Symmetry activates extrastriate visual cortex in human and nonhuman primates

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Humans often create and appreciate visual symmetry in their environment, and the underlying brain mechanisms have been a topic of increasing interest. Here, symmetric versus random dot stimuli produced robust functional MRI (fMRI) activity in higher-order regions of human visual cortex (especially areas V3A, V4, V7, and LO) but little activity elsewhere in brain. This fMRI response was found both with and without attention controls. Moreover, it was highly correlated with the psychophysical perception of symmetry. Similar symmetry responses were found by using line-based and dot stimuli and were found at a wide range of stimulus sizes and geometric configurations. Weaker symmetry responses were found in analogous regions of macaque visual cortex by using fMRI techniques with higher sensitivity. This evidence suggests that visual symmetry is specifically enhanced in the human brain, but that the underlying neural mechanisms may nevertheless be resolvable in nonhuman primates.

functional MRI | monkey | psychophysics

In different contexts and across many different cultures, humans create and appreciate geometrical order; often our species does not just passively coexist with entropy. Sometimes this preference for order may simply reflect practical constraints. For instance, houses are more likely to remain standing when the underlying structural geometry is orderly, and it may be easier to recall the location of objects in an orderly environment. However, in other instances (e.g., art and religion), the human preference for order does not have obvious survival value. The latter examples could conceivably reflect an intrinsic cognitive bias for order over randomness.

Visual symmetry is a special form of order that may reflect such intrinsic biases (1–3). For instance, human faces are perceived as sexually more attractive when they are bilaterally symmetrical (4–7); this conclusion has been interpreted as an (perhaps unconscious) awareness that genetically linked pathologies can produce bodily asymmetries. In many other instances (e.g., kaleidoscopes and primitive pottery decoration), symmetry may be simply pleasing to the mind's eye (for review, see ref. 8).

In an intriguing initial study, Tyler *et al.* (9) reported that symmetric visual stimuli produce increased fMRI activity in higher-tier human visual cortex. Here, we extended the results of that study in several directions.

First, we tested whether such fMRI activity is correlated with the "perception" of symmetry by using systematically graded levels of symmetry and psychophysical measurements. An excellent correlation was found, especially in higher-tier visual cortical areas V3A, V4d/v, V7, and lateral occipital (LO).

Second, animals do not create symmetric stimuli. It may well be, however, that animals appreciate symmetry, for example, in their selection of sexual partners. Is the symmetry response an evolutionary specialization that is unique to humans, or does the symmetry response exist in animals? To clarify this question, we tested for an analogous symmetry response by using fMRI in awake fixating monkeys, and many procedures were common to the human fMRI. Although it was much weaker than in human subjects, we did find an analogous fMRI response in macaques.

Third, in humans, we also tested a wide range of control stimuli to further characterize the "symmetry" response. Ultimately, is the response really selective for symmetry? Control experiments by using stimuli of widely differing size showed that the localization of the fMRI activity was not an artifact due to preferential activation of the larger receptive fields in the higher-tier cortical areas. Control of visual attention slightly decreased the amplitude of the symmetry response, but the topography of the response remained largely unchanged. Additional controls revealed that a symmetry response was produced by stimuli of one-, two-, and fourfold radial symmetry, as well as "repetition" (tiled) stimuli, although the response amplitude varied in accord with salience and previous psychophysical expectations. Finally, the symmetry response proved relatively stable, whether produced by either dot- or contour-based stimuli.

Fourth, in the initial study (9), a prominent symmetry response was reported in an area (DLO), based on the number of voxels responding to the symmetry tests themselves, relative to volumetrically equated regions in most (but not all) of the retinotopic areas and area MT+. Not surprisingly, this approach resulted in very large apparent symmetry responses in DLO. Here, we instead defined all regions of interest based on area-labeling tests that were independent of the symmetry stimuli, based on the percent activation in all of the voxels, in each region of interest. This approach revealed a more widespread symmetry response in human visual cortex that was highest in areas V3A, V4d/v, V7, and LO, marginally present in V3, and absent in areas V1 and V2.

Methods

Subjects. Nine human subjects were used, although (for practical reasons) each subject could not be used in all experiments. All subjects gave written consent. The experiments were approved by Massachusetts General Hospital Institutional Review Board (MGH-IRB). Subjects were aged 26–38 years with normal or corrected-to-normal vision. In addition, three male rhesus monkeys (2.5–3.5 kg) were scanned. All procedures for animals were approved by MGH-IRB in accordance with National Institutes of Health guidelines.

Visual Stimuli. In most symmetry tests (e.g., experiments 1–5), we generated kaleidoscopic (fourfold radial) symmetry patterns based on sparse (1.8% density) white dots on a black background, mirror-reflected along the vertical, horizontal, and intervening oblique axes (Fig. 1 *A* and *B*). Within each 45° wedge, the dots were randomly arranged. Visual stimuli were generated by a Macintosh (Apple) G3 or G4 laptop with MATLAB 5.2.1 and PSYCHTOOLBOX MAC 2.52 (10). In control experiments (e.g., see *Supporting Text* and Figs. 6–9), we also generated and tested stimuli with one- and twofold symmetry (folded along either horizontal or vertical axis), and "tiled" (repetition) patterns

Abbreviations: BOLD, blood oxygenation level-dependent; fMRI, functional MRI; LO, lateral occipital.

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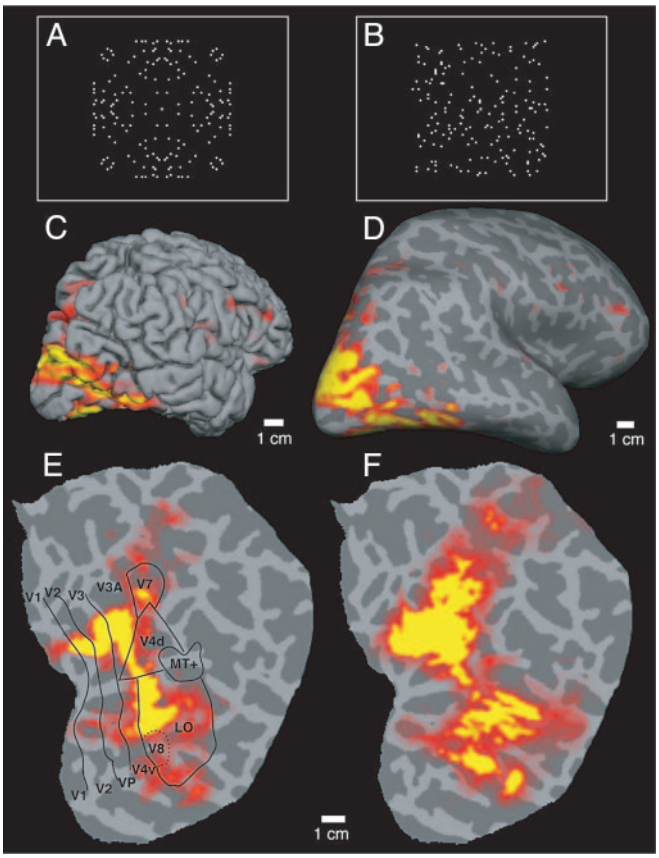

Fig. 1. Experimental stimuli and resultant brain activation. (*A*) Example of the symmetric dot stimuli. (*B*) Example of random dot control stimuli. In every stimulus, a small ''bull's eye'' fixation target was present at the center of the screen. (*C*) Example of relative brain activation (BOLD-based fMRI) produced by symmetric (compared with random) dot stimuli, shown in the normal ''folded'' format, in the right hemisphere (posterior-lateral view) from one subject. Activity threshold (gray-red), $P < 0.001$; red-yellow transition, $P < 10^{-10}$. (*D*) Same data as in *C*, now shown in the ''inflated'' cortex format. (*E*) Symmetry-biased activation in the ''flattened'' cortex format from the same subject as in *C* and *D* with visual areas also labeled. Only the posterior (visual) portion of cortex is displayed. (*F*) Symmetry-biased activation averaged across all imaging subjects presented with this subset of stimuli ($n = 5$), shown in the same format as *E*. Activity threshold in group data (gray-red), $P < 10^{-4}$; red-yellow activity transition, $P < 10^{-40}$.

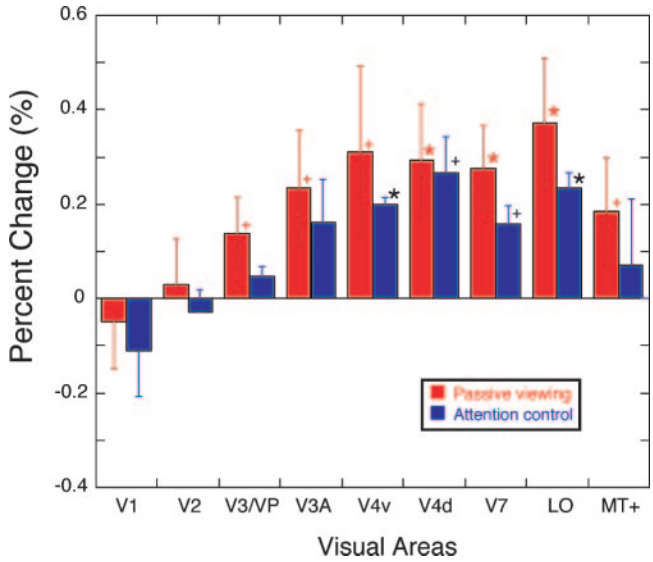

Fig. 2. fMRI differences produced by symmetric (relative to random) dot stimuli (e.g., Fig. 1 *A* vs. 1*B*), measured in specific visual cortical areas, with and without controls for attention. The red bars show the amplitude of the fMRI-based symmetry activation during simple passive viewing. The blue bars show analogous data acquired when subjects viewed the same stimuli while concurrently attending to nonsymmetric aspects of the stimuli. On average, these attention manipulations reduced the amplitude of the symmetry activation by 0.1% relative to passive fixation. Asterisks indicate visual areas that were activated significantly more (*t* test) by the symmetric stimuli compared with the random patterns: +, $P < 0.05$; *, $P < 0.01$. In no cortical area was there a significantly greater response to random than to symmetric dot arrays.

based on 2 × 2 or 4 × 4 tiles; these stimuli were otherwise equivalent to the fourfold radial dot patterns used in the main experiments. Except as noted, the stimulus was a square 16° on a side, and each dot was 0.16° wide.

To control for attention (e.g., experiments 2–5, Fig. 2, and *Supporting Text*, which is published as supporting information on the PNAS web site), subjects performed a detection task during presentation of the random dot stimuli. In half of the presentations, one of the dots was made slightly reddish. This probe dots' location, and the timing of its appearance, were randomized and unpredictable. Subjects indicated the presence of a reddish dot by a button box located inside the scanner. The threshold ratio of red/white in the probe dot was modulated by the staircase method to keep the subjects performance level constant and prevent pop-out effects. Except for the probe dot, the stimulus was equivalent to the other random dot stimuli.

To test the correlation of perception and fMRI (experiment 3), patterns comprised of symmetry plus noise were generated in a graded series (e.g., Fig. 3*A*). There were five conditions: 100% noise (i.e., random), 68% noise, 34% noise, 17% noise, and 0% noise (100% symmetric). For example, in the 17% noise conditions (Fig. 3*A*, *Upper Center*), initially we generated 100% symmetric dot patterns, then erased 17% of dots (randomly selected), then replaced that number of dots at random locations in the stimulus. In the 100% noise condition, the dot configuration was entirely random. Subjects were required to maintain central fixation while they performed the discrimination task. To measure the psychometric function (e.g., Fig. 3*B*), subjects were asked to press one of two buttons indicating whether a given stimulus appeared random or (at least partially) symmetric. Thirty stimuli were generated at each level of noise (150 total), and those stimuli were presented in random order.

Imaging. MRI data were acquired at 3 T by using procedures described in refs. 11 and 12. For further details, see *Supporting Text*.

Results

Experiment 1: Localization. To evaluate symmetry processing in the brain, we first presented symmetric versus random dot stimuli (e.g., Fig. 1 *A* and *B*) to normal human subjects during fMRI scanning. Subjects were instructed to view the sequence of stimuli while fixating on the center of the stimulus. A block design was used for maximal sensitivity. A new stimulus was generated every second to randomize dot position. Other aspects of the stimuli (e.g., dot size, number, and density) were equated across symmetric and random dot conditions.

Despite these overall similarities between stimuli, we found a robust increase in fMRI activation to the symmetric stimuli in the visual cortex (see Fig. 1 *E* and *F*) in each of the nine human subjects tested. The increase in fMRI activation for the symmetry stimuli, relative to the activation produced by fields of purely random dots, will be called the symmetry response.

This symmetry response was concentrated in visual cortical

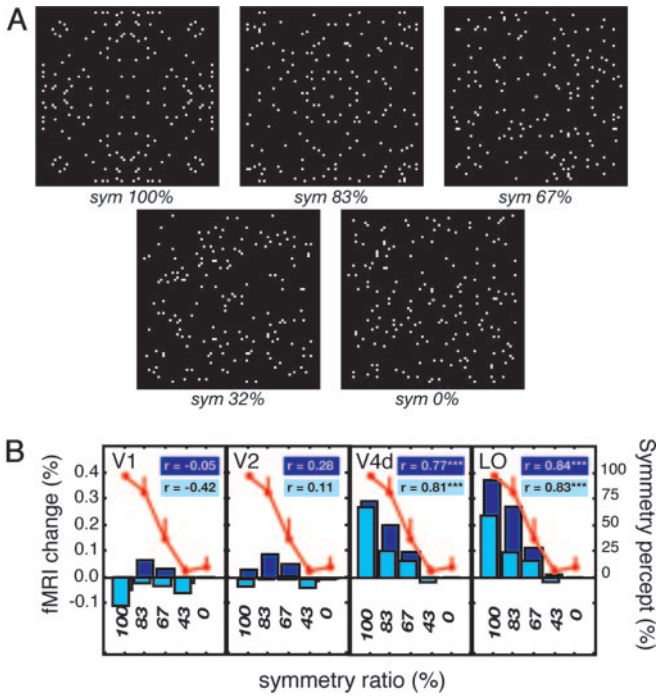

Fig. 3. Correlation between symmetry perception and brain activation in different visual areas. (*A*) Examples of test stimuli with different levels of noise ranging from 100% symmetry to random. (*B*) Correlation between fMRI signals in the passive-viewing (blue bars) and attention-controlled (cyan bars) experiments in representative visual areas, V1, V2, V4d, and LO (results from all visual areas tested are shown in Fig. 5). Baseline (zero) in the bar graphs corresponds to the averaged fMRI signal produced by the random dot stimuli. The *x* axis represents the symmetry ratio. The red graph shows the psychometric function of the symmetry percept; for ease of comparison, it is replotted for each visual area. The psychophysical threshold for symmetry detection was ≈50%. Asterisks superscripted to the correlation coefficients (blue for the main passive viewing, cyan for the attention controls) indicate statistical significance level: +, $P < 0.05$; *, $P < 0.01$; **, $P < 0.001$; ***, $P < 0.0001$. The fMRI and psychophysics were both averaged across all subjects.

areas known to have larger receptive fields, such as areas V3A, V4d/v, V7, and regions known to be involved in object recognition (e.g., LO) (13). In lower-tier areas known to have smaller receptive fields (e.g., V1 and V2), there was little or no significant symmetry-specific activation (see Fig. 1). The symmetry activation was largely confined to the visual cortex, with very little activation in higher-order brain regions beyond the visual cortex (e.g., Fig. 1 *C* and *D*) or subcortical regions (data not shown). The relative lack of activity outside visual cortex suggests that the symmetry response is due largely to intrinsic or bottom-up processing, not a reflection of top-down processing within the visual cortex.

Experiment 2: Effects of Attention. fMRI studies suggest that variations in visual attention could contribute to the blood oxygenation level-dependent (BOLD) response to this (or almost any) stimulus. Here, subjects might inadvertently attend more to the symmetric stimuli than to the random dots in the passive viewing conditions described above (e.g., Fig. 1 *A* and *B*). To test this hypothesis, we conducted additional fMRI experiments in which subjects were required to attend to nonsymmetric features in both the symmetric and random dot stimuli. In half of the 1-sec trials (randomly ordered), one randomly chosen dot was made slightly reddish by manipulating the color saturation, and the subjects were required to detect this threshold colored dot (see *Methods*). To keep attention load equal (and high) across all dot stimuli, this threshold dot saturation was maintained throughout the scan by using a dynamic staircase procedure with the subject performance converging at 68% correct.

Consistent with other studies (14), this attention to irrelevant stimulus features reduced the overall amplitude of the fMRI difference based on the relevant feature (here, symmetry). The effect of attention was statistically significant, when calculated over all visual cortical areas tested (paired *t* test, $P < 0.001$). However, in most areas, the effect of attention was small (average magnetic resonance signal change = 0.1%) relative to the effect of symmetry itself. Moreover, the same general set of visual areas (e.g., V3A, V4d/v, V7, and LO) remained selectively activated by the symmetric stimuli with or without the attention controls. Thus, most of the symmetry activation was apparently due to sensory factors, not uncontrolled attention.

Experiment 3: Correlation Between Percept and fMRI. Does this neural selectivity for symmetry have anything to do with the perception of symmetric stimuli? If so, variations in the perceptual salience of the symmetry might correlate with fMRI measures, as in previous studies correlating fMRI with visual perception (e.g., refs. 15–17).

We tested this hypothesis by first presenting subjects with a graded series of dot stimuli, ranging from fully symmetric to random (Fig. 3*A* and Fig. 5, which is published as supporting information on the PNAS web site), with and without the attention controls (see Fig. 3 *B* and *C*). This fMRI data were then compared to psychophysical measurements made outside the scanner, in which subjects were presented with these same stimuli and were asked to indicate whether the stimuli were symmetric.

The perception of symmetry decreased as dot position was increasingly randomized. In higher-order visual cortex, the symmetry-specific fMRI response decreased correspondingly as noise was added to the otherwise-symmetrical stimuli. By calculating the correlation between psychophysical and fMRI measurements during this series, it became possible to quantify which cortical visual area(s) are most likely to mediate the perception of symmetry. These relationships are shown in Fig. 3. Generally, we found that the same visual areas (e.g., V3A, V4d/v, V7, and LO) that showed the largest fMRI responses to the symmetric-random differences also showed the highest correlation to the variations in symmetry perception. Again, this relationship held whether attention was controlled.

For instance, BOLD signals were significantly larger for 100% symmetry patterns than for random patterns (paired *t* test: V3/VP, $P < 0.02$; V3A, $P < 0.02$; V4v, $P < 0.02$; V4d, $P < 0.001$; V7, $P < 0.005$; LO, $P < 0.005$; in the passive viewing experiment condition: V4v, $P < 0.01$; V4d, $P < 0.03$; V7, $P < 0.02$; LO, $P < 0.005$ with the attention controls). In V1 and V2, BOLD signals to 100% symmetry patterns were not statistically different from those to random patterns, with or without attention controls.

Experiment 4: Additional Controls. Most of our stimuli were based on fourfold mirror symmetry, but topographically similar results were also produced by other forms of mirror symmetry, such as twofold and onefold symmetry (see Fig. 6, which is published as supporting information on the PNAS web site). The fourfold symmetry produced slightly larger fMRI signals, consistent with an earlier fMRI study showing a minor advantage of radial stimuli (18). When the axis orientation was horizontal (up-down symmetry), the symmetry response was somewhat weaker than the vertical (left-right symmetry). This finding is in accord with previous psychophysics and single-unit studies (19). Interestingly, this selectivity for symmetry remained even when otherwise similar repetitive (tiled) dot arrays were used as control stimuli (see Fig. 7, which is published as supporting information on the PNAS web site). These fMRI differences support earlier

psychophysical and theoretical work that distinguished between mirror- and repetition-based dot arrays (20, 21).

We have shown that V1 and V2 did not produce any preferential symmetry response. However, it might be argued that the lack of symmetry response in these areas could be caused by a sampling bias because we sampled the entire extent of stimulus-activated V1 and V2. If, for instance, only the peripheral representations of these visual areas have a symmetry response, the sampling of the entire regions of V1 and V2 might have obscured such a tendency. To test this theory, we resampled fMRI responses separately from the foveal and peripheral (subdivided at 5° eccentricity) representations in V1 and V2. Fig. 8, which is published as supporting information on the PNAS web site, clearly shows that the BOLD response to symmetric and random stimuli were not statistically different between the fovea and peripheral parts in each of V1 and V2.

Similarly, one might argue that the symmetry response was largely confined to the higher visual areas (which have larger receptive fields) simply because our stimulus size was large (16° on a side). By this argument, if the stimuli were smaller, then the lower visual areas would have a correspondingly better chance to respond. We did a control experiment to test this idea, comparing the effects of dot array stimuli (symmetry versus random) by using large and small array sizes (16° and 4° on a side, respectively). Fig. 9, which is published as supporting information on the PNAS web site, shows that the higher-order visual areas were activated essentially equivalently, irrespective of the array size. If anything, the large array size produced more activity in lower-tier areas (e.g., V1, V2, etc.) than higher-tier areas. These two control tests largely discount concerns about stimulus size in the symmetry response.

A further issue that may arise in the interpretation of the above random-element targets is that the symmetry response in lateral occipital cortex may be attributed to a secondary perceptual effect of symmetry rather than to the direct results of symmetry processing. Despite the fact that the symmetry images contain the same local information as the nonsymmetric null stimuli, there is a tendency for the symmetric stimuli to evoke stronger percepts of contours and shapes than the nulls. Although these percepts are an inevitable consequence of the symmetry, they might be regarded as a separate neural process that does not, in itself, constitute symmetry processing.

To address this concern of the basis of the fMRI signal, we ran a further control study that manipulated nonsense contours. Bilateral symmetry modulation was applied to complex contour stimuli such that the contours were equally salient for both symmetric and nonsymmetric nulls. The contour stimuli were generated as smooth random modulations relative to a circle at 8° eccentricity, forming multilooped filigree figures (see Fig. 10*A*, which is published as supporting information on the PNAS web site). The fMRI responses to these stimuli were recorded in a paradigm that was similar to that of the main study. As in that study, strong symmetric/nonsymmetric activation again occurred in lateral occipital cortex (see Fig. 10*B*).

Experiment 5: Monkey fMRI. What are the evolutionary roots of this symmetry response: is it a general-purpose feature of mammalian visual processing, or is it a uniquely human specialization? To test for a symmetry-specific activation in our primate relatives, we measured fMRI responses in awake fixating macaques in response to the same dot-symmetry comparisons used in our human experiments (e.g., Fig. 1). Initially, when using the same scanner and conventional BOLD signals as in our human subjects, we did not find a significant symmetry response in macaques. By itself, this result would suggest that the neural symmetry activation is a unique specialization of the human brain.

However, it remained possible that a weaker symmetry sensitivity exists in macaque, below the threshold of the techniques used in humans. To test this theory, we used more-sensitive fMRI techniques, including BOLD imaging at 7 T and monoc-

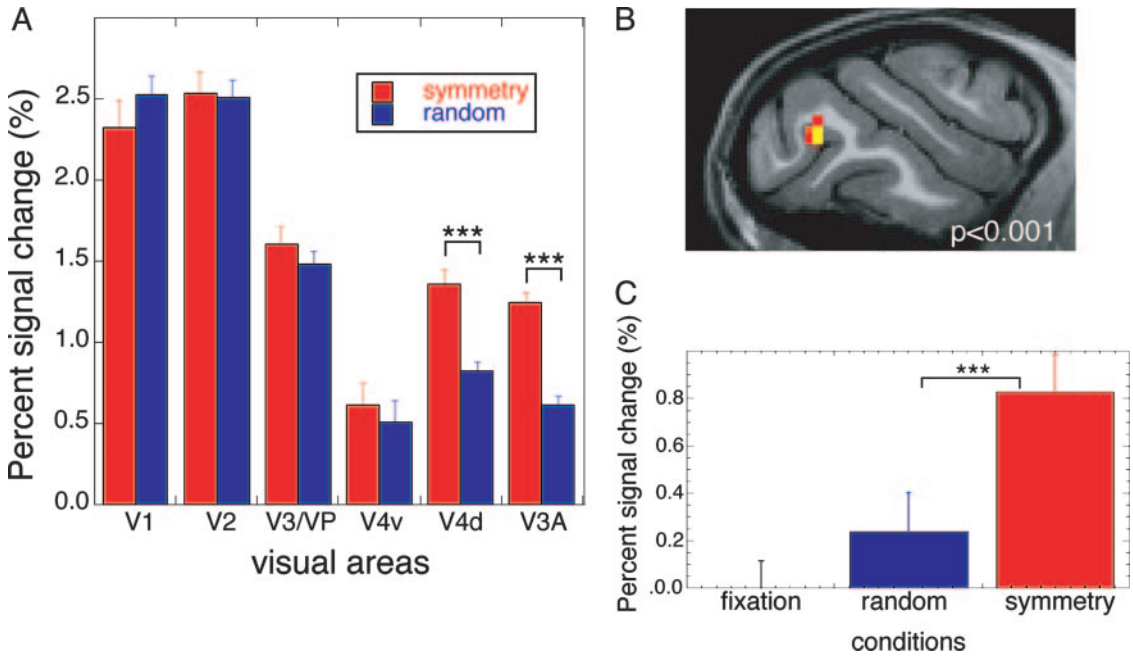

Fig. 4. Symmetry response in awake fixating monkeys. (*A*) Average response amplitudes (+1 standard error relative to activity during fixation on a uniform gray stimulus of equal mean luminance) from specific visual cortical areas by using an exogenous iron oxide-based contrast agent (monocrystalline iron oxide) at 3 T. Stimulus conditions are coded in different colors: symmetry, red; random dots, blue. Asterisks indicate statistically significant differences between symmetry and random conditions ($P < 0.001$). (*B*) A sagittal slice, showing significant fMRI activity (symmetry minus random) in a different monkey, in visual area V4d/TEO, based on BOLD-fMRI at 7 T. (*C*) Average of the fMRI response in this region, showing the mean percentage + 1 standard error, for the symmetry (red) and the random (blue) stimuli.

rystalline iron oxide imaging at 3 T. These extra efforts did reveal a small but analogous symmetry activation in apparently homologous areas of macaque visual cortex such as V3A, V4d, and TEO (see Fig. 4). Overall, our fMRI and related psychophysics (22) suggest that neural mechanisms tuned to visual symmetry are present in nonhuman primates, although they are less well developed than in humans.

Discussion

This study suggests that human visual cortex processes visual symmetry in a particular way and that areas V3A, V4d/v, V7, and LO are intimately related to this symmetry processing. Detailed control experiments confirmed that these regions were also activated when attention was controlled. Moreover, the magnitude of activation in these higher visual areas (V3A, V4d/v, V7, and LO) was highly correlated with the likelihood of symmetry perception. In contrast, the activity in lower visual areas such as V1 and V2 did not show any correlations with the likelihood of perception at all.

One might argue that some form of object-related preprocessing occurs during perception of the symmetric dots patterns and that the regions activated by symmetry were just responding to those object-like features or to components of structure, rather than to the symmetry itself. However, our control experiments suggested this result is unlikely. First, one control experiment (e.g., Fig. 7) showed that the cortical regions that were activated by symmetry responded more to symmetry than to tiling or repetitive patterns. Second, in the nonsense contour experiments, the symmetric stimuli would not have shown more activation than the asymmetric stimuli if those regions responded to any perception of objects components, but this did not occur. Collectively, these lines of evidence suggest that higher visual cortex including V3A, V4d/v, V7, and LO is prominently involved in the processing of symmetry.

The human cortical areas (e.g., V3A, V4d/v, V7, and LO) that were activated by symmetric stimuli here are also selectively activated by additional global stimulus comparison, as reported previously. For instance, the presence of binocular disparity activates V3A (23–25), kinetic boundaries activate V4d (26–28), radial and concentric gratings reportedly activate V4v (18), and object perception activates LO (13, 29). Moreover, cortical regions activated by various objects (29) generally overlap with the symmetry-selective regions found in the present study. Interestingly, some of the object-based stimuli that activate these regions also contain strong symmetries; thus, our data suggest that some part of the fMRI responses reported for objects of various types may arise from the presence of symmetry (30) in relation to asymmetric control stimuli.

In all three monkeys, extensive BOLD measurements at 3 T did not reveal a statistically significant symmetry response, although a robust symmetry response was easily produced in all human subjects with the identical stimuli, scanner, and analysis tools. Instead, we had to use much more sensitive fMRI techniques (7T BOLD, 3T monocrystalline iron oxide, and extensive signal averaging) to reveal the apparently homologous activation (e.g., Fig. 4). These differences in fMRI sensitivity strongly suggest that symmetry processing is weaker in monkeys than in humans. Despite this result, it is noteworthy that the symmetry response can be demonstrated in corresponding areas of macaque and humans because it opens up the possibility that single-unit recording and related classical neurobiological techniques can be used to clarify the neural mechanisms involved. It has been reported that single units in inferior temporal cortex (IT) mediate interhemispheric transfer in visual patterns (31) and mirror-image discrimination (19). However, in this study, we did not find a significant symmetry response in macaque IT. Because neurons in IT are known to be highly shape-specific (32), it remains possible that a difference in stimulus configuration, or in sensitivity of single units versus fMRI (33), accounts for this apparent discrepancy.

The strong correlation of the fMRI and psychophysical measurements of symmetry and the presence of a small symmetry activation in macaques suggest that cortical calculations of visual symmetry have a biological value not widely recognized at the neural level. Ultimately, a high perceptual sensitivity to symmetry may be linked with the presence of symmetry in normal phenotypes and, correspondingly, with the asymmetry in pathological specimens. For instance, predators must be highly sensitive to bilateral gait asymmetries because this trait can indicate a pathological vulnerability that can facilitate an attack. Even sexual selection is biased toward bilaterally symmetric partners (4, 5). In such cases, a high sensitivity to symmetry would have obvious survival value.

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