



The neural basis of visual symmetry and its role in mid- and high-level visual processing

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Symmetry is an important and prominent feature of the visual world. It has been studied as a basis for image segmentation and perceptual organization, but it also plays a role in higher level processes, such as face and object perception. Over the past decade, there has been progress in the study of the neural mechanisms of symmetry perception in humans and other animals. There is extended activity in the ventral stream, including the lateral occipital complex (LOC) and VO1; this activity starts in V3 and it occurs independently of the task (automatic response). Additionally, when the task requires processing of symmetry, the activation may emerge for objects that are symmetrical, even though they do not project a symmetrical image. There is also some evidence of hemispheric lateralization, especially for the LOC. We review the studies on the cortical basis of visual symmetry processing and its links to encoding of other aspects of the visual world, such as faces and objects.

Keywords: symmetry; regularity; LOC; fMRI; EEG; TMS

Introduction

It would be wrong to consider symmetry as a rare and special image property, or worse as a curiosity. On the contrary, symmetry has a central role in vision. At its essence, symmetry is a concept closely related to structure and regularity. More formally, symmetrical structures can be described as containing self-similarities. In 2D images, self-similarity results from rigid transformations that map one part onto another. Examples of symmetry can be found in visual art in different cultures and across the centuries. Although empirical work on symmetry perception has a long history, its neural basis has become clearer only in recent years. We review this progress here, starting with a brief historical background.

In his classic book, Ernst Mach¹ used symmetry to illustrate the importance of comparing formal properties of the incoming information with perceptual properties. He pointed out that reflectional symmetry was the only type of symmetry perceived

without effort, and that there is an advantage for vertical axis orientation (Fig. 1). These aspects have been confirmed by several empirical studies (e.g., Ref. 2). Reviews have been published (in chronological order) by Wagemans,^{3,4} Treder,⁵ Bertamini and Makin,⁶ van der Helm,⁷ and Cattaneo.⁸ A book on the subject based on a journal special issue was edited by Tyler.⁹ Here, we review the growing literature, with a focus on neural mechanisms that process visual symmetry.

Visual processing of symmetry and its role in figure–ground organization

Within the Gestalt tradition, the role of symmetry in perceptual organization has been studied since Bahnsen,¹⁰ a student of Edgar Rubin. As in the famous face–vase demonstration by Rubin, Bahnsen created displays in which two alternating regions could be perceived as figure or ground. He concluded that symmetrical regions tend to be perceived as figures. One argument is that

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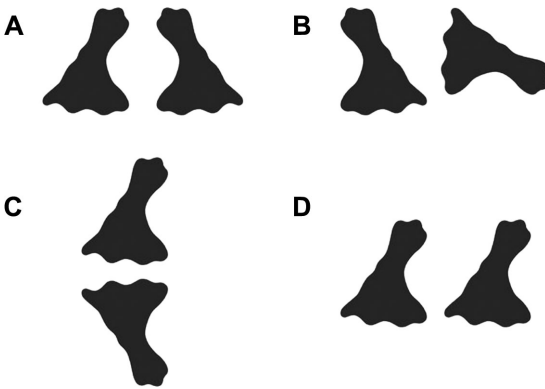


Figure 1. These shapes are taken from Mach's book (Chapter VI). Although they (A–D) are all isometries (rigid transformations preserving metric structure), only the first pair (A: vertical reflection) can be perceived without effort.

symmetry is a nonaccidental property and therefore is unlikely to be present in ground regions.^{9,11,12}

Empirical evidence has confirmed that symmetry is a grouping factor,^{13–16} although Kanizsa and Gerbino¹⁷ found symmetry to be less powerful than convexity for figure–ground organization. In an important study, Machlisen *et al.*¹⁴ tested the effectiveness of symmetry in a task of contour completion, where closed objects emerge after local information is integrated. They confirmed that symmetric shapes were easier to detect than asymmetric ones. In a study by Treder and van der Helm,¹⁸ participants responded to elements distributed over two depth planes. Detection of symmetry (but not of repetition) was poor when the corresponding elements were on different planes (i.e., at different depths). This supports the claim that symmetry is a cue for the presence of a single object. Repetition, instead, may be related to the presence of multiple objects. Consistent with this, detection of symmetry is faster when the elements form an object (e.g., because of closure of the contours).^{19–24}

A significant disruption to perception of symmetry is caused by a mismatch in the coding of contour information, that is, when convexities on one side correspond to concavities on the other and vice versa.^{19,25,26} Importantly, the link between symmetry and objectness is specific to reflection symmetry, and Bertamini *et al.*²⁷ found no within-object advantage for detection of rotated contours. This is consistent with the fact that symmetry signals a structure produced by a growth process.²⁸

One strategy to study to what extent the visual system is tuned to symmetry is to vary presentation time. Some studies have confirmed that symmetry can be detected with presentations between 100 and 150 milliseconds.^{29–32} A few studies have used even shorter presentations—50 (see Ref. 33) and 25 milliseconds.³⁴ Note that these results exclude any indispensable role for exploratory eye movements. Even though detection can happen for very short presentations, longer presentations do improve the probability of correct responses,³⁵ suggesting that there is information integration up to durations of a second or more. The visual system can also integrate position information presented at different points in time. Niimi *et al.*³⁶ used symmetrical dot patterns divided into two asymmetric groups. When these are presented successively, observers can detect symmetry using visual persistence.

Although detection of reflectional symmetry is not affected by number of elements, Sharman and Gheorghiu³⁷ found that dynamic flicker or motion of the elements improves symmetry detection. This was consistent with previous work by Niimi *et al.*³⁸ Perhaps the limited lifetime of the elements increases the number of relevant locations that are integrated.

Detection of reflectional symmetry is robust to local perturbations of position²⁹ and midpoint alignment.³⁹ Symmetry detection is also robust to phase variations, especially when they are orthogonal to the reflection axis.⁴⁰ It is also possible to perceive symmetry when elements are near isoluminance,⁴¹ although symmetry detection may be gated by feature attention to color.⁴² For dot patterns, elements near the axis of symmetry have great influence on perception of symmetry,³⁰ but the system does not rely exclusively on these locations, and the elements on the edges of a shape are also important.^{29,43}

In terms of type of elements, Locher and Wagemans³² found that shape and orientations of elements did not significantly affect perception of symmetry, although clusters of elements (higher order features) contributed to the emergence of symmetry. Hulleman and Olivers⁴⁴ argued that concavities contribute more than convexities to detection of bilateral symmetry, although it is likely that the effect is better described as the importance of parsing of the object.⁴⁵

Symmetry perception can overcome skew or depth rotation,^{46,47} as well as presentation away from fixation³⁰ and in the periphery.^{48,49} Performance in the periphery can be high when stimuli are scaled by a cortical factor,^{50,51} although it is subject to crowding.⁵² There is mixed evidence about the detrimental effect of a luminance mismatch of the elements,^{53–56} which is referred to as antisymmetry and discussed further below.

Formal models of symmetry perception

As shown in Figure 1, there are various types of regularity, although researchers have mainly studied reflectional symmetry. It is worth considering how models of symmetry perception generalize, because a model that deals with different regularities is more powerful than one limited to reflection.

Early work by Garner^{57–59} developed a transformational model, where perceptual regularity is linked to the number of alternative versions of the pattern (generated by rigid transformations). The holographic model, developed by van der Helm and Leeuwenberg⁶⁰ and expanded by van der Helm,⁶¹ takes a different approach. They noted that all visual regularities have a *holographic property* that can be described as a structure-preserving growth.⁶² A holographic regularity can be expanded one substructure at a time, and the global structure is preserved. For example, in reflectional symmetry, a single pair of dots symmetrically straddling the axis would count as a holographic substructure. We could add another pair, and the global reflection would be preserved, and so on. Therefore, any holographic regularity can be divided into substructures, all of which have the same regularity as each other. Unlike the earlier transformational model,⁵⁸ the holographic model provides an account of the residual structure in symmetry + noise patterns and of the perceptual structure of Glass patterns.^{63,64} The model explains why detection of reflectional symmetry is not affected by number of elements, while repetition is more difficult to detect with more elements.⁶⁵ We therefore include noisy symmetry, repetition, and Glass patterns in our review of symmetry perception.

Van der Helm and Leeuwenberg⁶⁰ proposed a formal way of quantifying goodness of different regularities, based on the Gestalt concept of simplicity and economy.^{66,67} The weight of evidence (W) is proportional to the number of holographic regular-

ities (E) as a fraction of total amount of information (N) ($W = E/N$).^{60,68} There has been some criticism of the holographic model⁶⁹ and a rebuttal.⁷⁰ However, there is agreement that, while the holographic model does not explain all known goodness phenomena,^{68,71} it can predict psychophysical discrimination performance.⁷² Even though the model was not biologically inspired, Makin *et al.*⁷³ found a good correlation between W and the amplitude of the neural response to symmetry and to Glass patterns.⁷³ This is discussed below.

The link between symmetry and efficient coding could explain why it is easier to see the difference between two symmetrical patterns than two asymmetrical patterns.^{74–76} It could also explain a more recent observation: a set of dots appears less numerous when arranged in a symmetrical pattern than in an asymmetrical pattern.⁷⁷ This decrease in perceived numerosity is consistent with a theory predicting inattention to redundant items when estimating number or density. Decreased numerosity also leads to decreased perceived duration,⁷⁸ a finding that supports a common magnitude coding.⁷⁹ Therefore, one would predict that symmetry would reduce perceived duration. However, the opposite pattern has been observed: symmetrical patterns appear to last longer.^{80,81} This could be explained by a different effect: the relationship between subjective duration and the size of a neural response to the stimulus.⁸²

Other formal models of symmetry detection have proposed an analysis of corresponding elements using oriented filters.⁸³ The input, therefore, could be signals from V1 and V2. This and other models use image measures to perform a correlation or to find corresponding structures between locations on either side of a reflection axis^{11,84,85} or a correlation between cells of a Voronoi tessellation.⁸⁶ Influential work by Dakin and Watt⁸⁷ and Dakin and Hess⁴⁰ proposed a model based on the outputs of filters oriented orthogonal to the axis. Spatial frequency filters extract oriented blobs from the image, and symmetry is detected from blob alignment. All spatial filter models include stages. For instance, the model by Gurnsey *et al.*⁸⁴ has three stages: a first stage extracts low spatial frequency information, a second finds an axis using a global differencing operation, and a third stage explicitly detects the symmetry axis.

Analyzing correlations over every possible axis and position is computationally demanding and

subject to noise in the image, as pointed out by Poirier and Wilson.⁸⁸ To address this, Poirier and Wilson proposed a model that is built on top of a shape model. Contour segments are obtained from non-Fourier V4-like units. This approach is particularly useful to address the key role of contours in shape and symmetry perception. Another solution to the combinatorial explosion is to make use of the higher order relationships in patterns with perfect bilateral symmetry (captured by “correlation quadrangles”) and bootstrap the pairwise matching along the local symmetry axis established by a small number of pairs.⁸⁹ This bootstrap model can also explain the advantage of higher order symmetry (i.e., multiple axes of reflection) and the differences between orthogonal and skewed symmetry.^{47,89}

Chen and Tyler⁹⁰ and Wu and Chen⁹¹ used a normalization process and nonlinear summation to account for symmetry detection carried out in parallel by multiple channels, selective for color and orientation. Moreover, they separated this perceptual stage from a later decision stage. This is a higher order mechanism that monitors all channels (unless cued toward one channel) to determine whether symmetry is present.

Several studies considered the perceptual consequences of a mismatch between element features other than location. For instance, in the case of luminance antisymmetry, all elements are arranged symmetrically, but black elements are paired with white and white with black. Antisymmetry and symmetry are perceptually comparable under some conditions, in particular when density is low,^{54,56} but in other cases antisymmetry discrimination is impaired.^{53,92,93} There are a few explanations for the relative perceptual weakness of antisymmetry. It could be that some visual filters do not carry symmetry information when luminance is mismatched;⁵⁴ that antisymmetry can only be discriminated with a slow, serial attentional mechanism;⁵³ or that antisymmetry perception is disrupted by interactions with other Gestalt grouping principles.⁹³

We have not discussed the many efficient computational and neural networks solutions to extract symmetry information from the image (for an overview of the computational approach, Ref. 94; for specific neural networks, see Refs. 95–97).

In summary, formal models of symmetry perception vary in their neural plausibility, mathematical precision, number of assumptions, and whether

they apply to all regularities (e.g., glass patterns, antisymmetry). Some are computational models that identify symmetry in an image and include biologically realistic features like spatial frequency filters and a separation between image analysis and decision stages.^{40,83,88,90} Others are more focused on formal properties of configurations and defining the difference between different kinds of regularity.^{58,60} We can describe this as a distinction between *process* models, which concern the way symmetry is extracted from the image, and *representational* models, which address the structure of a visual representation once it has been formed.⁶⁰ We anticipate that formal models of symmetry perception will converge with precise neuroscientific research in the future, owing to the improved flow of communication in both directions.

Neural mechanisms of symmetry perception

Brain regions involved in responding to visual symmetry have been mapped using functional magnetic resonance imaging (fMRI). Sasaki *et al.*⁹⁸ studied the contrast between patterns with symmetrical or random dots. They found symmetry-related activity in bilateral extrastriate regions of the occipital cortex but no activation of the primary visual cortex. The extrastriate visual regions included V3A, V4, V7, and the lateral occipital complex (LOC). Moreover, Sasaki *et al.*⁹⁸ found that V4 and LOC activity scaled with the proportion of symmetric dots in noisy configurations. They also found comparable activations in conscious macaque monkeys. Tyler *et al.*⁹⁹ also reported a symmetry activation in the left and right LOC and weaker symmetry-related activations in other extrastriate areas, while, again, there was no symmetry response in V1. Another fMRI study compared faces, inverted faces, 3/4 view faces, symmetrical abstract images, and asymmetrical abstract images.¹⁰⁰ Abstract images were made from phase-scrambled faces, so low-level features were controlled. Among other things, the authors found that only the intraoccipital sulci (IOS) and middle occipital gyri (MOG) were activated by abstract symmetry compared with abstract asymmetrical images. MOG partly overlapped with LOC. Meanwhile, the areas activated by upright faces compared with abstract asymmetrical images were the occipital face area (OFA), fusiform face area (FFA), MOG, and IOS. Further analysis showed that the FFA and OFA

response was mostly viewed invariant but reduced by face inversion, and that the right OFA had a special role in processing facial symmetry rather than abstract symmetry. This latter finding supports other behavioral evidence that facial symmetry discrimination employs dedicated circuitry not used in other symmetry discrimination tasks.¹⁰¹ Although more research is required, it seems that abstract symmetry perception is not identical to face perception, but neither is it completely independent from face perception (see section on transcranial magnetic stimulation (TMS) work for further evidence).

More recent fMRI work¹⁰² has found activations as early as V3 and in ventral occipital area VO1 as well as in LOC. Keefe and Morland (personal comm.) also found that responses scaled with coherence in dot patterns and with the number of folds and that, for both passive viewing and detection tasks, the strongest response was in ventral occipital VO1 and in the more ventral parts of the LOC.

In summary, many extrastriate areas are activated by symmetry, and often the strongest response is in the LOC. The LOC already has a well-established role in coding shape and segmented objects,^{103,104} and symmetry detection is intimately connected to these operations. Furthermore, in early blind participants, the right LOC responds to tactile symmetry.¹⁰⁵ However, the LOC has several subregions, and a full understanding of the extrastriate symmetry network will require more data from human visual maps.

Beck *et al.*¹⁰⁶ reviewed Sasaki *et al.*⁹⁸ and anticipated future work by saying that one important issue is “to determine whether stimulus symmetry is coded by single neurons within the areas identified in the Sasaki study or, alternatively, whether it results from a sophisticated population code that may be more easily revealed by a method that measures responses from large populations of neurons, such as fMRI” (p. 406). We do not have a conclusive answer to this question, as there have been few relevant single-cell recording studies. However, one recent publication provided fresh evidence about symmetry processing in monkey inferior temporal (IT) cortex (an area not activated in Sasaki *et al.*'s study). Pramod and Arun¹⁰⁷ used abstract shapes with parts placed on the right and left side of a reflection axis. They found that the neuronal response to the whole object was the sum of responses to the parts, regardless of symmetry. Symmetric objects

attained a special status only because they were more distinctive (compared with asymmetric objects). This was true because of selectivity to parts, a form of position invariance, for IT neurons. They concluded that the neural response to symmetry is driven by generic computations at the level of single neurons.

The neural response to symmetry can also be measured with event-related potentials (ERPs). There is a difference in posterior ERPs generated by images that contain symmetry and images that do not contain symmetry. Norcia *et al.*¹⁰⁸ used symmetrical and asymmetrical dot patterns. For electrodes over the occipital pole, they found that the symmetry ERP was more negative. This negativity started after P1 and N1 (220 ms after onset) and was then sustained. Jacobsen and Höfel¹⁰⁹ confirmed this ERP using abstract black and white patterns and replicated the effect in subsequent work.^{110,111} We refer to this as a sustained posterior negativity (SPN), and its amplitude is the difference between ERPs generated by symmetric and asymmetric patterns (Fig. 2). Although the onset latency may vary slightly from study to study, it is usually between 220 and 250 ms and therefore appears soon after the N1 component, and N1 itself can be weakly but significantly modulated by symmetry.¹¹² Source localization confirms that the SPN is generated by the extrastriate visual areas identified with fMRI.^{102,112}

The SPN is generated by the presence of regularity in the image, independent of the participant's task. The fact that this SPN is generated automatically has been supported by several published studies^{102,110,111,114–116} and in numerous unpublished ERP data sets. This automatic response to symmetry does not exclude a modulation of the response due to attention. For instance, Rampone *et al.*¹¹⁷ found that SPN amplitude was reduced when participants attended to superimposed words and was absent when negative words were presented. Attention to symmetry was also found to enhance the fMRI response to symmetry by Sasaki *et al.*⁹⁸ and more recently by Keefe and Morland (personal comm.). Although the SPN is sustained for long periods, amplitude peaks at around 300–400 ms (Fig. 2), and this early window provides the most reliable signal.⁷³

Early theories of the neural processing of symmetry had suggested a link between bilateral symmetry perception and the bilateral symmetrical anatomy of the cerebral hemispheres. Following Mach's

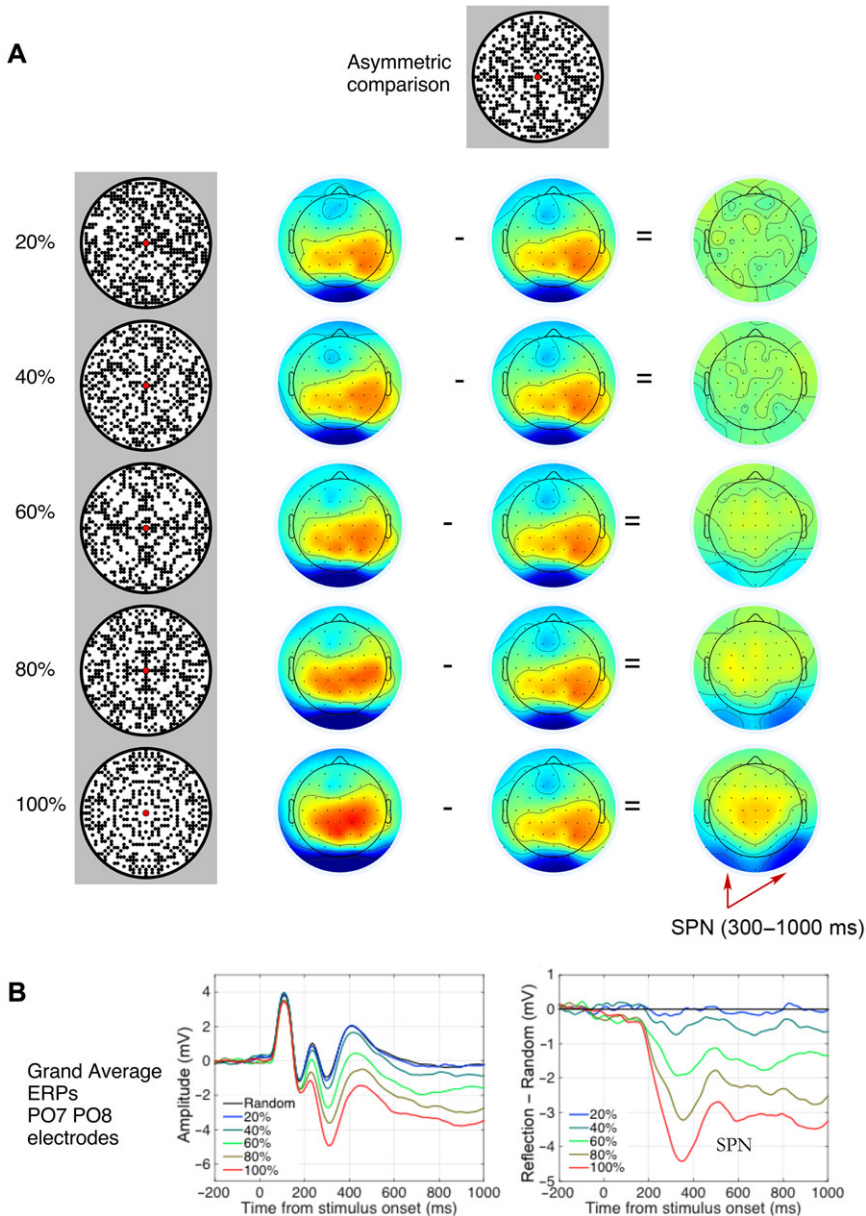


Figure 2. The sustained posterior negativity (SPN) scales parametrically with the proportion of symmetrical elements. Left panels in A show symmetry + noise displays from 20% to 100% symmetry in 20% increments. Each row shows grand-average topography (300–1000 ms) generated by the pattern and by an asymmetrical comparison. Difference plots are shown on the right column. Here, the SPN is seen as negative amplitude (blue) at posterior electrodes. (B) Grand-average event-related potentials (ERPs) from PO7/8 electrodes in all conditions (left) and the difference waves (right). It is possible to see how the SPN scales parametrically with P Symm. Data are from Ref. 113.

observation that vertical bilateral symmetry was the most salient visual regularity, Julesz³⁰ suggested a point-by-point matching process for corresponding locations presented in the left and right hemifield and processed in the right and left hemisphere,

respectively (see also Refs. 118 and 119). Some empirical support for this idea came from a study of two patients born without a corpus callosum.¹²⁰

However, the theory of a link between perception of bilateral symmetry and the cortical anatomy is

not tenable when considering that symmetry can be processed away from fixation and that reflectional symmetry is most salient when multiple axes are present. Wright *et al.*¹²¹ studied the SPN when patterns (diameter of 2.1°) were positioned to the left and right of fixation (3.2°). An SPN was present in the contralateral electrodes with respect to the location of the symmetric pattern. Moreover, the authors analyzed the contribution of the other pattern (other side of fixation), including the case when no second pattern was present. That is, their analysis compared the response to a symmetric pattern in one hemifield, when in the other hemifield there was a symmetric pattern, a random pattern, or no pattern. Information in the other hemifield made no significant contribution, suggesting that the two hemispheres could process symmetry independently.

Because of visuospatial superiority of the right cerebral hemisphere, there is a left-side superiority in many visual half-field tasks.^{122,123} Therefore, one might expect symmetrical patterns to be discriminated better when presented in the left hemifield. This was confirmed with a symmetry discrimination task for both right-handed and left-handed observers.¹²⁴ In addition, the opposite pattern of results was found in a subset of participants who were atypically right-hemisphere dominant for language processing. Verma *et al.*¹²⁴ concluded that, despite the variability, language and visuospatial functions are lateralized in opposite brain hemispheres. These findings suggest that symmetry detection is indeed a cognitive function lateralized to the right hemisphere for most of the population. Occipital alpha band desynchronization, a measure of cortical excitation, can also be right lateralized during symmetry discrimination tasks.^{116,125} More evidence for lateralization is discussed below based on TMS studies.

Finally, the importance of the ventral visual system in symmetry perception is also supported by neuropsychological evidence. Driver *et al.*¹²⁶ described a patient (CC) with right parietal lesions and hemispatial neglect. CC was unable to discriminate whether vertical objects were symmetrical because the left side was invisible to him. However, CC could explicitly discriminate horizontal symmetry and could use vertical symmetry implicitly in figure-ground segmentation. This suggests that CC could process symmetry preattentively using

the intact ventral stream. Vecera and Behrmann¹²⁷ described another patient (JW) with occipital and only mild right parietal damage. JW had normal spatial attention but no ability to discriminate symmetry. Furthermore, Milner *et al.*¹²⁸ found that symmetry discrimination was abolished in visual-form agnosia patient DF, who had an intact primary visual cortex and spared dorsal stream function. However, for a role of the dorsal areas for global form perception, see Lestou *et al.*¹²⁹

Type of symmetry and regularity

The latency of the SPN does not appear to depend on the type of stimuli. Although these studies were not designed to probe latency in detail, similar latencies have been reported using black and white geometrical patterns;¹¹² reflection, rotation, and repetition;¹¹⁴ closed and open contours;¹¹⁶ and square fields.¹¹⁷ In contrast, the amplitude of the SPN scales with the visual salience of different regularities.^{73,114} For instance, SPN amplitude increases monotonically with the proportion of symmetry in symmetry + noise patterns, as shown in Figure 2.¹¹³ Similarly, the blood oxygen level-dependent (BOLD) response in the extrastriate network increases with the proportion of symmetry.⁹⁸

In the Gestalt tradition, perceptual *goodness* is a concept that refers to the perceptual strength of salience of a visual configuration.¹³⁰ As mentioned above, van der Helm and Leeuwenberg⁶⁰ proposed a holographic weight-of-evidence model, which quantifies the goodness for configurations of discrete elements. Makin *et al.*⁷³ found that the holographic *W* score explained 86% of the variance in grand average SPN amplitudes across multiple experiments, and precise predictions of the holographic model were confirmed within experiments. Moreover, *W* and SPN amplitude correlate with preference for different kinds of abstract symmetry, both in British and Egyptian samples.¹³¹

Several important studies have measured the neural response to symmetry using the steady-state visual evoked potential (SSVEP) technique. Each trial presents a sequence of rapidly changing patterns. The periodic stimuli drive a periodic neural response. This neural response comprises the stimulus frequency and its harmonics.¹³² When the periodic stimulus involves alternation between symmetry and random patterns, the neural response to symmetry is isolated by odd

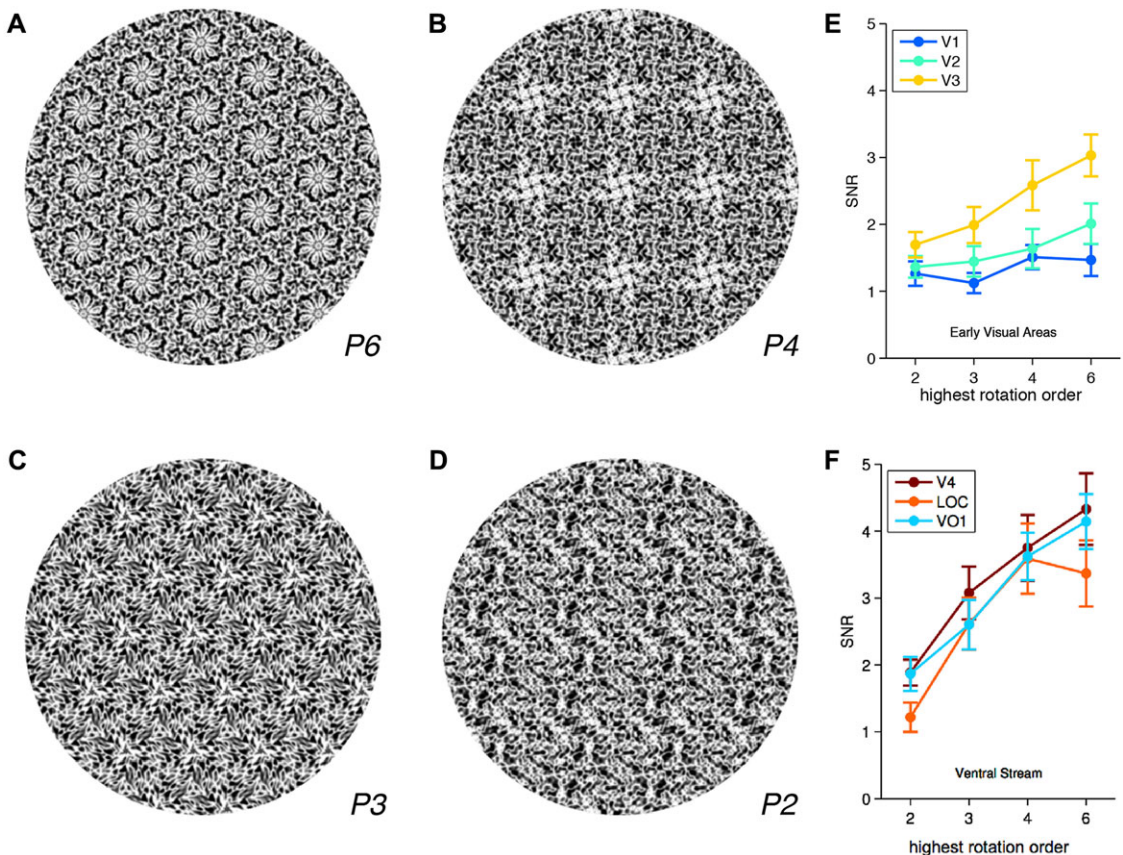


Figure 3. Wallpaper patterns (A–D) and cortical response distributions (E and F). Wallpaper patterns that differ in their highest rotation order are shown for groups P6, P4, P3, and P2 (A–D). These patterns produce parametric BOLD responses in V3, but not V2 and V1 (panel E) and in V4, LOC, and VO1 (panel F). Response magnitude is plotted in terms of signal to noise ratio of the amplitude at the paradigm frequency (10 cycles per 240-s scan) and the average of adjacent frequencies in the BOLD response spectrum. Data are from Ref. 102.

harmonic components.¹⁰⁸ Oka *et al.*¹³³ found that the amplitude of the odd harmonics scaled with the number of folds for reflection and that it was greater for symmetry than antisymmetry when density was high, but not when density was low. The same technique has shown that the neural response to radial and concentric Glass patterns is larger than to translational Glass patterns.¹³⁴

Image regularity has also been studied in relation to texture properties. Within a regularity space, textures inhabit a continuum from low to high regularity.¹³⁵ The highest regularity patterns are perfectly regular and comprise the 17 wallpaper or crystallographic groups.¹³⁶ Like symmetry, texture regularity is likely to be represented in extrastriate areas.¹³⁷ Kohler *et al.*¹⁰² used a combination of functional MRI and high-density

electroencephalography (EEG) to study textures in terms of the underlying symmetries. Kohler *et al.*¹⁰² used a set of four wallpaper patterns that differed only in their highest degree of rotation symmetry (Fig. 3A–D). They found responses that were parametric in the degree of rotation starting in V3 (Fig. 3E). Parametric responses to the highest degree of rotation symmetry were also found in areas V4, VO1, and LOC (Fig. 3F). EEG source localization suggested that responses in V3 and V4 (around 75 ms) lead to responses in LOC (around 110 ms). This is earlier than SPN onset in most studies (Fig. 2). The wallpaper patterns in Kohler *et al.*¹⁰² may have been more salient than the dot patterns of previous studies and thus have led to earlier latencies. Also, the experiments and analyses of the dot pattern studies were not designed

to discover the very earliest neural response to symmetry.

In a recent follow-up study, Alp *et al.*¹³⁸ measured SSVEP as participants viewed symmetric patterns composed of distinct spatial regions presented at two different frequencies (f_1 and f_2). They used a multiple-frequency tagging approach to measure intermodulation (IM) components that have been shown to reflect nonlinear processing at the neural level,¹³² here reflecting integration of spatially separated parts of the pattern. They compared SSVEPs measured for wallpaper patterns and control patterns for which all reflection symmetries were removed but whose local properties remained equal. Hence, both images were equal in terms of translation and rotation symmetry, but reflection symmetry could only emerge for the wallpaper pattern through integration of the image pairs. Both wallpaper and control stimuli produced IM components, indicating that integration occurs for both types of patterns. Importantly, however, low-frequency IM components differed between the reflection and control stimuli, indicating the presence of integration mechanisms specific to reflection symmetry. This confirms the special status of reflection symmetry noted already by Mach¹ and included as a core fact in the perception of symmetry and regularity to be explained in some models.^{60,89}

Extraction of symmetry from images

The tuning of the visual system to regularities has functional significance in relation to image segmentation and object representation. However, for this role to be adaptive, it is important to consider the issue of how regularities in the image relate to the regularities in the environment. For a regular abstract shape, as well as for the special case of the human face, only nonaccidental viewpoints give rise to symmetry in the image. In most cases, a symmetrical object will project an image altered by perspective distortions. Under these conditions, symmetry may still be perceived based on degraded image regularity⁴⁶ or following a normalization process.¹³⁹

Ventral regions of the human visual system compute object representations that are robust to transformations, like depth rotations, which preserve solid shape structure.¹⁴⁰ Recent computational models have shown that neurons that learn according to a broad class of Hebb-like rules have responses invariant to viewpoint.¹⁴¹

Makin *et al.*¹¹⁵ tested the SPN amplitude for symmetric configurations presented in perspective (Fig. 4). They found that, when observers performed a symmetry/random discrimination task, SPN amplitude was equivalent for 0° and 50° slants, thus showing complete view invariance. However, for participants who responded to the color of the patterns, SPN amplitude was proportional to the amount of regularity in the image and thus reduced for the slanted patterns. The patterns in Figure 4 have both vertical and horizontal reflection. Because only the vertical is affected by slant, a reduced SPN was recorded. For configurations with a single axis (the axis of depth rotation), the SPN was reduced further still.

The symmetry-sensitive network always responds to symmetry present in the image, as highlighted earlier. However, the study by Makin *et al.*¹¹⁵ demonstrated that it is possible to activate this network after a nonautomatic process that extracts symmetry in the object, perhaps through a perspective normalization process.¹³⁹ This theory has been recently supported by fMRI evidence.

In addition to extracting symmetry from perspective views of objects, it is important for the system to be robust to partial views of an object, as in the case of occlusion. A significant SPN has also been recorded for images where two (asymmetrical) parts of an object were shown in a way that only combining these parts over time would create a symmetrical object.¹⁴² These results show that the extrastriate symmetry network can integrate information presented at different points in time.

Neuroscientific techniques are now being used to answer questions about antisymmetry and the role of color channels. Antisymmetry generates an SPN under most conditions, even when participants are not actively attending to regularity.¹⁴³ However, in some conditions, SPN amplitude is reduced for antisymmetry⁷³ and can even be abolished when elements are not isolated (e.g., a checkerboard) (unpublished results). The mixed evidence on the salience of antisymmetry mentioned earlier^{53,93} is likely to result from a conflict between symmetry and other grouping principles. Within a checkerboard, for example, large regions of uniform color form structures with relevant convexities and concavities, thus creating antisymmetry not just at the luminance level but also at the level of part structure, as highlighted earlier in the review.²⁶

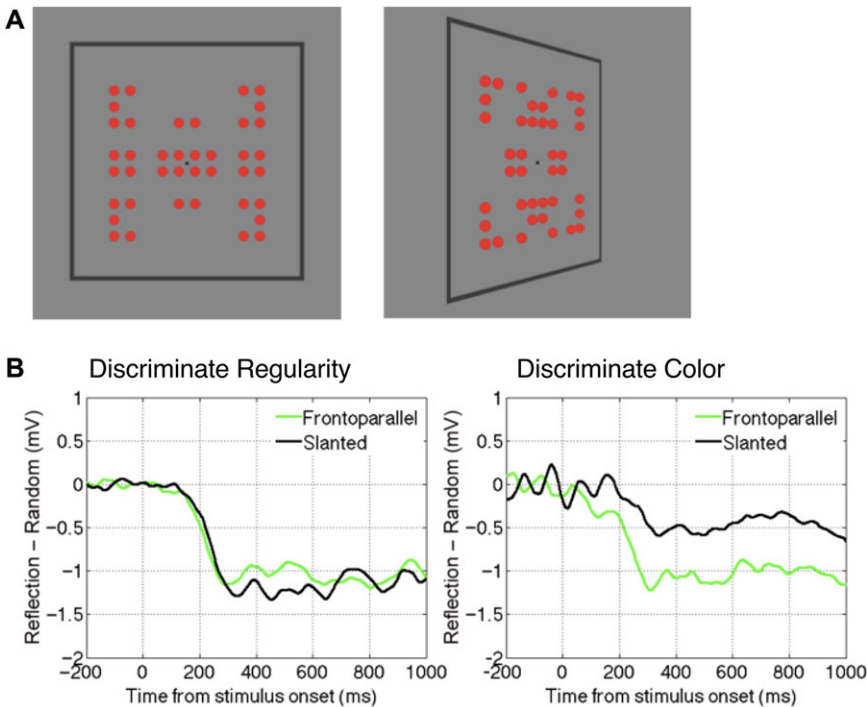


Figure 4. The images (A) show dot patterns with vertical and horizontal reflectional symmetry. They are presented within a plane slanted by 0° and 50° , respectively. When participants discriminate regularity, the SPN is unaffected by perspective. This view invariance suggests that the extrastriate network responds to symmetry in the object. Conversely, when participants discriminated color, the SPN was reduced in the 50° -slanted condition. This suggests that the extrastriate network only responded to symmetry in the image. Data are from Ref. 115.

Wu and Chen¹⁴⁴ and Gheorghiu *et al.*⁹² studied the relationship between symmetry and luminance or color of the elements. Moreover, Gheorghiu *et al.* distinguished between sensitivity and selectivity in symmetry perception. They found that antisymmetry was harder to discriminate than symmetry: color or luminance mismatches across the midline degraded performance. This result suggests that symmetry perception mechanisms are sensitive to color/luminance (mis)matches. However, performance when symmetry and noise dots were segregated by color or luminance (e.g., symmetry red and noise green) was equivalent to when symmetry and noise were not segregated by color (e.g., symmetry red and green, noise red and green). This suggests that symmetry perception mechanisms are not color or luminance selective. For instance, there is no red-symmetry or green-symmetry channel. However, segregation can enhance performance if the mapping is predictable, because it allows attention to focus on the potentially symmetrical dots.

Assessing the necessity of cortical regions in symmetry perception

The fMRI studies reviewed above have found a neural response to symmetry in a network of extrastriate areas upstream from V3. A limitation of this technique is its inability to reveal whether neural activity in each region is causally involved in perception. Necessity of neural activations in perceptual processes in human observers can be investigated with transcranial brain stimulation techniques. Of these techniques, TMS has been used to assess the cortical underpinnings of symmetry encoding. TMS can either enhance or suppress neural activity and behavior depending on stimulation intensity and cortical excitability.^{145,146}

TMS studies have revealed lateralization of symmetry processing, as well as links to the face-processing network. Using fMRI-guided TMS, Bona *et al.*¹⁴⁷ found that stimulation of right and left LO interfered with low-level symmetry detection in a task involving random-dot displays but with a larger

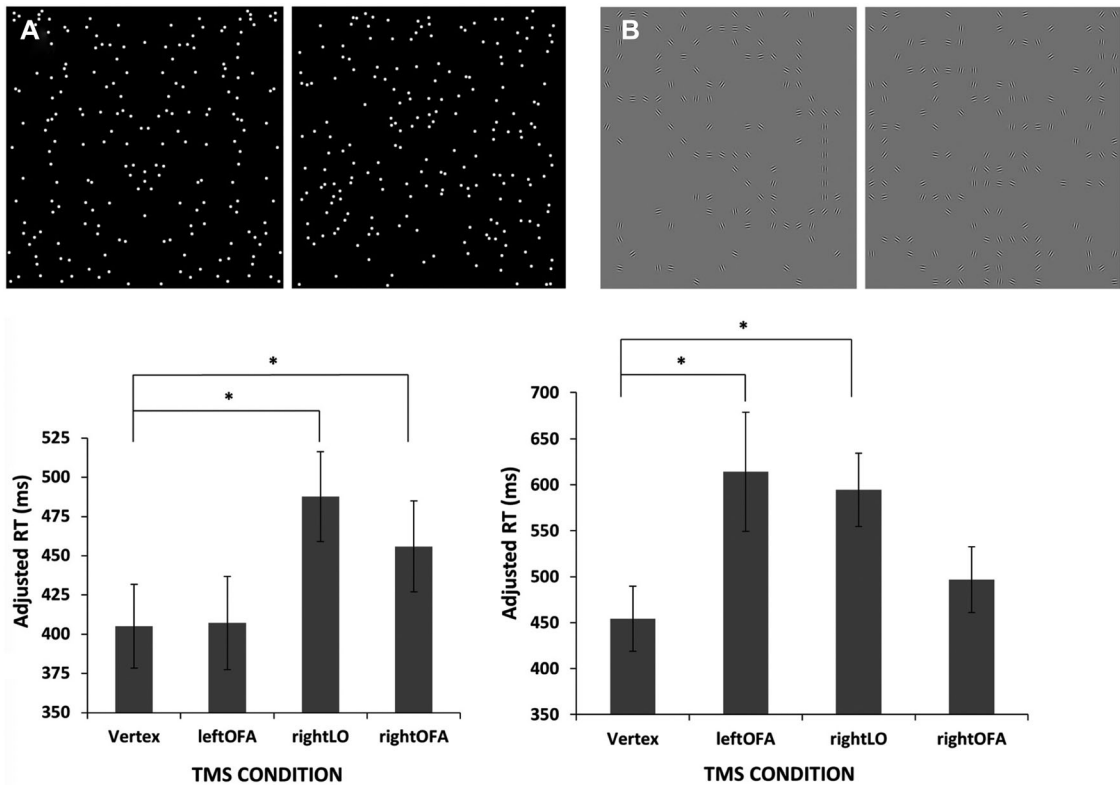


Figure 5. The face-processing network is implicated in low-level symmetry processing.¹⁴⁸ (A) In the symmetry condition, participants were asked to judge whether symmetry (along the vertical axis) was present in abstract dot configurations. (B) In the shape detection of task, participants were asked to judge the presence of a shape consisting of Gabors. The graphs show mean inverse efficiency (i.e., RT/accuracy) for each TMS condition in experiment 1a (A), which assessed symmetry detection in dot patterns, and experiment 1b (B), which assessed shape detection. The asterisks indicate significant pairwise comparisons (Bonferroni–Holm corrected). Error bars represent 1 SEM. In experiment 1a, TMS impaired symmetry detection in dot patterns when applied over the right OFA and right LO compared with vertex (baseline), whereas stimulation of the left OFA did not affect performance. In experiment 1b, TMS over the right LO and left OFA significantly impaired shape detection compared with vertex stimulation, whereas the right OFA TMS did not. Data are from Ref. 148.

effect for the right side. No such laterality effect was present for a shape-detection task based on edge integration rather than symmetry. This suggests that the right hemisphere is preferentially involved in symmetry processing, a phenomenon that may link to right hemisphere lateralization found in face processing. The SPN is also slightly right lateralized in some experiments, although not consistently.⁶

Moreover, as symmetry is an inherent property of faces, one might expect face-processing mechanisms to use it as an organizational principle. To investigate the role of the face-processing network in symmetry processing, Bona *et al.*¹⁴⁸ applied fMRI-guided TMS over participants' OFA during the same vertical symmetry–detection task used in their prior study. The results showed that both the right OFA

(but not its left homologue) and right LO impaired symmetry detection, whereas only right LO stimulation impaired shape detection based on contour integration. This finding is consistent with the fMRI study by Chen *et al.*,¹⁰⁰ which found OFA responses not only to faces but also to images that were not recognizable faces but contained symmetry. However, Chen *et al.*¹⁰⁰ concluded that the areas responding to symmetry per se were the MOG and IOS. Instead, the OFA and FFA did not show significant correlation changes for symmetry in scrambled images. Perhaps some neural mechanisms thought to be face specific may reflect selectivity to stimulus features, such as symmetry, a prominent cue in shape detection. Consistently with this view, a follow-up TMS study found that vertical but not horizontal

symmetry processing involved the right OFA.¹⁴⁹ The use of adaptation paradigms have potential to offer more insights into the neural tuning overlap between face and nonface symmetry.^{146,150}

A further experiment¹⁴⁸ showed that detection of facial symmetry (specifically, discriminating perfect symmetry relative to normal faces) was reliant on the right OFA but not on the right LO, indicative of the existence of face-specific symmetry mechanisms (Fig. 5). Therefore, the neural basis of symmetry processing appears to differ depending on whether symmetry is used as an organizational principle in stimulus identification at the early levels of stimulus processing or for fine-detail examination of an already detected stimulus.

Finally, another approach to causal relationships is to use response-locked averaging of the ERP during a symmetry-discrimination task.¹⁵¹ Response-locked averaging emphasizes neural activity that is more associated with timing of the behavioral response than with the timing of the stimulus presentation. Distributed inverse source imaging was used to examine responses in V3, V4, V3A/B, LO1, and LO2 areas previously implicated in symmetry processing. Using this method and the rotation groups of Figure 3, Kohler *et al.*¹⁵¹ found that area VO1 had the strongest and earliest response-locked activity of the set of visual areas examined. Other ventral surface areas (V3, V4, VO2) also had response-locked activity, but it was not observed in LO1. LO2 had response-locked activity immediately after the time of the button press. This analytical approach and stimulus/behavioral paradigm emphasize the role of ventral surface areas in symmetry perception. Ventral surface areas are difficult to target with TMS, given its preferential ability to target superficial gyri.¹⁵² Given this, future research should aim to pursue causal relationships in symmetry perception with multiple methodologies and multiple visual stimulus types.

Conclusions

The visual system responds strongly to regularity in the image. Neuroimaging evidence has corroborated the behavioral observations that regularity and symmetry in particular are salient features of the incoming visual information. Some aspects are well established, and we list them here. First, with respect to the location of the neural response, neural activation is widespread within the early ventral sys-

tem, including areas V3, V4, V7, and the LOC.^{98,102} However, no single area has been identified as exclusively specialized for the processing of symmetry. Rather, an extended network responds in a way that differs only quantitatively for different types of symmetry, including textures and Glass patterns, or for different levels of noise.¹¹³ Second, this extrastriate network responds to information in the image automatically, even when people are not attending to symmetry. This supports the view that symmetry is involved in basic form and shape perception. Third, in addition to the response to the image properties, the system can be activated also when information about symmetry is recovered from the image after a process of extraction (e.g., for symmetric patterns shown in perspective¹¹⁵). Finally, the network can code symmetry independently in each hemisphere, as shown by lateralized presentations.¹²¹ However, there is also evidence of hemispheric specialization, in particular for the right OFA and right LOC.¹⁴⁸

We have reviewed classic studies on perception of symmetry and focused on recent progress in understanding how symmetry is processed in the human brain. There has been good progress, and work is still ongoing. The evidence points to an overlap between visual processing of symmetry and visual processing of shape and objects, including faces.

Competing interests

The authors declare no competing interests.

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