



Research report

The causal role of the lateral occipital complex in visual mirror symmetry detection and grouping: An fMRI-guided TMS study

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ABSTRACT

Despite the fact that bilateral mirror symmetry is an important characteristic of the visual world, few studies have investigated its neural basis. Here we addressed this issue by investigating whether the object-selective lateral occipital (LO) cortex, a key brain region in object and shape processing, is causally involved in bilateral symmetry detection. Participants were asked to discriminate between symmetric and asymmetric dot patterns, while fMRI-guided repetitive TMS was delivered online over either the left LO, the right LO or two control sites in the occipital cortex. We found that the application of TMS over both right and left LO impaired symmetry judgments, with disruption being greater following right LO than left LO TMS, indicative of right hemisphere lateralization in symmetry processing. TMS over LO bilaterally also affected a visual contour detection task, with no evidence for hemispheric difference in this task. Overall, our results demonstrates that LO bilaterally plays a causal role in symmetry detection possibly due to symmetry acting as a strong cue in Gestalt processes mediating object recognition.

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1. Introduction

Bilateral vertical symmetry is an important feature of the visual world. Not only are faces and bodies symmetric, but so are many aspects of the natural world (trees, flowers, animals)

as well as manufactured objects (from tools to furniture and buildings). Bilateral symmetry is easily and rapidly detected by the human visual system, even in infancy (reviewed by Herbert & Humphrey, 1996) and most probably without involving attentional resources (Julesz, 2006; Wagemans,

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1995). Rapid symmetry detection may at least partially rely on low-level visual mechanisms based on spatial-filtering similar to those involved in texture processing (Dakin & Herbert, 1998; Dakin & Hess, 1997). Symmetry has been suggested to be one process involved in figure-ground segregation and perceptual grouping (Labonté et al., 1995; Machilsen, Pauwels, & Wagemans, 2009).

Symmetric stimuli are better recalled than asymmetric patterns and the symmetry advantage extends to haptically explored patterns (Cattaneo et al., 2010; Rossi-Arnaud, Pieroni, & Baddeley, 2006; Rossi-Arnaud, Pieroni, Spataro, & Baddeley, 2012). The fundamental significance of symmetry may come from its biological relevance, with symmetry being perceived as a marker of health (Grammer & Thornhill, 1994). Finally, a hierarchy seems to exist in symmetry salience, with the vertical axis of symmetry being more easily detected than other axis orientations (Herbert & Humphrey, 1996; Royer, 1981; Wagemans, Van Gool, Swinnen, & Van Horebeek, 1993).

Despite the prominent role of visual symmetry in our visual lives, only a few studies so far have investigated its neural basis. Psychophysical results have suggested that the corpus callosum is implicated in vertical symmetry detection (Herbert & Humphrey, 1996). Bilateral symmetry along the vertical axis is perceived faster and more accurately than symmetry at other orientations as a result of the bilateral symmetric organization of the visual system. This ‘vertical advantage’ has been replicated in numerous times, and holds for reaction times, accuracy and other discrimination measures (reviewed in Herbert & Humphrey, 1996). Hemispheric differences in symmetry detection have also been reported: results from a divided visual field paradigm have suggested a more prominent role of the right hemisphere (RH) in symmetry detection (Brysbaert, 1994). Using fMRI, Sasaki, Vanduffel, Knutsen, Tyler, and Tootell (2005) and Tyler et al. (2005) reported that the perception of symmetric dot configurations more strongly activated the lateral occipital (LO) cortex and higher-order visual regions as compared to random configurations. LO is a region involved in shape and object encoding in a modality-independent fashion (Amedi, Malach, Hendler, Peled, & Zohary, 2001; Grill-Spector, Kourtzi, & Kanwisher, 2001; Pietrini et al., 2004). It was concluded that cortical regions activated by various objects generally overlap with the symmetry-selective regions (Sasaki et al., 2005); this may reflect the sensitivity of LO to factors such as figure-ground segmentation and grouping processes, for which symmetry is a strong cue (Altmann, Deubelius, & Kourtzi, 2004; Machilsen et al., 2009).

Neuroimaging, however, only provides correlational evidence and cannot indicate whether a region is necessary for a specific function. The causal link between a brain region and perceptual functions can be investigated by using brain stimulation techniques, such as transcranial magnetic stimulation (TMS). The rationale is that if a cortical area is *causally* involved in a particular task, stimulating that area with TMS should affect performance in that task (Cowey, 2005). In the present study, we used fMRI-guided TMS to investigate the role of the left and right LO cortex in the detection of visual vertical symmetry. We found that LO, bilaterally, is causally involved in symmetry detection. Interestingly, TMS over the right LO disrupted symmetry detection to a greater extent

than TMS applied over the left LO, indicative of right hemisphere preference for symmetry processing. To tease apart effects relating to symmetry from those associated with figure-ground segregation processes, we carried out a second experiment in which left and right LO were stimulated during a shape detection task (in which contours emerged by virtue of collinearity of the Gabor elements). We found that TMS over left and right LO disrupted contour detection, and that the disruptive effect of LO TMS on symmetry detection is consistent with the notion that symmetry is one grouping principle in perceptual organization. However, the hemispheric difference we found in symmetry detection was not related to grouping processes in general, being absent in the shape detection task.

2. Experiment 1

2.1. Method

2.1.1. Participants

Fifteen students or staff members (8 males, mean age = 25.07, SD = 3.19) with normal or corrected-to-normal vision at Aalto University, Espoo (Finland) took part in Experiment 1. All participants were right-handed (Oldfield, 1971). Written informed consent was obtained from all participants and the study was approved by the local ethics committee. Participants were treated in accordance with the Declaration of Helsinki.

2.1.2. Stimuli

Stimuli consisted of dot patterns similar to those employed by Sasaki et al. (2005) and were created using a Windows PC using Matlab (r2008b) and PsychToolbox (version 3.0.9 – Flavor: beta – Corresponds to SVN Revision 2540). A total of 120 vertically-symmetric stimuli and 120 asymmetric stimuli were created, all consisting of 198 white dots on a black background. The patterns were relatively sparse, with the dots covering 1.8% of stimulus area. Each stimulus had a diameter of 16° of visual angle, and dot diameter was .16°. Symmetric stimuli were symmetric along the vertical axis (with the vertical axis of symmetry coinciding with the vertical midline of the display) and they were generated by first placing half of the dots randomly onto the left side of the stimulus, and then reproducing the same arrangement on the right side so that the resulting image was symmetric (with each dot on the left side of the image having a corresponding symmetric dot in the right hemisphere). For asymmetric stimuli, the dots were distributed in a pseudo-random manner over both the left and right half of the stimulus, with the constraint that the same number of dots appeared to the left and to the right of the midline (see Fig. 1A for examples of symmetric and asymmetric stimuli). In both symmetric and asymmetric stimuli, dots could appear on the vertical meridian (the axis of symmetry for symmetric patterns).

2.1.3. fMRI localization

Left and right LO were localized in each participant as the activation peak of clusters of voxels that responded more strongly to gray-level photographs of objects than to scrambled versions of the same images. The scrambled objects were

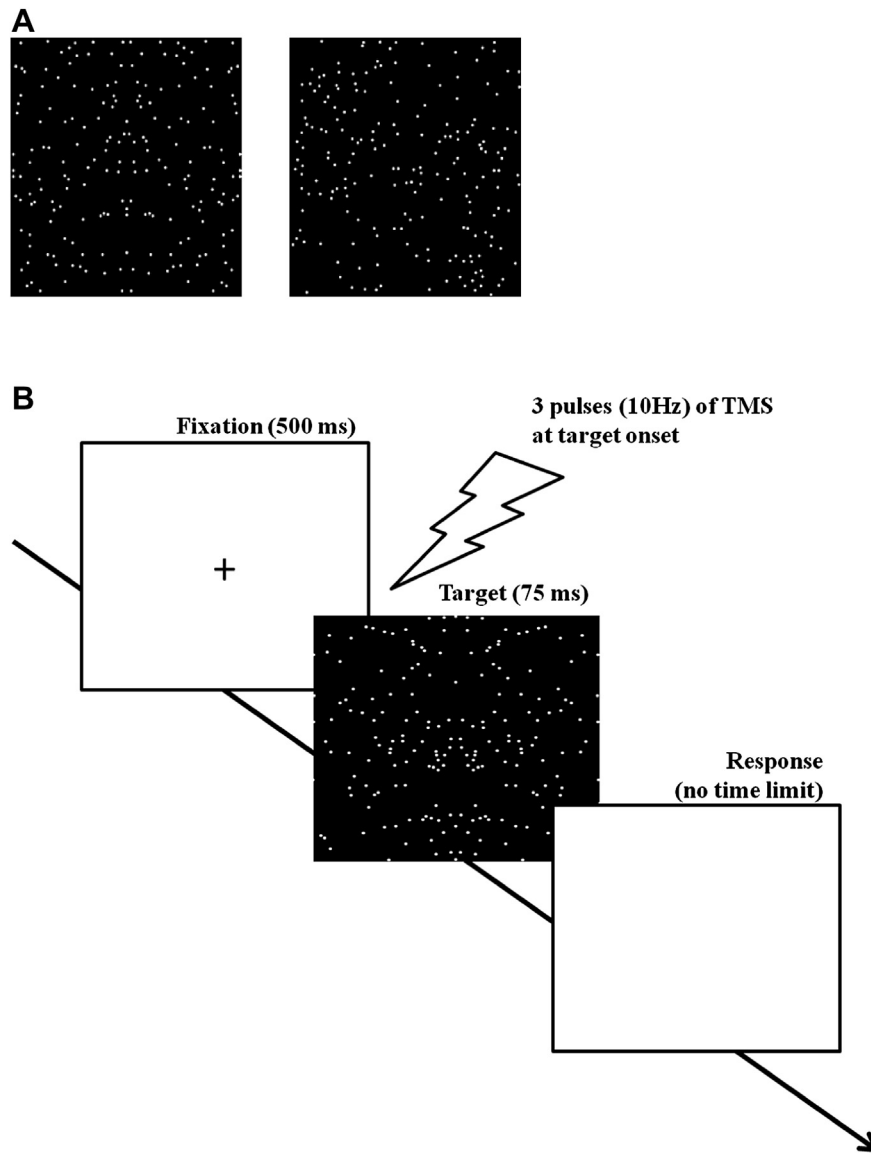


Fig. 1 – (A) Examples of symmetric (left) and asymmetric (right) stimuli used in the different experimental blocks. (B) Timeline of an experimental trial. Each trial started with a fixation cross appearing in the middle of the screen for 500 msec. The target stimulus was then presented for 75 msec and participants were instructed to indicate, as quickly as possible, whether the pattern was symmetric or asymmetric. A TMS train of 3 pulses (10 Hz) was given at stimulus onset.

constructed by randomly selecting an equal number of square tiles from the original object images, arranging them in a 16×16 grid of the same dimensions as the object images and permuting their positions. Measurements were performed using a 3T GE Signa Excite scanner (General Electric Medical Systems) equipped with an eight-channel receiver head coil. Functional volumes were acquired with echo-planar imaging using single-shot gradient-echo sequence with a repetition time of 2.0 sec. Twenty-nine slices with 3.0-mm slice thickness were acquired, with a field of view of 20 cm, resulting in $3.125 \times 3.125 \times 3 \text{ mm}^3$ voxel size. The imaging matrix was 64×64 , echo time 30 msec, and flip angle of 60. The duration of the object localizer was 432 sec. Data preprocessing, estimation and visualization were performed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>, cf. [Friston, Ashburner, Kiebel,](#)

[Nichols, & Penny, 2007](#)) MatlabTM toolbox. In preprocessing, functional images were corrected for inter-leaved acquisition order and for head motion. The first four images from the beginning of each run were excluded to reach stable magnetization. During the parameter estimation, the data were high-pass filtered with 128 sec cutoff, and noise autocorrelation was modeled with AR(1) model. The data were coregistered to high-resolution structural images which were standardized into MNI space using SPM8. The mean MNI coordinates for right and left LO were 44 (SD = 2.5), -78 (SD = 4.1), -13 (SD = 6.7) and -44 (SD = 4.4), -77 (SD = 5.7), -12 (SD = 9.5), respectively.

2.1.4. TMS

TMS pulses were delivered using a Nexstim stimulator (Nexstim Ltd, Helsinki, Finland) using a biphasic figure-of-eight

coil. In the left and right LO TMS conditions, for each participant the coil was placed over the identified activation peaks observed in that participant's object localizer; this was accomplished by using the Eximia NBS neuronavigation system (Nexstim Ltd, Helsinki, Finland), a coregistration software that allows fMRI-guided positioning of the TMS coil (e.g., Hannula et al., 2005). Fig. 2 shows the left LO and right LO sites

on a representative participant. To test for the specificity of any induced TMS effect over LO, two adjacent sites, one in each hemisphere, were used as controls. The coil was moved up 2 cm from left (CL) and right (CR) LO respectively. It is important to note that two adjacent areas can be selectively stimulated by TMS even when their distance is less than 2 cm (see Pitcher, Walsh, Yovel, & Duchaine, 2007).

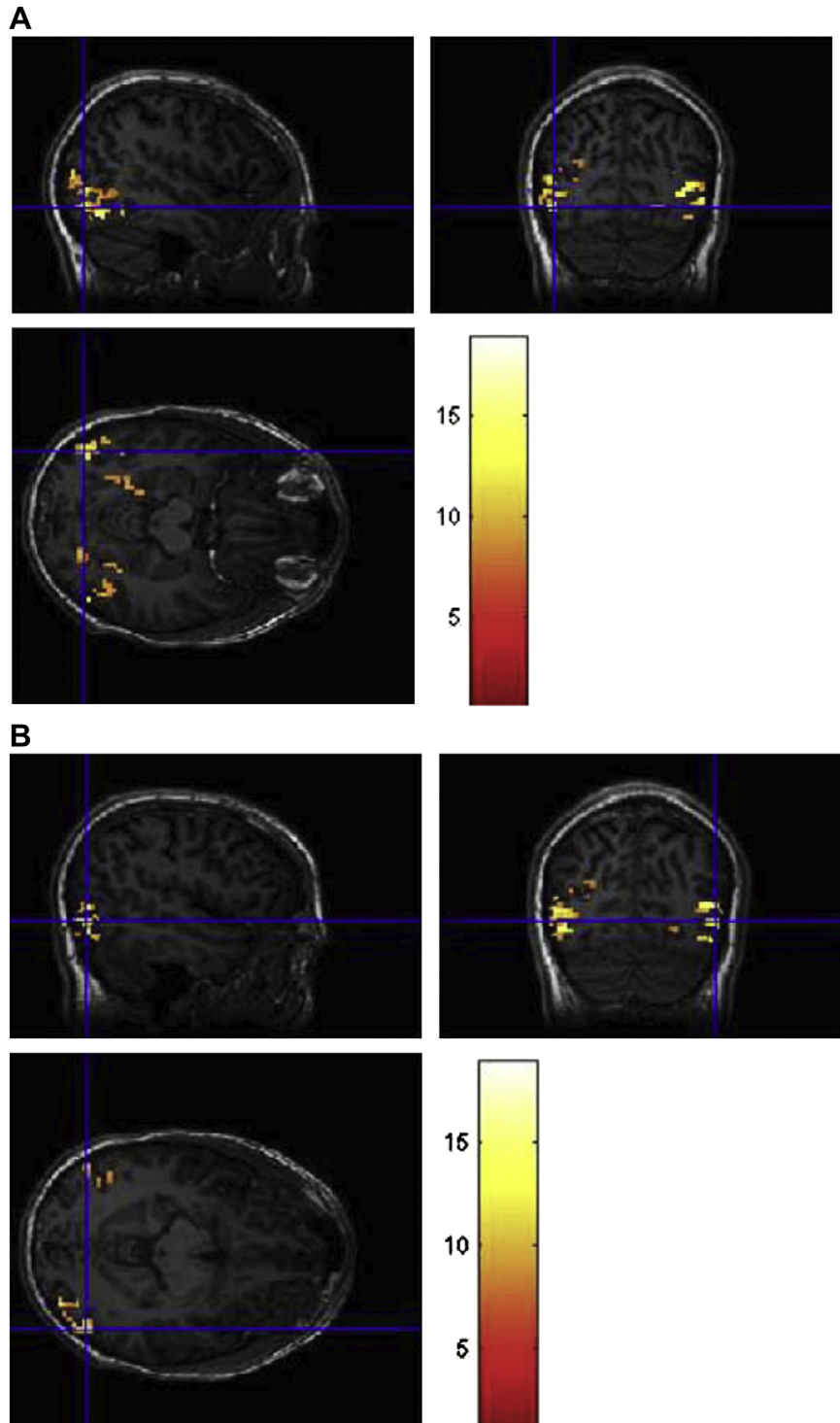


Fig. 2 – Axial, sagittal and coronal views (from upper left in clockwise order) of a representative participant showing the activation peak of the left (A) and right LO (B). The control sites (CL and CR) were localized such that the coil was moved up 2 cm dorsally from left and right LO respectively.

The coil was positioned over the stimulation sites such that the coil handle was pointing upwards and parallel to the midline as in previous studies targeting LO (e.g., Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009). In each trial of the TMS blocks (see below) a pulse train with a frequency of 10 Hz (consisting of 3 pulses) was delivered over one of the four targeted sites (see Cattaneo, Bona, & Silvanto, 2012; Cattaneo, Mattavelli, Papagno, Herbert, & Silvanto, 2011; Saad & Silvanto, 2013, for similar stimulation parameters). We chose the timing of the pulses based on previous ERPs evidence reporting that the N1 component (range 170–200 msec) was sensitive to the presence of symmetry in dot patterns (Makin, Rampone, Pecchinenda, & Bertamini, 2013) (other studies showing a deflection peak around 220 msec since stimulus onset, see Norcia, Candy, Pettet, Vildavski, & Tyler, 2002). Nonetheless, figure–ground-specific signals appear in the visual cortex at various stages within a large time window in the 50–300 msec range (see Neri & Levi, 2007). Moreover, previous TMS evidence (see Koivisto, Railo, Revonsuo, Vanni, & Salminen-Vaparanta, 2011) has shown that LO TMS decreases response speed at the SOAs of 150 and 180 msec after stimulus onset, and intracerebral recordings data from humans suggest that occipitotemporal areas in the ventral visual pathway are able to encode category-related information as early as 100 msec after stimulus onset (Liu, Agam, Madsen, & Kreiman, 2009). Since response latencies (RL) in ventral visual pathway are found as early as 100 msec, and they continue to at least to 200 msec, applying 10 Hz TMS at stimulus onset we aimed to be sure to cover the period of LO activity. Stimulation intensity was 40% of the maximum stimulator output. This intensity was determined on the basis of pilot studies indicating that this was the highest intensity we could use on LO (which is close to neck muscles) without causing participant discomfort. This stimulation intensity corresponds to approximately 80% of phosphene threshold of the early visual cortex, which is in the region of 45–50% with the Nexstim stimulator. This intensity range has been used in previous work in our laboratory (Saad & Silvanto, 2013).

2.1.5. Procedure

The stimuli were presented on an 18-inch monitor with a display resolution of 1600 × 1200. Viewing distance was 60 cm and the head position was maintained using a chin rest. E-prime 2.0 (Psychology Software Tools Inc., Pittsburgh, USA) was used for stimulus presentation and data recording. The timeline of an experimental trial is shown in Fig. 1B. Each trial started with a black fixation cross appearing in the middle of the display for 500 msec, followed by the target, i.e., a symmetric or asymmetric dot configuration, appearing for 75 msec. Simultaneously to the presentation of the target, participants received the TMS train. The experiment consisted of 5 blocks of 80 trials each (40 symmetric and 40 asymmetric stimuli, randomly ordered). In one block TMS was not delivered (NO TMS baseline block), in the other four blocks TMS was delivered at each of the different cortical sites, LOL, LOR, CL and CR. Participants were asked to judge whether the target was symmetric or asymmetric by left/right key pressing with their right index and middle finger. Both accuracy and response speed were emphasized. In each block the order of stimulus presentation was randomized. The order of TMS

blocks and response-key assignment were counterbalanced across participants. Prior to the experiment, all the participants performed a short practice session, consisting of one block of 40 trials (20 symmetric and 20 asymmetric, different from those used in the real experiment).

2.2. Results

One subject was excluded from analyses due to RL being more than 2 SD above the sample mean. Accuracy was above 90% in all the experimental conditions: mean for NO TMS = 96% (SD = 2.8), LOL = 94% (SD = 4.3), LOR = 93% (SD = 5.0), CL = 95% (SD = 2.6), CR = 94% (SD = 3.7). Statistical analyses were performed on mean RT adjusted for accuracy (i.e., inverse efficiency = mean RT/proportion of correct responses; see Bardi et al., 2013; Pasalar et al., 2010), to account for any possible trade-off between speed and accuracy, and normalized with respect to the baseline NO TMS condition (Alford, van Donkelaar, Dassonville, & Marrocco, 2007; Ellison, Battelli, Cowey, & Walsh, 2003). Mean RT in the NO TMS condition was 464 msec (SD = 211).

The impact of TMS on performance as a function of stimulation site is shown in Fig. 3. A repeated-measures ANOVA with TMS site (LO vs Control) and hemisphere (Left vs Right) as within-subjects factors revealed a significant main effect of TMS site, $F(1,13) = 6.28$, $p = .026$, $\eta_p^2 = .33$, indicating that when TMS was applied over area LO, bilaterally, there was a reduction in performance compared to when TMS was applied to the control sites. The analysis also revealed a significant effect of hemisphere, $F(1,13) = 6.51$, $p = .024$, $\eta_p^2 = .33$, and a significant interaction of site by hemisphere, $F(1,13) = 5.39$, $p = .037$, $\eta_p^2 = .29$. The main effect of hemisphere was a result of performance being worse overall when TMS was applied over the RH, but this effect must be considered in light of the significant interaction of site by hemisphere. To clarify this interaction, we looked at the simple main effect of hemisphere within each stimulation site (LO and control): performance did not differ between the left and right control sites,

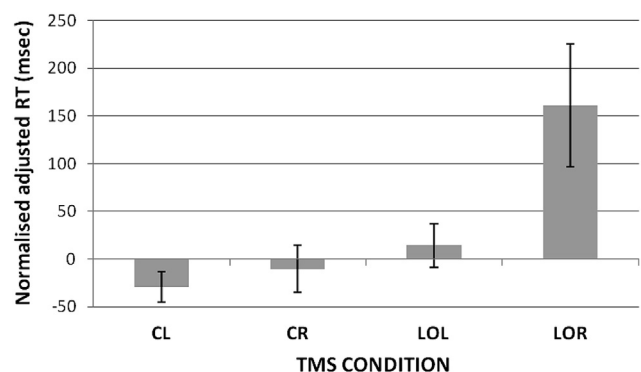


Fig. 3 – Participants' adjusted RT (= raw RT/accuracy), normalized to the baseline NO TMS condition (N = 14). Overall, TMS over both the left and right LO disrupted symmetry detection compared to TMS over the left and right control site. However, disruption was significantly higher following right LO than left LO TMS ($p = .021$), whereas no hemispheric difference emerged for the control sites ($p = .40$). Error bars indicate ± 1 SEM.

$t(13) = .87, p = .402$, whereas it was significantly worse for right LO TMS compared to left LO TMS, $t(13) = 2.62, p = .021$. Thus the key finding of Experiment 1 is that, although TMS to both the left and right LO impaired performance, the disruptive effect of TMS was larger for the right side.

3. Experiment 2

3.1. Method

3.1.1. Participants

Twelve participants (7 males, mean age = 23.25, SD = 2.3), all right-handed and with normal or corrected-to-normal vision, took part in Experiment 2, after providing a written informed consent. None of them previously participated in Experiment 1. The study was approved by the local ethics committee and participants were treated in accordance with the Declaration of Helsinki.

3.1.2. Stimuli

Stimuli consisted of different Gabor patches (GP) patterns (gray scale values ranging from 13 to 165) presented on a gray background (gray value 89). Each Gabor element was defined as the product of a sine wave luminance grating (frequency of 3.75 cycles/deg) and a two-dimensional Gaussian envelope (standard deviation of $.19^\circ$ in both dimensions). Each pattern had a diameter of 16° of visual angle and the GP diameter was $.8^\circ$. GPs were distributed on an invisible 20×20 grid. The number of GPs in the patterns ranged from 120 to 210. The minimum center-to-center distance between the Gabor elements was $.8^\circ$. A first set of 40 GPs was created in which GPs were carefully distributed and oriented to delineate a closed contour (see Fig. 4; with all contours defining unfamiliar shapes) embedded in a random GP background, similar to Kourtzi, Betts, Sarkheil, and Welchman (2005). The contour was built up from a variable number of GPs, that always corresponded to the 40% of the total number of GPs present on screen (the remaining 60% GPs were random background). A second set of 40 stimuli was generated consisting of GPs randomly distributed and oriented: for each stimulus of the first set, a corresponding random pattern was created for the second set, so that GP patterns in the two sets were perfectly matched in terms of the total number of GPs they contained. All stimuli were created using a Windows PC with Matlab (r2011a) and PsychToolbox (version 3.0.9 – Flavor: beta – corresponds to SVN Revision 2540).

3.1.3. fMRI localization and TMS

The fMRI localization procedure and TMS parameters were the same as in Experiment 1. The mean MNI coordinates for right and left LO were 44 (SD = 3.2), -76 (SD = 4.2), -13 (SD = 5.7) and -42 (SD = 5.1), -76 (SD = 5.9), -12 (SD = 8.1), respectively.

3.1.4. Procedure

The task was a shape detection task: participants were required to indicate with left/right key pressing (using their right index and middle finger) whether they could detect a shape in the stimulus. Otherwise, the procedure was the same as in Experiment 1. Participants performed 5 blocks consisting

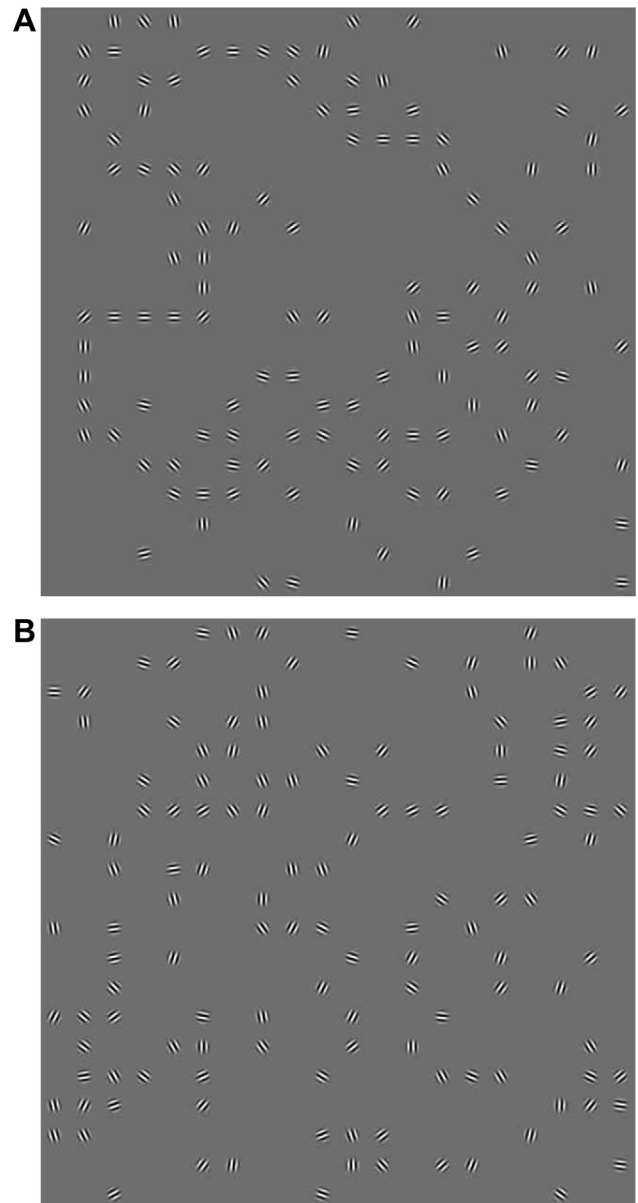


Fig. 4 – Examples of Gabor patches patterns used in Experiment 2: in (A) a shape is visible; in (B) Gabor patches are randomly distributed (contrast has been enhanced here for illustrative purposes).

each of 80 randomly presented trials (40 with no shape visible, and 40 with a shape embedded). In one block TMS was not delivered (NO TMS baseline block), in the other four blocks TMS was delivered at the same cortical sites as in Experiment 1, namely LOL, LOR, CL and CR. As in Experiment 1, participants received the TMS train simultaneously to the presentation of the target. The order of TMS blocks and response-key assignment were counterbalanced across participants.

3.2. Results

Accuracy was above 88% in all the experimental conditions: mean for NO TMS = 91% (SD = 5.4), LOL = 88% (SD = 8.0),

LOR = 88% (SD = 8.7), CL = 90% (SD = 6.4%), CR = 89% (SD = 8.1). Mean RTs in each TMS condition were adjusted to accuracy and normalized to the baseline No TMS condition as in Experiment 1. Mean RT in the NO TMS condition was 479 msec (SD = 146). The impact of TMS on performance as a function of stimulation site is shown in Fig. 5.

A repeated-measures ANOVA with TMS site (LO vs Control) and hemisphere (Left vs Right) as within-subjects factors showed a significant main effect of TMS site, $F(1,11) = 14.67$, $p = .003$, $\eta_p^2 = .57$, indicating that TMS over LO decreased performance compared to TMS applied to the control sites. The effect of hemisphere was not significant, $F(1,11) = .21$, $p = .654$, $\eta_p^2 = .02$, nor was the interaction TMS site by hemisphere, $F(1,11) = .97$, $p = .345$, $\eta_p^2 = .08$.

4. Discussion

In this study we applied TMS over the left and right LO cortices to investigate the role of these regions in bilateral symmetry detection. We found that application of TMS over both the left and the right LO significantly impaired participants' ability to discriminate vertically-symmetric dot patterns from asymmetric ones (Experiment 1), causally implicating these regions in symmetry detection. Right LO stimulation impaired symmetry detection significantly more than left LO stimulation, indicative of right-hemisphere lateralisation. Experiment 2 was included to verify whether the effects we report relate to symmetry perception as a cue in perceptual grouping mechanisms (cf. Machilsen et al., 2009). The second experiment showed that TMS over LO bilaterally impaired detection of contours defined by collinearity of Gabor elements (with no evidence of hemispheric differences). The lack of hemispheric differences in Experiment 2 suggests different underlying cortical processes for symmetry detection alone compared to perceptual grouping.

Clearly TMS over LO does not disrupt performance in all tasks. Several studies show that TMS over LO can selectively disrupt processing of specific visual stimuli, leaving

processing of other stimuli unaffected (see Dilks, Julian, Paunov, & Kanwisher, 2013; Pitcher et al., 2009). The lack of hemispheric differences observed in Experiment 2 also rules out the possibility that our results are merely a product of TMS being more effective in disrupting the right hemisphere. Furthermore, our MNI coordinates indicate that the left and right LO were equally distant from the scalp surfaces, thus it is unlikely that one hemisphere was more affected by TMS than the other.

Our finding of bilateral involvement of LO in both symmetry detection and collinearity-based grouping processing is in line with previous electrophysiological, neuroimaging and TMS evidence pointing to bilateral involvement of LO in object/shape detection (Ales, Appelbaum, Cottareau, & Norcia, 2013; Altmann et al., 2004; Ellison & Cowey, 2009; Ferber, Humphrey, & Vilis, 2005; Mullin & Steeves, 2011). Although earlier neuroimaging data did not reveal hemispheric differences in LO activation during symmetry detection (Sasaki et al., 2005), the greater TMS effects over the RH we observed are in line with previous data based on a divided visual field paradigm reporting a left visual field/RH advantage in symmetry detection (Brysbaert, 1994). This pattern of hemispheric lateralization may depend on well-documented hemispheric differences in global/local processing wherein the RH is specialized for configural/global visual processing and the LH for local feature processing (e.g., Christie et al., 2012; Yovel, Levy, & Yovel, 2001, for reviews; Fink et al., 1997; Han, He, & Woods, 2000; Lamb, Robertson, & Knight, 1989; Robertson, Lamb, & Knight, 1988). Indeed, it is likely that symmetry detection for patterns like those presented in the current study occurs through a coarse and global/parallel analysis of the stimuli instead of being computed through a point-by-point serial comparison (Barlow & Reeves, 1979; Dakin & Herbert, 1998; Huang, Pashler, & Junge, 2004; Julesz, 2006; Locher & Wagemans, 1993). TMS over the right LO may have been particularly detrimental to participants' performance by impacting global processing. The effect reported here is that symmetry detection remains very accurate in all TMS conditions, but more time is required to achieve that accuracy when RH LO is stimulated (Fig. 3).

A further factor contributing to a right LO critical locus is that the RH and the LH are predominantly biased toward low and high spatial frequency analysis, respectively (see Hellige, 1996). Global information about a stimulus is preferentially conveyed by low spatial frequencies, whereas local information by high spatial frequencies (Badcock, Whitworth, Badcock, & Lovegrove, 1990; Lamb & Yund, 1993; Peyrin, Chauvin, Chokron, & Marendaz, 2003). Low-frequency channels are believed to contribute more strongly to symmetry perception, at least in case of stimuli consisting of dense dot patterns (Dakin & Herbert, 1998; Julesz & Chang, 1979), and as also suggested by patients missing foveal vision and selectively relying on low spatial frequencies (De Stefani et al., 2011). It is hence possible that the stronger disruptive effects we observed on symmetry detection following right LO stimulation depended on TMS affecting magnocellular projections (coding low spatial frequencies) to extrastriate visual areas (cf. Kveraga, Boshyan, & Bar, 2007) although this remains a speculation and further research is needed to directly address this hypothesis.

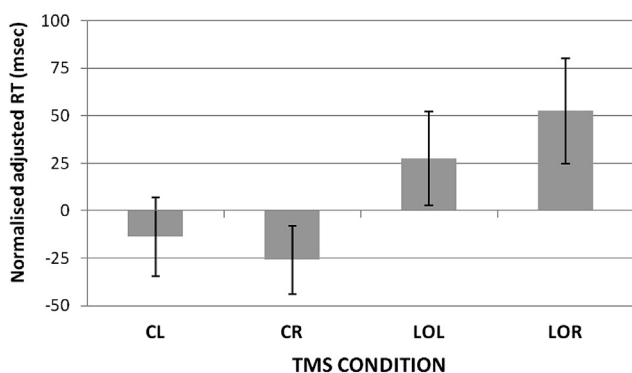


Fig. 5 – Participants' adjusted RT (= raw RT/accuracy), normalized to the baseline NO TMS condition (N = 12). TMS over LO bilaterally significantly impaired shape detection compared to TMS over the control sites. There were no hemispheric differences. Error bars indicate ± 1 SEM.

Nonetheless, one may object that most perceptual grouping processes – including figure-ground segmentation based on collinearity of GP – tap more Gestalt than analytical processing. A possible alternative explanation to account for the pronounced effects of RH LO stimulation may be found in the importance of symmetry as a cue in face detection, with face processing dominated by right hemisphere activity (e.g., Hillger & Koenig, 1991; Kanwisher & Yovel, 2006; Sargent, Ohta, & MacDonald, 1992). Indeed, symmetry detection and face detection appear to be closely linked. For example, Jones, Victor, and Conte (2012) have recently shown that face-likeness enhances symmetry perception. Chen, Kao, and Tyler (2007) found that the right occipital face area (OFA), adjacent to LO and other visual areas, shows differential activation between faces and asymmetric scrambled images but not between faces and symmetric scrambled images. Caldara and Seghier (2009) found that the right fusiform face area (FFA) is also sensitive to symmetry, with symmetrical patterns eliciting larger responses in right FFA compared to asymmetrical ones. In this view, the RH may have become more important in symmetry detection given its greater role in face recognition.

In a previous TMS study (Cattaneo et al., 2011) using an adaptation paradigm and different stimuli, we found evidence for bilateral involvement of LO in symmetry detection but no evidence of a RH specialization. However, in that study the TMS effects on symmetry detection depended on whether participants showed adaptation or not. Moreover, in that study we used sparse patterns comprising 24 dots, whereas in the present study the patterns were of much higher density (198 dots). It has been suggested (see Wagemans, 1997) that processing of dense dot patterns is based on low spatial frequency band information, for which the RH shows a preference (see Hellige, 1996), as discussed above. Thus, it is possible that these stimulus-related and paradigm differences explain the lack of a hemispheric difference in our previous study.

Finally, in interpreting our findings it is important to consider possible inaccuracies in the target sites localization procedure (especially considering the proximity between LO and the chosen control cortical sites) that are inherent to all localization methods, including fMRI-guided ones (see Bijsterbosch, Barker, Lee, & Woodruff, 2012; Thielscher & Wichmann, 2009). Furthermore, although the effects of right LO TMS in symmetry detection were very robust, the effects of left LO TMS were less so, as in Experiment 1 the normalized performance with left LO TMS (see Fig. 5) does not seem to differ much from zero. However, comparing the effects of left LO TMS to the No TMS condition would not be a proper comparison here because it would not take into account the nonspecific effects of TMS (e.g., tapping sensation on the scalp, sound of clicks) which may enhance reaction times. Indeed, in the present study there was a trend for such facilitation with both control sites. Comparing the effects of left LO TMS against its control site (Control Left) is thus more appropriate, as it takes into account such nonspecific effects.

In sum, our results reveal that LO bilaterally is causally involved in vertical symmetry detection, as well as in contour detection. Importantly, the right LO was found to play a more important role than the left LO in symmetry detection. The lack of any lateralization effect in the shape detection task

suggests that primarily right LO may be critically involved in symmetry detection whereas figure-ground segmentation based on other grouping principles (e.g., collinearity) relies on bilateral LO activity.

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