



Research report

Electrophysiological responses to symmetry presented in the left or in the right visual hemifield

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ABSTRACT

Symmetry is a highly salient feature in the visual world, abundant in both man-made and natural objects. In particular, humans find reflectional symmetry most salient. Electrophysiological work on symmetry perception has identified a difference wave known as the Sustained Posterior Negativity (SPN) originating from extrastriate areas. Amplitude is more negative for symmetrical than random patterns, from around 200 msec after stimulus onset. For the first time, we report responses to patterns presented exclusively in one hemifield. Participants were presented with reflection or random dot patterns to the left and right of fixation (3.2°). They judged whether the patterns were light red or dark red in colour. In Experiment 1, the pair always included one symmetrical and one random pattern. In Experiments 2 and 3 we varied the information presented contralaterally. The SPN was generated separately in each hemisphere in response to what was presented in the contralateral visual hemifield (a lateralised SPN). We conclude that a symmetry-sensitive network of extrastriate areas can be activated independently in each cerebral hemisphere.

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1. Introduction

Symmetry has a central role in the study of vision. Indeed, any system engaged in extracting structure from a rich image will either exploit regularities or become tuned to it (Enquist & Arak, 1994). Symmetry is a non-accidental property of an image, linked to the presence of objects in the environment, and therefore it can contribute to perceptual organization (Bertamini, 2010), to image

segmentation (Machilsen, Pauwels, & Wagemans, 2009), and to the recovery of 3D structure (Pizlo & Stevenson, 1999). This paper is concerned with the role of the two cortical hemispheres in the perception of symmetry. How the two hemispheres interact to process symmetry is a question that has been central to research in the topic since early work by Mach (1886/1959). We will review this background next, and then introduce our experiments that directly compared responses to symmetry presented to the left or the right hemifield.

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1.1. Symmetry perception

The study of perception of symmetry has a long history (Barlow & Reeves, 1979; Koning & Wagemans, 2009; Mach, 1886/1959; Tyler, Hardage, & Miller, 1995; For a recent review see; Treder, 2010), and over the last ten years a combination of psychophysics and imaging studies have led to a better understanding of how the human brain responds to symmetry (Bertamini & Makin, 2014; Chen, Kao, & Tyler, 2007; Kohler, Clarke, Yakovleva, Liu, & Norcia, 2016; Lux, Marshall, Neufang, & Fink, 2006; Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005).

Mach (1886/1959) noted that what is salient in perception is not the same as what is regular from a formal (mathematical) sense. Moreover, he speculated that bilateral symmetry, especially when the axis is vertical, might be salient because of the anatomical symmetry of the human visual system. Julesz (1971) explored this idea further. Given that the left half of the image would be processed in the right hemisphere, whilst the right half of the image would be processed in the left hemisphere, Julesz suggested that a point-by-point matching process occurs for corresponding locations. Braitenberg (1986, 1990) along with Milner and Jeeves (1979, pp. 428–448) suggested that the loci of this point-by-point matching were the fibres passing through the corpus callosum. The corpus callosum is the bundle of fibres that allows communication between the hemispheres. Its connections are widely spread in the extrastriate cortices both in humans (Clarke & Miklossy, 1990) and macaques (Van Essen, Newsome, & Bixby, 1982), with axons projecting densely between the areas where the vertical meridian of the visual field is represented. The premise of this callosal hypothesis is that each half of a pattern is processed in one hemisphere, and then mapped across the vertical midline via the corpus callosum.

Some psychophysical and neuropsychological evidence supports the callosal hypothesis. First, detection of symmetry is worse in peripheral vision (Gurnsey, Herbert, & Kenemy, 1998; Saarinen, 1988), where each half would not be projected symmetrically to the opposite cerebral hemisphere. Second, detection of vertical reflection patterns is more efficient than detection for other orientations, like horizontal or oblique (Barlow & Reeves, 1979; Bertamini, 2010; Corballis & Roldan, 1975; Koning & Wagemans, 2009; Julesz, 1971; Palmer & Hemenway, 1978). Corballis and Roldan (1975) found fastest responses for vertical orientation; when participants tilted their heads, the optimal orientation shifted in the direction of the head tilt. They concluded that retinal rather than gravitational coordinates explain the vertical advantage. Third, Herbert and Humphrey (1996) tested two individuals born without a corpus callosum. Both patients were poorer at detecting symmetry at fixation compared with matched healthy controls. However, other mechanisms may operate when symmetry is presented away from fixation, as both healthy participants and acallosal patients are still able to detect symmetry, albeit with a reduced sensitivity.

Recent reviews of the available evidence suggest that the strong version of the callosal hypothesis is unlikely to be correct. Symmetry can be detected when the axis does not

match the anatomical midline, and even when patterns are presented entirely to one hemisphere (Corballis & Roldan, 1974), and salience of a reflected pattern increases with an increase in number of axes (Treder, 2010). Moreover, there is evidence that the vertical advantage depends on expectations and priming (Rock & Leaman, 1963; Wenderoth & Welsh, 1998).

1.2. Brain responses to symmetry

Researchers have explored the neural basis of symmetry perception in humans using several approaches, from neuroimaging to neuropsychological fMRI. Although there is no single narrow area devoted to processing symmetry, an extended network has been identified, most sensitive to bilateral symmetry.

Neuroimaging studies have found that symmetric stimuli activate the left and right extrastriate cortex including V3a, V4, V5 the Lateral Occipital Complex (LOC) (Chen, Kao, & Tyler, 2007; Sasaki et al., 2005; Tyler et al., 2005). Transcranial magnetic stimulation (TMS) studies have shown the left and right LOC to be causally involved in detecting vertical and horizontal symmetry, although this has not been consistently found (Cattaneo, Mattavelli, Papagno, Herbert, & Silvanto, 2011). Recently, Bona, Herbert, Toneatto, Silvanto, and Cattaneo (2014; 2015) applied TMS over the left and right LOC, and found that this disrupted symmetry detection, but this disruption was greater in the right hemisphere. Interestingly, lateral occipital activation is also observed in haptic exploration of symmetry in the early blind (Bauer et al., 2015).

A connected debate in the literature relates to the functional role of dorsal regions (posterior parietal cortex, PPC; intraparietal sulcus, IPS) in global pattern processing and symmetry (Lestou, Lam, Humphreys, Kourtzi, & Humphreys, 2014). Contrary to strict hierarchical processing within the ventral visual stream, it has been proposed that the dorsal cortex contributes to formation of 'hypotheses' about objects. In particular, impairments in perceiving global forms emerge after damage to the dorsal visual stream (Riddoch et al., 2008; Shalev, Humphreys, & Mevorach, 2004).

Electrophysiological studies have also studied the extrastriate symmetry response. Norcia, Candy, Pettet, Vildavski, and Tyler (2002) examined the visual event-related potential (ERP) produced by symmetrical or random patterns. Amplitudes were comparable up until 220 msec after stimulus onset, afterwards the wave for the symmetric pattern was more negative than for the random pattern. Jacobsen and Höfel (2003) found the same ERPs. They referred to the difference between symmetry and random as the Sustained Posterior Negativity (SPN). The SPN is bilateral, and is likely to originate from both cerebral hemispheres. The SPN has been found consistently between around 220 msec and 1000 msec after stimulus onset.

We are confident that the SPN is an automatic visual response to symmetry, which is independent of the task participants are doing (Bertamini & Makin, 2014). We find a similar SPN wave when people are explicitly classifying the patterns as symmetrical or random, and when they are attending to an orthogonal visual dimension, like colour

(Makin, Rampone, & Bertamini, 2015) or the number of blocks (Makin, Rampone, Wright, Martinovic, & Bertamini, 2014). Furthermore, the SPN is comparable during oddball detection tasks, where participants are looking out for rare anomalous components (Höfel & Jacobsen, 2007a; Makin, Pecchinenda, Rampone & Bertamini, 2013). The SPN is found while participants deliberately misreported their responses (Höfel & Jacobsen, 2007b) and regardless of whether symmetry or random required a ‘yes’ response in a 2AFC task (Makin, Wilton, Pecchinenda, & Bertamini, 2012).

Makin, Rampone, Pecchinenda, and Bertamini (2013) reported that the SPN is produced by reflection, rotation and translation, although reflection produced the largest amplitude SPN. This is consistent with the original observations about the special salience of reflection by Mach (1886/1959) and Goldmeier (1937). It is also consistent with many psychophysical results showing that sensitivity to reflection is higher than sensitivity to other regularities (Makin, Pecchinenda, & Bertamini, 2012; Royer, 1981). The difference in amplitude between the regularities was unrelated to properties of the configuration (a single object or a gap between two objects, Makin et al., 2014). A comparable SPN is also produced regardless of whether symmetry is presented vertically or horizontally (Wright, Makin, & Bertamini, 2015).

1.3. A test using EEG and lateralised presentations

Based on the psychophysical and electrophysiological evidence, it seems logical to suggest that a specialized network spanning both hemispheres generates the SPN. However, little is known about how the two hemispheres communicate during symmetry perception. A strong interpretation of the callosal hypothesis, discussed above, states that the optimal stimulus has its axis aligned with the anatomical midline and projects to both hemispheres. A completely opposite view is that the symmetry sensitive network is activated independently of where the patterns are located in the visual field. These are both strong hypotheses. A third hypothesis is that each network responds to information in the contralateral hemifield, but that communication between the hemispheres contributes, for instance because of a specific role of the right parietal regions in processing symmetry (Bona, Cattaneo, & Silvanto, 2015).

We conducted three experiments to test how the SPN is affected by peripheral presentation. In Experiment 1, participants were presented with a pair of patterns (reflection and random) on either side of fixation. Reflection was confined to one visual hemifield, which was processed by the contralateral hemisphere. Random was simultaneously presented in the other hemifield, and processed by the contralateral hemisphere. On half of the trials, reflection was in the left hemifield and random in the right, whilst for the other trials reflection was in the right and random in the left. In Experiment 2, a single pattern was presented to just one hemisphere. Participants were presented with a reflection or a random dot pattern in one visual hemifield whilst the other hemifield contained no pattern. In Experiment 3, matching pairs of either symmetrical or random dot patterns were presented to both hemispheres. In all experiments, participants were required to make a colour judgement about the

presented patterns by deciding whether the patterns were light or dark red. Regularity was therefore not relevant for the task. The reason for this choice is that we are interested in the automatic activation of these areas, and previous work has shown that attention is not necessary for SPN generation (e.g., Makin et al., 2013).

If the SPN does not require co-activation of corresponding left and right anatomical loci, the same neural response to symmetry should be found in each hemisphere. Our experiments will therefore show whether each hemisphere has a symmetry sensitive network that can be activated independently, and whether this network can be activated even when the task of the observer is not actively involved in symmetry discrimination.

2. Experiment 1

2.1. Method

2.1.1. Participants

Twenty-four participants took part in the study (age 18–35, Mean age 24, 8 males, 2 left handed). Participants had normal or corrected-to-normal vision. Some received either course credit or financial reimbursement upon completion of the study. The study was approved by the University Ethics Committee and conducted in accordance with the Declaration of Helsinki (revised 2008).

2.1.2. Apparatus

EEG activity was recorded using a BioSemi (Amsterdam, The Netherlands) Active-Two amplifier in an electrically shielded and darkened room. EEG data was sampled continuously at 512 Hz from 64 scalp electrodes embedded in an elasticised cap arranged according to the standard international 10–20 system. The same apparatus was used in Makin et al. (2012) and other ERP-symmetry studies from our lab (reviewed in Bertamini & Makin, 2014).

In order to detect blinks and eye movements, vertical bipolar electrodes (VEOG) were positioned above and below the right eye. Horizontal bipolar electrodes (HEOG) electrodes were positioned on the outer canthi of both eyes. Stimuli were generated using the PsychoPy software (Peirce, 2007) and presented on a CRT monitor (1280 × 1024; 60 Hz, Mitsubishi; Tokyo, Japan). Participants were positioned 100 cm from the monitor with their head stabilized in a chin rest. They entered their responses by pressing either the ‘A’ or ‘L’ button of the computer keyboard.

2.1.3. Design

There was a single within-subjects factor with two levels (Arrangement [Reflection-Random, Random-Reflection]). There were 72 trials in each condition (144 trials in total). On each trial, both a reflection and a random pattern were simultaneously presented. The position of the patterns in the left and right visual hemifields was randomized and counterbalanced. Reflection-Random refers to the reflection pattern being presented in the left hemifield whilst random is presented in the right. Alternatively, Random-Reflection

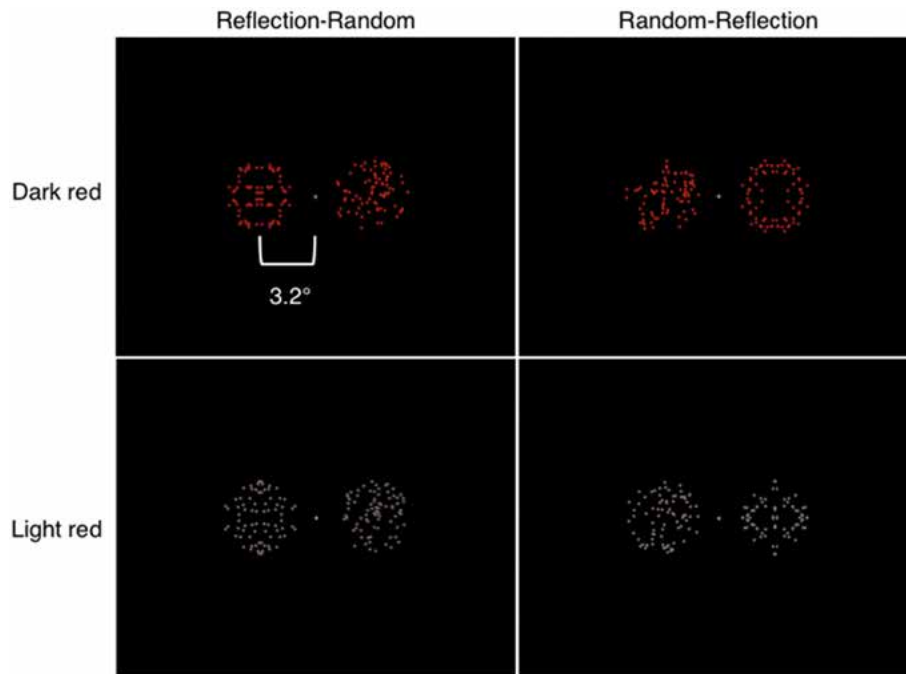


Fig. 1 – Example of the stimuli used in Experiment 1. Participants were required to make a judgement about whether both patterns were either dark or light red. Novel patterns were presented on each trial.

refers to the random pattern being presented in the left visual hemifield whilst reflection is presented in the right (Fig. 1).

2.1.4. Stimuli

Stimuli consisted of dot patterns (Fig. 1), which were presented either side of a grey fixation cross. On each trial, a reflection dot pattern was presented one side of fixation whilst a random dot pattern was presented on the other. Both patterns had a diameter of 2.1° and were positioned 3.2° either side of fixation. The presented pair of patterns were always the same colour (dark or light red). Each pattern was made up of 80 separate dots, with each dot having a radius of $.008^\circ$. Symmetric stimuli had a reflection about both horizontal and vertical axes. Novel patterns were used on each trial to avoid any effect of familiarity.

2.1.5. Procedure

Prior to the start of the experiment, participants completed a practice block, which consisted of 16 trials, and its design matched that of the main experiment. This allowed participants an opportunity to familiarise themselves with the task and to ask any questions. The experiment consisted of a total 144 trials. To allow participants to have a rest and break fixation, the experiment was divided into six blocks.

Participants were informed that they would be required to maintain fixation on the central cross and avoid blinking during the presentation of the patterns. Each trial began with a baseline period of between 1.5 and 2 sec, when the screen showed the central fixation cross. The patterns then appeared and stayed on screen for a further 1.5 sec. After each trial, participants were presented with a response screen, where they had up to 10 sec to report whether the patterns were light red or dark

red in colour. The response screen informed them to press the button on the right for 'dark red' and on the left for 'light red' or vice versa. The position of the words on the left and right side of the screen were counterbalanced across trials. This approach ensured that when the patterns were shown, participants would not be able to prepare their lateralized motor responses. Participants were not required to respond as quickly as they could, but were informed to be as accurate as possible.

2.1.6. EEG analysis

EEG data was processed using the EEGLAB toolbox in MATLAB (Delorme & Makeig, 2004). Raw EEG signals from the 64 electrodes were re-referenced offline to a scalp average and low pass filtered at 40 Hz. The data was then sampled at 128 Hz in order to reduce file size and segmented into -1 sec to 1.5 sec epochs with a baseline of -200 msec to 0 msec. Ocular, muscle and other artefacts were identified and removed using Independent Component Analysis (ICA; Jung et al., 2000). The data was then reformed as 64 independent components and an average of 7.6 components removed from each participant (min = 3, max = 14). Following ICA, trials that had amplitude greater than ± 100 μ V for any electrode were removed. For Reflection-Random 11.5% of trials were removed whilst 11.9% of trials were removed from Random-Reflection.

For analysis, N1 amplitude was calculated as mean amplitude between 190 and 220 msec. The SPN was broken up into two separate time windows of equal length: 200–600 msec and 600–1000 msec after stimulus onset.

The decision to consider an early and late SPN separately is justified by recent research. In this early time window, amplitude has been found to correlate with a mathematical index of perceptual goodness (Makin et al., 2016). The strength of the

correlation declines after an early peak, and there are more exceptions found. N1 and the SPN were measured from electrode clusters over the left (P1, P3, P5, P7, PO3 and PO7) and right hemispheres (P2, P4, P6, P8, PO4 and PO8). These electrodes were chosen due to the interest in the posterior response and because they were consistent with electrode selections used in previous research undertaken (e.g., Makin et al., 2015).

2.2. Results

2.2.1. Behavioral

Participants had to discriminate whether the presented patterns were either light or dark red. Overall, they made a correct colour discrimination on most of the trials (Reflection-Random = 96.6%, Random-Reflection = 97.5%). Response times were uninformative as judgements were unspedded, and entered after the patterns had disappeared from the screen.

2.2.2. ERPs

2.2.2.1. N1. Differences in N1 between regularities and random presented in the contralateral visual field have previously been found (Schadow et al., 2009). We thus examined N1 with a two factor ANOVA (Arrangement [Reflection-Random, Random-Reflection] \times Hemisphere [Left, Right]). There were no main effects or interactions.

2.2.2.2. SPN. Fig. 2 shows ERPs for reflection and random patterns arranged differently (Reflection-Random or Random-Reflection). When a hemisphere was processing reflection, amplitude was lower than when it was processing random. The SPN was apparent in each of the two hemispheres, but somewhat stronger in the right hemisphere.

We analysed the data with an Arrangement (Reflection-Random, Random-Reflection) \times Hemisphere (Left, Right) \times Time Window (200–600, 600–1000) repeated measures ANOVA.¹ There was no main effect of Arrangement [$F(1, 23) = 1.312, p = .264, \text{partial } \eta^2 = .054$] or Hemisphere [$F(1, 23) = .979, p = .333, \text{partial } \eta^2 = .041$], but there was a main effect of Time [$F(1, 23) = 48.889, p = .001, \text{partial } \eta^2 = .680$]. The only significant interaction was between Arrangement and Hemisphere [$F(1, 23) = 11.043, p = .003, \text{partial } \eta^2 = .324$].

We performed a post-hoc analysis on the data to explore more in detail the time course of the ERP. For the left electrodes, there was a difference between Reflection-Random and Random-Reflection arrangements between 200 and 600 msec [$t(23) = 2.373, p = .026, d = .250$]. Amplitude of the waveforms was lower in the left hemisphere when processing reflection than when it was processing random. However, in the left electrodes, there was no significant difference between arrangements in the later 600–1000 msec window [$t(23) = 1.271, p = .216, d = .140$]. Conversely, for the right electrodes, there was a difference between the two arrangements in both the earlier 200–600 msec time window [$t(23) = -3.526, p = .002, d = -.290$] and the later 600–1000 msec window [$t(23) = -2.563, p = .017, d = -.267$].

¹ The same ANOVA also was performed with colour (Light, Dark) as an additional factor. There were no main effects or interactions with colour.

3. Experiment 2

Experiment 1 found that the SPN could be generated in each hemisphere independently, by presenting patterns (reflection and random) in the left and the right visual hemifields simultaneously. To examine the interaction across hemispheres we conducted two further experiments. First, in Experiment 2, we present patterns to a single hemisphere, with nothing on the opposite side (Fig. 3).

3.1. Method

Twenty-four participants took part in the study [age 18–32, Mean age 19.8 (SD = 3.5), 4 males, 0 left handed]. The apparatus was the same as in Experiment 1. There was a single within-subjects factor (Arrangement [Reflection-Nothing, Random-Nothing, Nothing-Reflection, Nothing-Random]) with 36 trials per condition. On each trial, participants were presented with one pattern on one side of the fixation cross. Reflection-Nothing and Random-Nothing refers to the patterns being presented in the left visual hemifield whilst the other hemifield remains empty. Nothing-Reflection and Nothing-Random refer to the patterns being presented in the right visual hemifield with the left hemifield containing no pattern (Fig. 3). The stimuli and procedure were otherwise the same as in Experiment 1.

EEG analysis was the same as in Experiment 1. An average of 8.6 components were removed from each participant (min = 4, max = 18). For Reflection-Nothing 6.7% of trials were removed, for Random-Nothing 5.7%, for Nothing-Reflection 6.2% and for Nothing-Random 6.8%. As with Experiment 1, N1 amplitude was calculated as mean amplitude between 190 and 220 msec. The SPN was split into time windows of 200–600 msec and 600–1000 msec after stimulus onset. N1 and the SPN were measured from electrode clusters in the left (P1, P3, P5, P7, PO3 and PO7) and right hemispheres (P2, P4, P6, P8, PO8 and PO4).

3.2. Results

3.2.1. Behavioral

The task was the same as in Experiment 1. Overall, participants made the correct colour discrimination on most of the trials. Performance was comparable in each condition (Reflection-Nothing was 98.3%, Random-Nothing, 98.3%, Nothing-Reflection 97.9% and Nothing-Random 98.1%).

3.2.2. ERPs

3.2.2.1. N1. To examine N1 we performed a two factor ANOVA (Arrangement [Reflection-Nothing, Random-Nothing, Nothing-Reflection, Nothing-Random] \times Hemisphere [Left, Right]). As with Experiment 1, there were no main effects or interactions.

3.2.2.2. SPN. Figs. 4 and 5 shows the ERPs from Experiment 2. An SPN was produced in the hemisphere contralateral to the stimulus, and there was no *spill over* into the ipsilateral hemisphere. In other words, the contralateral hemisphere (i.e., the one which was processing the reflection or random

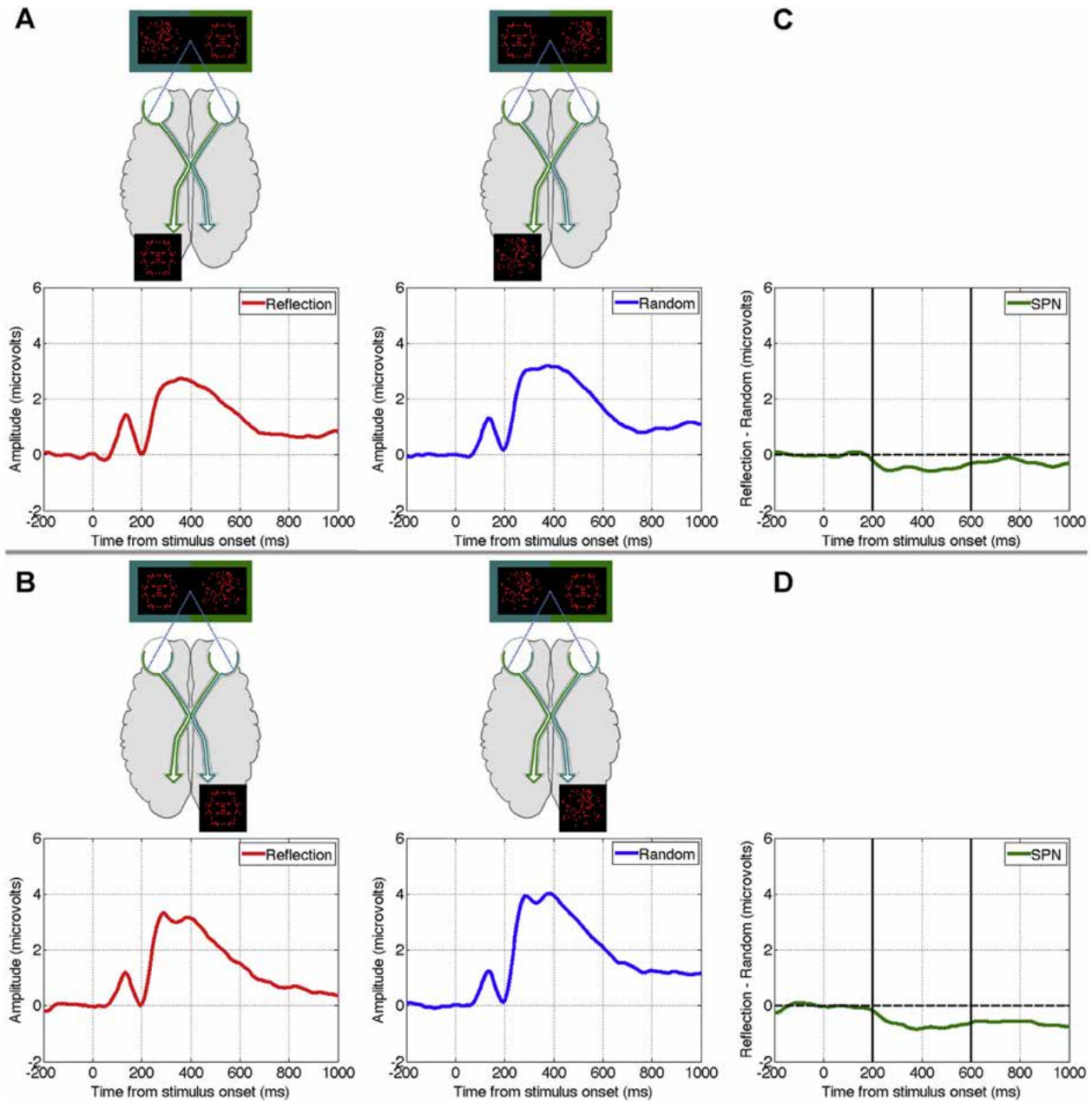


Fig. 2 – Experiment 1: Event Related Potentials (ERPs) from the left and the right hemispheres. Panels A and B show separate ERP plots for reflection and random over each hemisphere, with maps of the different stimulus arrangements and which hemisphere they are processed in. C) Difference wave for the left hemisphere. D) Difference wave for the right hemisphere.

patterns) generated the expected SPN response (with amplitude lower for reflection than random. Meanwhile, there was no SPN in the ipsilateral hemisphere (Fig. 5). See [supplementary information](#) for analysis of the SPN as a difference between Reflection and Nothing).

The SPN was explored with a three-factor repeated-measures ANOVA (Arrangement [Reflection-Nothing, Random-Nothing, Nothing-Reflection, Nothing-Random] \times Hemisphere [Left, Right] \times Time Window [200–600, 600–1000]).² There was

² The same ANOVA also was performed with colour (Light, Dark) as an additional factor. There were no main effects or interactions with colour.

no main effect of Arrangement [$F(3, 69) = 2.260, p = .089$, partial $\eta^2 = .089$], but there were significant effects of Hemisphere [$F(1, 23) = 8.341, p = .008$, partial $\eta^2 = .266$] and Time Window [$F(1, 23) = 70.009, p = .001$, partial $\eta^2 = .753$]. A significant interaction between Arrangement \times Time was found [$F(3, 69) = 6.165, p = .001$, partial $\eta^2 = .211$] along with a three-way interaction for Arrangement \times Hemisphere \times Time [$F(1.691, 38.886) = 46.751, p = .001$, partial $\eta^2 = .670$]. There were no interactions between Hemisphere and Time, or between Hemisphere and Arrangement.

First we consider left hemisphere electrodes for patterns presented in the right hemifield. For the 200–600 msec time window there was a difference between Nothing-Reflection and

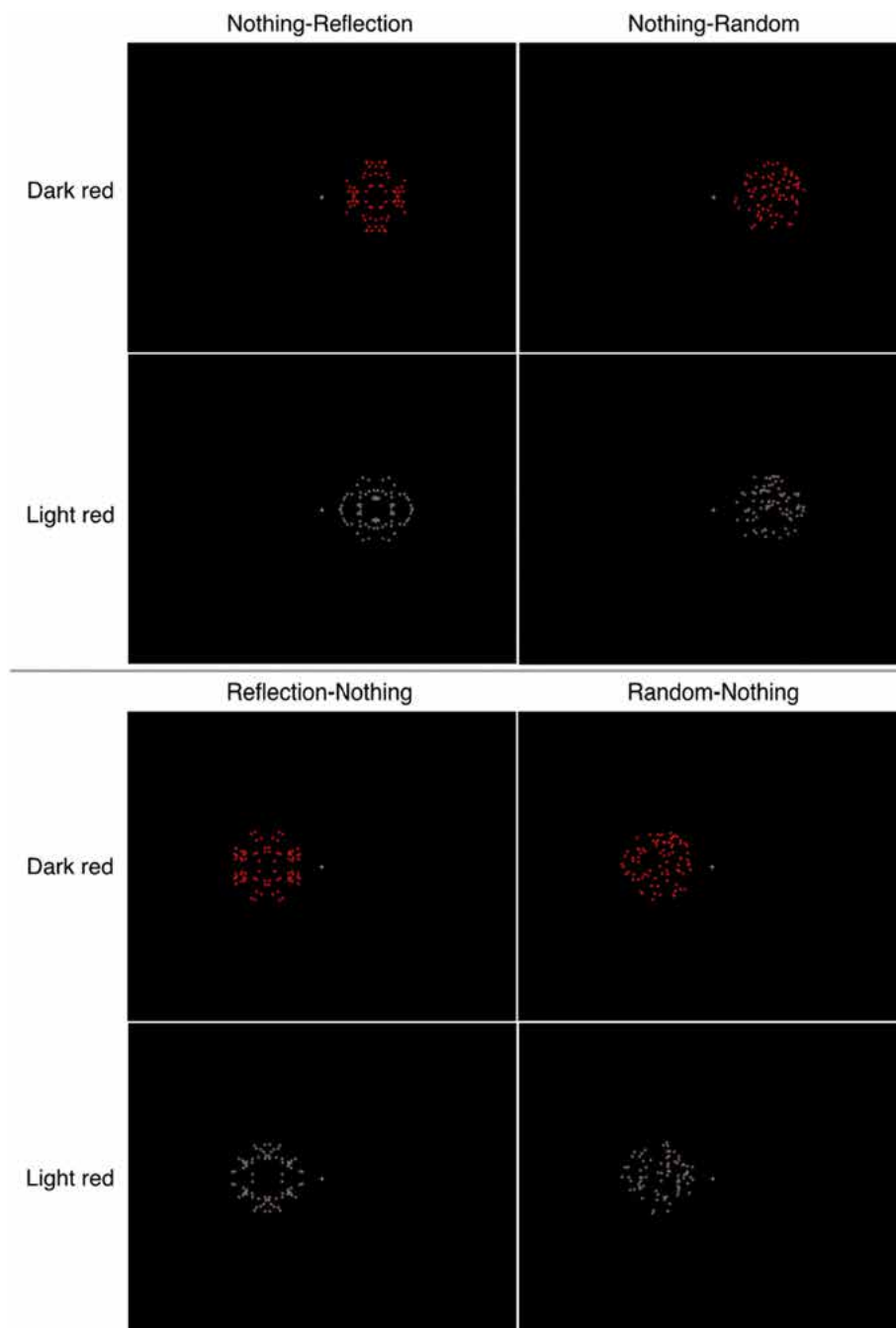


Fig. 3 – Example of the stimuli used in Experiment 2.

Nothing-Random [$t(23) = -3.671, p = .001, d = -.394$]; with amplitude lower for reflection than random. In contrast, there was no significant difference between Reflection-Nothing and Random-Nothing (because the stimuli were being processed in the opposite, right hemisphere). For the 600–1000 msec time window there was a difference between Nothing-Reflection and Nothing-Random [$t(23) = -2.921, p = .008, d = -.396$]. There was a marginally significant difference between Reflection-Nothing and Random-Nothing [$t(23) = 1.997, p = .058, d = .329$].

Next, we consider right hemisphere electrodes for patterns in the left hemifield. In the 200–600 msec time window there was a difference between Reflection-Nothing and Random-Nothing [$t(23) = -3.496, p = .002, d = -.420$]. There was no

significant difference between Nothing-Reflection and Nothing-Random. For the 600–1000 msec time window there was no significant difference between Reflection-Nothing and Random-Nothing or between Nothing-Reflection and Nothing-Random. The lack of a significant difference between Reflection-Nothing and Random-Nothing suggests that the SPN disappears at around 800 msec after stimulus onset (Fig. 4).

4. Experiment 3

Experiment 2 found that the neural response to symmetry was present in the hemisphere contralateral to the pattern (although this response was diminished in the right

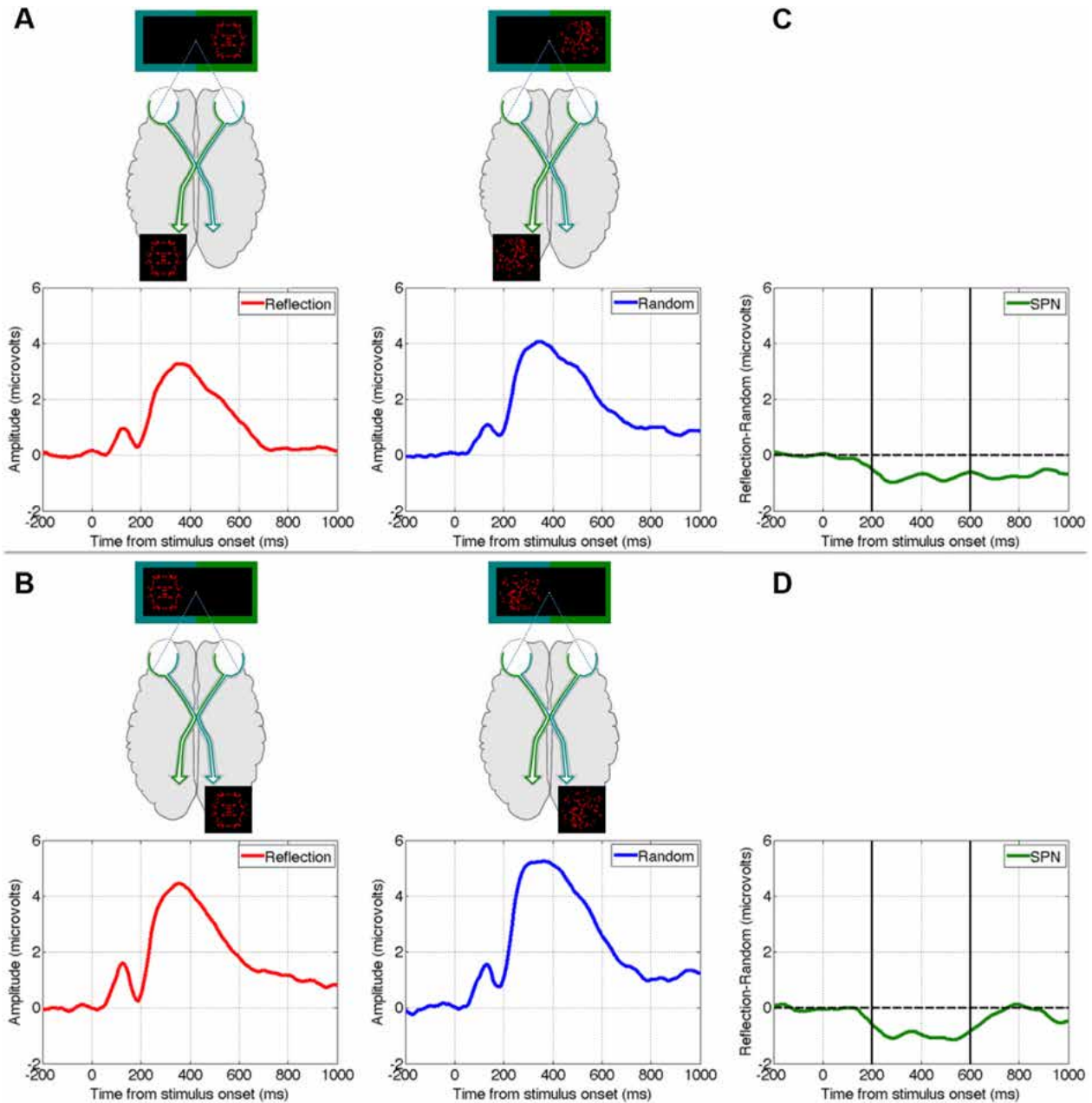


Fig. 4 – Experiment 2: Event Related Potentials (ERPs) from the left and the right hemispheres, focussing on the contralateral hemisphere, where patterns were processed. Conventions are the same as Fig. 2.

hemisphere after 600 msec), and that there was no response in the ipsilateral hemisphere. Experiment 3 further examined lateralized responses by comparing ERPs produced when the same type of patterns are presented on either side of the midline (Reflection-Reflection or Random-Random).

4.1. Method

The same participants took part in this experiment as in Experiment 2. The apparatus was the same as in Experiments 1 and 2. There was a single within-subjects factor (Arrangement [Reflection-Reflection, Random-Random]) with 72 trials

per condition. On each trial, participants were presented with two patterns on either side of the fixation cross (Fig. 6). These patterns were both reflection or both random. The procedure was the same as in Experiment 1.

EEG analysis was the same as Experiment 1. An average of 7.7 components were removed from each participant (min = 2, max = 13). For Reflection-Reflection 10.3% of trials were removed whilst 9.6% of trials were removed from Random-Random. The SPN was divided into two time windows: 200–600 msec and 600–1000 msec after stimulus onset and measured from electrode clusters in the left (P1, P3, P5, P7, PO3 and PO7) and right hemispheres (P2, P4, P6, P8, PO4 and PO8).

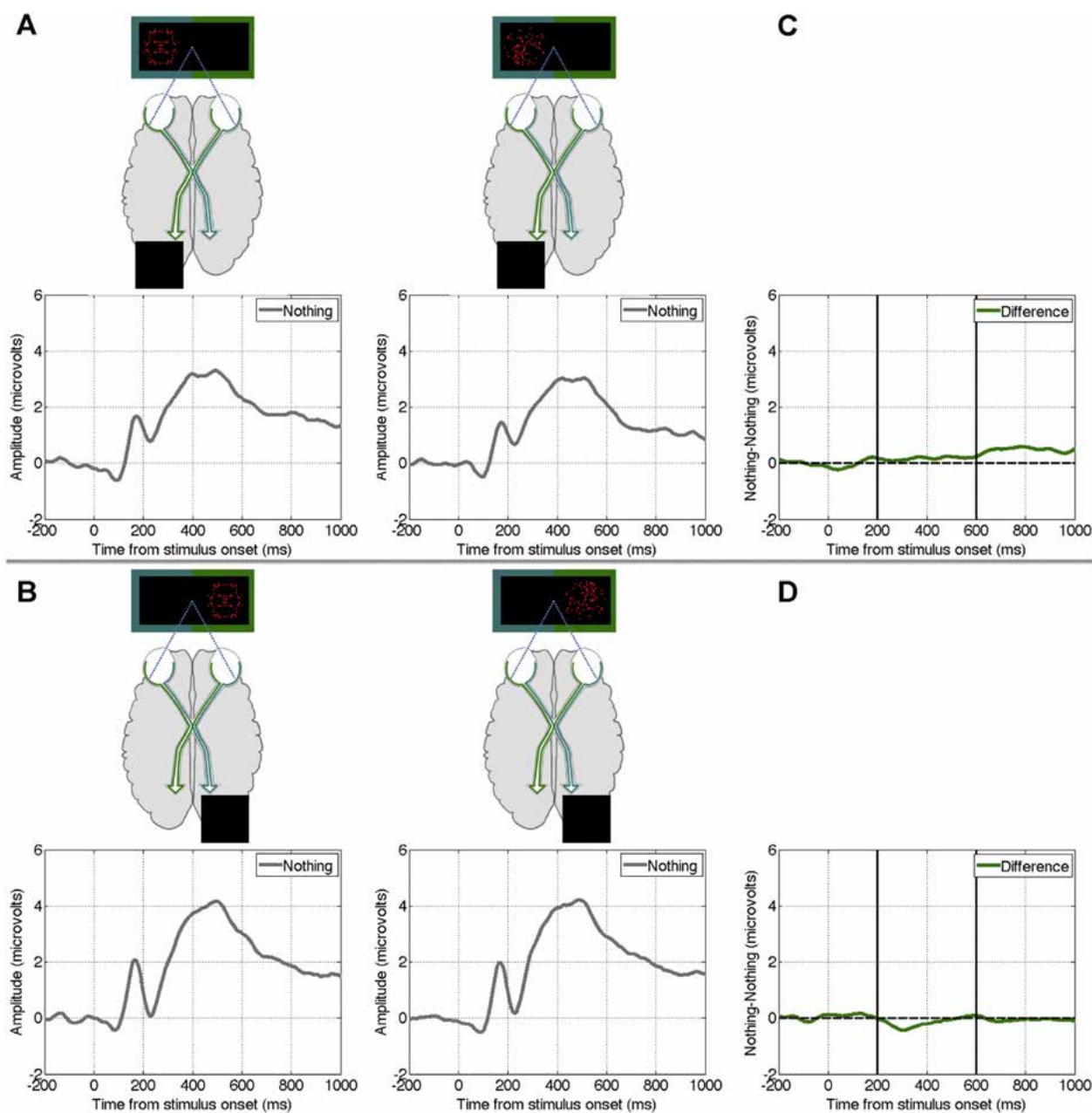


Fig. 5 – Experiment 2: Event Related Potentials (ERPs) from the left and right hemisphere, focussing on the contralateral hemisphere, opposite to the side where the patterns were processed. Conventions are the same as Fig. 2.

4.2. Results

4.2.1. Behavioral

Participants performed the same colour discrimination task as in Experiment 1. Overall, participants made a correct discrimination on most of the trials. Performance was comparable on Reflection-Reflection and Random-Random trials (97.8% vs 98.2%).

4.2.2. ERPs

4.2.2.1. N1. To examine N1, we performed a two factor ANOVA (Arrangement [Reflection-Reflection, Random-Random] \times Hemisphere [Left, Right]). There was a main effect of Arrangement [$F(1,23) = 5.766, p = .025, \text{partial } \eta^2 = .200$],

because amplitude was lower for Reflection-Reflection than Random-Random. There was no effect of Hemisphere or an Arrangement \times Hemisphere interaction.

4.2.2.2. SPN. An SPN was produced in both hemispheres, with reflection being lower in amplitude than random (Fig. 7). The SPN was explored with a three-way repeated-measures ANOVA (Arrangement [Reflection-Reflection, Random-Random] \times Hemisphere [Left, Right] \times Time Window [200–600, 600–1000]).³ There was a significant effect of

³ The same ANOVA also was performed with colour (Light, Dark) as an additional factor. There were no main effects or interactions with colour.

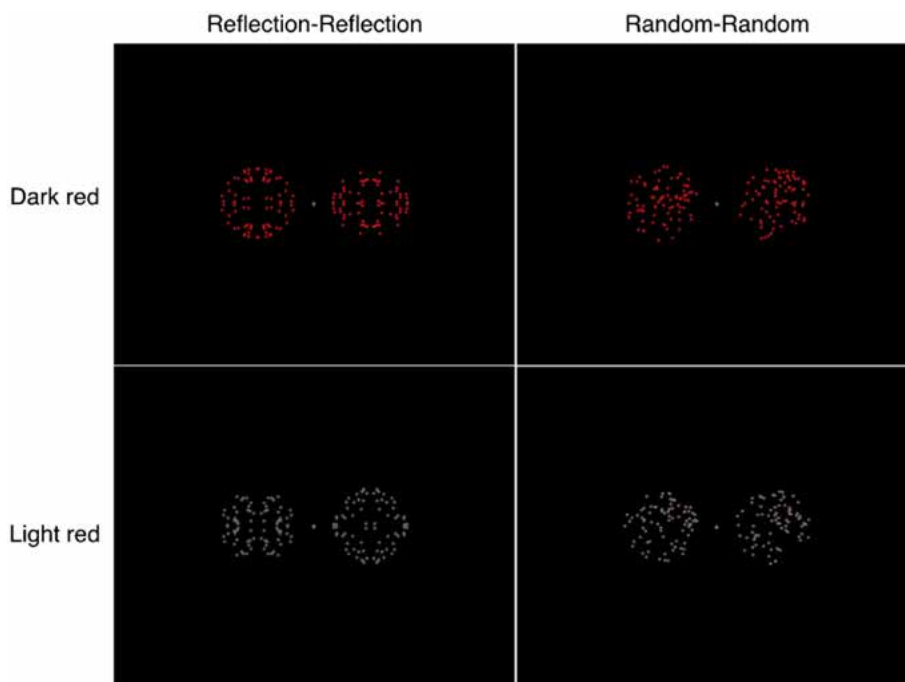


Fig. 6 – Example of the stimuli used in Experiment 3.

Arrangement [$F(1, 23) = 10.319, p = .004, \text{partial } \eta^2 = .310$], Hemisphere [$F(1, 23) = 20.400, p = .001, \text{partial } \eta^2 = .470$] and Time [$F(1, 23) = 60.300, p = .001, \text{partial } \eta^2 = .724$]. There was a significant interaction between Arrangement \times Time [$F(1, 23) = 6.975, p = .015, \text{partial } \eta^2 = .233$]. There were no Arrangement \times Hemisphere interaction or Arrangement \times Hemisphere \times Time interactions.

First we consider the left hemisphere. For the 200–600 msec window there was a significant difference between Reflection-Reflection and Random-Random [$t(23) = -3.554, p = .002, d = -.288$]. This significant difference between the arrangements persisted in the later time window [$t(23) = -2.088, p = .048, d = -.281$]. For the right hemisphere in the 200–600 msec time window there was a significant difference between Reflection-Reflection and Random-Random [$t(23) = -3.627, p = .001, d = -.259$]. Due to the SPN fading out at around 600 msec there was no significant differences in the later time window.

Fig. 8 shows a summary of the differences in amplitude across the three experiments. The SPN can be visualized here as lower blue bars than red bars. The pattern being processed in the hemisphere is labelled below, with the pattern in the opposite hemisphere in brackets. We can see that the SPN generated within a hemisphere is largely independent of what is being processed in the opposite hemisphere. This is true when the opposite hemisphere is processing a pattern of the opposite type (random or reflection) as in Experiment 1, nothing, as in Experiment 2, or a pattern of the same type, as in Experiment 3. This independence is of course most obvious in the 200–600 msec time window, when the symmetry response was present universally (left panels in Fig. 8).

First we consider the early response in left electrodes in Experiments 1 and 3, which were run on different groups of

participants. This can be examined statistically with a two factor mixed ANOVA. The within-subjects factor was Pattern processed (Reflection, Random). The between-subjects factor was Pattern in other hemisphere [Opposite type (Experiment 1) vs Same type (Experiment 3)]. This confirmed there was a difference between reflection and random responses in the left hemisphere [$F(1,46) = 16.764, p < .001, \text{partial } \eta^2 = .267$]. Crucially, there was no interaction, confirming that this response was independent of what the right hemisphere was doing [$F(1,46) = .194, p = .662$]. The same analyses confirmed independence of the early right-sided regularity response: There was again a main effect of Pattern processed [$F(1,46) = 24.894, p < .001, \text{partial } \eta^2 = .351$], which did not interact with pattern in other hemisphere [$F(1,46) = .478, p = .493$].

Next we compared the early symmetry response between Experiments 1 and 2 in the same way. In the left hemisphere, there was a main effect of Pattern processed [$F(1,46) = 18.477, p < .001, \text{partial } \eta^2 = .287$], which was independent of whether the other hemisphere was processing the opposite pattern or nothing [$F(1,46) = 1.085, p = .303$]. The same was true of the right hemisphere, where there was again a main effect of Pattern processed [$F(1,46) = 23.804, p < .001$] that was unaffected by Pattern in the other hemisphere [$F(1,46) = .773, p = .384$].

Finally, we used within participants ANOVAs to confirm hemispheric independence in Experiments 2 versus 3. In the left electrodes at the early time point, there was a main effect of Pattern processed [$F(1,46) = 20.595, p < .001, \text{partial } \eta^2 = .472$], which was independent of whether Nothing or the Same pattern was in the other hemisphere [$F(1,46) = .662, p = .424$]. The same was true in the equivalent analysis of the right hemisphere [$F(1,46) = 18.055, p < .001, \text{partial } \eta^2 = .440$], and no Pattern processed \times Pattern in opposite hemisphere interaction [$F(1,46) = 2.932, p = .100$].

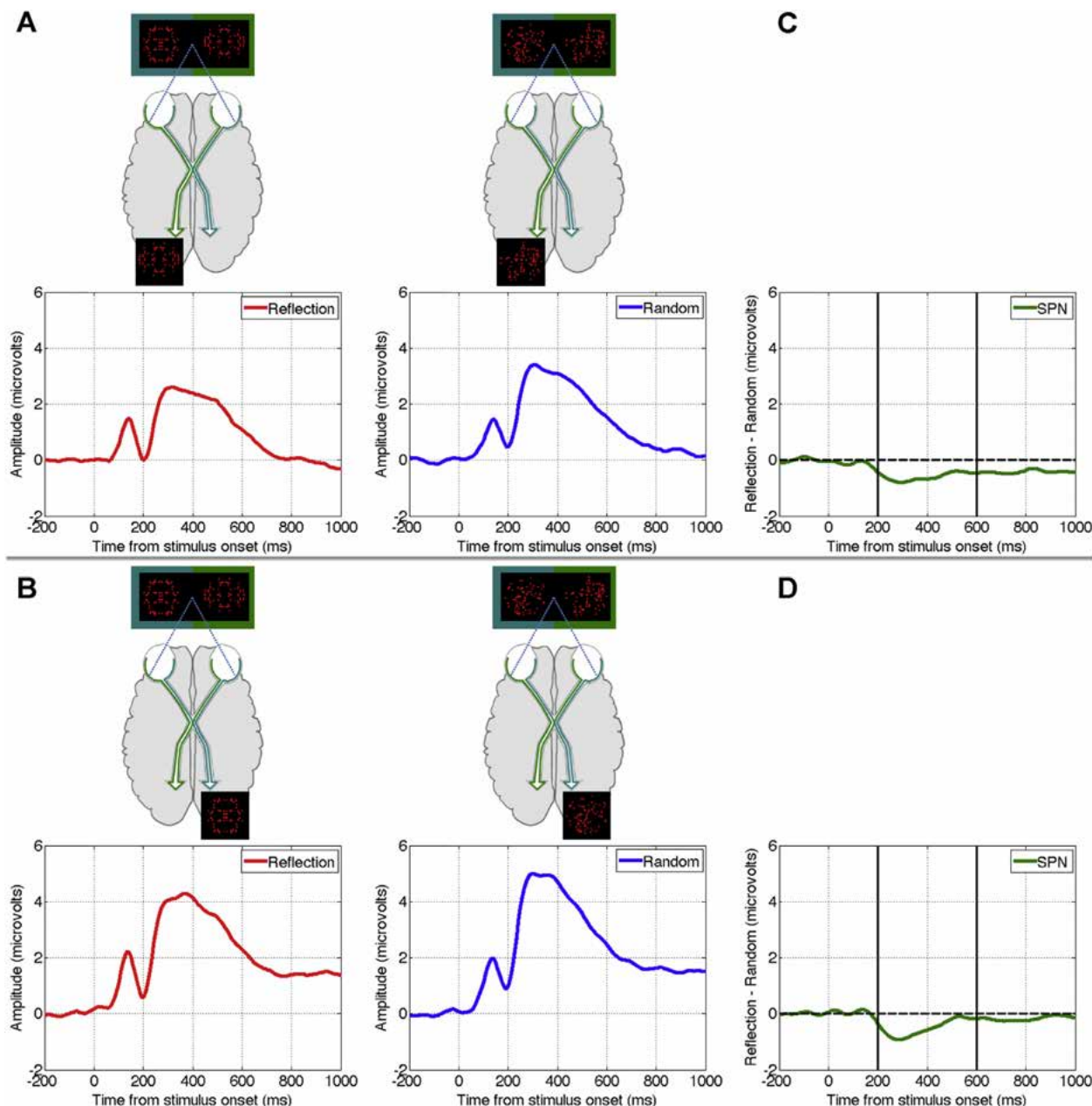


Fig. 7 – Experiment 3: Grand-Average Event Related Potentials (ERPs) from the left and the right hemispheres. Conventions are the same as Fig. 2.

In summary, 6 separate analyses of the early window confirmed that amplitude was more negative when a hemisphere is processing reflection than random, and that this SPN response is independent of what is being processed in the opposite hemisphere. Analysis of the late window is less instructive, because here the SPN faded in some conditions but not others. This fading was not predicted, but it is a separate issue.

5. General discussion

Neuroimaging studies have found a specialized symmetry sensitive network in extrastriate areas (Sasaki et al., 2005),

which is likely to generate the SPN (Bertamini & Makin, 2014; Makin et al., 2012). In this new series of experiments, we introduced a novel procedure. Reflection and random patterns were never presented at fixation: Instead they were presented as pairs, one on the left and one on the right of fixation. In Experiment 1, each pair comprised a reflection and a random pattern (Reflection-Random or Random-Reflection), thus the total amount of regularity in the entire visual field was always the same in each trial. In Experiment 2, patterns were only present on one side (Reflection-Nothing, Random-Nothing, Nothing-Reflection or Nothing-Random). In Experiment 3, reflection or random patterns were presented on both sides (Reflection-Reflection or Random-Random). This set of experiments allowed us to examine whether the SPN could be

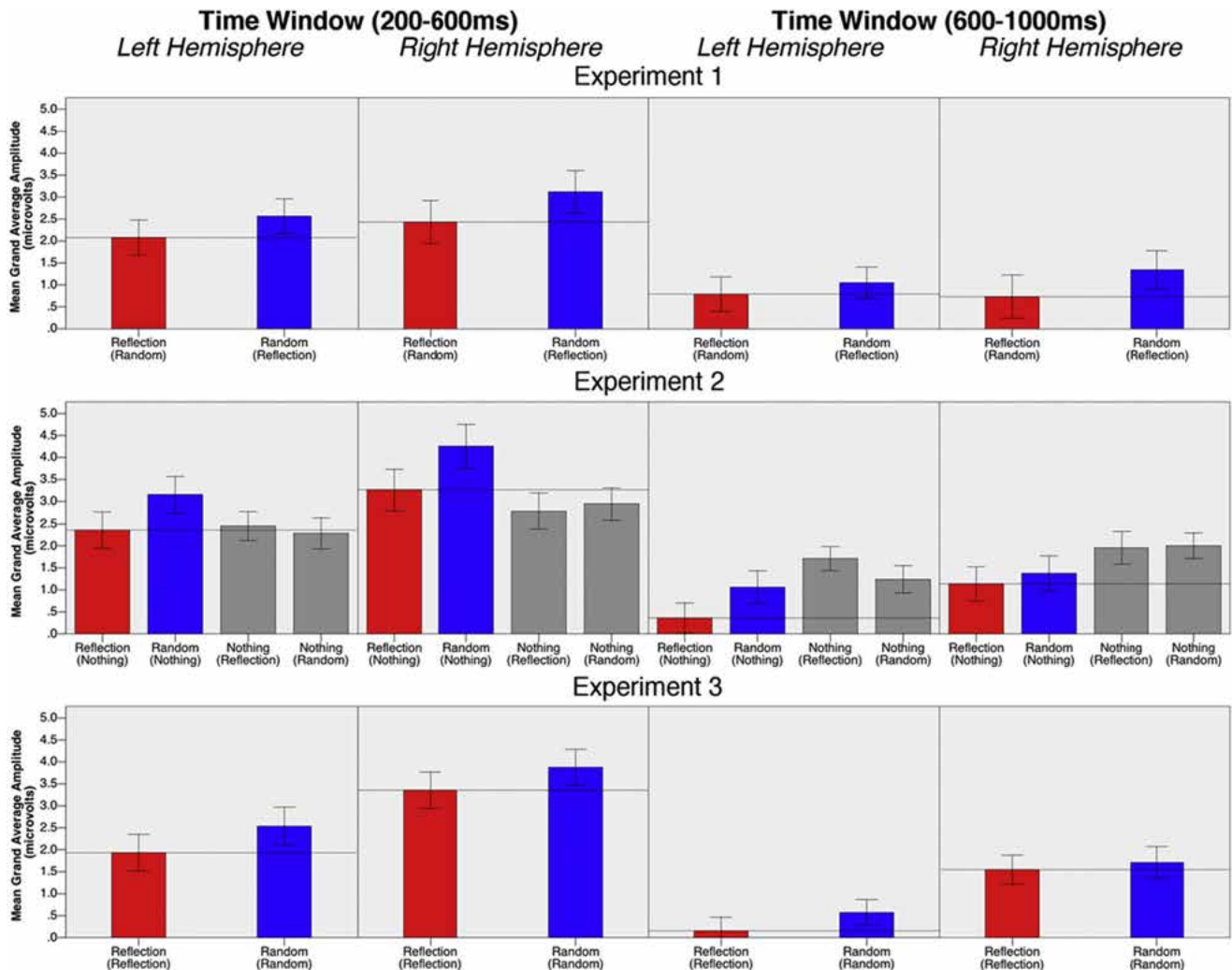


Fig. 8 – Mean Grand-Average Event Related Potentials (ERPs) of the SPN from the left and the right hemispheres for each experiment in the early (200–600 msec) and late time windows (600–1000 msec). Stimuli in brackets are those that were processed in the contralateral hemisphere. Error bars: ± 1 Standard Error.

generated separately in each hemisphere, and to what extent the response was influenced by the information in the other hemifield.

The results showed that the SPN wave (Reflection < Random) could indeed be generated within a single cerebral hemisphere, with the information being processed in the opposite hemisphere having no detectable effect on this lateralized neural response to symmetry. This clear-cut result was unexpected, but it was consistent in all three experiments.

In Experiment 1, lower amplitude was recorded over the hemisphere that was processing a reflection pattern compared to when it was processing a random pattern. In Experiment 2, there was an SPN in the hemisphere contralateral to the dot patterns, but no SPN in the ipsilateral hemisphere. In Experiment 3, there was an SPN in each hemisphere, even though there was no symmetry across the vertical midline. Previous studies had only presented symmetry at fixation, so each half of the pattern was always presented to a separate hemisphere. These experiments are the first to show that the neural response

to symmetry can be generated when patterns are presented in the periphery.

This contralateral SPN response was produced despite the fact that participants were not required to respond to the presence of symmetry (just to the colour of the elements). This is consistent with the results of Makin et al. (2015), and adds further support to the claim that the SPN is an automatic response to symmetry present in the image (Bertamini & Makin, 2014).

Interestingly, regularity did not consistently influence N1 amplitude in our study. It has previously been reported that N1 amplitude increases with gestalt like images (Brodeur et al., 2008; Herrmann & Bosch, 2001; Herrmann, Mecklinger, & Pfeifer, 1999). The N1 component is sometimes sensitive to symmetry (Makin et al., 2012; Makin et al., 2013) however this has not been found consistently (Höfel & Jacobsen, 2007a, 2007b; Jacobsen & Höfel, 2003; Norcia et al., 2002). In another study Schadow et al. (2009) found an effect of regularity on N1, however, they embedded their regular target (e.g., a circle) in noise consisting of Gabor elements and participants had to

find the target. Conversely, in our experiments, participants were always discriminating colour, not regularity itself. It could be that the N1 effect of regularity is task dependent, unlike the SPN, which is generated by symmetry even when people are attending to other properties of the patterns.

It is likely that eye movements create artifacts in EEG recordings (Dimigen, Valsecchi, Sommer, & Kliegl, 2009; Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008). Even when participants are required to fixate, they do not keep their eyes perfectly still. Microsaccades produce extraocular muscle activity, which then disseminates to the scalp EEG. Furthermore, microsaccades produce a small displacement of the retinal image, which can generate VEPs over occipital areas 100–140 msec later (Dimigen et al., 2009; Engbert & Kliegl, 2003; Hafed & Clark, 2002). It is conceivable that microsaccade frequency might differ between reflection and random conditions, and that this could contribute to the SPN. We note that the VEP following a microsaccade would be bilateral, although potentially modulated by arrangement of the retinal image as well. However, the fact that we get a similar SPN within a hemisphere, and for a variety of different stimulus arrangements, means this component is very unlikely to be generated by microsaccades.

The SPN we have observed in these experiments is similar to other attention-related ERP waveforms, particularly the Sustained Posterior Contralateral Negativity (SPCN). It has been found that amplitude is negative over the contralateral hemisphere to the attended visual stimulus (Lefebvre, Dell'acqua, Roelfsema, & Jolicoeur, 2011). In Experiment 1, participants might shift spatial attention to reflection patterns more consistently than random patterns. That might produce an SPCN, which could be misinterpreted as a lateralized SPN, generated by symmetry. However, this alternative 'spatial attention' explanation cannot account for the similarities between ERPs across our three experiments. In each experiment, spatial attention was pulled in different ways. For instance, in Experiment 2, patterns were present on one side and there was nothing on the other side. Here participants would presumably shift spatial attention to the pattern, be it reflection or random. This should produce a similar SPCN for reflection and random. Nevertheless, amplitude was more negative for reflection than random. Still, the spatial attention account could claim that deployment of spatial attention was more consistent in the reflection condition. However, this interpretation would be inconsistent with Experiment 3, where both left and right patterns were the same type. Participants may divide attention between left and right visual fields, or switch back and forward. The behaviour of the attentional spotlight in Experiment 3 is likely to be different from Experiment 2, but the posterior negativity was similar.

Furthermore, it is unlikely that the SPN for central stimuli is an attentional ERP component. For one thing, the SPN is similar when patterns are presented with either a horizontal or a vertical axis (Wright et al., 2015), even though axis orientation would alter the distribution of spatial attention. Moreover, SPN amplitude can be predicted by models that quantify perceptual goodness (Makin et al., 2016). It would be difficult to explain such precise SPN results by differences in the deployment of spatial attention. Finally, the

electrophysiological response to symmetry is localized to shape sensitive areas in the ventral stream, like the LOC (Kohler et al., 2016). We conclude that although there is some overlap between attention-related ERPs and the SPN in terms of latency and topography, these ERPs are generated by different mechanisms. It is parsimonious to treat the ERPs recorded here as a lateralized SPN, rather than a complicated and nuanced set of SPCN recordings.

5.1. Relationship to neuropsychological studies on symmetry perception and hemispheric specialization

There have been several recent papers examining the effect of brain lesions on symmetry perception, as well as the neuroimaging studies mentioned above. It is worth considering how our current results relate to this literature, and also to the wider work on hemispheric specialization and communication between hemispheres. To recap, neuroimaging studies have consistently shown that V1 and V2 are NOT activated by symmetry, while there are symmetry related activations in extrastriate areas, including V3a, V4 and LOC (Kohler et al., 2016; Sasaki et al., 2005; Tyler et al., 2005). The SPN is probably generated by this extrastriate network (Makin et al., 2016). The LOC is certainly important for coding visual structure. LOC lesions have strong effects on object perception (e.g., Ptak, Lazeyras, Di Pietro, Schnider, & Simon, 2014). In fMRI research, the LOC is functionally localizing by comparing objects and scrambled objects (e.g., Kim, Biederman, Lescroart, & Hayworth, 2009). TMS work has shown that the LOC is causally involved in symmetry perception (Bona et al., 2014, 2015).

Although most work has characterized the ascending local-global processing in the early visual stream (e.g., Kohler et al., 2016), recent neuropsychological work has shown that bilateral extrastriate network is also sensitive to top down inputs. For instance, Bauer et al. (2015) asked blindfolded participants to discriminate symmetrical from random arrangements of braille-like pin matrices using touch alone. One contrast revealed that haptic exploration of symmetrical patterns activated LO and other visual maps in congenitally blind patients, while this 'visual cortex' response to haptic symmetry was not found in blindfolded controls. This suggests that there is an innate symmetry sensitivity ventral visual stream. This can be exploited in early blind people so the network becomes tuned to haptic symmetry.

There is less evidence for dorsal stream activation in symmetry perception (e.g., Kohler et al., 2016). However, Lestou, Lam, Humphreys, Kourtzi, and Humphreys (2014) compared perception of Glass patterns with global structure (concentric and radial) with perception of local-structure translational Glass patterns and random dipoles, and found evidence for a dorsal contribution. They examined a patient with dorsal stream (Intra-Parietal Sulcus) lesions, another patient with early ventral stream lesions (V2–V4), and healthy control participants. The dorsal patient was uniquely impaired at detecting global structure in the concentric and radial Glass patterns. As expected, control participants showed higher BOLD responses for global Glass patterns in early ventral regions V3b and KO. However, for the dorsal patient, this V3b and KO effect was reversed, with a higher response to translation. This work suggests that the

feedforward, local to global, ventral stream account of regularity perception is simplistic, and that the dorsal stream may also play a role.

As well as ‘heterarchical’ and multimodal inputs to the extrastriate symmetry network suggested by recent neuropsychological studies, we can also consider horizontal interactions between left and right hemispheres during symmetry perception. In several previous studies, we have presented vertical reflection patterns centrally, and participants fixated in the centre of the pattern (Makin et al., 2013). To detect vertical, central reflection, the system must integrate position information initially represented on opposite sides of the brain. Indeed, neuropsychological evidence has shown that both sides of a symmetrical figure are represented in the visual system, even when there is damage to the occipito-parietal region of one cerebral hemisphere (Doricchi & Galati, 2000; Driver, Baylis, & Rafal, 1992). In the current work, we show that the same symmetry response can be generated when all symmetrical structure is presented within a single hemifield. The anatomical bilateral symmetry of the brain only has something to do with the perception of symmetrical patterns in a superficial way. This refutes a strong version of the callosal hypothesis, but is consistent with earlier work showing that symmetry perception was still present in patients born without a corpus callosum (Herbert & Humphrey, 1996). It is also consistent with the results of Wright et al. (2015), who found a similar SPN for horizontal and vertical reflections, even though only vertical reflection requires interhemispheric integration.

If there are separate symmetry processors in each hemisphere, as we claim, perhaps the one in the right hemisphere is somehow stronger, or more sensitive, than its counterpart on the left? Certainly there is converging evidence from TMS (Bona et al., 2014) and alpha desynchronization (Wright et al., 2015) that the right hemisphere is more important for symmetry perception. The SPN itself is sometimes larger over the right hemisphere when patterns are presented centrally (although this lateralization is not consistent, Bertamini & Makin, 2014; Makin et al., 2016). Furthermore, behavioural work has shown that symmetrical patterns are detected quicker when they are presented in the left visual hemifield, and thus processed in the right hemisphere (Brysbaert, 1994; Corballis & Roldan, 1974). Recently, Verma, Van der Haegen, and Brysbaert (2013) had participants fixate centrally whilst 2-D symmetrical and asymmetrical figures were presented to each visual hemifield. Participants with a left hemisphere dominance for language showed superior symmetry detection in the right hemisphere. Likewise, Wilkinson and Halligan (2002) found that symmetry detection and perceptual landmark judgements were both superior when stimuli were presented to the right hemisphere.

Several hemispheric specializations are well known: famously the left hemisphere being more specialized for language whilst the right is more dominant in spatial attention (Cai, Van der Haegen, & Brysbaert, 2013). More relevant for this paper is the evidence suggesting that the right hemisphere is dominant for global processing whilst the left is dominant for local processing (Van Kleeck, 1989). Neuropsychological studies have shown that lesions to the left or right

superior temporal gyrus and the temporo-parietal junction are associated with these differences in global/local processing (Lamb, Robertson, & Knight, 1990; Lux et al., 2004; Robertson, Lamb, & Knight, 1988). Symmetry perception is an excellent example of global processing, so we might expect right hemisphere specialization for symmetry perception.

However, despite previous work and prior plausibility, we did not find much evidence in support for a strong right lateralization of the symmetry response in this series of experiments. Right lateralization of the symmetry response was apparent in Experiment 1, but not in Experiments 2 or 3. Furthermore, the duration of the SPN was often different in each hemisphere: In Experiment 1 the SPN faded early in the left hemisphere, in Experiments 2 and 3 it faded earlier in the right hemisphere. Any amplitude differences between hemispheres were specific to later time windows. These details were not expected and will require further investigation before they can be usefully interpreted.

6. Conclusions

In the long history of the study of symmetry a key question has been why bilateral symmetry appears special, as a type of regularity available to observers without effort (as opposed to other regularities such as rotational symmetry). A possibility is that this may be related to the bilateral symmetry of the cortex, and this is also known as the callosal hypothesis. Until now, electrophysiological investigations on symmetry had only presented patterns centrally at fixation (Jacobsen & Höfel, 2003; Norcia et al., 2002; Wright et al., 2015). The contralateral hemisphere therefore processed each half of the pattern, and the network that was identified was spanning both hemispheres. Our results show a SPN response to symmetry presented only within the left or the right hemifield. We conclude that symmetry processing does not require stimulation of both hemispheres. Instead, we confirm a response generated by the known symmetry-sensitive network in which activation was present *independently within each hemisphere*. This is not consistent with the callosal hypothesis, which postulated a special role for inter-hemispheric connections in symmetry perception.

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Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2016.11.001>.

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