



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



Zaira Cattaneo^{a,b,*}, Silvia Bona^{a,d}, Juha Silvanto^c

^a Department of Psychology, University of Milano-Bicocca, 20126 Milan, Italy

^b Brain Connectivity Center, National Neurological Institute C. Mondino, 27100 Pavia, Italy

^c Department of Psychology, Faculty of Science and Technology, University of Westminster, 309 Regent Street, W1B 2HW London, UK

^d Advanced Magnetic Imaging Centre, Aalto Neuroimaging, OV Lounasmaa Laboratory, School of Science, Aalto University, 00076 Espoo, Finland

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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

* Corresponding author.

E-mail address: zaira.cattaneo@unimib.it (Z. Cattaneo).

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; Sliwiska 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 Gledhill, 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

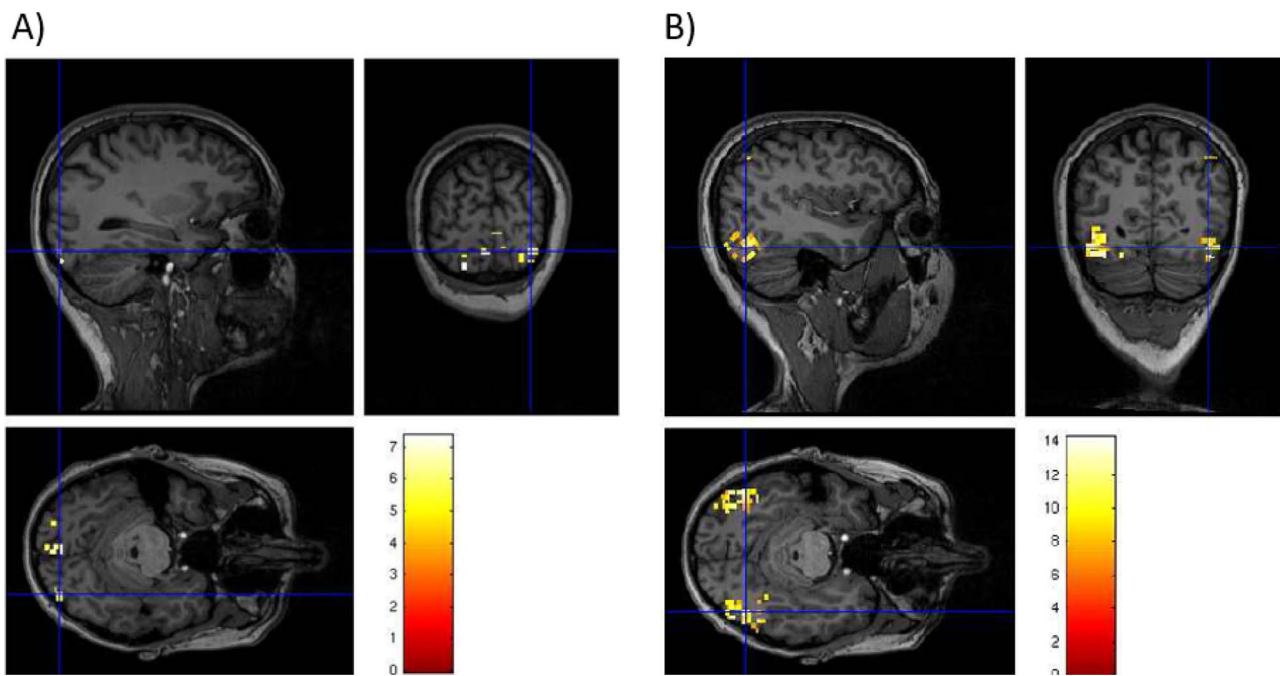


Fig. 1. Axial, sagittal, and coronal view (from lower left in clockwise order) in a representative participant of the activation peaks for faces versus objects in right OFA (A), and objects versus scrambled objects in right LO (B).

intensity of 40% of the maximum stimulator output for all participants, on the basis of our prior studies on OFA and LO function (e.g. Bona et al., 2015, 2016). This intensity corresponds to approximately 80% of the phosphene threshold of the early visual cortex, as reported by prior studies using the same stimulator machine (i.e., 45–50% with the Nexstim stimulator, Saad and Silvanto, 2013). A fixed TMS intensity has been used in most studies targeting OFA (Pitcher et al., 2007; Solomon-Harris et al., 2013) and LO (Cattaneo et al., 2015; Mullin and Steeves, 2011; Pitcher et al., 2009). Timing of stimulation was decided on the basis of our prior work in which TMS was found to impair symmetry detection with the same stimulation parameters. Electrophysiological studies found responses to symmetry in extrastriate visual areas approximately 250 ms after stimulus presentation (for a review, see Bertamini and Makin, 2014), whereas category-specific responses in extrastriate visual cortex have been detected already at 100 ms following stimulus onset (e.g., Pitcher et al., 2012; Sadeh et al., 2010). During the stimulation, the coil was held tangentially to the scalp over the individual peaks of activation acquired during the fMRI scan, with the coil handle pointing upwards and parallel to the midline (e.g. Kadosh et al., 2011; Muggleton et al., 2006; Pitcher et al., 2009). The coil was kept in place by the experimenter and its position was constantly monitored by using the eXimia NBS System. Vertex was localized as the midway point in between theinion and the nasion and equally distant from the left and right inter-trachial notches and was chosen as control site to control for the non-specific TMS-induced somatosensory effects evoked by the pulses.

2.4. Stimuli

Stimuli were presented on an 18-in. monitor with a display resolution of 1600 × 1200. Participants sat at a viewing distance of 60 cm and with their head stabilized by means of a chin rest. Stimulus presentation and response recording were controlled by E-prime v2.0 (Psychology Software Tools). The stimuli were the same as used in Bona et al. (2014, 2015) and similar to those employed by Sasaki et al. (2005). A total of 120 vertically symmetric and 120 non-symmetric stimuli was generated, consisting of 198 white dots on a black background; the patterns were of medium density, with the dots covering

1.8% of image area. Each pattern had a diameter of 16° of visual angle; dot diameter was .16°. To create the vertically symmetric configurations, half of the dots was first placed randomly into the left side of the image and subsequently the same arrangement was reproduced in the right hemispace, so that the resulting image was perfectly symmetric (i.e., with each dot on one half having a corresponding symmetric dot in the other half). The horizontally symmetric configurations were generated by rotating the vertically symmetric stimuli by 90 degrees. In non-symmetric patterns, the dots were distributed in a pseudo-random manner over both left and right hemispaces on the images, with the constraint that the same number of dots appeared in both sides. An example of the three configuration types is shown in Fig. 2.

2.5. Procedure

The two different types of symmetry (vertical and horizontal) were tested in separate blocks, of which participants were informed in advance. The timeline of an experimental trial is illustrated in Fig. 2d: the beginning of each trial was signaled by a black fixation cross appearing in the center of the display for 500 ms; this was followed by the target, i.e., a symmetric (along the vertical or the horizontal axis depending on the block) or a non-symmetric dot configuration, which remained visible for 75 ms. The TMS train (3 pulses at 10 Hz, i.e., pulse gap of 100 ms) was given concurrently with target presentation over one of the three target sites (right LO, right OFA, or Vertex). The task was a symmetry detection task: specifically, participants had to indicate as accurately and quickly as possible whether the displayed target was either symmetric or non-symmetric, by pressing the corresponding key with their right index and middle finger. Each experimental block consisted of 80 trials (40 symmetric and 40 non-symmetric targets, appearing in random order). For each symmetry type three blocks were run, one for each stimulation site (right LO, right OFA, and Vertex): thus, a total of six blocks was performed by each participant. The order of TMS blocks and the order of the two symmetry types were counterbalanced across participants, with the constraint that the three TMS blocks of each symmetry type were always performed in a row, before moving to the other type. The experiment was preceded by a short practice session (with no TMS) for each symmetry type, consisting of 20

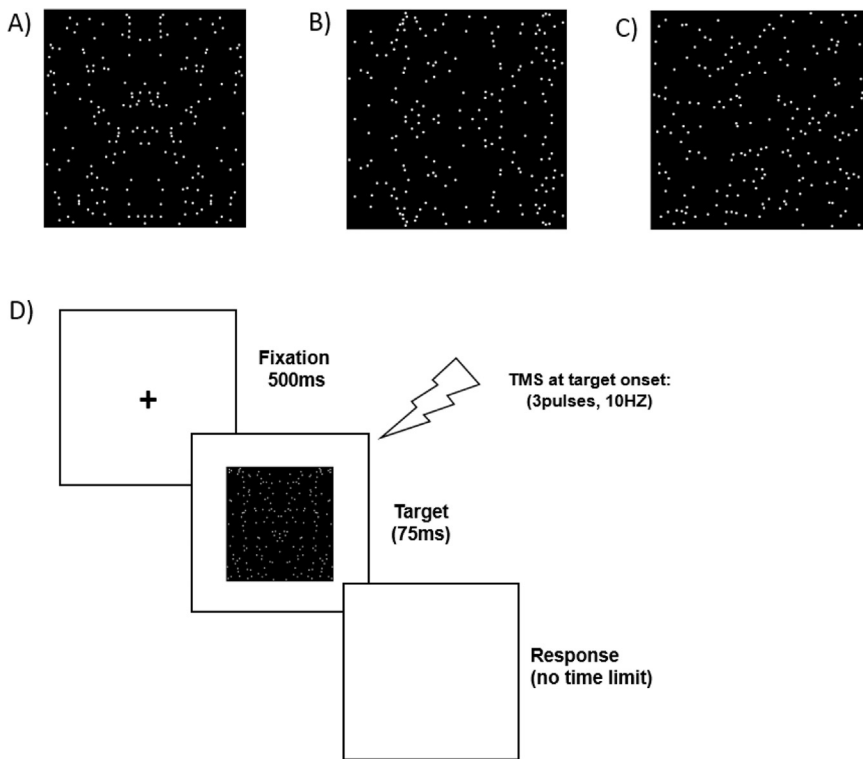


Fig. 2. Examples of a vertically symmetric (A), horizontally symmetric (B) and non-symmetric (C) dot configuration, respectively. Timeline of an experimental trial (D): a 500 ms black fixation cross was followed by the target (75 ms) consisting of either a symmetric (along either the vertical or the horizontal axis, depending on the block) or a non-symmetric dot pattern. Participants indicated whether the stimulus was symmetric or not. The TMS pulse train (3 pulses, 10 Hz) was administered at the target onset.

trials (10 symmetric and 10 non-symmetric patterns). As expected given the stimulated regions (see [Schaeffner and Welchman, 2017](#)) and the TMS intensity used, none of our participants reported phosphene perception during the experiment.

3. Results

The dependent variables were accuracy scores and response latencies for correct responses (see [Fig. 3](#)). Trials in which participants' RT were ± 3 SD compared to their block mean were excluded from the analyses (following this criterion 1.2% of trials were excluded). A repeated-measures ANOVA was carried out on each dependent variable, with TMS site (right LO, right OFA, Vertex) and Symmetry axis (Vertical vs. Horizontal) as within-subjects variables.

Detection accuracy was overall high in all task conditions. Mean accuracy for vertical symmetry was 93% (SD=8.3) for Vertex TMS, 91% (SD=6.3) for LO TMS, and 92% (SD=7.1) for OFA TMS. Detection accuracy for horizontal symmetry was 90% (SD=8.0) for Vertex TMS,

85% (SD=9.4) for LO TMS, and 88% (SD=8.9) for OFA TMS. The ANOVA on mean accuracy scores revealed a significant main effect of Symmetry axis, $F_{(1,20)} = 23.23$, $p < .001$, $\eta_p^2 = .54$, with participants being overall more accurate in detecting vertically than horizontally symmetric patterns. The main effect of TMS was significant, $F_{(2,40)} = 4.03$, $p = .025$, $\eta_p^2 = .17$, whereas the interaction TMS by Symmetry axis was not, $F_{(2,40)} = 1.58$, $p = .22$, $\eta_p^2 = .07$. Post-hoc comparisons revealed that TMS over LO overall impaired symmetry detection compared to vertex (control) stimulation irrespective of axis of orientation, $t_{(20)} = 2.46$, $p = .023$. The comparisons LO-TMS vs. OFA-TMS, $t_{(20)} = 1.56$, $p = .13$, and Vertex-TMS vs. OFA-TMS, $t_{(20)} = 1.55$, $p = .14$, did not reach significance.

The ANOVA on mean correct RT (see [Fig. 3](#)) revealed a significant effect of Symmetry axis, $F_{(1,20)} = 4.62$, $p = .044$, $\eta_p^2 = .19$, due to participants being overall faster in detecting vertical than horizontal symmetry. The main effect of TMS, $F_{(2,40)} = 5.91$, $p = .006$, $\eta_p^2 = .23$, and the interaction TMS by Symmetry axis, $F_{(2,40)} = 3.63$, $p = .036$, $\eta_p^2 = .15$, were significant. Post-hoc comparisons showed that both TMS over LO, $t_{(20)} = 2.78$, $p = .011$, and TMS over OFA, $t_{(20)} = 2.79$, $p = .011$, delayed participants' detection of vertically symmetric patterns compared to Vertex-TMS. No difference in detection of vertical symmetry was observed between LO and OFA-TMS, $t_{(20)} = 1.04$, $p = .31$. For the Horizontal symmetry condition, post-hoc comparisons showed that TMS over LO significantly delayed detection compared to OFA-TMS, $t_{(20)} = 2.34$, $p = .030$, and compared to the control condition, $t_{(20)} = 1.89$, $p = .073$ (in this case, the effect did not reach full significance). In turn, no difference in detection of horizontally symmetric pattern was observed for OFA-TMS compared to the control (Vertex) condition, $t_{(20)} < 1$, $p = .57$.

4. Discussion

The aim of this study was to compare the neural bases of vertical and horizontal symmetry detection. This was accomplished by asking participants to detect (in separate blocks) vertically or horizontally symmetric dot configurations while online TMS was applied over either right OFA, right LO or Vertex. Stimulating right OFA significantly

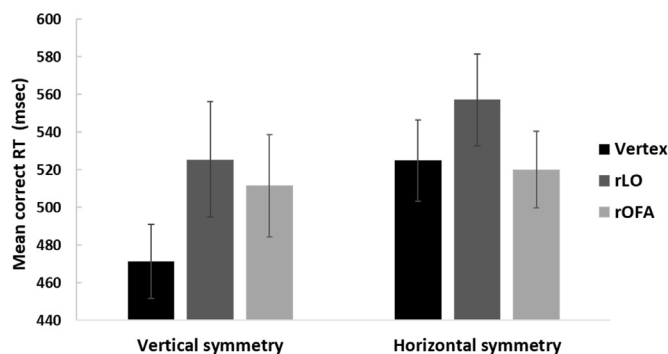


Fig. 3. Mean ($N = 21$) correct response latencies (RT) for detection of vertical and horizontal symmetry as a function of TMS site. Vertical symmetry was affected by stimulation of both right LO and right OFA. In turn, TMS affected perception of horizontal symmetry only when delivered over right LO, whereas stimulation of right OFA had no impact. Error bars represent ± 1 SEM.

delayed detection of vertically symmetric configurations while horizontally symmetric targets were not affected. In contrast, interfering with right LO activity delayed correct detection of both vertically and horizontally symmetric patterns (also significantly reducing accuracy). Hence, we demonstrate that whereas the right LO plays a causal role in encoding of both vertical and horizontal symmetry, the right OFA is causally involved in detection of vertical symmetry only. The neural bases of these two types of symmetry therefore partially differ.

As stated in the Introduction, the existing evidence on whether vertical and horizontal symmetry involve distinct neural mechanisms has been unclear. While electrophysiological studies have shown that the sustained posterior negativity (SPN) is similar for vertically and horizontally symmetric patterns (Wright et al., 2015), event-related desynchronization of the occipital alpha rhythm is differently affected by these two stimuli (Wright et al., 2015). Furthermore, prior fMRI evidence indicates that neural responses in LO to vertical symmetry appear to be stronger than for horizontal symmetry (Sasaki et al., 2005). Our findings support the view that these two types of symmetry do have distinct neural basis, in terms of partially distinct brain regions being necessary for their detection. Moreover, the impact of LO-TMS on reaction times suggest that LO, although coding both horizontal and vertical symmetry, may be more sensitive to the presence of the latter, in line with neuroimaging evidence (Sasaki et al., 2005) and with results of a prior TMS-adaptation study (Cattaneo et al., 2011). It should be noted on this regard that TMS is more likely to affect RTs in case of high accuracy (see Devlin and Watkins, 2008), which was around 90% at baseline in the present study.

This pattern of results is likely to reflect the different contexts in which vertical and horizontal symmetry appear in the visual world. As discussed earlier, fast and efficient detection of vertical symmetry provides an evolutionary advantage in the form of aiding recognition of animals and faces, given that most animals are mirror symmetric along the vertical axis. This can also explain the role of OFA in encoding vertical symmetry. A strong link exists between face and symmetry processing, with symmetry functioning as a cardinal cue in face detection (Anderson and Gledhill, 2013; Rhodes et al., 2005; Simmons et al., 2004). For example, the presence of symmetric face components is known to heighten face processing (Little and Jones, 2006; Troje and Bühlhoff, 1998) and, likewise, encoding of symmetry is facilitated by face-likeness (Jones et al., 2012). The role of OFA in detecting vertical symmetry in dot configurations may very well reflect its well-known role in face processing. Similarly, the involvement of LO in vertical symmetry detection is not surprising, given that LO is a key region for object processing (Ales et al., 2013; Grill-Spector, 2003; Grill-Spector et al., 2001; Mullin and Steeves, 2011) and given that large proportion of objects are symmetric along the vertical axis. Indeed, vertical symmetry is widely known to facilitate perception of both objects and shapes (Labonté et al., 1995; Machilsen et al., 2009).

In contrast, horizontal symmetry is much less frequent (and thus likely less salient) than vertical symmetry in the natural world. Empirical evidence from human observers is consistent with distinct mechanisms underlying the detection of these two types of symmetry; for example vertical symmetry is detected much faster and effortlessly (the so-called “vertical advantage”, Barlow and Reeves, 1979). Our finding of LO involvement in horizontal symmetry is in line with prior fMRI evidence which have implicated the LO in symmetry detection along different axes, including vertical and horizontal (Sasaki et al., 2005; Tyler et al., 2005). Given that objects tend not to be symmetric along horizontal axis, it is difficult to explain the role of LO in horizontal symmetry detection in terms of its object-selectivity. Rather, it may reflect the role of LO in perceptual organization in general (Grill-Spector, 2003; Malach et al., 1995; Treder and van der Helm, 2007) which is likely to arise from LO exhibiting larger receptive fields than lower-order visual areas which are necessary for extrapolating symmetry in a global fashion (Treder, 2010; Tyler et al., 2005). Indeed, fMRI studies have implicated LO in processes such as perceptual

completion (Murray et al., 2002; Ritzl et al., 2003) and integrating local features into a global figure (Grill-Spector et al., 2001; Konen and Kastner, 2008).

The sensitivity of OFA to vertical symmetry is likely to be important for its role at the earliest stage of face processing, in terms of extracting low-level features allowing face detection (Pitcher et al., 2011b). In support of this view, a prior behavioral study (Jones et al., 2012) has shown that face-likeness of a stimulus facilitates detection of its symmetrical structure even when presented in an inverted orientation (inversion typically disrupting face configural processing, see Taubert et al., 2011). This finding, together with prior evidence showing that OFA may have little sensitivity to face inversion (Pitcher et al., 2011a; Yovel and Kanwisher, 2005), suggests that the interaction between symmetry and face detection in OFA is likely placed at the parts-based level of analysis of a given stimulus. In turn, sensitivity to symmetry in OFA may be less important at higher-level stages of processing, such as in face identity encoding (e.g., Ambrus et al., 2017; Solomon-Harris et al., 2013).

Our findings may also help clarify the role of OFA in non-face visual categorization. Indeed, right OFA has been found to be implicated in shape recognition (Silvanto et al., 2010), shape vs. texture discrimination (Lowe et al., 2017), in disambiguating Mooney objects (Bona et al., 2016; Renzi et al., 2015) and in identifying specific exemplars within an object-category (Haist et al., 2010). Hence, the selective involvement of OFA in vertical vs. horizontal symmetry detection we observed in our study may also be related to object processing, given that most objects are symmetric along the vertical rather than horizontal axis (see Treder, 2010). On this regard, the reported involvement of OFA in recognizing Mooney objects (which can be detected only on the basis of their global configuration due to their lack of distinguishable and interpretable local parts, see Latinus and Taylor 2005, 2006; McKeef and Tong, 2006), suggests that rOFA is likely implicated in early, low-level figure-ground segmentation in which symmetry is an important cue (Wagemans et al., 2012).

In our study we used repetitive TMS at fixed timing and thus did not investigate the time course of symmetry processing. Future studies could use chronometric TMS to examine this. Comparing the critical time window of OFA in symmetry detection with that of face processing (e.g., Pitcher et al., 2007), would allow to clarify the interaction between symmetry and face detection in this region. Moreover, future research may further disentangle the role of OFA in symmetry and face detection by employing priming or adaptation paradigms (e.g. Cattaneo and Silvanto, 2008; Cattaneo et al., 2012): this would allow to examine whether the same neural populations in OFA are indeed responsible for face and symmetry detection.

In sum, our results shed light on the cortical underpinnings of vertical and horizontal symmetry encoding and demonstrate that the two symmetry orientations rely on partially different neural networks: in particular, we revealed that while right LO plays a causal role in perception of both symmetry orientations, the role of right OFA is limited to vertical symmetry and does not extend to horizontal orientation. We propose that this pattern might reflect the different functional roles of vertical and horizontal symmetry in low-level and high-level visual perception.

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