RESEARCH ARTICLE

Lori L. Beason-Held · Keith P. Purpura
Jack S. Krasuski · Richard E. Desmond
David J. Mangot · Eileen M. Daly · Lance M. Optican
Stanley I. Rapoport · John W. VanMeter

Striate cortex in humans demonstrates the relationship between activation and variations in visual form

Abstract Electrophysiologic and functional imaging studies have shown that the visual cortex produces differential responses to the presence or absence of structure within visual textures. To further define and characterize regions involved in the analysis of form, functional magnetic resonance imaging (fMRI) was used to detect changes in activation during the viewing of four levels of isodipole textures. The texture levels systematically differed in the density of visual features such as extended contours and blocks of solid color present within the images. A linear relationship between activation level and density of structure was observed in the striate cortex of human subjects. This finding suggests that a special subpopulation of striate cortical neurons participates in the ability to extract and process structural continuity within visual stimuli.

Key words Visual perception · Object recognition · Functional magnetic resonance imaging · Neuroimaging · Human

Introduction

The ability to identify defining borders between objects or individual components of a scene is an important process involved in the perception of complex images within our visual environment. To subsequently recognize specific objects contained within the scene, the brain must also be able to detect and differentiate between variations in regularity and form. The visual system is very capable of performing these operations and appears to do so in a rapid and effortless fashion, suggesting that early stages of processing may play an important role (Thorpe et al. 1996; Ullman 1996).

Psychophysical studies of texture perception have shown that briefly presented visual textures sharing the same spatial power spectra or spatial frequency content determined by two-point spatial correlation statistics are usually not readily differentiated by human subjects (Julesz et al. 1973). This finding is consistent with a model of the early visual system which holds that the retina, thalamus, and striate cortex are dominated by receptive field mechanisms sensitive to differences in the spatial frequency content of images (DeValois and DeValois 1988). Thus, textures that fail to differentially activate these receptive field mechanisms are difficult to discriminate. Conversely, stimuli selected from classes of textures with different spatial power spectra can be rapidly discriminated and are useful assays of the spatial contrast sensitivity function of the visual pathway.

Julesz and colleagues also demonstrated that rapid discrimination of isodipole textures (i.e., textures sharing the same mean luminance and spatial frequency content) is possible if particular form elements produced by special four-point spatial correlation rules are included within the images (Julesz et al. 1978; Victor and Conte 1989, 1991; Victor and Zemon 1985). The types of receptive field mechanisms that can detect these form elements in the absence of spatial frequency cues are not those known to exist in the subcortical visual pathways, suggesting that nonlinear cortical mechanisms must be involved in detecting this type of structure (Victor 1986). This finding also suggests that the perception of recognizable images such as faces, buildings, and natural scenes may rely on similar mechanisms, because these images are likewise determined by their higher-order

L.L. Beason-Held (✉) · J.S. Krasuski · R.E. Desmond
D.J. Mangot · E.M. Daly · S.I. Rapoport · J.W. VanMeter
Laboratory of Neurosciences, NIA, National Institutes of Health,
Bldg. 10, Rm. 6C414, 9000 Rockville Pike,
Bethesda, MD 20892, USA
e-mail: LBH@Box-L.nih.gov
Tel: +1-301-4964754, Fax: +1-301-4020074

K.P. Purpura
Department of Neurology and Neuroscience,
Weill Medical College of Cornell University, New York, USA

L.M. Optican
Section on Neural Modeling, NEI, National Institutes of Health,
Bethesda, Md., USA

J.W. VanMeter
Sensor Systems, Sterling, Va., USA

(greater than second-order) spatial correlations (Field 1994). It is likely that the higher-order correlation rules produce specific spatial features that are detected by receptive field mechanisms in the visual system.

Electrophysiologic studies in humans and monkeys have shown that the visual system responds differentially to textures where the four-point spatial correlation rule results in the presence of extended contours and rectangular blocks of a single color relative to textures made up of a random arrangement of pixels (Purpura et al. 1993, 1994; Victor and Conte 1989, 1996). Visual evoked potential (VEP) studies in humans also suggest that the amplitude of the response to these isodipole textures is related to the density of form elements contained within the images. For example, a fully correlated texture exhibiting regular extended contours and solid blocks of color can be spatially decorrelated in a systematic fashion so that examples of textures are generated that exhibit a range of apparent features or form elements (see Fig. 1). VEPs have demonstrated that stimulation with textures exhibiting systematic or parametric differences in spatial correlations results in a linear increase in response amplitude as the density of form elements increases (Victor and Conte 1991).

In the present experiment, functional magnetic resonance imaging (fMRI) was used to determine anatomic regions of the human brain that similarly demonstrate a linear relationship between activation level and the density of structure in isodipole textures. Healthy young adults were shown examples of four levels of isodipole textures where the degree of spatial correlation (alpha level) ranged from alpha=0 in the random textures to alpha=1 in the fully correlated textures.

Materials and methods

Subjects

Eight healthy control subjects, seven women and one man (aged 20–37 years; right-handed), participated in the study. All were medically screened to exclude brain or systemic diseases that might affect brain function. Visual fields and acuity were screened, and subjects with suboptimal visual acuity wore corrective lenses during scanning. Following full explanation of purpose, procedures, and risks of the study, informed consent was obtained from each subject.

Visual stimulation

Four levels of textures were used in this experiment (Fig. 1). Details of the construction of isodipole textures can be found elsewhere (Julesz et al. 1978; Victor and Conte 1991). In brief, to construct a class of textures that share the same average spatial power spectrum but differ in their "higher-order" spatial correlations, the coloring of each element (black or white) in the initial row and column of the texture is determined by chance. For the "random" class of textures, the color of all other interior elements is also determined by chance. Construction of the spatially correlated class of textures begins the same way, but interior elements are colored using a different strategy. Here, the color of each new element is based on the colorings of three other elements in the texture. These elements lie at three of the vertices of any rectangle that ex-
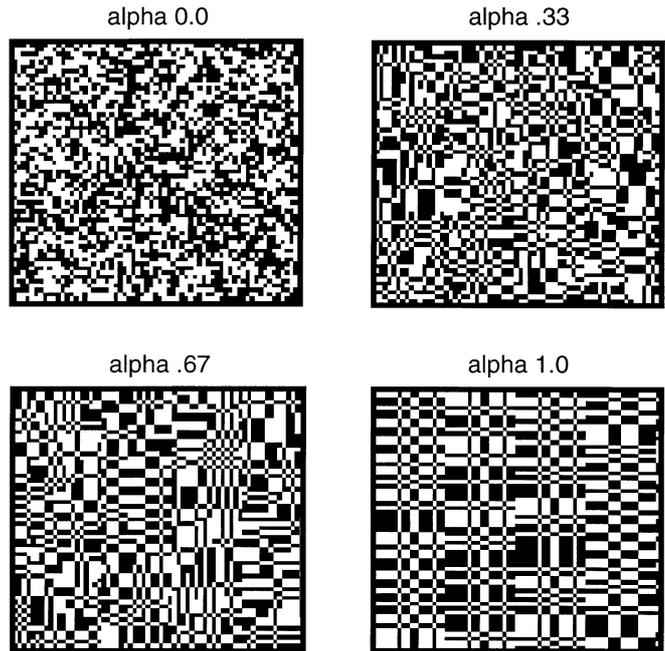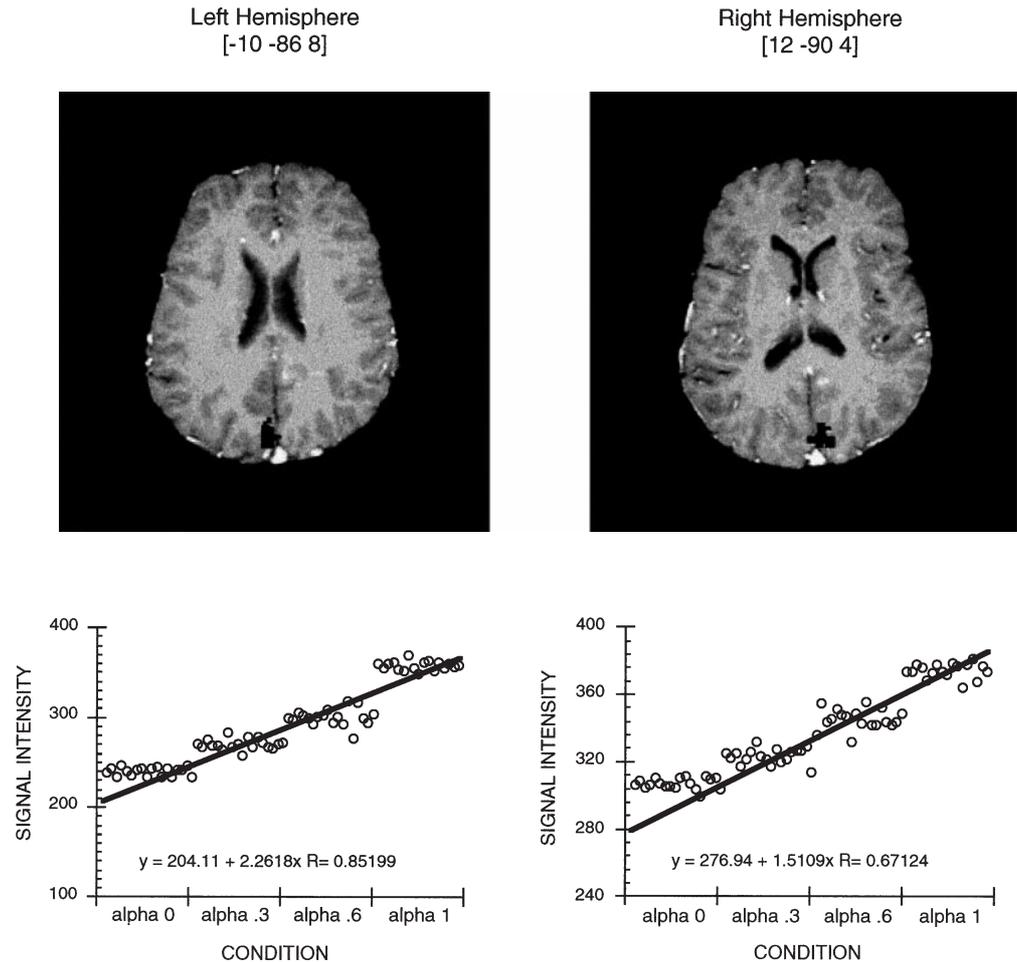

Fig. 1 Examples of textures from the four alpha classes. Correlated textures used in this study (alphas 0.33–1) were created using a variation of the standard technique used elsewhere (Purpura et al. 1994). Here, each frame was assembled by placing four separately constructed regions side by side in the display. This manner of display breaks the standard "even" correlation rule (Victor 1985) across the joining boundaries, but the isodipole characteristics of the texture are maintained

ists parallel to the initial row and column of the texture, with the new element located at the fourth vertex of the rectangle. If there are three white or black elements at the other three vertices, the new element must be white or black, respectively. If there are two white elements, the new element must be black and vice versa. This class of textures is referred to as "even," for there are an even number of black and/or white elements at the four vertices of every rectangle. This correlation rule results in textures that are rich in the form elements of extended contours and solid blocks of uniform color at multiple spatial scales, features that are absent in the random textures.

The fourth-order correlation rule that controls the construction of an even texture can be extended to produce new families of textures with different densities of form elements (Victor and Conte 1989). Disorder can be introduced into the even textures by altering the probability that the coloring of any element of the texture will follow the correlation rule. For example, in the fully correlated even textures, the probability that each texture element follows the specified coloring scheme is 1.0. Suppose, however, that we stipulate that an element in an even texture can flip from black to white or vice versa with a probability of 0.05. This translates to an alpha level (or degree of spatial correlation) of 0.67 (see Victor and Conte 1989 for details). For a probability of 0.12, the degree of correlation is 0.33. When the probability of faithful rendition falls to 0.5, the texture becomes fully decorrelated, i.e., random. As one can see in Fig. 1, as the textures become more decorrelated, the number of extended contours and blocks of solid color diminishes and hence the density of salient form elements drops. Four spatial correlation levels were used in this experiment: alpha=0.0, alpha=0.33, alpha=0.67, and alpha=1.0.

The stimuli were projected onto a 24×30-inch viewing screen using a Macintosh Quadra computer and a Sony video projector. The screen subtended 16×18° of visual angle and could be viewed from inside the magnet bore with the use of mirrors. The smallest

Fig. 2 Data from a representative subject showing significant differential responses to increases in the degree of salient form elements (alpha level). The brain slices illustrate clusters within the striate cortex (area 17) that demonstrate a significant linear response in relation to texture alpha level. The area of activation is shown in *black. Below each slice,* the adjusted MR signal response of the local maxima within the activated cluster is shown across the four alpha conditions. The *circles* represent data points from each of the 18 epochs collected per condition. Talairach coordinates of the local maxima are shown in *brackets*

Left Hemisphere
[-10 -86 8]

Right Hemisphere
[12 -90 4]

$y = 204.11 + 2.2618x$ R= 0.85199

$y = 276.94 + 1.5109x$ R= 0.67124

pixel (area of black or white) in the textures subtended 0.3° of visual angle. Textures were rendered with 100% luminance contrast.

Four series were administered in which the subject saw fixation and activation conditions in alternating 60-s epochs. Each series included three epochs of both fixation and activation conditions. Each epoch consisted of six scans. For a given series, the activation condition consisted of a stream of novel textures from one of the four alpha classes (presentation interchange rate, 800 ms). The four series were presented in a random order across subjects to control for presentation effects. Subjects were instructed to keep their gaze focused on the center of the viewing screen throughout both fixation and texture stimulation conditions.

Brain imaging

All imaging was performed on a 1.5-T Signa General Electric scanner using a whole-brain Medical Advances head coil. A gradient-echo echoplanar sequence was used for functional blood oxygenation level-dependent (BOLD) imaging (Ogawa et al. 1993). The following sequence parameters were used for all subjects: 25-cm field of view (FOV); 64×64 acquisition matrix; 10 s TR; 40 ms TE; 90° flip angle; and 4-mm slice thickness. Within each series, 18 scans or whole-brain volumes were collected for both activation and fixation conditions. Each volume consisted of approximately 30 axial slices, depending on head size.

Structural scans were obtained using a spoiled GRASS sequence (25 cm FOV; 256×256 acquisition matrix; 150 ms TR; 9 ms TE; 60° flip angle; 4-mm slice thickness). Axial slices were obtained in the same location and orientation as the functional volumes.

Data analysis

The data were analyzed on a single-subject basis using Statistical Parametric Mapping (SPM 97; Welcome Department of Cognitive Neurology, London, England). For each subject, all series were registered to the first volume collected (Woods et al. 1992) and warped into the stereotactic space (Friston et al. 1995) of Talairach and Tournoux (1988). For a given series, scans from the activation epochs were concatenated in order of acquisition. Activation scans from all series were then normalized using the ratio adjustment or proportional scaling method. Following application of a high-pass filter, the data were analyzed on a voxel-by-voxel basis using a delayed boxcar function (6-s temporal lag). Significant voxels were obtained by using parametric weights across the activation conditions of the four series to distinguish regions demonstrating a linear relationship between alpha level and brain signal intensity. Voxels with $P \leq 0.001$ were considered significantly correlated with a linear increase in textural structure or alpha level. Following conversion of the *t*-values to *Z*-scores, a cluster analysis was performed on the positively correlated voxels to determine significant areas of correlation based on intensity and spatial extent (*Z*-score threshold 3.04; spatial probability threshold 0.05; Friston et al. 1994). All presented results meet statistical significance based on this measure. Significant clusters were mapped onto each subjects structural scan to confirm anatomical localization.
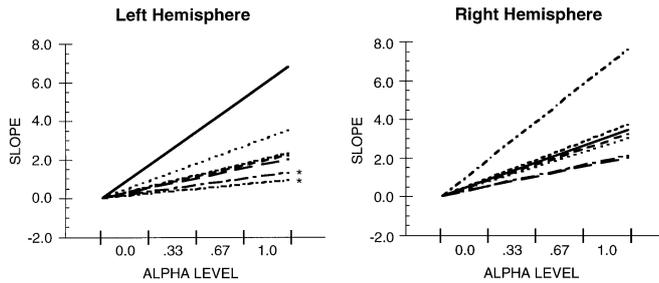
Fig. 3 Single-subject activation data for both cerebral hemispheres. Representation of individual slope values across the four alpha levels of activated clusters in the striate cortex. Because two subjects had the same slope value in the left hemisphere (2.20), the lines have been adjusted slightly to aid visualization. *Asterisks* denote slopes that did not reach significance in the left hemisphere of two other subjects

Results

Seven of the eight subjects demonstrated significant linear trends in brain signal intensity which were related to the density of salient visual form elements within the texture stimuli. While the eight subject demonstrated activation similar to the other subject, the regions did not meet the spatial extent threshold defined by the cluster analysis. Results from a representative subject are shown in Fig. 2.

Of the seven subjects demonstrating significant results, all showed involvement of the striate cortex or Brodmann area 17. A linear signal response was observed in this region in relation to increasing alpha levels of the textures. In five subjects, activation of the striate cortex was seen bilaterally. In the remaining two subjects, activation of the striate cortex was seen in the right hemisphere only. Four of the seven subjects also demonstrated involvement of areas outside of the striate cortex. Two subjects demonstrated activation of the fusiform gyrus (Brodmann area 18/19), one subject demonstrated activation of the posterior cuneus (Brodmann area 18), and one demonstrated involvement of the hippocampal region. Figure 2 illustrates the signal response with regard to alpha level in the striate cortex of subject D.L.

To assess hemispheric differences, the data values were extracted and a standard least-squares fit was performed to analyze the slopes of the activation patterns for each subject (Fig. 3). While the two subjects showing significant activation in the right hemisphere only also demonstrated positive slopes in the left hemisphere, these did not reach statistical significance. Statistical analysis (paired *t*-test) of the slopes did not reveal significant differences in activation between the right and left hemispheres.

Discussion

This fMRI study demonstrates that changes in the density of salient texture features produces different levels of activation in striate cortex (Brodmann area 17). In this study, subjects viewed different ensembles of textures, each with a different density of extended contours and colored blocks but all sharing the same spatial power spectra. The higher the density of these form elements, the greater the activation in this area of the brain. The neural basis of this pattern of activation may lie with a special subpopulation of local circuits that are widely distributed across the cortical tissue.

In the monkey, electrophysiologic studies have shown that the striate cortex or V1 is involved in the extraction of local features within visual textures (Purpura and Victor 1990; Purpura et al. 1994). VEP and local field potentials have shown that the striate cortex is activated by a rapid interchange between random textures (alpha=0) and fully correlated or even textures (alpha=1). That is, the amplitude of the response increases when the stimulus changes from a random to a fully correlated texture. Intracortical field potentials further show that this response is uniform throughout all layers of the striate cortex, and single-unit recordings indicate that this sensitivity to differences in local feature density extends down to the level of the receptive fields of single simple and complex cells. The results presented here support these findings in that an increase in activation level within striate cortex is observed when subjects are presented with textures exhibiting increasing form or structure.

Studies of texture perception in humans have also demonstrated differential responses to isodipole textures. The ability of the human visual system to perceive differences in form elements present in these images has been demonstrated using both psychophysical and VEP techniques. With regard to psychophysics, it has been shown that subjects can readily discriminate between a random texture and one exhibiting form elements even with brief presentation rates (50 ms). When tested with the same type of textures used in the present experiment, subjects could reliably discriminate between a random texture and textures with spatial correlation levels as low as alpha=0.1 (Victor and Conte 1991).

VEP recordings in humans show the same electrophysiologic response to fully correlated and random texture interchange that is seen in the monkey (Victor and Conte 1989, 1991). The antisymmetric or odd harmonic component of the VEP waveform that is sensitive to the form elements within visual textures (Victor 1985) indicates that the two texture levels differentially drive neural populations in the visual pathway. Furthermore, this antisymmetric component also demonstrates a linear relationship with alpha level (Victor and Conte 1989): the greater the density of form elements the greater a proportional increase in the amplitude of the component. Because the VEP is a population response, an increasing amplitude in one of its components suggests that an increase in the density of local features recruits greater numbers of a particular cortical subpopulation of neurons. The fMRI results described here suggest that striate activity is responsible, at least in part, for the signal trends observed in the human VEP studies.

Activation of the striate cortex in response to any one texture level can be explained by the fact that the textures are rich in high-contrast edges that are present in two orientations. These visual components are capable of activating large populations of neurons through the spatial frequency and orientation tuning properties of receptive fields known to be widely represented in this region. The differential activation generated in the striate cortex by the four texture levels, however, suggests the presence of a spatial linking mechanism in V1, and thus the presence of a special subpopulation of neurons with this receptive field mechanism that are capable of driving the BOLD signals reported here.

The spatial linking operation is actually a two-stage mechanism involving two spatial scales (Victor and Conte 1989). First, local edge detection is performed by neurons with receptive fields on the order of the smallest texture elements. In this study, the smallest texture element is 0.3° on a side. Second, a stage of integration occurs that cooperatively links the outputs of neighboring local edge detectors sharing a common orientation preference. This second stage involves a threshold function that limits the recruitment of edge-detector subunits unless these subunits are aligned along an extended contour or the perimeter of a larger block. The space constant of the integration stage can be extrapolated from a previous VEP/modeling study (Victor and Conte 1989) and is on the order of 1° of visual angle. This means that the linking operation of any one neuron would include enough visual space to capture between two and three of the smallest texture elements. Different texture element sizes would recruit different subpopulations of neurons with receptive field sizes matched to the lengths of the element edges and with larger or smaller space constants for integration.

Detailed physiological descriptions of the two stages in the proposed spatial linking mechanism are currently not available. One candidate receptive field property that could play a role in the first stage is that of length tuning (Hubel and Wiesel 1965; Orban 1984). Length and width tuning are now recognized as properties arising from end-zone and flanking suppression, respectively, of the classic excitatory receptive field (DeAngelis et al. 1994). Endstopped (length-tuned) cortical neurons show a significant decrease in response as a patch of grating or a bar is extended past the boundaries of the classical receptive field into the receptive field end-zones. Length tuning could enhance the extraction of local edges of a particular size from the textures and various length tunings may operate at different spatial scales. As the amount of sporadic decorrelation increases, the lengths of the available contours would decrease and this would change the distribution of the recruited endstopped cells.

However, length tuning probably does not play a role in the second critical stage of integration in the spatial linking mechanism. It is currently thought that endstopped neurons play more of a role in texture segregation than in feature binding within a texture (Rao and Ballard 1999). Endstopped neurons show the greatest attenuation when the orientation of the edges falling within the end-zones matches that of the edges in the receptive field center. The spatial linking model described above requires a facilitatory interaction between edge detectors sharing the same orientation preference. While this binding stage has yet to be described in detail through physiological recordings, it has proved to be a useful construct for explaining how contour integration works in the human visual system (Field et al. 1993).

Previous neuroimaging studies have shown that many extrastriate cortical areas become active when subjects either passively observe complex visual stimuli or actively participate in pattern and object recognition (Grady et al. 1998; Hirsch et al. 1995; Malach et al. 1995). The number and strength of activation in these areas depends on the nature of the tasks, types of visual stimuli, and history of testing. Using PET (Beason-Held et al. 1998b), we have shown that fully correlated textures produce enhanced activation throughout the ventral "what" pathway (Ungerleider and Mishkin 1982). This activation was also seen to shift in a posterior-to-anterior distribution as the scanning proceeded over the course of 1.5 h. With fMRI (Beason-Held et al. 1998a), we found that striate cortex generates a stable BOLD signal to stimulation with both random and fully correlated textures. However, the responses to fully correlated textures significantly exceeded those generated by random textures. Here, we have shown that the degree of BOLD activation is linearly related to the density of feature elements in the textures. This finding demonstrates that increased activity in the striate cortex occurs in response to enhanced regularity and continuity within the correlated textures, independent of spatial frequency and orientation properties common to all texture levels. This result may also be responsible for signal changes observed previously in human VEP studies (Victor and Conte 1989, 1991). Together with monkey studies (Purpura and Victor 1990; Purpura et al. 1994) and human psychophysical studies (Victor and Conte 1989), our work emphasizes the importance of early visual areas in the perception of form in our visual environment. In particular, our results strengthen the view that the striate cortex might play a more significant role in the extraction of visually salient features than has been thought traditionally.

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