



Not all visual symmetry is equal: Partially distinct neural bases for vertical and horizontal symmetry



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ABSTRACT

Visual mirror symmetry plays an important role in visual perception in both human and animal vision; its importance is reflected in the fact that it can be extracted automatically during early stages of visual processing. However, how this extraction is implemented at the cortical level remains an open question. Given the importance of symmetry in visual perception, one possibility is that there is a network which extracts all types of symmetry irrespective of axis of orientation; alternatively, symmetry along different axes might be encoded by different brain regions, implying that there is no single neural mechanism for symmetry processing. Here we used fMRI-guided transcranial magnetic stimulation (TMS) to compare the neural basis of the two main types of symmetry found in the natural world, vertical and horizontal symmetry. TMS was applied over either right Lateral Occipital Cortex (LO), right Occipital Face Area (OFA) or Vertex while participants were asked to detect symmetry in low-level dot configurations. Whereas detection of vertical symmetry was impaired by TMS over both LO and OFA, detection of horizontal symmetry was delayed by stimulation of LO only. Thus, different types of visual symmetry rely on partially distinct cortical networks.

1. Introduction

Mirror (reflective) symmetry is an important cue in visual perception for both animals and humans and it is extracted fast and pre-attentively from visual scenes (e.g., Barlow and Reeves, 1979; Wagemans et al., 1991; for reviews, see Bertamini and Makin, 2014; Cattaneo et al., 2014; Treder, 2010). The salience of vertical symmetry is likely to have emerged to facilitate recognition of animals (mostly symmetric along the vertical axis) and of human bodies and faces (e.g., Treder, 2010). Although symmetry along other axes of orientation also acts as a grouping principle of perceptual organization (e.g., Wagemans et al., 2012) and may also convey important information about the environment (for instance, images reflected in still water appear symmetric along the horizontal axis, see Cavanagh et al., 2008), the vertical axis of symmetry is the most salient for the visual system (for review, Wagemans, 1995). Indeed, several psychophysical studies have found faster and more efficient detection of vertical symmetry relative to symmetry along other orientations (Barlow and Reeves, 1979; Herbert and Humphrey, 1996; Machilsen et al., 2009; Wagemans, 1995; Wenderoth, 1994).

Whether detection of different types of reflective symmetry involves

different cortical networks is not clear. This is because most studies so far have focused on the neural basis of vertical mirror symmetry detection, with only little available evidence on other axis orientations. Neuroimaging findings suggest that the critical cortical region mediating vertical symmetry detection is the lateral occipital (LO) complex, together with other regions in the extrastriate visual cortex, such as V3, V4 and V7 (Sasaki et al., 2005; Tyler et al., 2005; see also Bauer et al., 2015, for supramodal evidence). Interestingly, the magnitude of activation in these areas seems to be higher for 4-fold symmetry than for 2-fold or 1-fold symmetry and for vertical than for horizontal symmetry (Sasaki et al., 2005). On one hand, electrophysiological studies have shown that the sustained posterior negativity (SPN), a component thought to be generated by automatic visual symmetry analysis in the extrastriate visual cortex (Makin et al., 2013, 2014; see Bertamini and Makin, 2014, for review), is similar for vertically and horizontally symmetric patterns (Wright et al., 2015). On the other hand, event-related desynchronization of the occipital alpha rhythm - observed in tasks requiring the detection of visual regularities including symmetry (Makin et al., 2012, 2015) - is differently affected by horizontally and vertically symmetric stimuli (Wright et al., 2015). Moreover, a prior study combining adaptation with TMS over LO found clearer effects on

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detection of vertical than horizontal symmetry (Cattaneo et al., 2011). Taken together, available evidence suggests that there may be some differences in the neural underpinnings of horizontal and vertical (reflective) symmetry detection (Cattaneo et al., 2011; Sasaki et al., 2005; Wright et al., 2015).

A series of transcranial magnetic stimulation (TMS) studies have showed that the LO region plays a causal role in symmetry detection (Bona et al., 2014, 2015; Cattaneo et al., 2011; for a recent review, Cattaneo, 2017), supporting and extending prior neuroimaging evidence (Sasaki et al., 2005). Moreover, Bona et al. (2015) demonstrated that detection of vertical symmetry also causally involves a key node of the face-processing network, the right occipital face area (OFA; Minnebusch et al., 2009; Pitcher et al., 2007, 2009). However, no “virtual lesion” TMS study so far has directly investigated whether LO and OFA are causally involved to a similar extent in horizontal and vertical symmetry detection; this was the aim of the present study. This was accomplished by means of fMRI-guided TMS, a tool that permits to assess the functional relevance of a targeted brain site in a specific cognitive process (Parkin et al., 2015; Sack et al., 2009; Silvanto and Pascual-Leone, 2012; Sliwinska et al., 2014; Walsh and Cowey, 2000). Participants were instructed to discriminate between symmetric (along either the vertical or the horizontal axis) and non-symmetric dot patterns while receiving TMS over either the right OFA, the right LO or Vertex (as a baseline). The case of OFA is particularly intriguing because its involvement in vertical symmetry detection has been linked to its role in face recognition (Bona et al., 2015; see also Chen et al., 2007), with symmetry acting as a strong cue in recognizing faces, at least when they appear in standard top-down orientation (e.g., Anderson and Gleddie, 2013; Rhodes et al., 2005; Simmons et al., 2004). If the role of OFA in symmetry detection is strictly dependent on the vertical orientation of the symmetry axis (faces appearing symmetric along the vertical axis), then interfering with OFA may not affect horizontal symmetry detection. In turn, interfering with LO activity may also affect horizontal symmetry, although the effects may be less evident than with vertical symmetry (see Cattaneo et al., 2011; Sasaki et al., 2005).

2. Methods

2.1. Participants

Twenty-three neurologically healthy students (9 males, mean age: 24.91, SD: 2.83) with normal or corrected-to-normal vision from Aalto University, Espoo (Finland) took part in the experiments. One participant was excluded due to long RTs (more than 2 standard deviations from the participant's mean RT) and one further participant interrupted the experiment because of TMS-induced discomfort; therefore the final sample included 21 subjects (8 males; mean age: 24.4, SD: 2.23). All participants were right-handed (Oldfield, 1971). The protocol was approved by the local ethics committee and a written informed consent was filled out by all subjects. Participants were treated in accordance with the Declaration of Helsinki and were screened for contraindications to fMRI and TMS. The study included two sessions: in the first session the fMRI localization was carried out whereas the TMS experiments were performed in the second session.

2.2. fMRI localization of LO and OFA

fMRI localization was performed at the Advanced Magnetic Imaging (AMI) center, Aalto University (Espoo, Finland) using a 3 T MAGNETOM Skyra whole-body scanner (Siemens Healthcare, Erlangen, Germany) equipped with a 30-channel head-neck coil. Each participant underwent three functional runs, one for LO and two for OFA (note that a piloting study in our lab suggested that consistent localization of OFA may need more trials compared to LO localization), as done in prior studies (Bona et al., 2015, 2016). LO and OFA were

both localized in the right hemisphere. Indeed, prior findings suggest that right OFA but not its left homologous is involved in vertical symmetry detection (Bona et al., 2015), possibly reflecting the role of right but not left OFA in face processing (e.g., Pitcher et al., 2011b; Rossion et al., 2003). Moreover, although both the left and right LO are involved in symmetry detection, the latter seems to play a clearer role (Bona et al., 2014). The stimuli were displayed in the middle of the screen on a 18-in. monitor (display resolution: 1280 × 1024) using Presentation software (Neurobehavioural System) and viewed at a distance of 40 cm through a mirror inserted in the head coil. All stimuli were gray-scale images measuring approximately 16 × 16 degrees of visual angle. Specifically, three different stimulus categories were employed: faces, objects and scrambled images of the same objects. Scrambled images were created by randomly selecting an equal number of square tiles from the original object image and modifying their position within a grid of the same dimension as the original objects. Participants were instructed to fixate the centre of the images, marked with a fixation cross. Right LO was determined by selecting the activation peak of clusters of voxels responding more intensively to images of objects compared to scrambled objects (as in Bona et al., 2015, 2016). Functional volumes were collected in a single run lasting 432 s with gradient-echo EPI sequence. The following imaging parameters were used: 23 slices with 3.5 mm slice thickness, repetition time = 2 s, echo time = 30 ms, voxel size = 3.125 × 3.125 × 3 mm³, flip angle = 75. Right OFA was identified as the activation peak of the cluster of voxels exhibiting stronger activation to faces relative to objects. The functional images were collected over 2 functional runs, each one lasting 271.2 s. Otherwise, the same parameters as for LO localization were employed. For each participant, a high-resolution T1-weighted MPRAGE anatomical image was also acquired.

Following data collection, SPM8 Matlab™ toolbox (<http://www.fil.ion.ucl.ac.uk/spm>) was used for data preprocessing, parameter estimation and visualization. During the preprocessing, the functional data were corrected for head movements and slice acquisition time. To allow a stable magnetization, the first four volumes of each runs were excluded. In the parameter estimation, the data were high-pass filtered with 128 s cutoff, and noise autocorrelation was modeled with AR(1) model. The functional data of each participant were co-registered with their individual anatomical scan, which were standardized into MNI space. The mean MNI coordinates for right OFA were: 46 (SD=4.6), -75 (SD=5.4), -5 (SD=7.4); and for right LO were 39 (SD=4.7), -79 (SD=9.03), -9 (SD=4.8); these coordinates are consistent with those reported in previous fMRI-guided TMS studies targeting the same regions (e.g., Pitcher et al., 2009; 2011). Fig. 1 shows the location of right LO and right OFA sites in a representative participant. Although LO and OFA are located at a distance of approximately 2 cm on the scalp, as reported by prior studies (Pitcher et al., 2007; see also Silvanto et al., 2010), several studies indicate that despite their proximity these two regions can be selectively affected by fMRI-guided TMS stimulation, as reflected in double dissociations in the encoding of distinct stimulus categories such as faces and objects (e.g., Dilks et al., 2013; Gilaie-Dotan et al., 2010; Pitcher et al., 2009, 2011a; Solomon-Harris et al., 2013).

2.3. TMS stimulation

TMS was delivered using a 70 mm biphasic figure-of-eight coil connected to a Nexstim stimulator (Nexstim Ltd., Helsinki, Finland). The stimulation targets were individually localized by means of eXimia Navigated Brain System (Nexstim Ltd., Helsinki, Finland), a co-registration software that enables real-time fMRI-guided placement of the coil (e.g., Hannula et al., 2008; Niskanen et al., 2010). On each trial, a train of 3 TMS pulses with a frequency of 10 Hz was delivered at target onset over one of the targeted sites (right LO, right OFA, Vertex) (see Bona et al., 2015, 2016; Cattaneo et al., 2012; Heuer et al., 2016; for similar stimulation parameters). The stimulation was set at a fixed

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