The Human Expression of Symmetry:
Art and Neuroscience

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Abstract

Symmetry is an important visual property for humans and for organisms in general. It is useful for discriminating living organisms from inanimate objects, for identifying face orientation and the direction of attention, and in the selection of desirable mates. Its importance to humans is expressed in its ubiquitous use as a design principle in objects of human construction (from buildings to Persian rugs). Symmetry is also expressed in less explicit form in the compositional structure of paintings, such as portraits, in the art of many eras.

A particular example of hidden symmetry in art is the placement of the eye in portraits. A survey of portraits over the past two millennia revealed that one eye has tended to be placed symmetrically at or near the vertical axis of the canvas throughout history. This placement violates the inherent symmetry of the face and body, which is placed asymmetrically, but expresses a deeper symmetry of centration of the 'window on the soul'. Most artists seem to be unaware of the accuracy of the symmetric placement. Overall, there is no bias in either which eye was centered or whether the face was turned left or right. Thus, the symmetry of eye placement seemed to be a core principle rather than a manifestation of some other asymmetry.

How rapidly is symmetry detectable by humans? Does it require comparisons among the reflected elements or is it apprehended in a single glance? The stimulus duration required for threshold detection is invariant at about .05 seconds over all regions of the retina. This duration is too brief for serial eye-movement or attentional comparisons and implies that human symmetry processing is global and hard-wired.

To explore the brain representation of symmetry for the first time, functional magnetic resonance imaging (fMRI) was used to identify occipital cortical areas activated by the presence of simple bilateral or multiple symmetries in fields of otherwise random dots. A variety of translational or reflection symmetries produced preferential activation of a dorsal region of the occipital lobe whose function is otherwise obscure. These stimuli produced little or no

differential activation of other known visual areas. Since symmetry is a common property of objects and faces, activation of this specialized occipital region seems to be encoding the presence of symmetry in the visual field.

Perceptual Processing of Pattern Symmetries

Visual perception begins with the projection of a visual image onto the array of retinal cones that each respond over as little as one minute of visual arc in central vision. In a series of transformations spanning many synapses and interconnections, visually responsive neurons in the brain become sensitive to areas of the visual scene that is more than 1000 times greater than individual cones. The large spatial extent of these cortical receptive fields raises the question of the types of visual computations that require such long-range connections in these portions of the brain. These computations may be useful for a variety of visual functions, including perceptual rescaling (color constancy, compensation for viewing angle, size constancy), estimating object properties (size estimation, perceptual grouping), and specific cues that are important for object recognition and classification (figure/ground segregation, contour completion, texture segmentation). The full response of the organism then involves the integration of the perceptual properties of objects into the matrix of meaningfulness and the set of appropriate responses that may be evoked.

Symmetry is an example of a cue that plays a profound role in object properties and requires long-range integration of object features across parts of the image. In many cases symmetry information is not present in the local features and can be found only by comparing information distributed across long distances in the visual field (Tyler et al., 1995; Szlyk et al, 1996). The reason for the perceptual salience of symmetry is unknown, but it can been argued that symmetry is a useful cue for discriminating living organisms from inanimate objects. That it is an important visual cue to humans is evident in the recurrence of symmetric patterns and designs throughout human history in the constructed environment from architecture and art to furniture and transportation.

An important issue relating to symmetry is that it is closely bound to the things commonly classified as 'objects'. Most objects, from umbrellas to dogs, have one or more axes of symmetry. Indeed, it is hard to think of a common object (other than a carefully selected rock) that exhibits no symmetry axes at all. Therefore, most studies of object processing, either with perceptual or brain response output variables, implicitly confound symmetry with object processing because they typically use scrambled images as controls, which destroy the symmetry relations in the objects just as they destroy the object coherence (edges, surfaces and so on). Nevertheless, it is perfectly possible to create asymmetric objects, for example by splitting pairs of bilaterally-symmetric objects down their symmetry axis and assembling

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asymmetric chimeras. So the concept of 'object' does not imply symmetry, even though they are commonly associated. To understand fully the neural basis of object processing, therefore, the stimuli need to be deconfounded from the symmetry property, in case much of what is thought to be (categorical) object processing is actually (perceptual) symmetry processing. Such issues tend to be underplayed by cognitive neuroscientists but are the natural domain of vision scientists, who focus on control of details of the physical stimulus before addressing its cognitive properties.

The artistic tendency to center one eye symmetrically in portraits

How then, is the ubiquitous property of symmetry in constructed objects expressed in the queen of the arts – painting? Painters have long been renowned for their multiplicity of compositional styles and avoidance of rules of composition. Nevertheless, the importance of the center of the canvas has long been appreciated; manuals of artistic composition highlight the importance of the central vertical line in various ways. How are such rules applies to the field of portraiture? There seem to be no formalized compositional rules about how to the place the features of the sitter in relation to the frame of the canvas, other than that it should form a "balanced composition". Nevertheless, it turns out that there is a high consistency to place one eye close to the center vertical to the picture frame throughout the history of Western portraiture.

To illustrate the degree to which an eye tends to be set near the center vertical, twelve classic portraits from the past six centuries are reproduced in Fig. 1. Selection for this figure was based on the artistic significance of the portraits with the heads in a variety of poses, with no attempt at a scientific sampling. From the perspective of frame geometry, many of the examples illustrate the lengths to which portrait artists seem to go to set one eye on the center line, even when they depart from the classic three-quarter pose. Several cases illustrate how clever composition generates the overall impression that the face is symmetrically located in the frame. Only when the guide lines are drawn through the pictures does it become clear that one eye is near the exact horizontal center.

Lateral Placement of the Eyes in Portraits

To quantify the relation between the position of the most-centered eye and the frame of the canvas, the horizontal and vertical position of the eyes was measured in portraits available from various sources. If eyes were positioned according the center of symmetry of the face, both eyes would be the same distance from the axis and the choice of the most-centered eye will make little difference to the result. Even if the head were close to the center vertical and there

were a random amount of head turn, the choice of the closer eye as the one for analysis would narrow the (Gaussian) distribution by only the square root of 2.

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Fig. 1. A selection of classic portraits over the past six centuries, reproduced to the full width of the original frame (with the exception of that of George Washington, from the $1 bill) and cropped at the bottom to match an arbitrary vertical dimension. The white line marks the horizontal center. Portraits are by Rogier van der Weyden (c. 1460) Sandro Botticelli (c. 1480), Leonardo da Vinci, 1505), Titian (Tiziano Vecellio; 1512), Peter-Paul Rubens (1622), Rembrandt van Rijn (1659), Gilbert Stuart (c. 1796, as reproduced on the U.S. $1 bill), Graham Sutherland (1977) and Pablo Picasso (1937).

Portraits were gleaned from a variety of published summary sources that contained a large number of reproductions of hand-composed portraits. To be included, the portrait had to be of a single person with no other dominant objects (such as the easel that it often included in self-portraits), and depiction of the body did not go below the waist, to ensure that the head rather than the figure was the principal element of the composition. A preliminary survey indicated that there was little tendency to center an eye in side-view or profile portraits (as in coins, medallions, stamps and so on), so these were excluded from the analysis.

Fig. 2 vividly illustrates how one eye is placed in a narrow distribution peaking at the lateral center in Western portraits over the centuries. Although this position may be related to previous compositional principles, consideration of the variety of hypotheses from the artistic literature implies that it would have been difficult to foresee this outcome before the study was conducted. In particular, many portraits are designed with an asymmetric composition that makes it hard to evaluate the symmetry of the eyes in the frame. Thus, it seems that the centering of one eye is appreciated at some subconscious level in the brain, while hidden from the domain of conscious judgments. In fact, a survey of classical texts on composition has turned up only one mention of the idea that the eyes as such should be positioned relative to the frame of the picture; the typical emphasis is on the placement of centers of mass or on eye placement relative to the vanishing point in cases of central perspective.

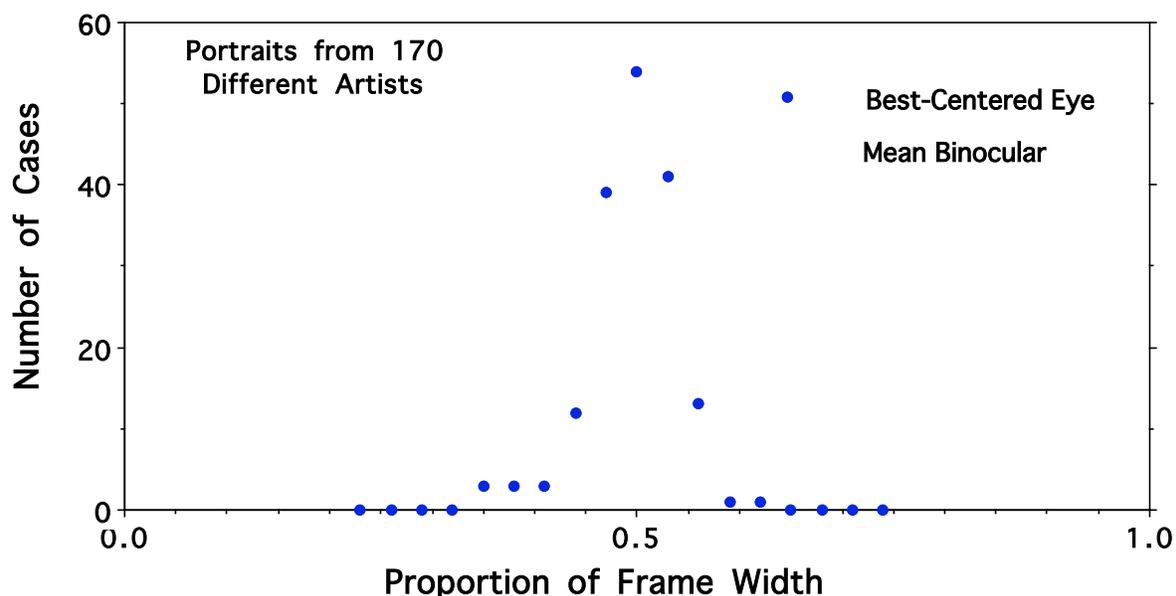## Shape of Distribution Indicates Placement Principle

Fig. 2. Histograms of lateral location of the best-centered eye (filled symbols, solid curve) compared with the mean binocular position (dashed curve) in portraits over the past 600 years. Note that the mean binocular curve is bimodal as expected if either one eye or the other is placed close to the center.

This distribution not only characterizes a tendency for the average portrait, it is also typical of many individual artists, including those who bucked the mainstream and developed highly individual artistic styles. Analysis of portraits by artists as idiosyncratic as Durer, Rembrandt, Modigliani, Picasso and Bacon, each of whom placed major emphasis on the portrait, reveals essentially the same distribution as that shown in Fig. 2. Picasso, in particular, specialized in breaking almost any artistic canon one can name, but adhered to the eye centering principle with uncanny accuracy. Thus, this principle seems to have a powerful hold on the preferred perceptual organization of individual representation. This is not to say, of course, that there are not exceptions and outliers. An artist is free to use a perceptual principle in either a positive of negative sense according to the goals of the picture, or to ignore it altogether if some other organizing principle is being employed. My intention is not to promote a constraint, but to follow an exploratory vein that may tell us something about the organization of human perception.

Now, what about the height of the eye? Would that have the some tight distribution, and also be centered vertically in the frame? Although the spread of the distribution was somewhat broader, none of the portraits had an eye below the vertical center, so there was a strong tendency for them to be high in the frame. A rule of great antiquity in art is that of the Golden

Section, the geometric ratio of 0.62 : 0.38 at which the ratio of the smaller segment to the larger is equal to the ratio of the larger section to the whole. It turns out that the vertical distribution of eyes peaks almost exactly at the Golden Section level, and was almost as narrow as for the width distribution. This analysis suggests that one can draw a box at this position that is only about 3% of the total frame area but will have an eye located in it in almost 90% of all portraits.

Finally, one can raise the objection that there is nothing special about the eye itself; the same kinds of regularities might be found for any principal feature in portraits. In fact, both the mouth and the nose distributions were as much as three times broader than the best-eye distribution, so it looked as though the eye was the dominant feature in terms of accuracy of placement. Similarly, the hands, another feature of interest, were distributed so widely that it did not even seem worth measuring their positions. It is instructive to look around the world and see how often an eye appears on the center-line of a frame, in photos, advertisements, movies and so on. There really does seem to be something special about that location that catches your attention.

Long range symmetry processing out to far periphery

Detection of mirror-symmetric objects in the visual field may be adaptive to survival in the animal world, where recognition of predators and prey could be based in part on discrimination of an animal's bilateral symmetry from the generally asymmetric background flora. In particular, when an animal turns to face the observing organism, seeing a meal or a mate, it displays its symmetry and becomes perceptually salient. Human symmetry detection has been well studied in the fovea,[Julesz, 1971 #8; Bruce, 1975 #12; Corballis, 1974 #24; Barlow, 1979 #1; Jenkins, 1982 #16] where it can be discriminated from noise for presentations less than 100 msec.[Barlow, 1979 #1; Carmody, 1977 #13; Tyler, 1995 #38] The rapidity of this processing suggests that it is an example of perceptual pop-out mediated by a specialized cortical mechanism in a lower cortical representation area such as V1 or V2, as supported by recent neurophysiological evidence of specialized responses to the medial axis of textured stimuli placed symmetrically in the receptive field.[Lee, 1995 #46]

Most previous studies of symmetry detection in both the fovea and periphery have shown its dependence on short-range mechanisms only,[Mach, 1886 #9; Julesz, 1971 #8; Kahn, 1981 #41; Jenkins, 1982 #16; Saarinen, 1988 #21; Locher, 1989 #43; Herbert, 1993 #42; Wenderoth, 1995 #35] implicating local, polarity -specific mechanisms by analogy with those in the other modalities. Three studies that used a longer range configuration [Corballis, 1974 #24; Barlow, 1979 #1; Labonte, 1995 #209] used low density random patterns in which the longer range of symmetry processing could have been mediated by "short range" mechanisms relative

to the low-spatial-frequency content of the patterns (since the range criterion is generally proportional to the spatial frequency content of the pattern). The discovery that it is polarity-insensitive complex cells that signal the symmetry axis of symmetric patterns [Lee, 1995 #46] makes it important to evaluate the role and extent of the long-range class of mechanisms in symmetry detection.

We therefore designed experiments to determine the range of pattern matching involved in human perception of mirror symmetry and to evaluate the relative sensitivity of local (linear receptive field) or long-range (polarity-insensitive pattern-matching) mechanisms as a function of retinal eccentricity. For a vertical axis of symmetry, pairs of sectors in a vertical configuration (Fig. 3a) contain information local to the symmetry axis, while pairs in a horizontal configuration (Fig. 3b) require long-range comparisons across the visual field

The experimental test images were scaled with eccentricity to compensate for the rapid fall-off of spatial resolution in the periphery. To minimize *a priori* judgments of the scaling factor involved, we employed a self-scaling image configuration (Tyler, 1982 #47; Watson, 1987 #44] by changing the viewing distance of the observer from the display. Thus, all aspects of the stimulus were scaled in direct proportion to retinal eccentricity, obviating the need to derive a functional relation for each aspect for human vision. (Without some scaling, the stimulus would soon become invisible beyond the fovea). The overall retinocortical scaling factor in effect may then be evaluated from the residual sensitivity variations with stimulus eccentricity. The stimuli consisted of bilaterally reflected, randomly-coloured blobs scaled in proportion to distance from the fovea, in opposing sectors of either a vertical or horizontal pair. The outer diameter of each sector was twice the inner diameter, as shown for two size scales in Fig. 3. The local symmetry axis was visible in the vertical pairs of sectors, whereas horizontal sectors presented widely separated symmetric regions with no information near the symmetry axis. This configuration was designed to allow evaluation of the presence or absence of short-range symmetry information at each eccentricity.

Fig. 3. Stimuli for testing symmetry discrimination across retinal eccentricity. Blobs randomly colored either black or white, each blob consisting of pixels in a random Gaussian density distribution, were bilaterally reflected about a vertical axis. Each stimulus consisted of a pair of quadrant annuli, or sectors, presented at 6 viewing distances to cover eccentricities on the retina of 1-2° to 32-64°; at the greatest eccentricity, pairs spanned 128° of the visual field. Either vertical (a) or horizontal (b) sector pairs were selected, with the remaining quadrants masked to match the mean-luminance background. Pre- and post-test intervals were masked with random dynamic modulation of the blob structure to obliterate processing based on afterimages. c) Demonstration stimuli illustrating the ease with which long-range

symmetry is perceived. By fixating the eyes on the central fixation Fs at a various viewing distances from 10 cm to 1 m, the viewer may assess how readily long-range symmetry is perceived in the high-density and low-density patterns.

Sensitivities in vertical and horizontal sector pairs at eccentricities ranging from fovea to extreme periphery are shown in Fig. 4. The principal result for both observers is that, under the self-scaling regime, duration sensitivity is essentially uniform across eccentricity for both horizontal and vertical sectors (except in the fovea), implying that the self-similar scaling matched sensitivities within a factor of about $\sqrt{2}$ for this task. Beyond the fovea, the slopes of the eccentricity functions do not differ significantly from zero for any condition. The observers were able to discriminate symmetric from non-symmetric patterns for presentations of less than 50 msec at any eccentricity. This performance is particularly remarkable in the case of the horizontal sector configuration. At the greatest eccentricity, immediate comparisons may be made between the two patterns over as much as ~90° of the visual field (or over at least 64° between the edges of the patterns), which we believe to be the longest retinal range ever established for any pattern-matching task.

The remarkable pattern-processing abilities revealed by the symmetry discrimination across the entire range of visual eccentricity pose a challenge for models of pattern recognition in visual cortex. In the case of the horizontal configuration, pattern-processing mechanisms must be matching up the symmetric information from one cortical hemisphere to the other on the basis of an extremely short stimulus presentation followed by a masking stimulus. The peak response evoked by the median axis of a textured strip when it is centered within the receptive fields of some complex cells in V1[Lee, 1995 #46] could subserve a limited form of this pattern-matching role, although such cells have been demonstrated only up to a range of 6°. Perhaps cells with specialized symmetry responses of sufficiently long range to account for the present results range may be found in higher cortical representation areas, possibly even aggregated to for a cortical representation specific to bilateral symmetry detection.

Fig. 4. Sensitivities for two pattern densities in sector pairs at mean retinal eccentricities ranging up to $\pm48°$. Sensitivity was measured as the reciprocal of duration required to reach a threshold criterion of 60% correct. Top, discrimination of symmetry in vertical sectors for two observers; bottom, symmetry discrimination in horizontal sectors for two observers. Left side of plots (short-dashed lines) are reflected versions of the data shown on the right sides, to emphasize that the symmetric stimuli were presented in both hemifields.

Minimum duration for symmetry detection is essentially uniform over retinal eccentricity ($\pm$!0.2 log unit in each condition), indicating no measurable reduction in sensitivity for bilateral symmetry even in the extreme periphery.

Mapping the human brain response to symmetry stimuli

Our psychophysical results imply that symmetry is an object property that requires long-range integration of scene features for its perception. In many cases symmetry information is not present in the local features and can be found only by comparing information distributed across long distances in the visual field. This section describes functional magnetic resonance imaging (fMRI) to investigate activity in the visual cortex while observers view patterns containing large-scale symmetry. The object of the study was to determine whether the property of symmetry would activate known retinotopic regions of cortex or elicit specialized responses.

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The stimuli were fields of white dots 26° in diameter at 25% density on a dark background organized in patches of symmetry structure alternated with a sequence of control stimuli of purely random dots. Examples of the symmetry stimuli we used are shown in Fig. 5. A particularly effective version was the four-axis reflection symmetry pattern exemplified in Fig. 5a, alternating with a purely random pattern such as Figure 5b. The stimulus sequence consisted of an 18 s period of blank or symmetric patterns which changed every 1.5 sec, followed by 18 s of purely random dot patterns, also updated every 1.5 sec. The control stimulus consisted of a blank, dark field alternated with purely random dot patterns (Figure 5b). The alternation sequence was repeated 5-6 times per scan.

We use the term multiple symmetries in the physicists' sense of any regular similarity in pattern across regions of an image. It thus includes not just reflection symmetry around various

| a | b | c |
| Four-fold Reflection | Random | Repetition |
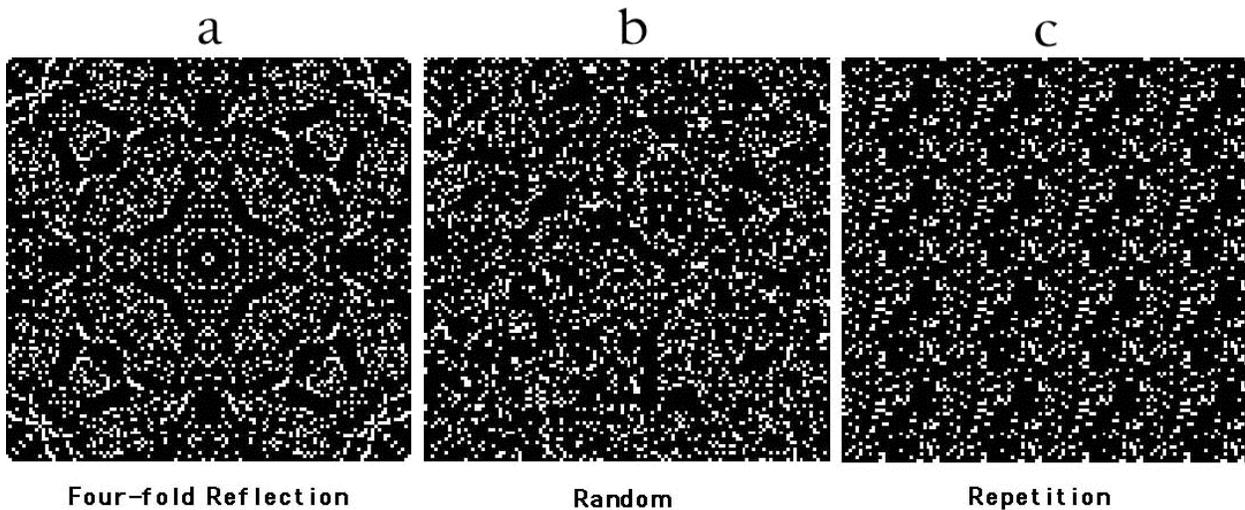
axes but translational symmetry and other transformations. As examples of the symmetry stimuli for fMRI testing, Fig. 5a shows a sample of four-axis symmetry, one of the most perceptually salient of our stimuli. Note that very little of the symmetry can be detected by local spatial analyses spanning the size of classical receptive field sizes found in primary visual cortex, typically less than 0.5° in diameter. A purely random dot pattern of the type used for control stimuli is shown in Fig. 1b. Although replete with contours and blobs, its pattern structure does not resonate visually like a symmetric pattern. A second type of mathematical symmetry, repetition symmetry, is shown in Fig 1c. Around the fixation center there is literally no information that the pattern deviates from random. It is only by a comparison across one repetition cycle, a long-range pattern match, that information about the pattern structure becomes available.

In Fig. 6, symmetry activation is compared with the location of the retinotopic visual areas. The computed spatial distribution of fMRI symmetry activation across slices is projected onto the 3D brain renderings of one occipital lobe in three orientations. To meet the significance criterion, voxel responses must respond within a 6-sec window following the onset of the symmetry phase of the stimulus, and reach a stimulus correlation level of 0.40 - 1.00 (orange > yellow > white coding). This activation forms a vertically extended region around and including much of the middle occipital gyrus (MOG), reaching up to near the parietal-occipital border. The 3D images illustrate that there was virtually no activation in response to the symmetry condition on the medial surface of the occipital lobe on which are represented the major portions of visual projection areas V1, V2 and V3 (medial rendering at right in Fig 6b). These projection areas have a retinotopic mapping from adjacent points in the visual field to adjacent points on the cortical surface (Tootell et al., 199?). Compared with the positions of known visual areas mapped by the standard rotating checkerboard wedge technique (Engel et al., 1995), the symmetry activation is lateral to the retinotopically organized areas (V1-4), but medial and posterior to the motion-specific area, V5/MT+, shown in cyan. Moreover, the symmetry-specific activation that we report is primarily dorsal with respect to the location of the object-specific lateral occipital area, LO, which has been reported to fall mostly on the ventrolateral surface of the cortex, between areas V4 and V5/MT+.
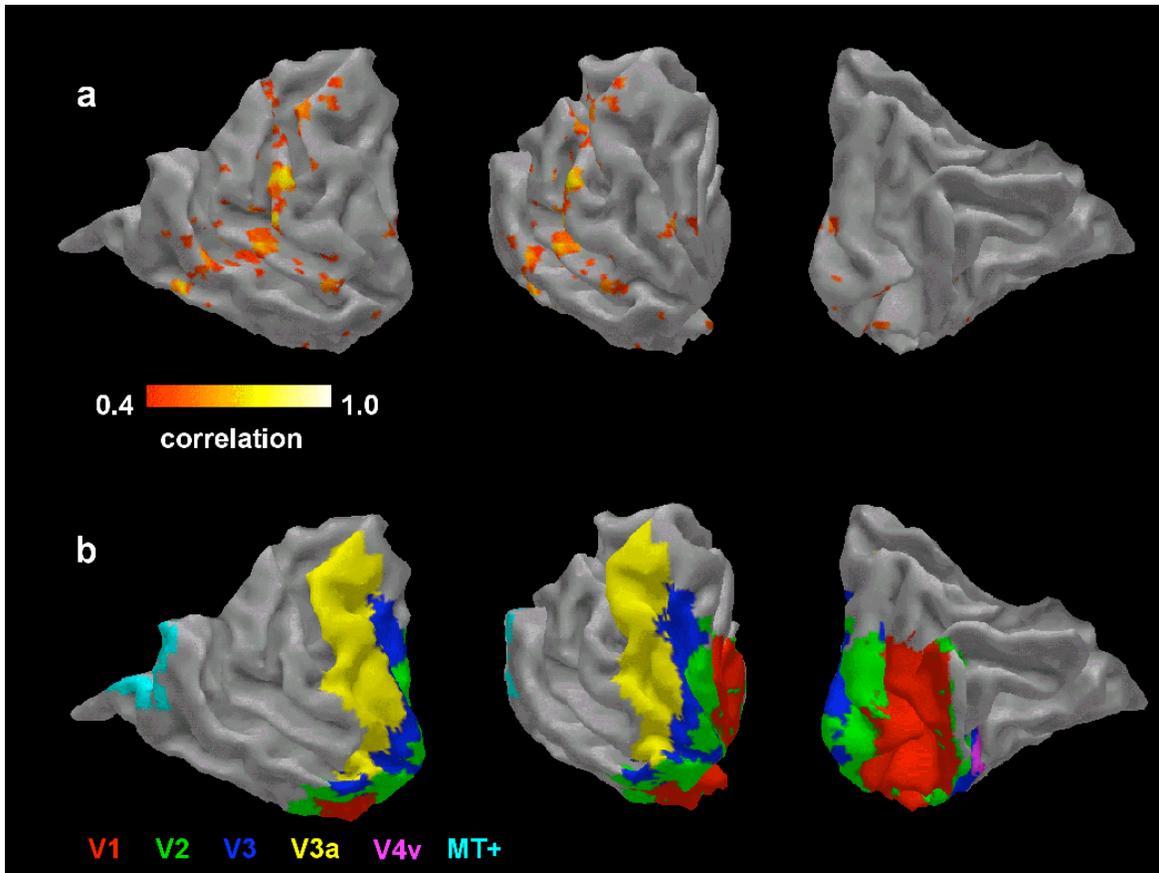
Figure 6. Three-dimensional renderings of the left occipital lobe in one subject (CT) depicting a) regions that responded to the presence of four-axis symmetry (fMRI activation shown in orange) compared with b) the positions of the retinotopic visual areas: V1 (red), V2 (green), V3 (blue), V3a (yellow), V4v (magenta) and V5/MT+ (cyan). Left, middle and right panels depict lateral, posterior and medial views, respectively. Images are rendered near the boundary between the cortex and white matter.

The data are consistent with the idea that regions in and near the MOG are involved in the processing of long-range stimulus structure. Because there is little symmetry-related activity in the early, retinotopically organized visual areas, the responses cannot be explained by the long-range connections present in area V1 (see Callaway, 1998 for review), area V2 (von der Heydt & Peterhans, 1989; Merigan et al., 1993) or other retinotopic areas (Reppas et al., 1997). Instead, the symmetry-specific responses imply the existence of neurons with larger receptive fields that are driven by patterns of activity spread across the mosaic of neurons in earlier visual areas. The role of the MOG in long-range visual processing is supported by studies that found a nearby and perhaps overlapping occipital region with a large representation of the ipsilateral

visual field (Tootell et al., 1998) Occipital regions including the MOG have also been implicated in the processing of illusory contours (Hirsch et al., 1995; Mendola et al., 2000) and at least a subset of the MOG (the KO region) may be involved in the detection of motion boundaries(Van Oostende et al., 1997). The detection of both types of stimuli benefits from the long-range integration of visual information.
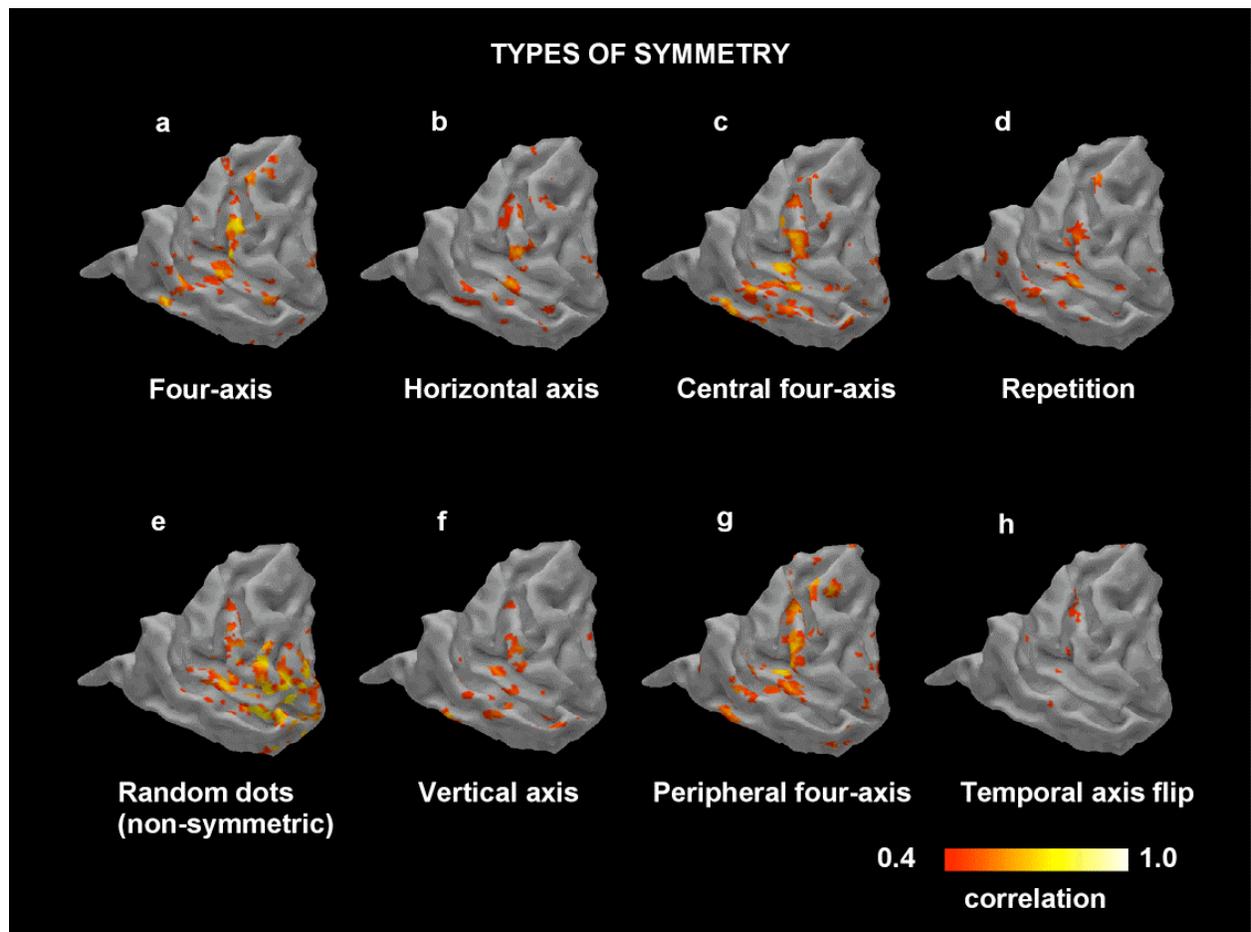

Fig. 7. Comparison of significant activation of the lateral left occipital lobe of one observer (CWT) by eight varieties of pattern stimulation. (Similar results were seen in both hemispheres and in the other two observers.) a) Responses to four-axis symmetry stimuli (Fig. 5a) vs. purely random dots (Fig. 5b). b) Responses to one-axis symmetry around the horizontal meridian. c) Responses when four-axis symmetry is restricted to the central part (0 to 6.5 deg eccentricity) of the stimulus. d) Responses to translational symmetry of repetitive random-dot tiles (wallpaper stimulus, Fig. 5c). e) Responses to the control stimulus, blank (dark) field vs. random dot patterns (Fig. 5b). f) Responses to one-axis symmetry around the vertical meridian. g) Responses when four-axis symmetry is restricted to the peripheral part (6.5 to 13 deg eccentricity) of the stimulus. h) Response to flipping the random dot field around a randomly-chosen axis every 1.5 seconds.

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Based on the stimulus properties, we conjecture that the symmetry information is unavailable to neurons that receive input from only a small portion of the visual field. Still, it is possible that the signals we observe are driven mainly by neurons with small receptive fields near the main axes of symmetry. To press this hypothesis and to determine whether symmetry is processed retinotopically within the MOG, we performed three additional experiments. First, we compared fMRI responses when the orientation of a single symmetry axis was either horizontal or vertical. Second, we compared activity when the symmetry was restricted either to the central visual field or to the periphery. Third, we measured responses to repetition symmetry (Figure 1c), which has long-range structure, but no foveal focus.

Fig. 7 summarizes the fMRI responses in the lateral occipital lobe of one observer for a number of symmetry patterns. Figure 7e shows the fMRI response in a baseline scan in which non-symmetric, random dot patterns were alternated with a blank (dark) field. Significant activity is present both in retinotopic areas such as V3a (see same subject in Fig. 3b) and in the mid-occipital region adjacent to the MOG. Figures 7a-d,f-h show fMRI responses when the various types of symmetric patterns derived from random dots are alternated with purely random dots. Figures 7b and 7f compare the activity when a single symmetry axis is oriented either horizontally or vertically. The spatial distributions of the activity largely overlap, implying that the responses are not retinotopically organized with respect to axis orientation. The distributions are also quite similar to the activation region for four-axis symmetry (Fig. 7a), indicating that the inclusion of three more axes after the first confers only a small advantage. The lack of retinotopic organization is confirmed in Figs. 7c and 7g, which compare fMRI responses when the symmetry of the random texture is restricted to the central 1/4 or peripheral 3/4 of the stimulus field. The two conditions again activate largely overlapping regions of the MOG, although the central symmetry stimulus activated the ventral LO region more strongly in this observer (Malach et al, 1995; Tootell et al., 1996). Figure 7d shows the response to repetition or translational (wallpaper) symmetry. In this stimulus, there is no local information concerning symmetry at all, but only long-range structure (Figure 1c) at the distance of one repetition cycle. Again, the significant activity is found in a region of cortex, including the MOG, that overlaps with that for one-axis (Fig. 7b,f) or four-axis (Fig. 7a,c,g) reflection symmetry. Results similar to those in Fig. 7 were obtained in both hemispheres and in the other two observers, although not all conditions were tested in all observers.

Fig. 7h provides an important control against the idea that the responses represent the activity of attending to or looking for symmetry rather than a direct response to the presence of the symmetry pattern. For this condition, the texture was completely random, but the pattern on each 1.5 s frame was derived from the previous by flipping it around a horizontal, vertical,

left- or right-oblique axis, randomly selected on each trial. The observer often found it difficult to detect the symmetry transform in this condition, and hence was making maximum effort to determine which axis had been selected for each flip. Nevertheless, the response is much reduced in this condition relative to any others, indicating that it is the presence of pattern symmetries rather than the effort to observe them that is the basis for the signal we record. However, it is noteworthy that the small focus of significant response for the axis flip condition again lies in the MOG region, suggesting that the weak symmetry signal of the temporal sequence is again processed in the same brain region as for the spatial symmetries.

In conclusion, this initial evaluation of cortical processing of symmetry established that symmetry/random alternation is a sufficient stimulus for significant fMRI activation in a little-understood region of the human occipital lobe in and around the middle occipital gyrus. The activation did not appear to be retinotopically organized. The high level of activation in the MOG may represent part of a general class of computations that require integration of information across a large span of the visual field. These observations provide an approach to the exploration of the corresponding processing in homologous areas of other species by classic neurophysiological and neuroanatomical techniques.

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