled any response.

Other visual areas also seem to encode surfaces, including CIP, which responds to the surface slant generated by pictorial cues (Tsutsui et al., 2002). The present study shows a specificity of the human CIP area for another surface attribute—brightness. Together with the known selectivity of this area for 3D structure from motion, stereo, and texture gradient (Taira et al., 2001; Tsao et al., 2003; Vanduffel et al., 2002), CIP may be a visual area dedicated to constructing 3D space perception to guide actions such as grasping behavior.

At present it is not known how the raw luminance signal is coded in real-life 3D scenes when inspected with free eye movements that generate transient and fast changes. It is possible that in these natural conditions luminance information is processed by a more widespread cortical neuronal circuitry involving both the dorsal and ventral pathways and that the brightness is computed at various stages of analysis that includes a top-down cognitive component (Adelson, 1993). We cannot completely rule out the possibility that the selective neuronal activity found here results in part from the simplicity of the stimulus, which comprises only one surface in the scene may engage only partially higher cognitive processes whose weak activity could not be detected. But in any event, LO and CIP would seem to be implicated in illusory brightness perception.

As attention modulates the BOLD response of visual cortex (Tootell et al., 1998), it is theoretically possible that some of the activity (particularly for the CIP response) could reflect differences in allocation of attentional resources (for example, by subjects paying more

attention to edges than lines). However, several facts argue against the involvement of attention. First, attention not only increases BOLD response but also improves psychophysical performance at thresholds (Lee et al., 1999; Morrone et al., 2002), and we found no difference in increment thresholds for edge or line stimuli. Second, our subjects were instructed to attend to the changes in the noise (that should in any event attract transient attention even without consciously attending to them), thereby directing attention all over the whole stimulus, rather than to a particular location. Third, many visual areas are strongly modulated by attention (like MT, V3, and even V1) but did not show any response to the illusory brightness. On the other hand, both for LO (Denys et al., 2004; Sasaki et al., 2005) and CIP (Tsao et al., 2003), attention seems not to be essential to elicit a specific response.

These data are consistent with many theories (Kingdom and Moulden, 1992; Marr, 1982; Morrone and Burr, 1988; Watt and Morgan, 1985) that the primary role of early analysis is the extraction of salient information, followed by a synthesis of this sparse information for the computation of the surface and objects. Interestingly, the selectivity for the illusion arises in associative areas where neurons have large receptive fields capable of integrating the information along contours. However, our data do not show a progressive trend in responsiveness to the illusion that increases with the size of the neuronal receptive fields (Press et al., 2001; Smith et al., 2001): no selective response was ever observed in occipital regions corresponding to V2, V3, or V4. In addition, the present results show that the BOLD response of the selective areas is nonlinear and probably subject to a strong contrast gain. The response to the edge pattern is only marginally stronger than the response to the line stimuli when presented against noise alone. Nevertheless, the direct contrast between line and edge shows a strong response about half the size of the individual edge or line responses. This strong nonlinear behavior suggests that the mechanisms involved in contour integration may be more complex and sophisticated than a simple linear integration of information. The present results do not support other simple models, such as an unspecific boost of low spatial frequencies (Dakin and Bex, 2003), or a role of a parallel luminosity channel (Cohen and Grossberg, 1984; Grossberg and Todorovic, 1988), given that both the edge and line stimuli have the same low spatial frequency content. However, they support the idea that features are detected and classified by V1/V2, from which higher cortices compute surface brightness.

Experimental Procedures

Stimuli

The COC illusion was generated by band-pass filtering a 1D profile containing a central square of 15°. The filter equation (in c/deg) is given by

$$G(w) = e^{-(w^2/2\sigma_H^2)} - e^{-(w^2/2\sigma_L^2)} \quad (1)$$

where w is the spatial frequency and $\sigma_H = 4.3$ and $\sigma_L = 0.17$ c/deg . The low-pass filtering was introduced to increase the RMS contrast of the stimuli. The 1D profile was used to generate horizontal and vertical stripes that were added appropriately to make the 2D stim-

ulus of Figure 1A. The vertical and the horizontal edges overlapped for about 0.6°.

The line stimulus (Figure 1B) was generated by applying the Hilbert transform to the 1D profile (for details see Burr et al., 1989; Morrone and Burr, 1988). The overall power spectra of the two stimuli differed less than 0.1%. The RMS contrast of the stimuli was 4%, corresponding to a Michelson contrast of 41.5% for the single line and of 20% for the single edge. The stimuli were embedded in random Gaussian noise of RMS contrast of 14%, refreshed every 300 ms. The incongruent edges stimulus (Figure 4A) was generated by inverting the polarity of the horizontal edges of Figure 1A before adding it to the vertical edges.

Stimuli were generated in advance as AVI uncompressed movies in MATLAB (245 gray levels) and displayed at 60 Hz through liquid crystal goggles (VisuaStim XGA - Resonance Technology at a resolution of 800 × 600 pixels, subtending 30° × 22.5° at an apparent distance of 1.2 m, with mean luminance of ~30 cd/m²). Extreme care was taken to γ correct and linearize the system, photometrically and by matching psychophysically the apparent luminance on the goggles with the apparent luminance of well-calibrated monitor.

Detection thresholds were measured in three subjects for similar conditions as in the scan, with a two-alternative forced-choice procedure. To localize retinotopic representation, we used a checkerboard stimulus (0.5° each square, alternating in contrast every 300 ms) presented centrally and extending from ±5° and presented in a square peripheral frame between 6.5° and 8.5° eccentricity.

Subjects and Procedure

Twelve healthy young volunteers with normal vision each participated in two to four recording sessions. The subjects were instructed to keep fixation to the central square and to pay attention to the changing visual noise.

For eight subjects it was possible to record in the same session the response to edge stimuli versus noise, to line stimuli versus noise, and to edge versus line stimuli. In six subjects (four from the previous group) we recorded the response to edge versus noise and to edges versus inverted edges.

In another two different subjects (plus two from the first group) we recorded the response to the edge versus noise alone, the line versus noise alone, and to the central and peripheral localizer checkerboard stimuli to check that the line stimulus was an appropriate localizer for the edge stimuli.

BOLD responses were acquired by 1.5 T General Electric LX Signa Horizon System (GE, Milwaukee, WI), equipped with Echo-speed gradient coil and amplifier hardware, using a standard quadrature head-coil. Activation images were acquired using echoplanar imaging (EPI) gradient-recalled echo sequence (TR/TE/flip angle = 3 s/50 ms/90°, FOV = 280 × 210 mm, matrix = 128 × 128, acquisition time: 3 min 12 s). Volumes consisted in 18 contiguous 4 mm thick axial slices, covering from the inferior temporal-occipital edge to the middle-parietal region (from about z = -28 to 45 mm), acquired every 3 s. Time course series of 64 images for each volume were collected in the six phases, the first epoch lasting 12 s more. An additional set of anatomical high-resolution 3D Fast SPGR data set (TR/TE/flip angle = 150 ms/2.3 ms/120°; RBW = 12.8 kHz; FOV = 280 × 280 mm, matrix = 256 × 256; isotropic dimension: 1.1 mm, NEX:2; acquisition time: 12 min 26 s) was acquired.

Two types of analysis were performed. For generating a statistical map of the BOLD response, Brain Voyager 2000 4.6 software package (Max-Planck Society, Germany and Brain Innovation, Maastricht, the Netherlands) was used. All volumes from each subject were adjusted with the application of rigid body transforms for residual motion-related signal changes. Functional data were smoothed spatially (Gaussian kernel of 4 mm full-width at half-height) but not temporally. Statistical activation maps were obtained using cross-correlation or general linear model analysis, with threshold at $p < 0.002$ and cluster size limit of two voxels. A more permissive threshold ($p < 0.05$) was used to check that there was no difference in the primary visual cortex activations between the line and edge stimuli, even relaxing the statistical criterion. Then EPI images were coregistered with the 3D anatomical data in order to define the Talairach-Tournoux coordinates and to generate the flat image of the brain.

A voxel-by-voxel analysis was performed in MATLAB. The regions of interest were defined differently for the associative and the primary visual cortex. To include all weak activity (both positive and negative), the ROI for the associative areas extended over a cylinder of 5 voxels diameter centered on the center of the maximum active voxels (selected with $p < 0.001$) in response to the edge versus line stimulus. (For two subjects in which we did not record in the same scan session the response of edge versus lines, the edges versus incongruent edges stimulus was used to locate the ROI.) When the activity extended over two or more sequential slices, the center of the cylinder followed the center of the most active regions. The ROI for primary visual cortex was defined as all active voxels for edge versus noise that were anatomically situated along the calcarine sulcus. Two independent analyses of the edge versus noise data were performed with two different threshold at $p < 0.001$ and $p < 0.05$, yielding similar results. Having defined for each subject the various ROIs, these were used to analyze the response of all scans in the same recording session. For each voxel of a ROI, the linear trend was calculated and subtracted. Activity was then normalized by the mean of all voxels of the ROI, and the amplitude and phase of the fundamental or second harmonic component of each voxel response in synchrony with the stimulus (expressed in percent of modulation) was calculated. Estimates of amplitude and phase of the response for each ROI were computed from the vectorial average of the single-voxel response, with the SE evaluated by the dispersion of the voxel population in the 2D polar plot. The ROI time course is the averaged activity of each normalized voxel, either individual or averaged over subjects (in the latter, the average was not weighted for voxel number). The plot of Figure 4 reports the projected amplitude of the modulation of the individual ROI averaged between subjects (for details see Boynton et al., 1999). The phases used for projecting the individual ROI amplitude were calculated from the phase of the vectorial average of all ROI responses to the edge stimulus versus noise collected from different scans and different subjects, equal to 106°, 95°, and 105° for V1, LO, and CIP, respectively.

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