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Selectivity for Polar, Hyperbolic, and Cartesian Gratings in Macaque Visual Cortex

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The neural basis of pattern recognition is a central problem in visual neuroscience. Responses of single cells were recorded in area V4 of macaque monkey to three classes of periodic stimuli that are based on spatial derivative operators: polar (concentric and radial), hyperbolic, and conventional sinusoidal (Cartesian) gratings. Of 118 cells tested, 16 percent responded significantly more to polar or hyperbolic (non-Cartesian) gratings than to Cartesian gratings and only 8 percent showed a significant preference for Cartesian gratings. Among cells selective for non-Cartesian gratings, those that preferred concentric gratings were most common. Cells selective for non-Cartesian gratings may constitute an important intermediate stage in pattern recognition and the representation of surface shape.

Neurons in the primary visual cortex (area V1) typically display tuning for elementary stimulus dimensions such as position, orientation, and spatial frequency (1). In the macaque monkey, subsequent stages of form processing are believed to take place in a hierarchy of extrastriate areas that includes areas V2, V4, and the inferotemporal cortex (IT) (2, 3). Although complex pattern recognition probably occurs in area IT and some IT cells are selective for faces, hands, or other highly complex stimuli (4, 5), little is known about the intermediate stages of processing involved in the generation of these higher order receptive field properties. We have addressed this problem by analyzing the receptive field characteristics of cells in area V4, an intermediate stage of the visual hierarchy. The stimulus set used in our experiments (Fig. 1A) was designed to meet several criteria: (i) it is rich enough to elicit responses from cells with complex

tuning properties, (ii) it is mathematically defined and permits calculation of tuning curves, (iii) it is based on specific computational theories of vision, and (iv) psychophysical and physiological observations have suggested the existence of cells tuned to these stimuli.

The stimuli were sinusoidally modulated gratings from three distinct classes, which we call Cartesian, polar, and hyperbolic. Each class is defined by the coordinate system in which the modulation functions form a linear, orthogonal basis. Thus, the Cartesian modulation functions form a basis in Cartesian coordinates whose cardinal axes generate conventional horizontal and vertical gratings. The intermediate functions generate Cartesian gratings at intermediate orientations. The polar functions form a basis in polar coordinates whose cardinal axes generate concentric and radial gratings, and the intermediate functions generate spiral gratings. Finally, the hyperbolic functions form a basis in hyperbolic coordinates whose cardinal axes generate hyperbolic gratings that differ in orientation by 45°, and the intermediate functions generate hyperbolic gratings at intermediate

orientations. The three stimulus classes are closely related to Lie differential operators, which take continuous derivatives of an image with respect to different coordinate systems. These operators may aid perceptual constancy by compensating for affine transformations of the retinal image that arise from changes in viewpoint and object orientation (6–8). The stimulus classes are also related to those used to identify cells in the medial superior temporal area that are selective for changes in rotation and in expansion and contraction (9): when integrated over time, rotating flow fields form concentric patterns, and expanding and contracting flow fields form radial patterns. Similar stimuli have been used in psychophysical studies (10) and have provided some support for mechanisms selective for polar or hyperbolic stimuli.

We first looked for cells in area V4 that respond more strongly to polar or hyperbolic gratings than to any Cartesian grating. We recorded extracellularly from single units in area V4 of anesthetized, paralyzed macaque monkeys (11, 12). In our primary test, we used polar and hyperbolic gratings that varied in spatial frequency and phase and Cartesian gratings that varied in orientation, spatial frequency, and phase (Fig. 1A). Figure 1, B to D, illustrates three types of selectivity that we encountered. The cell represented in Fig. 1B responded vigorously to concentric stimuli but poorly to all Cartesian gratings. The cell represented in Fig. 1C also preferred non-Cartesian stimuli, but the most effective stimulus was a hyperbolic grating. The cell represented in Fig. 1D preferred Cartesian gratings and was tuned for both orientation and spatial frequency.

All 118 V4 neurons studied with this stimulus set gave responses significantly above the base-line rate. With a *t* test, we compared the normalized firing rate obtained with the best Cartesian grating to that obtained with the best non-Cartesian grating (13). By this measure, 19 cells (16%) showed a statistically significant preference for non-Cartesian gratings, whereas 10 (8%) preferred Cartesian gratings (14). Out of 19 cells classified as non-Cartesian, 12 preferred concentric gratings, only 3 preferred radial gratings, and 4 preferred hyperbolic gratings. The preferences seem to reflect a continuum of selectivity rather than distinct cell classes. For the remaining 89 cells (78%), the responses to the best Cartesian and non-Cartesian gratings could not be distinguished statistically. Many cells in this last category showed sharp tuning profiles in both Cartesian and non-Cartesian stimulus spaces, which suggests a form of multiplexing in the representation of pattern information.

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Could some previously described property of V4 cells account for the preference for non-Cartesian gratings seen in some cells? Many cells in V4 are selective for stimuli smaller than their classical receptive field (CRF) (15), and length suppression along a cell's preferred orientation might make a non-Cartesian grating more effective than any full-sized Cartesian grating. If so, a Cartesian grating that covered only a portion of the CRF would be even more effective than the optimal non-Cartesian grating. We therefore varied the length of Cartesian gratings by truncating them along the axis parallel to the grating orientation (Fig. 2A). The results in Fig. 2, B and C, represent the same cells as do the results in Fig. 1, B and C. The cells responded only weakly to Cartesian gratings of any length, although they still responded to the optimal non-Cartesian grating. We examined ten

cells initially classified as non-Cartesian (seven concentric and three hyperbolic) using this procedure. Eight of the cells retained their preference for non-Cartesian gratings, whereas only two cells responded comparably to the best non-Cartesian grating and to a Cartesian grating of the optimal length and orientation. Thus, it appears that size selectivity for Cartesian gratings generally does not account for non-Cartesian response preferences in V4 cells (16).

Cells in V4 also have large nonclassical suppressive zones surrounding the CRF (15). If we had misplotted the receptive fields of non-Cartesian cells, the stimuli might have encroached on this suppressive zone. Depending on the particular form of the suppressive interaction, this influence could have produced an apparent preference for non-Cartesian over Cartesian grat-

ings, although Cartesian stimuli placed in the CRF might have produced a stronger response. Therefore, we displayed both Cartesian and non-Cartesian gratings at four different positions centered on the circumference of the estimated CRF and at a fifth position centered in the CRF (Fig. 3A). Responses shown in Fig. 3, B and C, are for the same cells represented in Fig. 1, B and C. For both cells there was no position at which any Cartesian grating elicited a response comparable to that for the best non-Cartesian grating. We used this procedure to examine ten cells initially classified as non-Cartesian. Six of the cells displayed consistent non-Cartesian stimulus

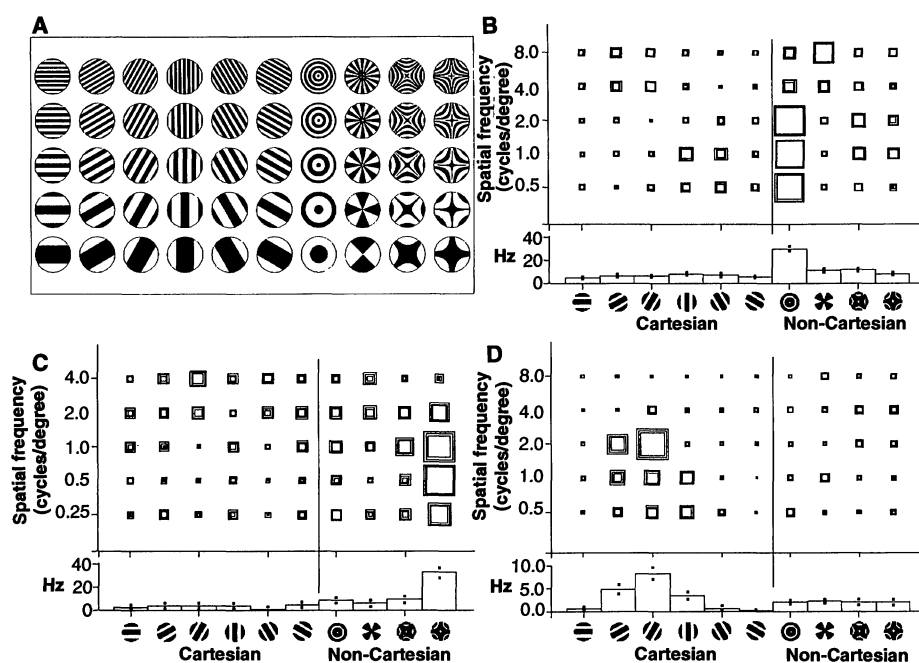


Fig. 1. (A) Stimulus set of Cartesian and non-Cartesian sinusoidal gratings. Gratings shown are square-wave gratings and the frequencies of high-frequency gratings have been reduced. Rings surrounding gratings represent borders of the stimuli, which were aligned as closely as possible with the classical receptive field (CRF). Gratings used in experiments were quantized to 250 luminance levels and were displayed for 0.5 s on a neutral gray background. All gratings were sinusoidal functions of x and y , respectively:

$$C_0 = \cos(2\pi\theta x), C_{90} = \cos(2\pi\theta y),$$

$$P_c = \cos(2\pi\theta \sqrt{x^2 + y^2}), P_r = \cos\left[2\pi\theta \tan^{-1}\left(\frac{y}{x}\right)\right]$$

$$H_0 = \cos(2\pi\theta \sqrt{|x^2 - y^2|}), H_{45} = \cos(2\pi\theta \sqrt{|xy|})$$

where C_0 and C_{90} represent 0° and 90° Cartesian gratings, respectively; P_c and P_r are polar concentric and polar radial gratings, respectively; and H_0 and H_{45} are 0° and 45° hyperbolic gratings, respectively. (B) Responses of a single V4 concentric cell to Cartesian and non-Cartesian gratings. The abscissa specifies grating type (six Cartesian grating orientations, concentric and radial gratings, and two hyperbolic grating orientations). The marginal histogram gives the mean relative firing rates and standard error of the means collapsed across spatial frequency. Squares in the two-way plot give normalized relative firing rates and standard errors. (C) Responses of a single V4 hyperbolic cell to Cartesian and non-Cartesian gratings. (D) Responses of a single V4 Cartesian cell to the same stimulus set.

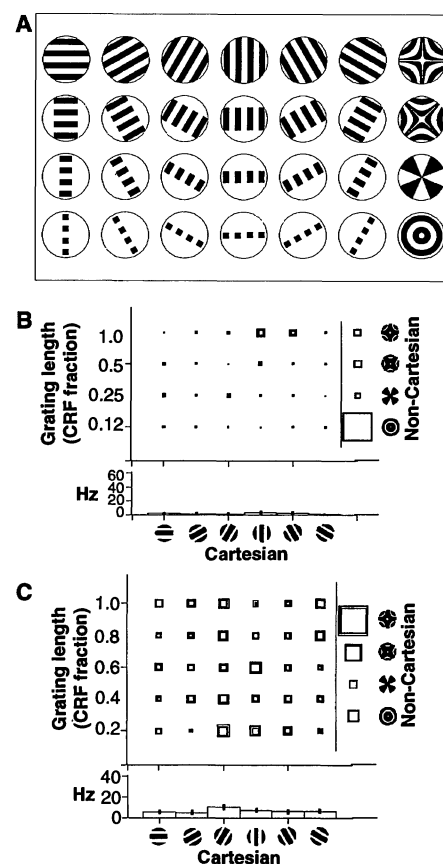


Fig. 2. (A) Cartesian and non-Cartesian gratings used in the length control test (schematic representation of gratings as in Fig. 1A). The same six Cartesian grating orientations were selected as in the previous test, but the length of the gratings was varied along the axis parallel to the grating orientation. Cartesian and non-Cartesian gratings were interleaved. The spatial frequency used for each cell was the most effective of those tested in the series illustrated in Fig. 1. (B) Responses of the same concentric cell whose responses are shown in Fig. 1B. The first six columns show responses to Cartesian gratings at the six orientations, and the last column shows responses to the non-Cartesian gratings. (C) Responses of the same hyperbolic cell whose responses are shown in Fig. 1C.

preferences across all positions where these cells were driven strongly. Another cell preferred hyperbolic patterns at one position and radial patterns at another. The remaining three cells responded equally to the best non-Cartesian grating and to a Cartesian grating at an offset position. In no case did a cell respond significantly better to a Cartesian grating at an offset position than to the best non-Cartesian grating. Thus, it appears that preferences for non-Cartesian patterns are not, in general, due to nonclassical surround interactions.

Many of these cells displayed insensitivity to spatial phase as well as to local stimulus position. The stimuli illustrated in Fig. 1A were each presented at two or three spatial phases. The particular cells tested were not phase-dependent, so the data include all phases collapsed together. Significant phase dependence was evident in only 3 of the 19 non-Cartesian cells and in only

1 of the 9 Cartesian cells. In this respect, most cells were more like complex cells in area V1 than simple cells (1).

Our standard stimulus set included Cartesian gratings generated according to modulation functions that fell along the cardinal axes of the space (horizontal and vertical gratings) as well as four intermediate orientations. In contrast, the non-Cartesian stimuli only included those with modulation functions that fell along the cardinal axes of their respective spaces: concentric and radial gratings (polar class) and orthogonal hyperbolic gratings (hyperbolic class). Given this difference and the conservative criterion that was used to classify cells as non-Cartesian, it is notable that twice as many cells preferred non-Cartesian to Cartesian gratings. We suspected that this bias would be even greater if the non-Cartesian stimulus spaces were sampled more densely. Accordingly, we recently added spiral gratings and hyperbolic gratings at additional orientations to our stimulus repertoire. Some cells prefer spiral gratings over other non-Cartesian and Cartesian stimuli, and these cells have smooth tuning functions in the polar stimulus space (Fig. 4, A and B). We also found cells that are tightly tuned to particular hyperbolic grating orientations. Our preliminary results suggest that the proportion of non-Cartesian cells may be significantly larger than our initial estimates and that these

cells may occur in spatially segregated clusters.

Previous studies have reported a small proportion of cells in areas V4 and IT that respond vigorously to complex stimuli such as faces (4), Walsh patterns (17), Fourier descriptors (18), and assorted elaborate two- and three-dimensional stimuli (5). Here we report responsiveness to complex, periodic patterns in area V4. Our procedure includes interleaved presentation of several stimulus classes (Cartesian, polar, and hyperbolic) and has controls that allow us to determine whether non-Cartesian response preferences are due to selectivity along some simpler dimension. In addition, our stimuli vary systematically along several dimensions, which allows us to estimate tuning curves for a cell's responses to the various stimulus classes.

The functional role of non-Cartesian cells in vision is not yet clear. We suspect that they may play a role in the perception of solid shape. As noted earlier, the derivation of a stable, canonical representation of objects is likely an important aspect of vision. Several theories based on Lie groups have been proposed to account for this function (6–8). These theories postulate the presence in the visual system of a family of continuous differential operators that normalize the visual image by removing the effects of two-dimensional affine transformations. Because the three stimulus classes we have examined are closely related to Lie orbits (the continuous vector fields of Lie operators), our findings are superficially consistent with this idea. However, several features of our data are incompatible with current proposals, including (i) the lack of phase sensitivity, (ii) the distribution and restricted size of local receptive fields, (iii) the unequal proportions of concentric, radial, and hyperbolic cells, and (iv) tuned responses across multiple stimulus classes in a significant subpopulation of cells.

Other proposals for visual object representation use transformational invariants or symmetry groups but do not rely on Lie group theory (19). Cells selective for non-Cartesian stimuli might play a role in such processes by responding to regions of symmetry or high informational content in a visual scene. Another class of theories presupposes that object recognition is based on a rich representation of the surface structure and topology of objects from the observer's point of view. Some theories center on invariants in the visual scene such as relationships between the reflectance map and the underlying three-dimensional surface structure of objects (20). Non-Cartesian cells might mediate the construction of such a representation by acting as efficient filters for the extraction of the relevant information from the retinal image.

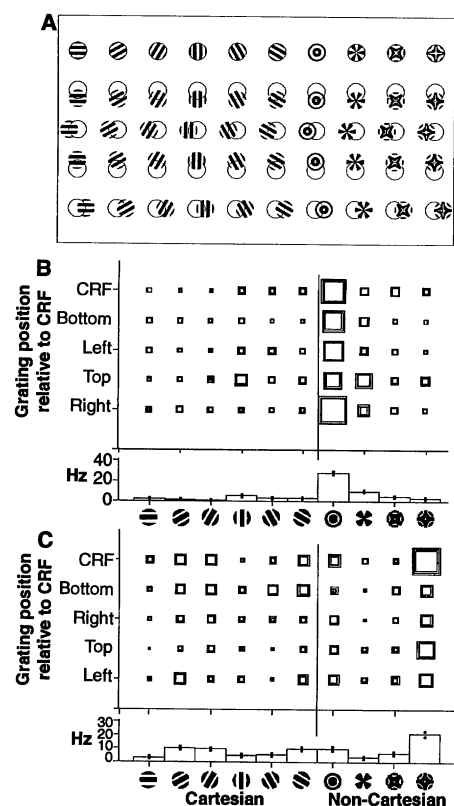


Fig. 3. (A) Diagram of grating placement in the position control test (schematic representation of gratings as in Fig. 1A). Cartesian and non-Cartesian gratings were centered at four positions around the circumference of the original CRF location and at one position within the CRF. The spatial frequency used for each cell was the most effective of those tested in the series illustrated in Fig. 1. (B) Responses of the same concentric cell whose responses are shown in Figs. 1B and 2B. (C) Responses of the same hyperbolic cell whose responses are shown in Figs. 1C and 2C.

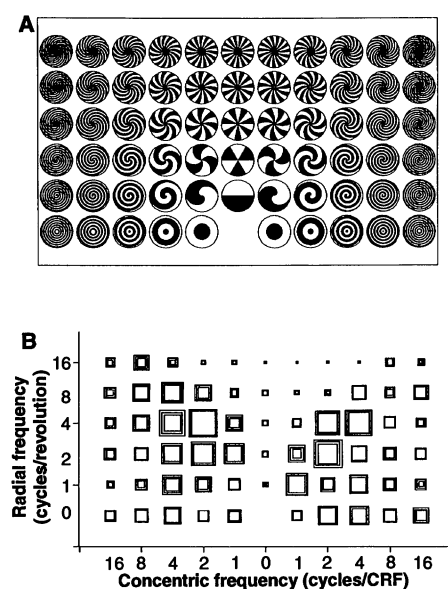


Fig. 4. (A) Gratings of the polar class (schematic representation of gratings as in Fig. 1A). The cardinal axes are concentric (abscissa) and radial (ordinate) gratings, and the intermediate gratings are spirals. Two spiral polarities are shown. (B) Responses of a single V4 cell to concentric, radial, and spiral gratings. The cell responded better to spiral patterns than to any concentric or radial pattern.

The process whereby theory motivates experiments and experiments guide theory is central to the emerging field of computational neuroscience. The present experiments, for example, were motivated in part by theoretical proposals, but those proposals now require substantial revision to become compatible with our findings. This cycle will surely continue because the algorithms implemented by the brain are likely to be far more complex and sophisticated than anything yet conceived by experimentalists or theorists.

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11. Recordings were made from four macaque monkeys (*Macaque nemestrina*) anesthetized with Sufentanil (5 to 12 μg per kilogram of body weight per hour, intravenously). Appropriate anesthesia doses were determined for each animal before paralysis. During Flaxedil-induced paralysis (7 to 15 μg kg^{-1} body weight hour^{-1} , intravenously) anesthesia was monitored and adjusted according to standard criteria for electrocardiographic and electroencephalographic responses, including the absence of responses to noxious stimuli. Single-unit recordings were made with Levick-type electrodes inserted into the prelunate gyrus and lunete sulcus through a customized recording chamber. Additional details concerning recording and surgical procedures are given by D. J. Felleman and D. C. Van Essen [*J. Neurophys.* **57**, 889 (1987)] and by J. F. Olavarria, E. A. DeYoe, J. J. Knierim, J. F. Fox, and D. C. Van Essen [*ibid.* **68**, 164 (1992)].
12. The receptive field of each isolated unit was determined with a computerized visual stimulator. The stimuli were shown in the optimal color for each cell as determined in a preliminary test. They were displayed for 0.5 s on a gray background with a luminance that was roughly equal to the mean luminance of the stimuli (~ 10 cd m^{-2}). The stimuli covered the estimated receptive field and spanned a range of spatial frequencies surrounding the preferred frequency of a cell. Two or three phases were tested. Cartesian sinusoidal gratings were mixed with non-Cartesian gratings to facilitate comparisons of response rates. The partially randomized stimulus sequence was shown between three and eight times as needed to achieve consistent estimates of response magnitudes.
13. Cells were classified by comparison of the response rate obtained with the optimal Cartesian grating to that obtained with the optimal non-Cartesian grating. Response distributions were normalized and were then compared with a *t* test. Because there were more Cartesian than non-Cartesian gratings in the stimulus set, this is a conservative test with a bias against classification of cells as non-Cartesian.
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16. Additional evidence against size selectivity as a cause of non-Cartesian stimulus preferences comes from our anecdotal observation that many non-Cartesian cells responded only weakly to the bars of variable size and orientation used in our manual receptive field plotting procedure. Also, in the preliminary results of a test that systematically varied the width and length of Cartesian gratings, size selectivity failed to account for the response characteristics of 14 of 20 cells initially classified as non-Cartesian.
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TECHNICAL COMMENT

Tritium and Radiocarbon Dating of Canada Basin Deep Waters

Two of us (R.W.M. and E.C.C.) recently applied radiocarbon data to determine the rates of nitrate (NO_3^-) regeneration and oxygen (O_2) depletion in the Canada Basin of the Arctic Ocean (1). A one-dimensional, time-dependent diffusion model was used to calibrate the age of the deep water. The combination of this model with a model of an organic carbon (C) flux (2), suggested (1) how C fluxes into the basin might reflect primary productivity within the central Arctic Ocean. We wish to correct an error in the age estimates of the basin water (1) and to suggest where the basin-derived estimate of C flux might fit into the larger scheme of primary production in the Arctic Ocean.

The bottom waters of the Canada Basin

are old and appear not to be affected by recent inputs from dense waters produced on the shelves (1, 3, 4). This point is central to the assumption of a stagnant basin that undergoes property exchange only by top-down diffusion or by particle flux. However, as seen in table 1 of (1), detectable quantities of tritium have penetrated the top of the basin. While not contradicting the proposed model, the tritium data imply that radiocarbon from bomb tests has also penetrated the top of the basin, and this must be accounted for before radiocarbon ages can be used to calibrate the model. For the Arctic Ocean, tritium and ^{14}C data (3, 5) suggest an appropriate correction to be 3.5 per mil in ^{14}C for each 0.1 tritium unit (TU) above the "pre-

bomb value" [assumed to be about 0.10 TU (6)]. We have rerun the model, making this correction and choosing -55 per mil for the value of the prebomb ^{14}C concentration (3, 6). The new calculation yields an effective deep water age of about 500 years, not 983 years as estimated in (1); the new vertical diffusion coefficient is about $3.9 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$ [the estimate in (1) was $2.3 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$].

The new calculations, which reduce the deep water age by about a factor of 2 and increase the vertical diffusion, show that larger fluxes are required to reproduce the NO_3^- and O_2 profiles than was assumed in (1). Thus, for the 1500-m boundary, we estimate the NO_3^- flux to be 5.9 $\text{mmol m}^{-2} \text{ year}^{-1}$, the O_2 utilization rate to be 63 $\text{mmol m}^{-2} \text{ year}^{-1}$, and the respective C fluxes to be 0.47 to 0.58 $\text{g m}^{-2} \text{ year}^{-1}$. For the deep Atlantic Ocean, W. S. Broecker *et al.* (6) correlated the change (Δ) in ^{14}C with ΔO_2 content and arrived at a slope of 0.8 $\text{mmol m}^{-3} \text{ O}_2$ per mil $\Delta^{14}\text{C}$. As radiocarbon decays at 10 per mil per 80 years, Broecker *et al.* concluded that (6) the mean O_2 utilization rate was 10 mmol m^{-3} per