Dynamics of perceptual decisions about symmetry in visual cortex

Peter J. Kohler [a,*], Benoit R. Cottereau [b,c], Anthony M. Norcia [a]

[a] Department of Psychology, Stanford University, Jordan Hall, Building 420, 450 Serra Mall, Stanford, CA 94305, United States
[b] Université de Toulouse, Centre de Recherche Cerveau et Cognition, Toulouse, France
[c] Centre National de la Recherche Scientifique, Toulouse Cedex, France

ABSTRACT

Neuroimaging studies have identified multiple extra-striate visual areas that are sensitive to symmetry in planar images (Kohler et al., 2016; Sasaki et al., 2005). Here, we investigated which of these areas are directly involved in perceptual decisions about symmetry, by recording high-density EEG in participants (n = 25) who made rapid judgments about whether an exemplar image contained rotation symmetry or not. Stimulus-locked sensor-level analysis revealed symmetry-specific activity that increased with increasing order of rotation symmetry. Response-locked analysis identified activity occurring between 600 and 200 ms before the button-press, that was directly related to perceptual decision making. We then used fMRI-informed EEG source imaging to characterize the dynamics of symmetry-specific activity within an extended network of areas in visual cortex. The most consistent cortical source of the stimulus-locked activity was VO1, a topographically organized area in ventral visual cortex, that was highly sensitive to symmetry in a previous study (Kohler et al., 2016). Importantly, VO1 activity also contained a strong decision-related component, suggesting that this area plays a crucial role in perceptual decisions about symmetry. Other candidate areas, such as lateral occipital cortex, had weak stimulus-locked symmetry responses and no evidence of correlation with response timing.

Symmetry is a highly salient feature of the natural world, found in both plants and animals as well as human artifacts. There is a large literature investigating the role of symmetry in visual perception that has proceeded along three separate, but related lines of inquiry. First, the computational operations necessary to detect symmetry have commanded a strong interest, mainly concerned with the necessity of comparing features from spatially distant parts of the visual field (Cohen and Zaidi, 2013; Dakin and Watt, 1994). This computational demand suggests a close relationship between symmetry and global integration processes involved in the perception of contours and motion (Lorenceau and Shiffrar, 1992; McDermott and Adelson, 2004).

The second line of inquiry considers the prevalence of symmetry in natural objects, which means that symmetry can serve as a powerful cue for the detection, recognition and classification of objects. Symmetry has been shown to have strong effects on multiple aspects of object processing, such as shape discrimination (Delius and Nowak, 1982), mate selection (Møller, 1992), and shape constancy operations (Li et al., 2013). Symmetry may also influence scene perception, reducing the number of perceived elements in a scene (Apthorp and Bell, 2015).

The third line of inquiry proposes that symmetry may play a key role in neural representations, because the neural code of an input image can

be made more effective by coding repeating image elements in terms of their symmetries, rather than coding each image element independently. Because symmetries are ubiquitous in the natural world, taking them into account makes for a highly efficient coding strategy (Mumford and Desolneux, 2010).

This longstanding interest in symmetry has understandably generated a strong interest in identifying the neural mechanisms supporting symmetry perception. The first push in that direction used electroencephalography (EEG) to study event-related potentials (ERPs) associated with processing of reflection symmetry, and found a differential response in posterior electrodes over occipital cortex, beginning at ~220 ms, well after the response to the contrast change evoked by the image update (Norcia et al., 2002). This initial EEG study has been followed by several others measuring similar *Sustained Posterior Negativity* (SPN) responses to different types of symmetric patterns (Bertamini and Makin, 2014; Jacobsen and Höfel, 2003; Makin et al., 2014, 2012, 2016; Palumbo et al., 2015). Interestingly, while SPN latency is fairly consistent across different stimuli and experiments, the amplitude has been found to scale parametrically with the strength of the symmetry in a presented image (Palumbo et al., 2015). Recent work has suggested that SPN amplitude may in fact index a more general neural response to the perceptual

* Corresponding author.
  E-mail address: pjkohler@stanford.edu (P.J. Kohler).

goodness of visual regularities (Makin et al., 2016).

Functional MRI studies on symmetry began with two studies published the same year, that both focused on reflection symmetry in dot patterns. The first study found a particularly strong response to symmetry in dorsal lateral occipital cortex, compared to retinotopic cortex (Tyler et al., 2005). The second study used an ROI definition procedure that was independent of symmetry responses, and found several areas in extra-striate visual cortex that were sensitive to reflection symmetry (Sasaki et al., 2005). Some areas remained sensitive even when attention was controlled – these areas included object-sensitive lateral occipital cortex (LOC), ventral V4 (adjacent to ventral V3, presumably defined as a quarter-field representation of the contralateral upper visual field, following Hadjikhani et al., 1998), V3A, V7 (commonly referred to as IPS0, see Swisher et al., 2007), and an area the authors called dorsal V4, which appears to correspond to either V3B or LO1. Another group of areas had significant responses only during passive viewing, including V3 and the motion-sensitive area MT+ (Sasaki et al., 2005).

We have recently expanded on this existing work, using a combination of EEG and functional MRI to measure responses to a novel set of stimuli comprised of wallpaper patterns (Kohler et al., 2016). Wallpapers are a class of regular textures that result from combinations of the four fundamental types of symmetry reflection, translation, rotation and glide (Fedorov, 1891; Polya, 1924). We focused on a subset of four of the 17 distinct wallpaper groups – those that contain rotation symmetries of various order. Using a combination of functional MRI and EEG source-imaging we showed that visual areas V3, hV4, VO1 and LOC had responses that varied parametrically with the order of rotation symmetry (Kohler et al., 2016). This sensitivity to rotation symmetry was not observed in V1 or V2, suggesting that the information conveyed by this form of regularity is not encoded prior to V3. EEG source-imaging allowed us to study the temporal order of symmetry processing across visual areas, and to determine that the onset of the symmetry responses occurred earlier in V3 and hV4 than in LOC. This result suggests that symmetry information is propagated along the ventral stream in a bottom-up fashion (Kohler et al., 2016).

The literature thus suggest that multiple visual areas process symmetry, but the causal role of the individual areas in symmetry perception remains poorly understood. A recent study found that reflection symmetry processing was disrupted when TMS was applied to LOC, but was unaffected when TMS was applied to V1/V2 (Bona et al., 2014; Cattaneo et al., 2011). This suggests that under the conditions of these experiments, LOC likely had a causal role in reflection symmetry perception, whereas V1/V2 did not. While these results indicate that LOC may be part of the cortical network supporting symmetry perception, they do not speak to the possible causal involvement of other areas that are responsive to symmetry, such as mid-level extra-striate areas e.g. V3, hV4 or VO1.

Here we present an EEG study in which we took a different approach to addressing the causal role of different visual areas in symmetry perception. We collected EEG measurements of the neuronal response to rotation symmetry, in the tradition of the initial ERP studies of symmetry. We expanded on the existing EEG and fMRI literature, however, by using an experiment design that made it possible to relate EEG measurements of brain activity directly to trial-to-trial variability in behavior. Our stimuli were textures from the four wallpaper groups containing rotation symmetries of varying order, that we have previously studied (Kohler et al., 2016). We asked participants to make speeded judgments about whether a presented texture image contained rotation symmetry or not. This approach allowed us to take two separate analysis approaches: Stimulus-locked analysis, which identified encoding-related activity analogous to that studied in our previous work, and response-locked analysis, which identified activity that can be directly related to the timing of button-press responses made by participants in each trial, and thus to the timing of the underlying perceptual decision making process. We first identify a set of electrodes over occipital cortex that have the most pronounced differences in the encoding-related activity evoked by

symmetry and no-symmetry stimuli, indicating that they are responding to symmetry. These electrodes also have decision-related activity that is separable from the encoding-related activity. We then use source imaging to localize both encoding- and decision-related activity in visual cortex. We can now ask which of the known symmetry-responsive visual areas show encoding-related responses to symmetry, and which of them also have activity that can be uniquely related to the perceptual decisions about symmetry.

This response-locked analysis approach has been successfully applied to investigations of the causal role of different visual areas in decisions about other perceptual domains such as shape discrimination (Ales et al., 2013) and disparity detection (Cottereau et al., 2014). Here response-locked analysis was used to determine which of the several areas that are capable of encoding symmetry are used to decode symmetry for perception. Considering that symmetry makes key contributions to multiple domains of visual perception, it is perhaps not surprising that a large number of visual areas are sensitive to symmetry. It is important, however, to clarify the contribution of each area to the ongoing perception of symmetry itself. This is the first study to approach this problem by coupling the trial-to-trial variability of brain and behavior.

Materials and methods

Participants

Twenty-five participants (11 females, mean age 27.8 ± 11.7) took part in the EEG experiment. Structural MRI data were collected in fifteen of these participants (6 females, mean age 30.8 ± 13.6), so that individualized head models could be constructed for distributed inverse source modeling. All participants were pre-screened to confirm that they had normal or corrected-to-normal visual acuity on the Bailey-Lovie chart and normal stereopsis on the RandDot test (http://precision-vision.com/products/stereo-vision-tests/randot-stereo-test.html). Their written informed consent was obtained prior to the experiment under a protocol that was approved by the Institutional Review Board of Stanford University.

Wallpaper stimulus generation

The four wallpaper groups used in this study, *P2*, *P3*, *P4* and *P6*, all contain rotation symmetries, but the maximum order of rotation symmetry is different from group to group. Rotation symmetry around a point can be defined in terms of its order n, which means that the object can be rotated by an angle $360°/n$ without changing. Each group contains rotation symmetry around several points that vary in order. For P2, the maximum order of rotation symmetry is 2, for P3 it is 3, for P4 it is 4 and for P6 it is 6 (we encourage the reader to identify rotation symmetries of different order in Fig. 1A).

Exemplars from the different wallpaper groups were generated using a modified version of the methodology developed by Clarke et al. (2011) that we have described in detail elsewhere (Kohler et al., 2016). Briefly, exemplar patterns for each group were generated from random-noise textures, which were then repeated and transformed to cover the plane, according to the symmetry axes and geometric lattice specific to each group. The use of noise textures as the starting point for stimulus generation allowed the creation of an almost infinite number of distinct exemplars of each wallpaper group.

To control for the contribution of low level stimulus features to the measured evoked responses, phase-randomized control exemplars were generated that had the same power spectrum as each exemplar image for each group. The phase scrambling operation eliminates rotation, reflection and glide-reflection symmetry relationships, but preserves the power spectrum. As a result of the phase scrambling operation, all scrambled control exemplars, regardless of which wallpaper group they are derived from, degenerate to another symmetry group, namely *P1*. P1 is the