

Symmetry perception in humans and macaques

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The human ability to detect symmetry has been a topic of interest to psychologists and philosophers since the 19th century, yet surprisingly little is known about the neural basis of symmetry perception. In a recent fMRI study, Sasaki and colleagues begin to remedy this situation. By identifying the neural structures that respond to symmetry in both humans and macaques, the authors lay the groundwork for understanding the neural mechanisms underlying symmetry perception.

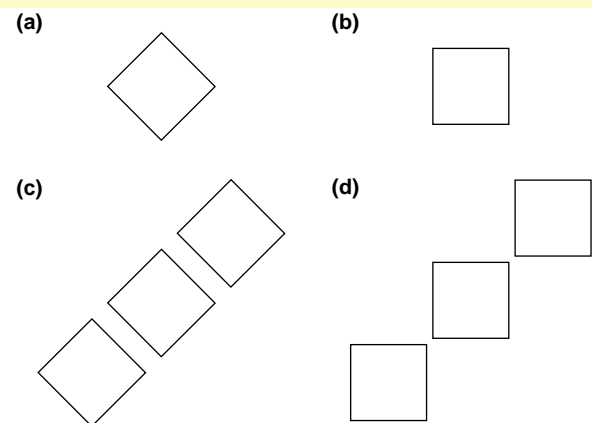
Bilateral symmetry pervades both the animal and plant kingdom as well as the man-made world, so perhaps it is not surprising that humans show a remarkable sensitivity to visual symmetry [1]. Infants as young as 4 months are able to discriminate mirror symmetry from other forms of symmetry, and in adults symmetry has been shown to influence various perceptual processes from figure-ground segregation [2] (see Box 1) to judgments of facial attractiveness [5]. Moreover, sensitivity to symmetry does not appear to be a uniquely human trait and, in fact, it not only crosses class but also phyla boundaries, with preferences for bilateral symmetry being shown in various species of birds as well as bees [6]. In a recent study, Sasaki, Vanduffel, Knutsen, Tyler and Tootell [7] not only extend this list to include rhesus macaques (*Macaca mulatta*), but also take an important step in understanding its neural underpinnings by identifying the cortical regions that respond to mirror symmetry in both humans and macaques.

Symmetry-related activity in humans

Using fMRI, Sasaki and colleagues found that symmetric dot patterns evoked more activity than random dot patterns in human visual cortex, more specifically in areas V3A, V4, V7 (an area just anterior to V3A), and the lateral occipital complex (LOC). It is interesting to note that symmetry-related activity was absent in early visual cortex, and instead was confined to more advanced extrastriate areas with large receptive fields that may mediate the integration of information from large portions of the visual field. Importantly, the activity within this extrastriate network of areas correlated strongly with the subjects' perception of symmetry. Stimuli that were perceived as being more symmetric evoked greater activity than stimuli that were perceived as being less symmetric, suggesting that the response differences did indeed reflect selectivity for symmetry. Interestingly, the

Box 1. Symmetry and perceptual organization

Mathematically, a figure is symmetrical if it is unchanged across a class of Euclidian transformations, which include translations, rotations and reflections. However, often what is meant by the term symmetry is more specifically reflectional or 'mirror' symmetry, and in fact Ernst Mach [3] suggested that observers are more sensitive to mirror symmetry than to repetition (i.e. translational symmetry). Since then, symmetry in general, and mirror symmetry in particular, has been the cornerstone of several theories of how we organize our perceptual world. Symmetry has been shown to help observers segregate figures from their background [2]. All else being equal, observers will often perceive a mirror symmetrical region as figure over a non-symmetrical region. It has been suggested that symmetry can influence perceived shape. The shape in Figure 1a can be seen as either an upright diamond or a tilted square [3], depending on your perceptual frame of reference. It has been suggested that there is a bias to choose an axis of mirror symmetry as the frame of reference [4]. The square/diamond is ambiguous because it has multiple axes of symmetry. However, if the square/diamond is placed in a context like the one in Figure 1c it looks much more like a square – it seems that a tilted frame of reference is adopted in this context. Again, this can be explained by appealing to symmetry, but this time in terms of the global axis of symmetry: as a group, the set of three shapes in Figure 1c have a diagonal axis of symmetry and thus a diagonal frame of reference. Similarly, the same square as in Figure 1b looks more like a diamond in Figure 1d because the symmetry axis of the group (i.e. the diagonal) defines the orientation of the individual shapes [4].



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Figure 1. Examples of symmetry influencing shape perception. (a) This shape can be seen as either an upright diamond or a tilted square, depending on the perceptual reference frame adopted. Embedded in the context shown in (c) it appears more like a square. Similarly, the square in (b) appears more like a diamond in (d). These effects have been explained as resulting from a strong bias to choose the global axes of symmetry in (c) and (d) as the perceptual frame of reference.

correlation between symmetry perception and fMRI signals held even when subjects were not attending to the symmetry of the stimulus and instead detected the presence of a small reddish dot in the stimulus. This is an important control as it demonstrates that the effects were not simply artifacts of observers finding symmetric stimuli more interesting. Moreover, it is consistent with behavioral studies suggesting that the detection of mirror symmetry may be preattentive, depending strongly on stimulus-driven factors [8]. Finally, Sasaki and colleagues found symmetry-related responses in extrastriate cortex for a range of stimuli varying in properties and size suggesting that the neural activity evoked in extrastriate cortex reflected a generalized response to symmetry.

Symmetry-related activity in monkeys

Sasaki and colleagues took their experiments a step further by scanning awake behaving monkeys that were trained to maintain fixation for several minutes while viewing the same symmetric dot patterns as the human subjects. Symmetry-related responses were found in areas V3A, V4 and TEO of macaque visual cortex. However, the symmetry responses in macaques were only revealed with more sensitive scanning techniques including a higher field magnet and the use of a contrast agent, suggesting that symmetry processing was in general weaker in monkeys than in humans. The study is one of the first to use the same methodology and experimental design in both humans and monkeys to reveal similarities and differences in the functional organization of visual processes. The macaque brain has been the most widely studied animal model for human neocortical organization and function. Studies such as this will help to advance our understanding of the validity of the model. For example, one important issue is to determine which brain regions in the two species are analogous. Area V3A appears to have a similar topographic organization in the two species and is therefore assumed to be analogous [9]. However, the definition (and naming conventions) of human ventral V4 are heavily debated [10], and it is not clear whether an area analogous to macaque dorsal V4 even exists in the human. Similarly, an area anterior to V4 has been termed human TEO, but a correspondence to macaque TEO has not yet been established [11]. Future parallel fMRI studies in the two species will help to establish 'homology' of areas based on functional criteria, that is, by demonstrating similarities in neural response properties.

Towards understanding the neural mechanisms underlying symmetry perception

Importantly, the Sasaki study also paves the way for future single-cell physiology studies seeking to understand the neural mechanisms underlying symmetry perception. There is surprisingly little known about symmetry perception at the behavioral and the neural levels in the macaque. The few relevant studies have dealt with complex stimuli such as faces [12] or mirror image confusions [13], and were focused on infero-temporal (IT) cortex. Interestingly, IT cortex was not activated in the Sasaki study. Future studies, using the regions localized

with fMRI as target sites for electrode placement, may determine whether the effects found in IT for complex images are related to those found here in more intermediate visual areas. Such an approach will also help to further the understanding of the general relationship between the BOLD signal and electrophysiological neural signals [14], as well as to interpret differences in activation patterns between fMRI and single-cell physiology studies that have been found previously [15]. One important issue in the domain of symmetry perception will be 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.

In summary, the approach taken by Sasaki and colleagues is exciting, and opens several promising research avenues. First, by establishing a correlation between psychophysical perception and neural activity in humans, the study paves the way for a deeper understanding of the relationship between symmetry perception and its underlying neural basis. Second, the parallel investigation of symmetry perception in humans and macaques lays the groundwork for future physiology studies directed at a better understanding of the cellular mechanisms that are involved in this fundamental perceptual ability.

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