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School of Psychology

**The electrophysiological response to visual symmetry:
Hemisphere lateralisation and visual clutter**

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degree of Doctor in Philosophy

by

Damien Wright

Supervisor:

Marco Bertamini

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Abstract

The experiments reported in this thesis explore the electrophysiological response to visual symmetry. Symmetry is an important visual feature in object recognition and image segmentation that is efficiently processed by the visual system. Neuroimaging and electrophysiological research has provided a greater understanding of how the human brain processes symmetry. ERP research has identified a neural signature for symmetry processing termed the Sustained Posterior Negativity (SPN): Lower amplitude is observed in posterior electrodes for symmetrical than random patterns from around 200ms after stimulus onset. This thesis will address four important and novel questions: (1) Can the SPN be produced independently within each hemisphere? (2) Is right lateralised alpha desynchronisation during regularity discrimination the result of hemisphere specialisation or directed spatial attention? (3) Does visual crowding influence the SPN? and (4) How does figure-ground assignment influence the neural response to symmetry? The current studies show for the first time that the SPN can be produced to stimuli in the periphery with symmetry processed by independent symmetry sensitive networks within each hemisphere. It also offers evidence that the right hemisphere may be specialised for symmetry perception. Moreover, figure-ground assignment and visual crowding are shown to modulate the SPN. Together these experiments highlight that this automatic response to symmetry is processed independently in each hemisphere and is subject to bottom-up stimulus characteristics.

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1. Introduction and Overview

This thesis is concerned with the human perception of visual symmetry, its function and neural mechanisms. Symmetry perception has a long history dating back to the work of Mach (1886/1959), with it being of interest to many different fields. In respect to vision, symmetry has been linked to the detection of objects and image segmentation. Recently, psychophysics and neuroimaging studies have allowed for an improved understanding of how the human brain processes visual symmetry (Bertamini & Makin, 2014; Dakin & Watt 1994; Kohler et al., 2016; Sasaki, Vanduffel, Knutsen, Tyler & Tootell, 2005; Wagemans, 1995).

EEG research has identified a symmetry specific ERP component: the Sustained Posterior Negativity (SPN). This is a late component where the amplitude is lower for symmetrical than random patterns from around 200ms after stimulus onset. There has been a growing body of research examining this ERP response to symmetry (Bertamini & Makin, 2014). However, many questions are still to be addressed.

The aim of this chapter is to introduce the importance of symmetry perception, and recent developments in the study of the neural response to visual symmetry. I will firstly outline why symmetry is such a significant feature to be investigated and why it is ubiquitous in everyday life. In section 1.1 I will provide a definition as well as highlight the different types of symmetry that exist. Following this I will outline a number of the symmetry perception models that have been proposed. In section 1.3 I will then highlight the neural areas that are thought to be involved in symmetry processing, before reviewing the electrophysiological literature. This chapter will provide only a brief introduction, as each individual chapter has its own introduction that will provide a more specific review of the literature and the experimental hypotheses. At the end of this chapter is an overview, which provides a summary of the hypotheses, main findings and conclusions of each chapter.

Symmetry is an important and abundant feature in the world around us. It occurs frequently in nature for example, it can be seen in insects and animals such as in the wings of a butterfly and the human body. Plants also exhibit many types of symmetry in the shape of their leaves and petals, the repetition of the leaves all over the plant and the cylindrical symmetry in their structure. Alongside this, symmetry can be observed in many man-made objects. The reflectional symmetry seen in Acheulean hand axes dating from 500,000 years ago is the earliest example of a human interest in this regularity (Hodgson, 2011). Symmetry is often incorporated into the design of buildings such as the Taj Mahal and in works of art; with it claimed to be the foundation of both science and nature (Rosen, 2009).

The visual system is adapted to efficiently process symmetry (Barlow & Reeves, 1979; Carmody, Nodine, & Locher, 1977; Wagemans, Gool, & d'Ydewalle, 1991). Two explanations have been proposed for this adaption. Firstly, it has been linked to genetic and evolutionary factors; suggesting that symmetry is important in signalling reproductive fitness of other members of the species (Møller, 1992; Rhodes, Proffitt, Grady & Sumich, 1998). Human mate choice is driven by reproductive fitness, with attractiveness indicating genetic quality. Reflectional symmetric faces and bodies are judged as more attractive than less symmetrical ones (Bertamini, Byrne & Bennett, 2013; Penton-Voak et al., 2001; Tovee, Tasker, & Benson, 2000). Deviations from reflectional symmetry result when an individual is confronted with developmental stress (e.g. disease or parasites) and they are unable to resist these circumstances. When choosing a mate, an individual would attempt to maximise their chances of reproductive success by choosing a mate with good genetic fitness, which would be indexed by reflectional symmetric features. A preference for symmetry in other objects such as works of art and buildings could be explained by this mechanism overgeneralising. Sensitivity for reflectional symmetry is found not only cross-culturally but also throughout the animal kingdom such as in rhesus monkeys, dolphins, swordtail fish, bees and various bird species (Benard, Stach, & Giurfa, 2006; Delius & Nowak, 1982; Møller 1992; Swaddle & Cuthill, 1994). This genetic and evolutionary theory proposes that the adaption of the visual system to symmetry is driven by natural selection. Although this is a well-known example, the evidence for a link between a preference for symmetry and evolutionary factors is not particularly strong. For example, the effect size for a preference for reflectional symmetric faces and bodies has been reported to be small and may even be zero once corrected for publication bias (a negative association between effect size and sample size; van Dongen, 2011). In addition, human facial symmetry has been found to correlate weakly with health (Rhodes et al., 2001; For a review see Møller & Swaddle, 1997).

A second explanation suggests that symmetry is important in signalling objects through image segmentation and object representation (Li, Pizlo, & Steinman, 2009; Machilsen, Pauwels, & Wagemans, 2009). Reflection is processed quickly and efficiently, particularly for vertical orientation (Mach, 1886/1959; Bertamini, 2010; Bertamini, Friedenber, & Argyle, 2002; Bertamini, Friedenber & Kubovy, 1997; Friedenber & Bertamini, 2000). This ease at which the visual system processes symmetry emphasizes its importance in perceptual organisation. Gestalt psychologists identified symmetry as a grouping principle due to its high level of ‘goodness’ (Koffka, 1935/1962). Reflection is said to be a cue to a single object, whilst repetition is easier to detect when it forms two objects (Corballis & Roldan, 1974; Koning & Wagemans, 2009; Bertamini 2010; Treder & van der Helm, 2007). The importance of symmetry in object representation is further emphasised through the key role it plays in figure-ground assignment: symmetrical regions tend to be perceived as the figure in ambiguous figure-ground displays (Driver et al., 1992; Kanizsa & Gerbino, 1976).

1.1. Defining symmetry

Symmetry has been studied across many fields including physics, computer vision and mathematics. One branch of mathematics, group theory is a mathematical method that describes groups of patterns (both number and geometric groups). As a result symmetry is closely connected with this method. Patterns can be classified in a number of ways including Euclidian plane isometries, the 7 frieze groups and the 17 wallpaper groups (Grünbaum & Shephard, 1987; Figure 1.1). In geometry, an object is classed as symmetrical if it remains invariant after a Euclidian transformation. When people think of symmetry they tend to think of mirror symmetry, but symmetry actually belongs to a group of isometries, which contains reflection (sometimes referred to as mirror or bilateral symmetry), translation, rotation and

glide reflection. Reflection consists of an object being divided by one plane so that the halves are mirror images. Increasing the number of planes the object is divided into will also increase the number of axis. Translation is the transposition of an object without reflecting or mirroring whilst rotation is where the pattern looks the same after being turned around an axis of angle. Glide reflection is a more complex symmetry, which combines reflection and translation along the direction of the mirror line. Throughout this thesis, the word 'symmetry' and 'regularity' will be used in the general sense to refer to all rigid transformations, which include reflection, translation and rotation. Furthermore, when stimuli are referred to as being 'random', it is to indicate that they are non-symmetric in shape.

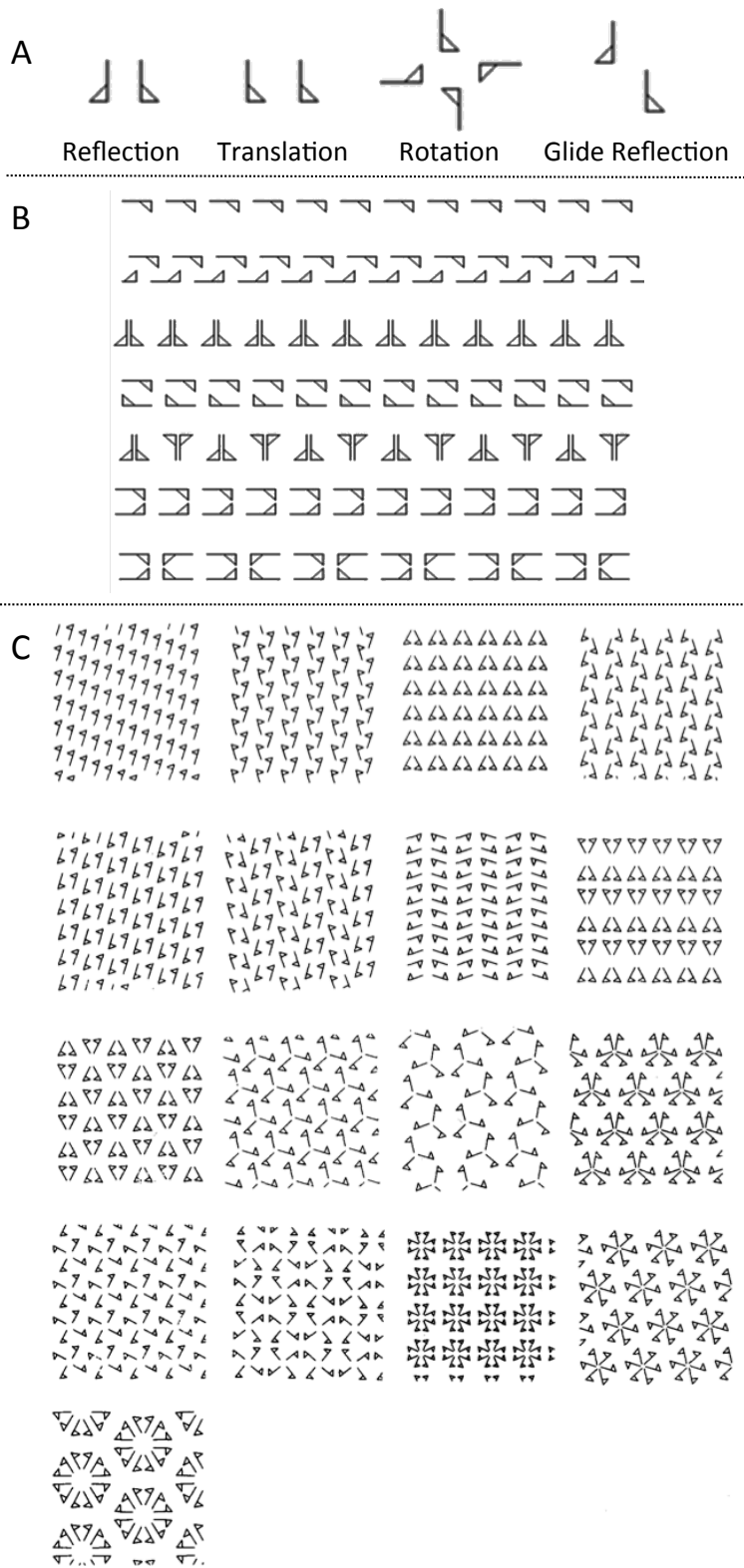


Figure 1.1. Classification of plane isometries, frieze patterns and wallpaper groups. A) Reflection, translation, rotation and glide reflection symmetries. B) 7 Frieze patterns (Reprinted from Liu, Collins & Tsin, 2004. Used with permission from IEEE). C) 17 wallpaper group patterns (Reprinted from Grünbaum, Grünbaum, & Shephard, 1986. Used with permission from Elsevier).

1.2. Models of symmetry perception

A number of models have been developed to explain the mechanisms of human symmetry perception. These consist of process, spatial filtering (which can be considered as process models) and representational models. Despite there being a number of formal models for symmetry detection there is not yet one that has been fully tested and agreed upon.

Process models attempt to describe the mechanisms of detection and how symmetry is extracted from visual information. Wagemans et al. (1993) proposed one such model whereby higher order structures are formed by joining symmetric positioned dot pairs with virtual lines. These virtual lines can also create virtual quadrangles and trapezoids, which can establish a reference frame that indicates the likely direction in which other dot pairings are to be found. This enhances the local pairing of elements in the whole pattern allowing for an efficient and rapid representation of the symmetry to be built from an initial random pairing of elements. This approach explains a number of the behavioural findings, for example, why fronto-parallel reflection is detected more easily than skewed reflection (Wagemans, Van Gool & d'Ydewalle, 1991).

A number of spatial filtering models have also been proposed (Dakin & Hess, 1997; Julesz & Chang, 1979; Kovesi, 1997; Osorio, 1996; Poirer & Wilson, 2010; Rainville & Kingdom, 1999). These models suggest that symmetry detection may take place in early visual areas as evidence indicates that these areas contain mechanisms sensitive to spatial frequency. Dakin and Watt (1994) proposed symmetry detection to be achieved through a two-stage spatial filter-processing model. The first stage of the Dakin and Watt model consists of a filtering process, whereby the symmetrical pattern is horizontally filtered followed by thresholding (which removes values close to the mean grey level). This breaks down the pattern leaving just spatial frequency information as a number of black and white

'blobs' aligned across the vertical axis. The second stage involves blob alignment; a procedure that measures how well the centre of each blob aligns with the symmetry axis. Here, the spatial filtering scale that is used determines the amount that the blobs are aligned across the axis. The alignment of these blobs could be used to determine the presence of an object in the image.

Another class of models, representational, focus on the detectability or salience of the symmetry. The two main models are the Holographic weight of evidence approach and the Transformational approach. The holographic approach by van der Helm and Leeuwenberg (1996) formalises regularities mathematical with the formula: $W = E/N$. E is the number of non-redundant pairings; N is the total number of elements in the stimulus whilst W is the perceptual goodness or saliency of the pattern. For example, for reflection E would be equal to the number of dot pairs in the pattern and N is the total number of dots. The holographic model accounts for a number of the findings in the symmetry literature. For instance, the salience of the symmetry decreasing as noise added to the pattern increases and that reflection is more salient than translation and rotation (Barlow & Reeves, 1979; Dakin & Herbert, 1998). Alternatively, the transformational approach defines symmetry according to a block structure (Garner, 1974). For reflection each half of the pattern would be assigned block structure, whilst for translation each repeat would be identified as a block. However, this model cannot explain how reflection is more salient than either translation or rotation.

1.3. Brain responses to symmetry

Neuroimaging studies have identified a number of areas that are active during symmetry perception including the Lateral Occipital Complex (LOC), V3a, V4 and V7. Activations have not been reported in either V1 or V2 (Chen, Kao & Taylor 2007; Kohler et al., 2016; Sasaki et al., 2005; Tyler et al., 2005). This is somewhat interesting, as symmetry

coding has been suggested to depend on spatial filter properties, which would require engagement of these areas. Sasaki et al. (2005) showed that activity in these extrastriate visual areas correlated with the saliency of reflection symmetry, with higher activation being produced for vertical than horizontal as well as for 4-fold compared with one/two-fold reflection symmetry. More recently, Kohler et al. (2016) found similar supporting evidence using rotation.

Transcranial Magnetic Stimulation (TMS) studies have also provided additional support for the involvement of the extrastriate areas in symmetry perception (Cattaneo et al., 2011; Bona et al., 2014; Bona, Cattaneo & Silvanto, 2015). In an fMRI guided TMS study, Bona et al. (2014) applied TMS over either the left or right LOC. TMS disrupted reflection symmetry detection over both hemispheres with the effect being stronger in the right hemisphere. Cattaneo, Mattavelli, Papagno, Herbert and Silvanto (2011) also found that disrupting the LOC bilaterally through TMS altered symmetry discrimination. TMS applied to V1/V2 regions did not influence reflection symmetry detection.

So far, it appears that higher visual areas (V3, V4, V7 and LOC) seem particularly involved in symmetry processing. This seems logical given that symmetry is a global feature and areas such as the LOC have been shown to be important in shape processing and perceptual organization (Grill-Spector, 2003; Malach et al., 1995). However, early visual areas may still be involved. For example, van der Zwan, Leo, Joung, Latimer, and Wenderoth (1998) found that cells in V1 coded information about the orientation of the axes of symmetry.

1.4. Electrophysiological response to symmetry

Event Related Potentials (ERPs) are voltage fluctuations, which can be induced by physical or mental activity and averaged from electroencephalogram (EEG) data. ERPs have been

recorded from posterior electrodes in response to the presentation of reflection and random patterns whilst participants judged whether the patterns were reflectional or not (Norcia et al., 2002). It was found that ERPs were similar at P1 and N1 however at around 200ms after stimulus onset, the waves diverged with reflection being more negative in amplitude than random (Figure 1.2). Jacobsen and Höfel (2003) later referred to this component as the Sustained Posterior Negativity (SPN). The SPN is described as a difference between the ERP wave for a symmetrical pattern and the ERP wave for a random pattern from around 200ms after stimulus onset. Negativity is used as a relative term to simply mean that symmetry is lower in amplitude than random.

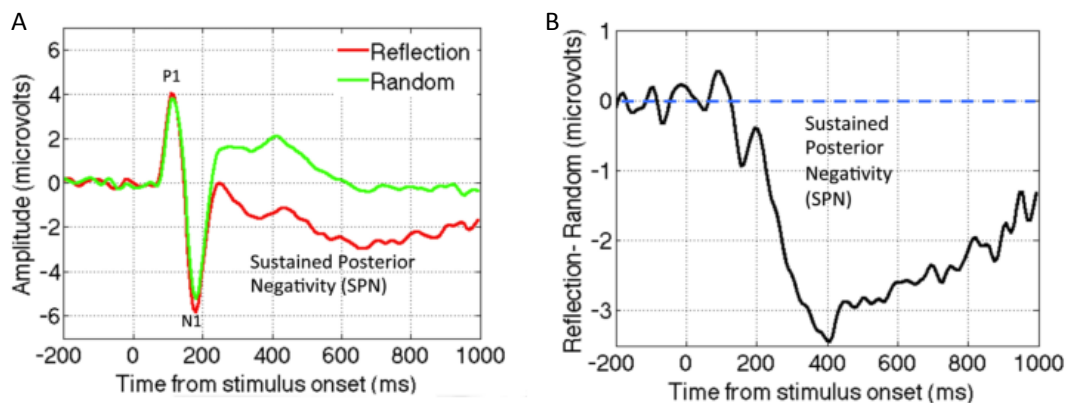


Figure 1.2. The Sustained Posterior Negativity (SPN). A) Grand-average waveforms for a reflection pattern and a random pattern recorded from posterior brain regions. B) Grand-average waveforms shown as a difference wave (Reflection – Random). Figure adapted from Bertamini & Makin (2014).

The SPN has been found to be present when viewing symmetry under various conditions. Makin, Rampone, Pecchinenda, and Bertamini (2013) showed that reflection produced the largest SPN. This is consistent with psychophysical findings, which have shown that reflection is the most salient of the regularities (Bertamini, 2010; Koning & Wagemans, 2009). Amplitude of the SPN in an early part of the SPN window also closely reflects perceptual goodness (Makin et al., 2016). When attending to symmetry, the SPN is view

invariant (Makin Rampone, & Bertamini, 2015). The SPN is task independent with it observed even when participants are engaged in tasks where stimulus regularity was not important. For example, it is produced (although reduced) when participants are required to attend to the features of a reflectional pattern (e.g. colour) or to words superimposed on the presented pattern (Makin, Rampone, & Bertamini, 2015). Furthermore an SPN is present when participants are required to deliberately misreport their actual judgments and so give incorrect responses about the presented stimuli (Höfel & Jacobsen, 2007b). The SPN has also been recorded during an oddball detection task whereby participants had to detect two squares amongst the presented dot pattern (Makin, Rampone, Pecchinenda, & Bertamini, 2013).

The SPN seems to be generated by extrastriate visual areas (V3a, V4, V7, LOC). Makin et al. (2012) performed a source localization analysis and found posterior brain regions produced the SPN. More precisely the SPN is likely to be generated by the LOC, which has been deemed the foremost symmetry area. Palumbo, Makin and Bertamini (2015) found that SPN amplitude, like LOC activation, scaled with the amount of reflectional symmetry in the image. Although not firm evidence, this is consistent with the findings from the neuroimaging studies (Chen, Kao and Taylor 2007; Kohler et al., 2016; Sasaki et al., 2005; Tyler et al., 2005). Overall, the SPN appears to be a response to visual symmetry in the image by a network of symmetry sensitive extrastriate visual areas in both hemispheres.

1.5. Chapters' overview

The aim of this thesis is to examine the neural response to visual symmetry. In this section I will provide an outline of the main research questions and summarize the results of each experimental chapter.

This thesis begins with an investigation into the neural response to patterns presented in the left or in the right visual hemifield (**Chapter 2**). To date, symmetry perception and the

SPN have assumed to be produced by a network spanning both hemispheres. Previous work had only examined the SPN in relation to symmetry presented in central vision (which generates bilateral hemisphere activation; e.g. Palumbo, Makin, & Bertamini, 2015). It may be that the SPN is only produced to symmetry in central vision, however it is possible that the SPN will be produced independently in each hemisphere when symmetry is presented in the contralateral visual field. For the first time, we present patterns in the periphery to investigate whether the SPN can be produced independently within each hemisphere. Participants were presented with different stimulus arrangements whilst fixating centrally. Following this they then performed a discrimination task that involved reporting whether the stimuli were light or dark red. In **Experiment 1(2)**¹, a reflection and a random pattern were simultaneously presented either side of fixation. In **Experiment 2(2)**, a single pattern (reflection or random) was presented in either the left or the right visual field. In **Experiment 3(2)**, participants were presented with matching patterns either side of fixation. Across the three experiments, the SPN was found within each hemisphere and, surprisingly, it was unaffected by what was presented to the other hemisphere. This suggests that each cerebral hemisphere has its own independent symmetry sensitive network in the extrastriate visual areas. It can also be concluded that symmetry perception does not require stimulation of both hemispheres to be achieved.

Another way of examining EEG is by looking at neural oscillations (Klimesch, Sauseng, & Hanslmayr, 2007; Pfurtscheller & Lopes da Silva, 1999). The study in **Chapter 3** provides an investigation into lateralised alpha event related desynchronization (ERD) during regularity discrimination. Neural oscillations are large assemblies of neurons that fire together in synchrony. They are ubiquitous in the brain and they play a key role in brain processes. Alpha oscillations (8-13Hz) occur in posterior brains regions. Oscillations are measured in

¹ The value in the brackets reports the number of the chapter (e.g. Experiment 1(2) is Experiment 1, Chapter 2).

power with a reduction in alpha power (or alpha event related desynchronization) reflecting an indirect index of excitation of the visual cortex. Two previous studies that have examined alpha ERD during regularity discrimination have reported a right lateralised hemisphere response which could either be a result of directed spatial attention or hemisphere specialisation (Makin et al., 2012; 2014). In the experiment in Chapter 3, alpha desynchronization was recorded over posterior brain regions whilst participants viewed reflection or translation patterns on either a vertical or horizontal axis of orientation. After stimulus presentation, participants had to classify the patterns as either reflection or translation. Alpha ERD was found in both the left and right hemispheres. However, this response was greater in the right hemisphere than the left. These results suggest that the right hemisphere is more specialised for regularity discrimination. However, the role of spatial attention cannot be completely ruled out as participants may still have moved their attention to the left regardless of pattern orientation.

Chapter 4 investigates how flanking objects influence the SPN. Both peripheral presentation and the presence of other objects can impair symmetry perception. Visual crowding is the reduced ability to perceive a target when flanked by objects. This effect is most prominent in peripheral vision. The strength of crowding is determined by the position of the flankers to the target as well as the features that these objects share. In chapter 2 it was demonstrated that the SPN could be produced to patterns presented in peripheral vision. Behaviourally it has been shown that reflection symmetry is subject to visual crowding (Roddy & Gurnsey, 2011). The SPN may be modulated when reflection is presented in the periphery amongst other objects (either reflection or random in shape). In **Experiment 1(4)**, participants were presented with a target (reflection or random) that was flanked by two random (non-symmetric) objects. Flankers could be positioned both above and below the target or either side. Participants were required to judge whether the target was symmetrical or

not. There are two hypotheses. The first hypothesis predicts that as the SPN is a response to symmetry in the image, this response will be produced whenever symmetry is present. This response would not be influenced by the position of the flankers. Alternatively, it has been found that the SPN responds to symmetry in the image with saliency of the symmetry increasing ERP amplitude. A second hypothesis therefore would predict that how easily the symmetry is perceived may impact on this response. Therefore, the size of the SPN will be determined by the strength of crowding. It was found that the SPN response in an early time window (200-600ms after stimulus onset) scaled with the strength of crowding. Crowding can also be affected by target-flanker similarity. For example, when the target and flankers share dissimilar features crowding is reduced (Kooi et al., 1994). As the SPN is a response to symmetry, this response may scale with the amount of symmetry in the image. Conversely, based on the results of Experiment 1(4) the SPN may be modulated by the strength of crowding. In **Experiment 2(4)**, the target and the flankers could be either all reflection, all random or different (e.g. a reflection target with two random flankers or vice versa) in shape. We found that when there was crowding the SPN was no longer present. In an attempt to reduce crowding and thus induce the SPN in **Experiment 3(4)** we varied two features (shape and contrast polarity) of the targets and the flankers. Black targets were presented amongst two white flankers. Again, the target and flankers could either be all reflection, all random or different in shape. It was found that, consistent with Experiment 1, the SPN response scaled with the strength of crowding. We conclude that the SPN is an automatic response to symmetry, which is present in the periphery and influenced by the presence of other objects.

Chapter 5 examines the electrophysiological response to symmetry during figure-ground assignment. Reflectional symmetry and convexity are both important cues in figure-ground assignment. When participants are presented with ambiguous figure-ground displays, both convexity and reflectional symmetry are important factors in determining what is

perceived as the figure (Driver et al., 1995; Kanizsa & Gerbino, 1976; for a review see Bertamini & Wagemans, 2013). We examined how figure-ground assignment would affect the SPN. To test this, we adapted stimuli used by Kanizsa and Gerbino (1976), which consisted of displays containing multiple red and green regions. When regions had convex parts they would be perceived as the figure whilst the concave parts would be seen as the ground. In **Experiment 1(5)**, we were interested in the ERP when reflection was perceived as being the figure and when it was perceived in the ground. Participants were presented with displays in which regions were either reflection with convex contours (reflection in the figure) or reflection with concave contours (reflection in the ground) or random. Participants had to judge which part of the display was the figure. The SPN was lower in amplitude when reflection was the figure than when reflection was the ground. There was no difference in ERPs between random and reflection in the ground. However, in this first study, reflection and convexity were confounded. Consequently the lower amplitude ERP for reflection in the figure could either be the result of reflection or convexity. In order to rule out the SPN was a response to convexity we conducted **Experiment 2(5)**. In this experiment, we modified the stimuli we had used in the first experiment, so that the displays contained reflection and random shapes, which could be either convex or concave in shape. Participants were required to either judge whether the presented shapes were red or green or if they were reflection or random. It was expected that we would find an SPN only for regions that were made of reflection convex contours. We found that there was a difference in ERPs for convexity when the displays were collapsed by regularity (reflection and random). However, regardless of the task for both the convex and concave displays there was no SPN (no difference between reflection and random). This lack of a difference between reflection and random for either convex or concave shapes was puzzling. In **Experiment 3(5)**, the same stimuli were presented as those from Experiment 2 except the fixation cross was moved to the axis of symmetry.

Previous SPN experiments had always presented symmetry with the fixation cross on the axis of symmetry. The lack of an SPN for Experiment 2 may have resulted from this, as attention may not have been centred on the symmetry. Yet for Experiment 3(5) an SPN was not found between reflection and random for either convex or concave. In **Experiment 4(5)**, the stimuli were modified so that the background matched the colour of the rest of the screen. Participants were presented with either one or three convex or concave shapes. For one shape there was no significant differences between conditions. However, for the three shapes there was found to be a significant difference between reflection convex and random convex but not between reflection concave and random concave. Overall the results suggest that the SPN is dependent on figure-ground assignment.

2. Can the SPN be produced independently within each hemisphere?*

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2.1. 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 200ms 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 reflection 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.

2.2. 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 organisation

(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 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 reflection presented to the left or the right hemifield.

2.2.1. Symmetry perception

The study of the 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; Lux et al., 2006; Kohler et al., 2016, 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 reflectional 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) 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 reflection 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 & Hemingway, 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 reflection 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 reflection, 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).

2.2.2. 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 reflectional 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, Vanduffel, Knutsen, Tyler & Tootell, 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 et al. (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 reflection 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 et al, 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 et al. (2002) examined the visual event-related potential (ERP) produced by

symmetrical or random patterns. Amplitudes were comparable up until 220ms after stimulus onset, afterwards the wave for the reflectional 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 220ms and 1000ms 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 reflectional 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 reflection or random required a 'yes' response in a 2AFC task (Makin, Wilton, Pecchinenda & Bertamini, 2012).

Makin et al. (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).

2.2.3. 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 et al., 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 reflectional 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.

2.3. Experiment 1

2.3.1. Method

2.3.1.1. 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).

2.3.1.2. 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 and 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 (1280x1024; 60Hz, Mitsubishi; Tokyo, Japan). Participants were positioned 100cm 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.

2.3.1.3. 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 refers to the random pattern being presented in the left visual hemifield whilst reflection is presented in the right (Figure 2.1).

2.3.1.4. Stimuli

Stimuli consisted of dot patterns (Figure 2.1), 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 0.008° . Symmetric stimuli had a reflection about both horizontal and vertical axes. Novel patterns were used on each trial to avoid any effect of familiarity.

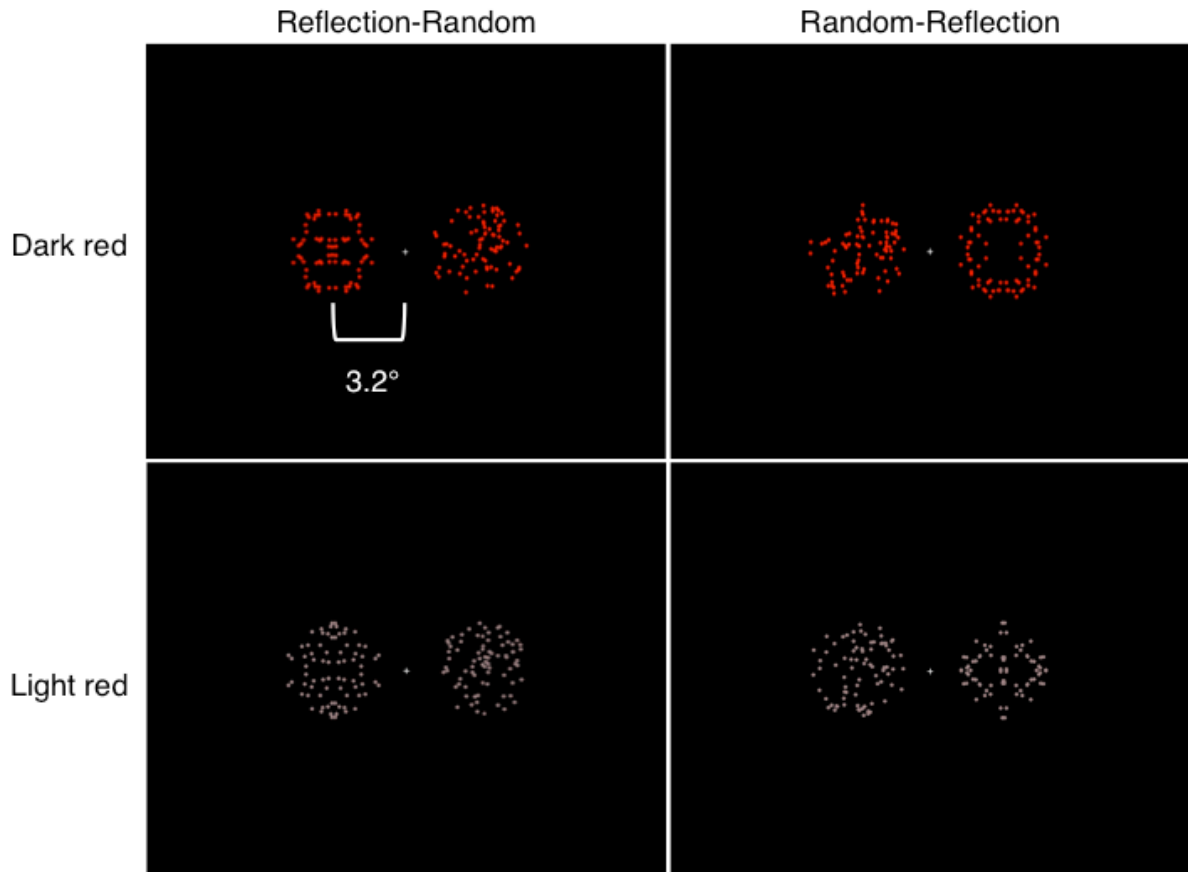


Figure 2.1. Example of the stimuli used in Experiment 1. Participants were required to make a judgment about whether both patterns were either dark or light red. Novel patterns were presented on each trial.

2.3.1.5. 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 seconds, when the screen showed the central fixation cross. The patterns then appeared and stayed on screen for a further 1.5 seconds. After each trial, participants were presented with a response screen, where they had up to ten seconds 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.

2.3.1.6. 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 40Hz. The data was then sampled at 128 Hz in order to reduce file size and segmented into -1s to 1.5s epochs with a baseline of -200ms to 0ms. 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 $\pm 100 \mu\text{V}$ 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 220ms. The SPN was broken up into two separate time windows of equal length: 200-600ms and 600-1000ms 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, Rampone & Bertamini, 2015).

2.3.2. Results

2.3.2.1. Behavioural

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 judgments were unspedded, and entered after the patterns had disappeared from the screen.

2.3.2.2. Event-Related Potentials

2.3.2.2.1. 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] x Hemisphere [Left, Right]). There were no main effects or interactions.

2.3.2.2.2. SPN

Figure 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.

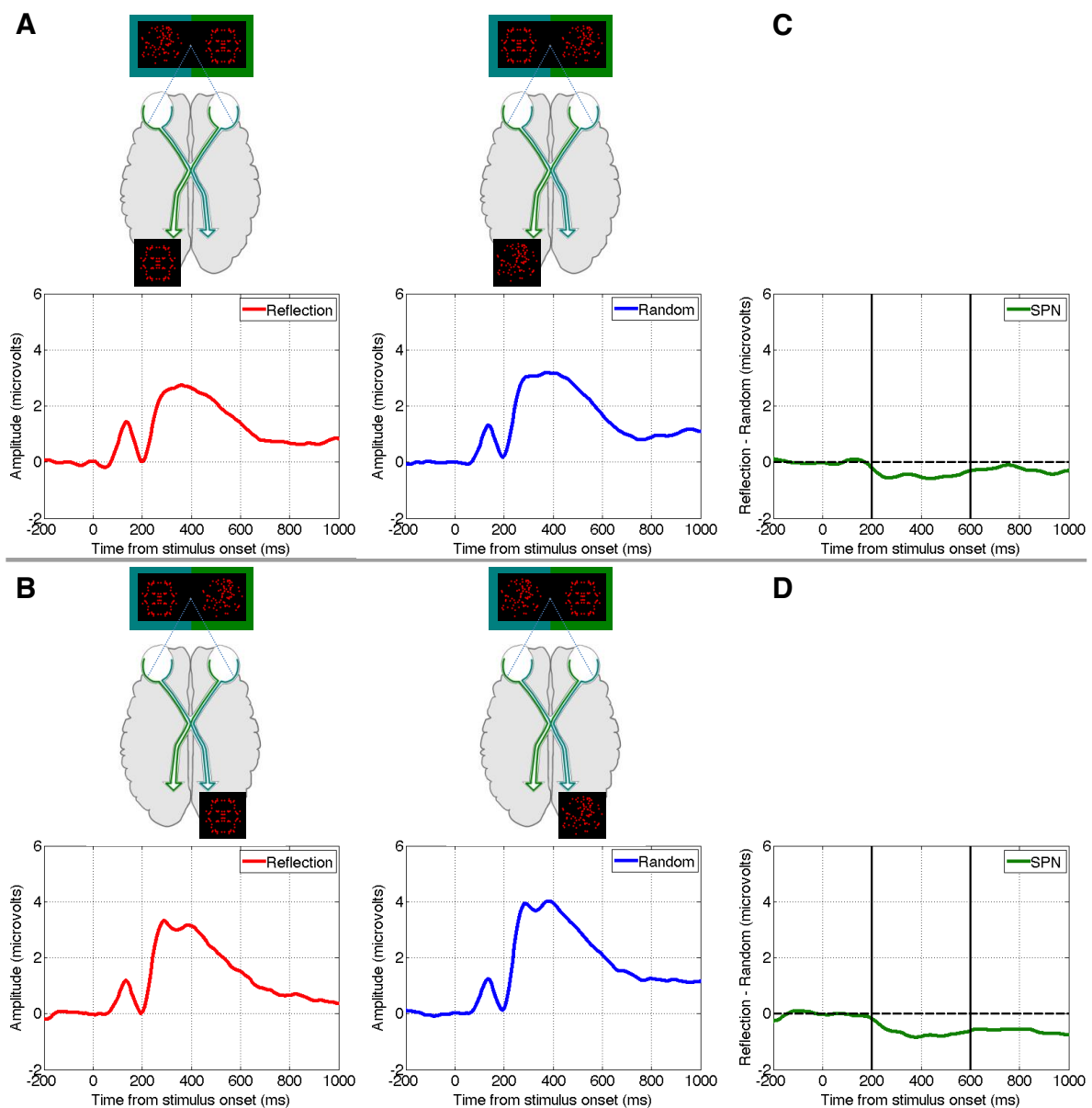


Figure 2.2. Experiment 1: Event Related Potentials (ERPs) from the left and the right hemispheres. Panels A and B show separate ERP plots for reflection and random over each hemisphere, with maps of the different stimulus arrangements and which hemisphere they are

processed in. C) Difference wave for the left hemisphere. D) Difference wave for the right hemisphere.

We analyzed the data with an Arrangement (Reflection-Random, Random-Reflection) x Hemisphere (Left, Right) x Time Window (200-600, 600-1000) repeated measures ANOVA². There was no main effect of Arrangement ($F(1, 23) = 1.312, p = 0.264, \text{partial } \eta^2 = 0.054$) or Hemisphere ($F(1, 23) = 0.979, p = 0.333, \text{partial } \eta^2 = 0.041$), but there was a main effect of Time ($F(1, 23) = 48.889, p = 0.001, \text{partial } \eta^2 = 0.680$). The only significant interaction was between Arrangement and Hemisphere ($F(1, 23) = 11.043, p = 0.003, \text{partial } \eta^2 = 0.324$).

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 200-600ms ($t(23) = 2.373, p = 0.026, d = 0.250$). 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 600-1000ms window ($t(23) = 1.271, p = 0.216, d = 0.140$). Conversely, for the right electrodes, there was a difference between the two arrangements in both the earlier 200-600ms time window ($t(23) = -3.526, p = 0.002, d = -0.290$) and the later 600-1000ms window ($t(23) = -2.563, p = 0.017, d = -0.267$).

2.4. 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

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

experiments. First, in Experiment 2, we present patterns to a single hemisphere, with nothing on the opposite side (Figure 2.3).

2.4.1. 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 (Figure 2.3). The stimuli and procedure were otherwise the same as in Experiment 1.

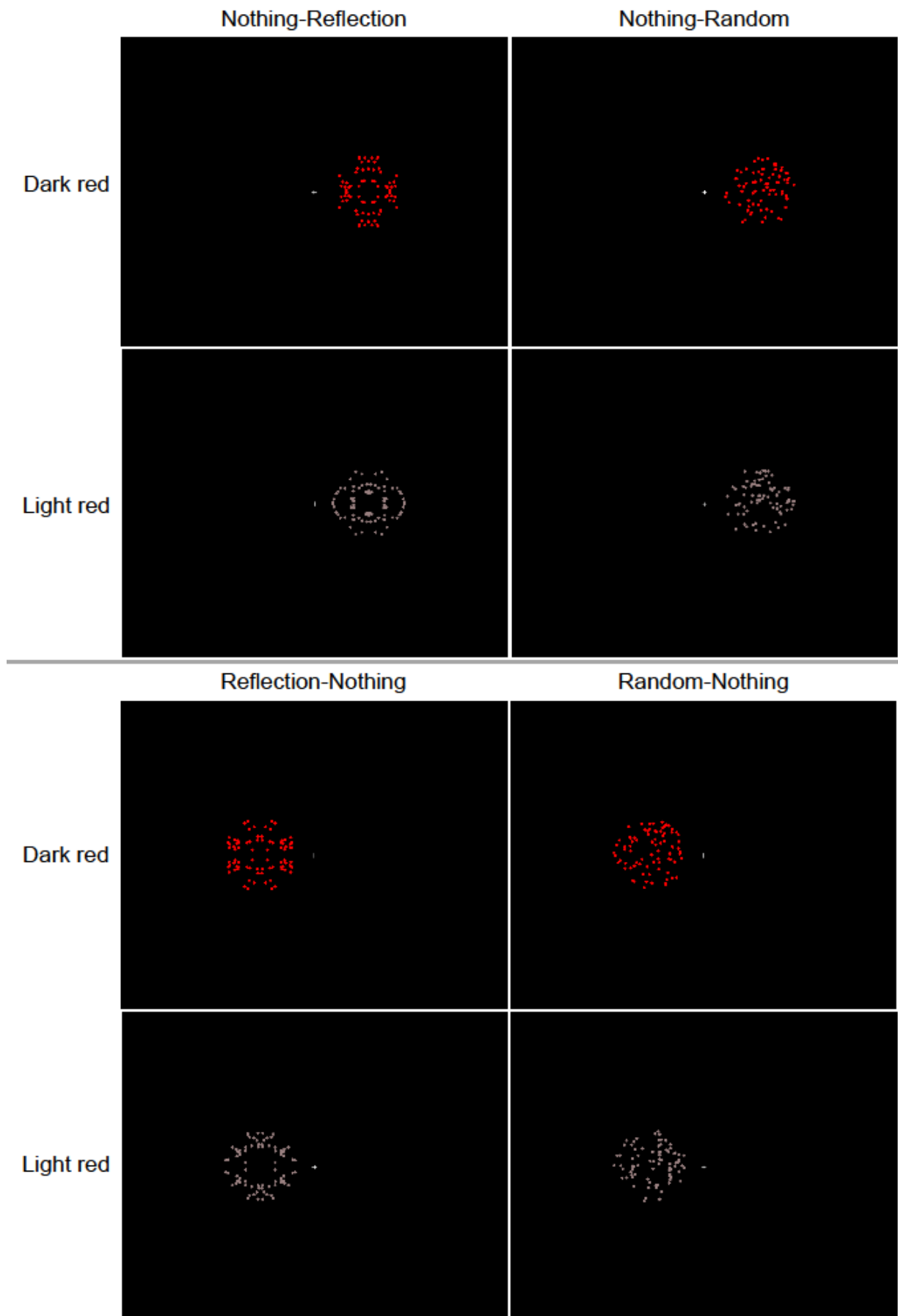


Figure 2.3. Example of the stimuli used in Experiment 2.

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 220ms. The SPN was split into time windows of 200-600ms and 600-1000ms after stimulus onset. N1 and the SPN were measured from electrode clusters in the left (P1, P3, P5, P7, PO7 and PO3) and right hemispheres (P2, P4, P6, P8, PO8 and PO4).

2.4.2. Results

2.4.2.1. 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%).

2.4.2.2. Event-Related Potentials

2.4.2.2.1. N1

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

2.4.2.2.2. SPN

Figures 2.4 and 2.5 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 patterns) generated the expected SPN response (with amplitude lower for reflection than random. Meanwhile, there was no SPN in the ipsilateral hemisphere (Figure 2.5). See Appendix 1 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] x Hemisphere [Left, Right] x Time Window [200-600, 600-1000])³. There was no main effect of Arrangement ($F(3, 69) = 2.260$, $p = 0.089$, partial $\eta^2 = 0.089$), but there were significant effects of Hemisphere ($F(1, 23) = 8.341$, $p = 0.008$, partial $\eta^2 = 0.266$) and Time Window ($F(1, 23) = 70.009$, $p = 0.001$, partial $\eta^2 = 0.753$). A significant interaction between Arrangement x Time was found ($F(3, 69) = 6.165$, $p = 0.001$, partial $\eta^2 = 0.211$) along with a three-way interaction for Arrangement x Hemisphere x Time ($F(1.691, 38.886) = 46.751$, $p = 0.001$, partial $\eta^2 = 0.670$). 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 200-600ms time window there was a difference between Nothing-Reflection and Nothing-Random ($t(23) = -3.671$, $p = 0.001$, $d = -0.394$); 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 600-1000ms time window there was a difference between Nothing-Reflection and Nothing-Random ($t(23) = -2.921$, $p = 0.008$, $d = -0.396$). There was a marginally significant difference between Reflection-Nothing and Random-Nothing ($t(23) = 1.997$, $p = 0.058$, $d = 0.329$).

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

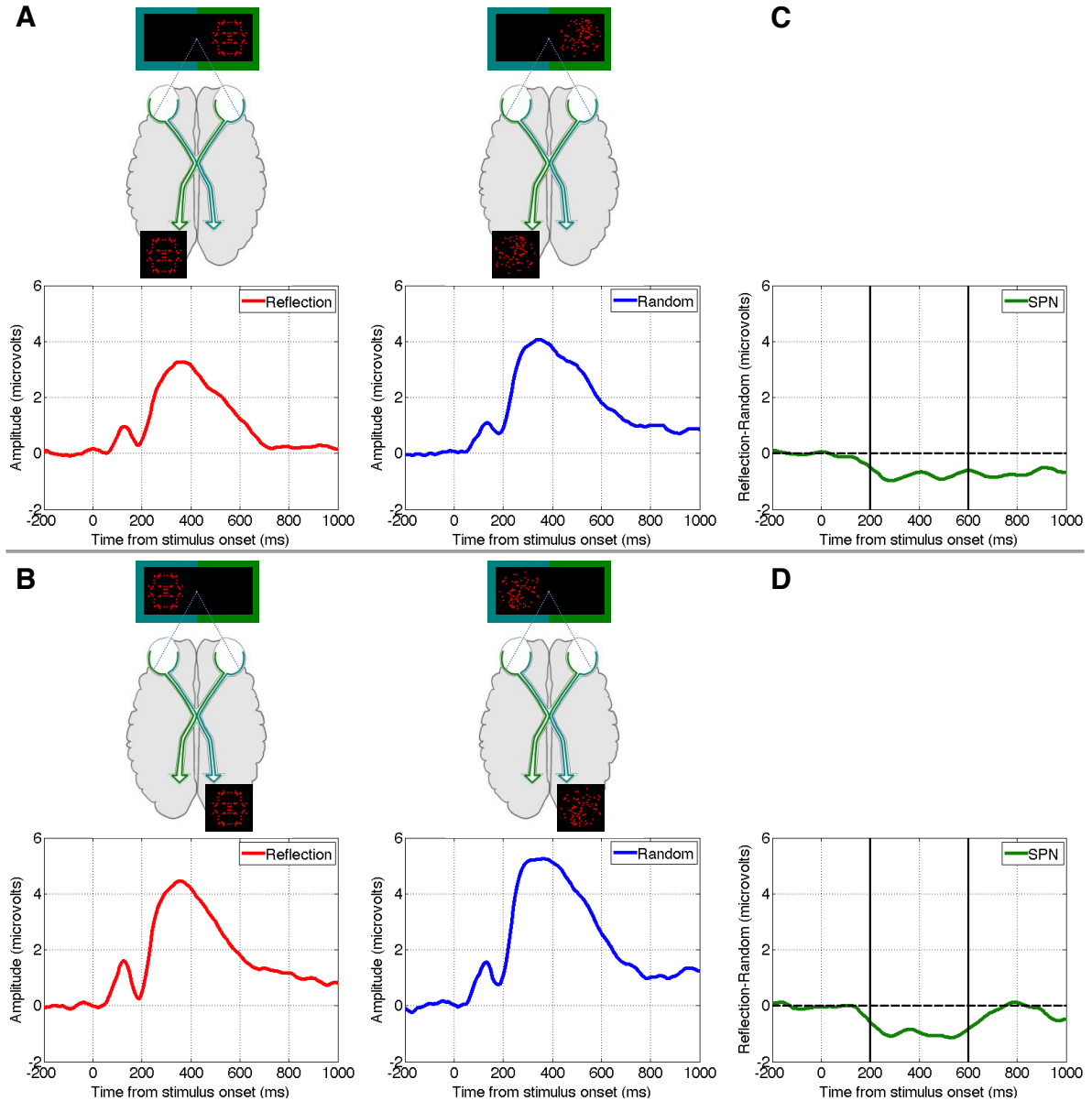


Figure 2.4. Experiment 2: Event Related Potentials (ERPs) from the left and the right hemispheres, focusing on the contralateral hemisphere, where patterns were processed. Conventions are the same as Figure 2.

Next, we consider right hemisphere electrodes for patterns in the left hemifield. In the 200-600ms time window there was a difference between Reflection-Nothing and Random-Nothing ($t(23) = -3.496$, $p = 0.002$, $d = -0.420$). There was no significant difference between Nothing-Reflection and Nothing-Random. For the 600-1000ms 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 800ms after stimulus onset (Figure 2.4).

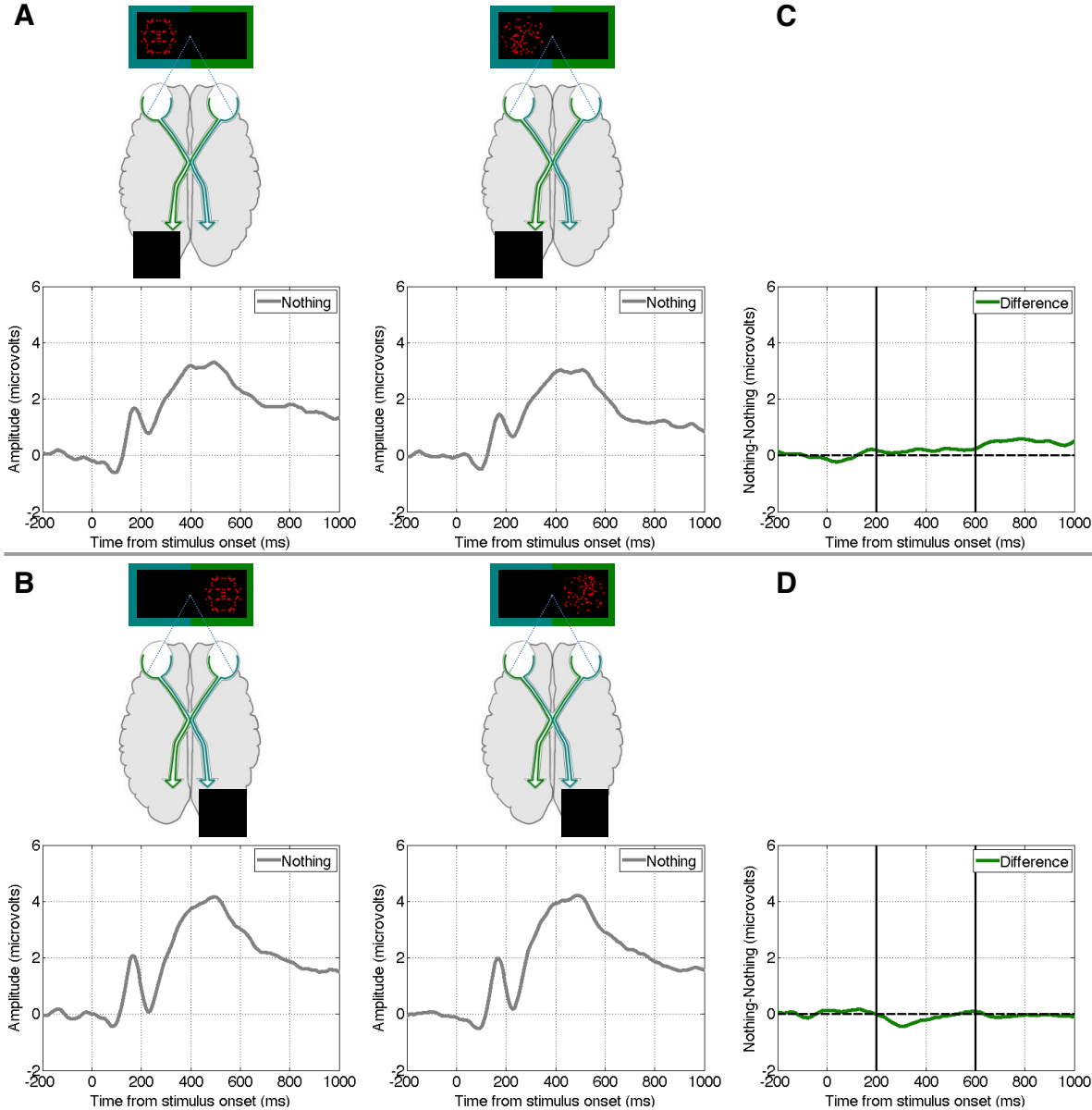


Figure 2.5. Experiment 2: Event Related Potentials (ERPs) from the left and right hemisphere, focusing on the contralateral hemisphere, opposite to the side where the patterns were processed. Conventions are the same as Figure 2.2.

2.5. 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 hemisphere

after 600ms), 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).

2.5.1. 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 (Figure 2.6). 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: 200-600ms and 600-1000ms 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).

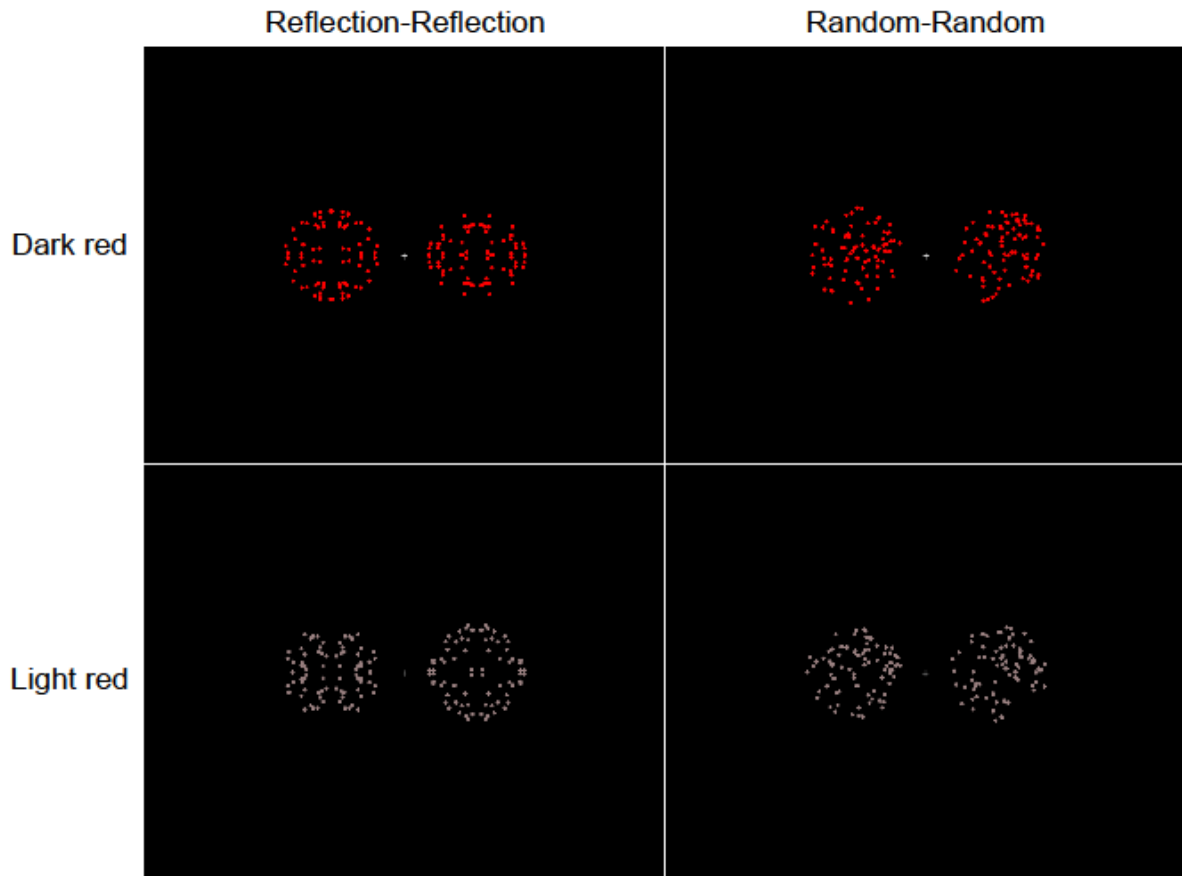


Figure 2.6. Example of the stimuli used in Experiment 3.

2.5.2. Results

2.5.2.1. Behavioural

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%).

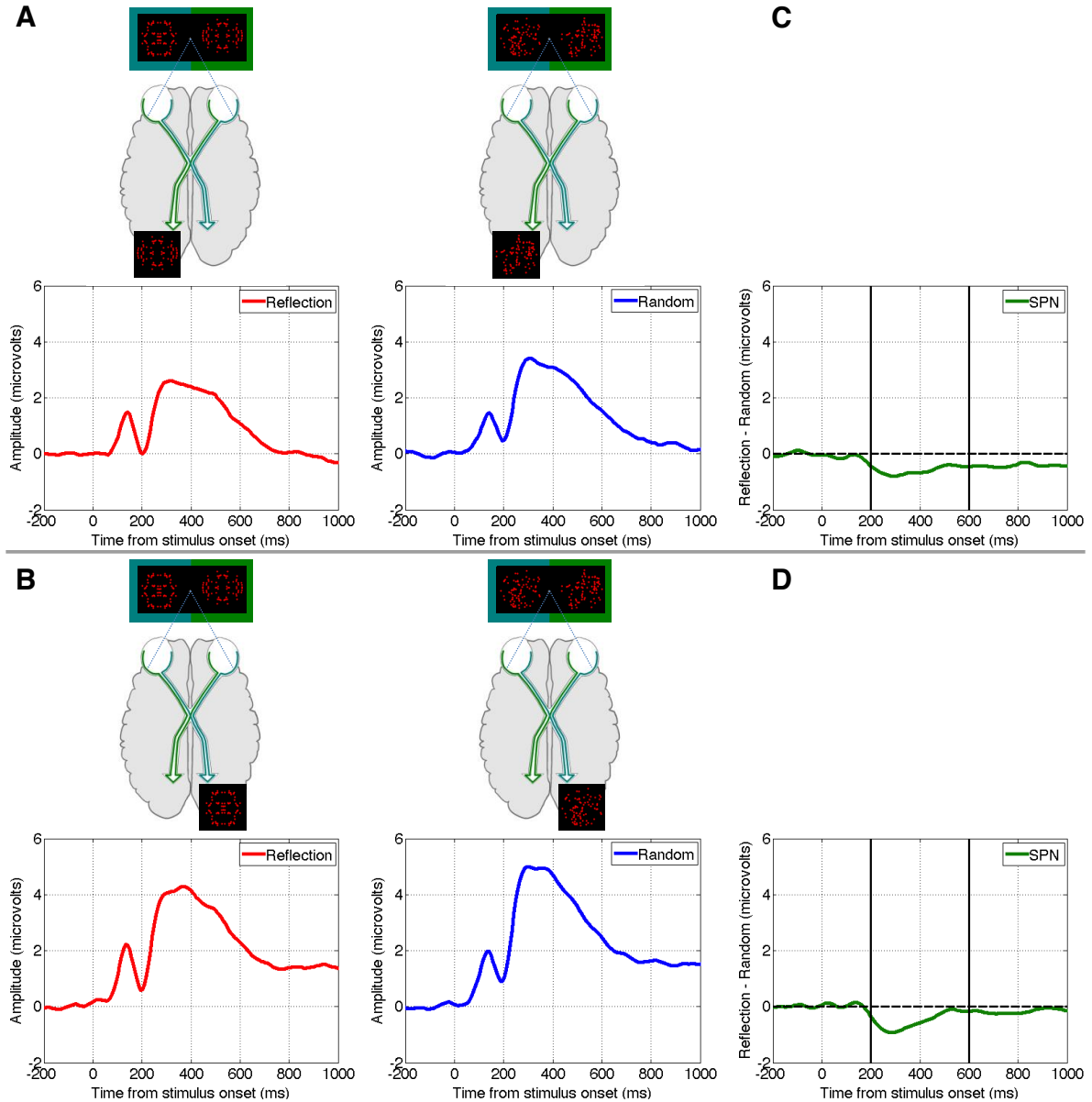


Figure 2.7. Experiment 3: Grand-Average Event Related Potentials (ERPs) from the left and the right hemispheres. Conventions are the same as Figure 2.2.

2.5.2.2. Event-Related Potentials

2.5.2.2.1. N1

To examine N1, we performed a two factor ANOVA (Arrangement [Reflection-Reflection, Random-Random] x Hemisphere [Left, Right]). There was a main effect of Arrangement ($F(1,23) = 5.766$, $p = 0.025$, partial $\eta^2 = 0.200$), because amplitude was lower for Reflection-Reflection than Random-Random. There was no effect of Hemisphere or an Arrangement x Hemisphere interaction.

2.5.2.2.2. SPN

An SPN was produced in both hemispheres, with reflection being lower in amplitude than random (Figure 2.7). The SPN was explored with a three-way repeated-measures ANOVA (Arrangement [Reflection-Reflection, Random-Random] x Hemisphere [Left, Right] x Time Window [200-600, 600-1000])⁴. There was a significant effect of Arrangement ($F(1, 23) = 10.319, p = 0.004, \text{partial } \eta^2 = 0.310$), Hemisphere ($F(1, 23) = 20.400, p = 0.001, \text{partial } \eta^2 = 0.470$) and Time ($F(1, 23) = 60.300, p = 0.001, \text{partial } \eta^2 = 0.724$). There was a significant interaction between Arrangement x Time ($F(1, 23) = 6.975, p = 0.015, \text{partial } \eta^2 = 0.233$). There were no Arrangement x Hemisphere interaction or Arrangement x Hemisphere x Time interactions.

First we consider the *left* hemisphere. For the 200-600ms window there was a significant difference between Reflection-Reflection and Random-Random ($t(23) = -3.554, p = 0.002, d = -0.288$). This significant difference between the arrangements persisted in the later time window ($t(23) = -2.088, p = 0.048, d = -0.281$). For the *right* hemisphere in the 200-600ms time window there was a significant difference between Reflection-Reflection and Random-Random ($t(23) = -3.627, p = 0.001, d = -0.259$). Due to the SPN fading out at around 600ms there was no significant differences in the later time window.

Figure 2.8 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

⁴ The same ANOVA also was performed with colour (Light, Dark) as an additional factor. There were no main effects or interactions with colour.

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 ms time window, when the symmetry response was present universally (left panels in Figure 2.8).

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 ($F(1,46) = 16.764, p < 0.001$, partial $\eta^2 = 0.267$). Crucially, there was no interaction, confirming that this response was independent of what the right hemisphere was doing ($F(1,46) = 0.194, p = 0.662$). The same analyses confirmed independence of the early right-sided regularity response: There was again a main effect of Pattern processed ($F(1,46) = 24.894, p < 0.001$, partial $\eta^2 = 0.351$), which did not interact with pattern in other hemisphere ($F(1,46) = 0.478, p = 0.493$).

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 ($F(1,46) = 18.477, p < 0.001$, partial $\eta^2 = 0.287$), which was independent of whether the other hemisphere was processing the opposite pattern or nothing ($F(1,46) = 1.085, p = 0.303$). The same was true of the right hemisphere, where there was again a main effect of Pattern processed ($F(1,46) = 23.804, p < 0.001$) that was unaffected by Pattern in the other hemisphere ($F(1,46) = 0.773, p = 0.384$).

Finally, we used within participants ANOVAs to confirm hemispheric independence in Experiments 2 vs. 3. In the left electrodes at the early time point, there was a main effect of Pattern processed ($F(1,46) = 20.595, p < 0.001$, partial $\eta^2 = 0.472$), which was independent of whether Nothing or the Same pattern was in the other hemisphere ($F(1,46) = 0.662, p =$

0.424). The same was true in the equivalent analysis of the right hemisphere ($F(1,46) = 18.055$, $p < 0.001$, partial $\eta^2 = 0.440$), and no Pattern processed \times Pattern in opposite hemisphere interaction ($F(1,46) = 2.932$, $p = 0.100$).

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.

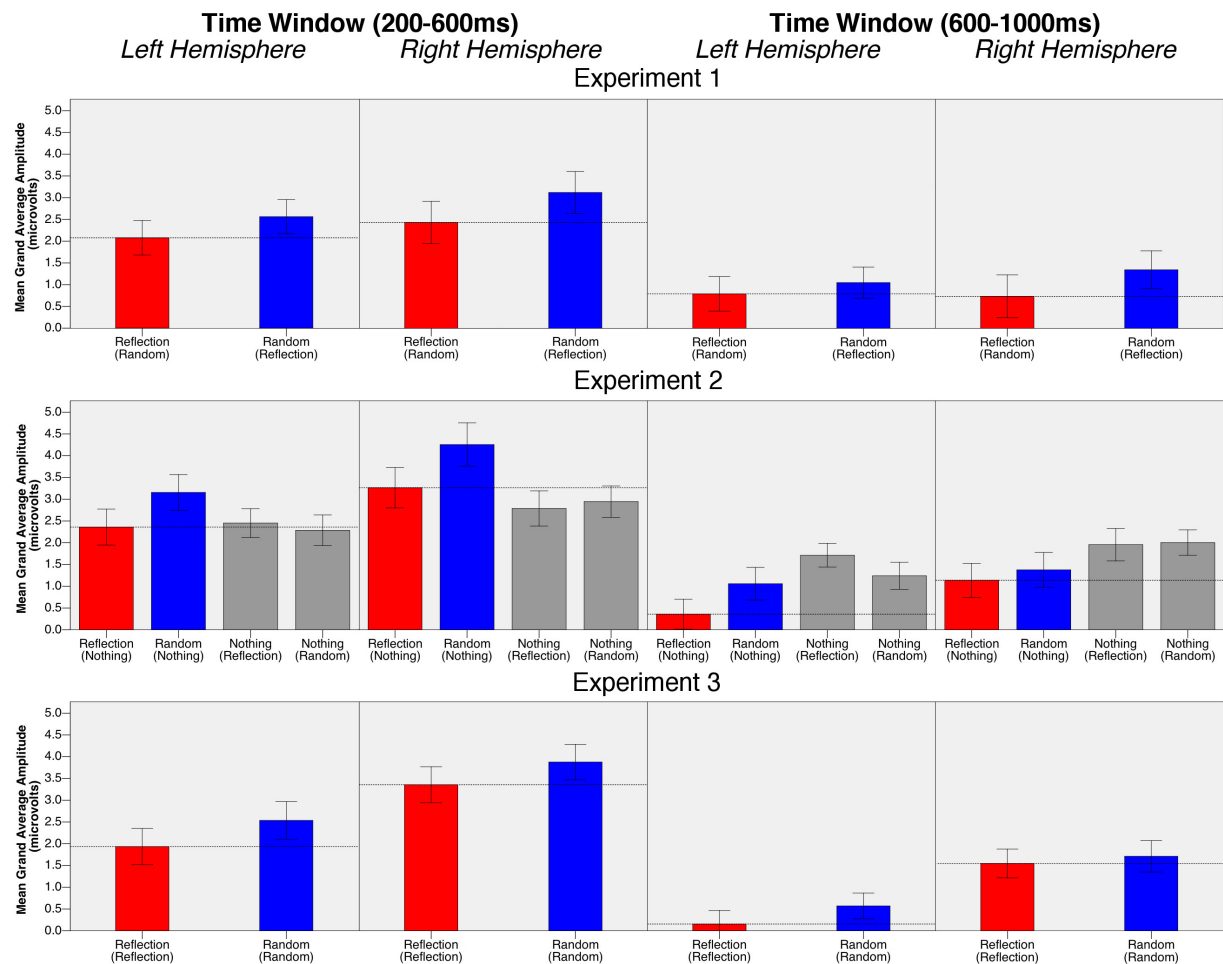


Figure 2.8. Mean Grand-Average Event Related Potentials (ERPs) of the SPN from the left and the right hemispheres for each experiment in the early (200-600ms) and late time windows (600-1000ms). Stimuli in brackets are those that were processed in the contralateral hemisphere. Error bars: ± 1 Standard Error.

2.6. 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 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, Rampone & Bertamini (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 et al., 1999). The N1 component is sometimes sensitive to symmetry (Makin et al., 2013; Makin, Wilton et al., 2012) however this has not been found consistently (Höfel & Jacobsen, 2007; Jacobsen & Höfel, 2003; Norcia, Candy, Pettet, Vildavski, & Tyler, 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 et al., 2009; Yuval-Greenberg et al., 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 100-140ms 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 behavior 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 ERP 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.

2.6.1. 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 (Sasaki et al., 2005, Tyler et al., 2005, Kohler et al., 2016). 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 et al., 2014). In fMRI research, the LOC is functionally localizing by comparing objects and scrambled objects (e.g. Kim et al., 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 the bilateral extrastriate network is also sensitive to top down inputs. For instance, Bauer et al.

(2015) asked blindfolded participants to discriminate reflectional from random arrangements of braille-like pin matrices using touch alone. One contrast revealed that haptic exploration of reflectional patterns activated LO and other visual maps in congenitally blind patients, while this ‘visual cortex’ response to haptic reflection 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 et al. (2015) 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 response 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 center 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 et al., 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 reflection 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 reflectional symmetric and asymmetrical figures were presented to each visual hemifield. Participants with a left hemisphere dominance for language showed superior reflectional symmetry detection in the right hemisphere. Likewise, Wilkinson and Halligan (2002) found that symmetry detection and perceptual landmark judgments 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 et al., 1990; Lux et al., 2004; Robertson et al., 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.

2.7. Conclusions

In the long history of the study of symmetry a key question has been why reflection 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 reflectional 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 and Höfel, 2003; Norcia et al., 2002; Wright, Makin & Bertamini, 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 sustained posterior negativity (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.

3. Is right-lateralized alpha desynchronization during regularity discrimination the result of hemispheric specialization or directed spatial attention?*

*This study has been published as Wright, D., Makin, A.D.J, & Bertamini, M. (2015). Right-lateralized alpha desynchronisation during regularity discrimination: Hemispheric specialization or directed spatial attention? *Psychophysiology*, 52(5), 638-647.

3.1. Abstract

When actively classifying abstract patterns according to their regularity, alpha desynchronization (ERD) becomes right lateralized over posterior brain areas. This could reflect temporary enhancement of contralateral visual inputs and specifically a shift of attention to the left, or right hemisphere specialization for regularity discrimination. This study tested these competing hypotheses. Twenty-four participants discriminated between dot patterns containing a reflection or a translation. The direction of the transformation, which matched one half onto the other half, was either vertical or horizontal. The strategy of shifting attention to one side of the patterns would not produce lateralized ERD in the horizontal condition. However, right-lateralized ERD was found in all conditions, regardless of orientation. We conclude that right hemisphere networks that incorporate the early posterior regions are specialized for regularity discrimination.

3.2. Introduction

Natural processes often produce emergent symmetry, which can be seen in countless examples from crystals, to galaxies, to animal phenotypes (Tyler, 1995). Psychophysical studies have shown that reflection symmetry is more salient, and more easily detected, by the human visual system than other regularities, such as translation or rotation (Bertamini, 2010;

Julesz, 1971; Koning & Wagemans, 2009), despite the fact that these patterns all share the presence of a rigid transformation (Mach, 1886/1959; Makin, Pecchinenda, & Bertamini, 2012). Reflectional symmetry is particularly salient when the axis of reflection is vertical (Barlow & Reeves, 1979). Sensitivity to reflection could be adaptive because reflectional symmetry signals reproductive fitness in potential mates (Møller, 1992; Rhodes, Proffitt, Grady, & Sumich, 1998), or because it is often a property of whole objects and therefore plays a role in image segmentation and object identification (Pizlo & Stevenson, 1999).

Symmetry refers to the property of a stimulus, which is defined as a geometric invariance under a rigid transformation such as reflection, rotation, or translation. Therefore, multiple symmetries can be present in a stimulus, and in the case of reflection there may be single or multiple axes. In this experiment, when we refer to symmetry we are concerned with the rigid transformations, which include reflection, translation, and rotation. When we discuss symmetry discrimination, we mean discrimination between two different transformations, here, reflection and translation.

The neuroimaging literature on symmetry has reported activations in a number of areas including the lateral occipital complex (LOC), V3a, V4, and V7, but not in the primary or secondary visual cortices (Chen, Kao, & Tyler, 2007; Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005; Tyler et al., 2005). Transcranial Magnetic Stimulation (TMS) studies have largely corroborated these results. Cattaneo, Mattavelli, Papagno, Herbert, and Silvanto (2011) found that adaptation to reflection symmetry was altered by disruption of either left or right LOC; however, no such effect was produced by V1 disruption. More recently, Bona et al. (2014) showed that TMS disruption of either left or right LOC impaired symmetry discrimination, but the effect was stronger on the right. We examine the issue of right lateralization with a different technique in the current work.

Several studies have used Event Related Potentials (ERPs) to study symmetry perception. Norcia, Candy, Pettet, Vildavaski, and Tyler (2002) presented participants with reflection or random patterns in quick succession. Amplitude in posterior electrodes was more negative for symmetrical patterns after around 220 ms from stimulus onset. Jacobsen and Höfel (2003) measured ERPs while participants judged abstract patterns as symmetrical or random. Again, amplitude at posterior electrodes was relatively negative for symmetrical patterns for a prolonged period after the visual evoked potential. They termed this component the sustained posterior negativity (SPN). The SPN was recorded in subsequent experiments when participants were engaged in oddball detection rather than symmetry discrimination (Höfel & Jacobsen, 2007a) or when participants were deliberately misreporting their responses (Höfel & Jacobsen, 2007b). Makin, Wilton, Pecchinenda, and Bertamini (2012) recorded the SPN, and found that it was unaffected by whether reflection or random patterns were designated as targets in their two-alternative forced choice discrimination task. Makin, Rampone, Pecchinenda, and Bertamini (2013) reported an SPN for different regularities, although reflection produced the largest response. Finally, Makin, Rampone, Wright, Martinovic, and Bertamini (2014) found that the SPN was larger for reflection than translation, independently of the requirements of the discrimination task, and independently of whether the regularity was the property of a single object or the gap between two objects. So far, it seems reasonable to conclude that the SPN is generated by automatic visual symmetry analysis in the extrastriate visual cortex, and this activity seems to systematically map onto some, but not all, psychophysical findings.

Makin, Wilton et al. (2012) also analyzed their EEG data in another way, measuring event-related desynchronization (ERD) of the occipital alpha rhythm. This response is fundamentally different to the SPN. ERD was comparable for reflection and random trials, and was significantly greater over the right posterior region. Makin et al. (2014) replicated

this right lateralization, and found that it was only present when participants were actively discriminating regularity (reflection or translation) and not when they were discriminating the number of objects in the display (one or two), even though the visual stimuli were identical in both tasks. It seems that alpha ERD picks up a different aspect of visual symmetry perception to the SPN: The SPN is the neural response to symmetry—it is a difference wave that distinguishes symmetry from random, and between different types of symmetry. Regularity detectors generate the SPN. Conversely, posterior alpha ERD is the same for all regularities and for random patterns. It is right lateralized, across all conditions, but only when people are engaged in a symmetry discrimination task. Right lateralization of posterior alpha ERD is thus a correlate of engagement with a task about regularity rather than regularity detection.

For many years, alpha oscillations have been associated with cortical off states. For example, alpha power is greater with the eyes closed, or when participants are not engaging in a task (Pfurtscheller & Lopes da Silva, 1999). Attention has also been shown to modulate alpha rhythms: with a decrease in alpha and an increase in beta power during attentional tasks (Gómez, Vázquez, Vaquero, López-Mendoza, & Cardoso, 1998; Vázquez, Gómez, Vaquero, & Cardoso, 2001). According to the inhibition-timing hypothesis, synchronized alpha oscillations (~8–12 Hz) reflect top down inhibition rather than purely “cortical idling.” Conversely, a reduction in alpha power, desynchronization, reflects neural excitation produced by task engagement (Klimesch, Sauseng, & Hanslmayr, 2007). The right-lateralized alpha response probably arises from greater activation in the posterior right hemisphere compared to the left during regularity discrimination tasks. However, these findings are inconclusive, because lateralization could arise from either transitory enhancement of contralateral visual inputs, or from functional differences between the cerebral hemispheres.

In our previous work, the axis of orientation was always vertical (Makin et al., 2014; Makin, Wilton et al., 2012). This may have encouraged participants to explore the regularity by shifting attention back and forth across the midline. Although eye movements were suppressed in these experiments, participants may still have moved covert attention. It is conceivable that visual exploration begins with a systematic shift to the left after early visual processing, and that this manifests as right-sided alpha desynchronization. Alternatively, there may be genuine hemispheric differences in regularity processing, with more regularity sensitive systems in the right posterior regions.

This later hypothesis is plausible because of the differences in cognitive functions of the two hemispheres. The exact nature of hemispheric specialization is still debated, but important differences have been suggested. Beyond the well-established left specialization for language and right specialization for spatial processing (Cai, Van der Haegen, & Brysbaert, 2013), it has been proposed that the left hemisphere preferentially processes high spatial frequencies whereas the right hemisphere preferentially processes low spatial frequencies (Sergent, 1983). In addition, the left hemisphere may be involved in processing local elements whereas the right is more involved in global element processing (Van Kleeck, 1989). Finally, there is strong evidence that the right frontoparietal network is specialized for mental object rotation (Parsons, 2003) and directing of visuospatial attention (Mesulam, 2002).

Most relevantly for the current study, there is some evidence for right hemisphere specialization for symmetry detection. First, Corballis and Roldan (1974) found that symmetrical patterns could be detected slightly faster when presented to the left visual hemifield (i.e., processed by the right hemisphere), and Brysbaert (1994) replicated this modest effect. Wilkinson and Halligan (2002) considered the similarities between symmetry perception and line bisection (where people place a mark in the center of a horizontal line, or attempt to identify noncentral bisections). A right hemisphere advantage was found for both

tasks. Stronger evidence for right hemisphere dominance in symmetry detection comes from a recent study by Verma, Van der Haegen, and Brysbaert (2013), who briefly presented reflectional symmetric or asymmetrical block shapes to either hemisphere while participants fixated centrally. For the neuro-typical participants who were left hemisphere dominant for language, reflection symmetry detection was superior when images were presented to the right hemisphere. For a subgroup of unusual right hemisphere language participants, this bias was absent or sometimes reversed. In short, it is likely symmetry detection systems are present in both cerebral hemispheres, but that the right hemisphere dominates in most people. However, the existing literature documents right hemisphere advantage when reflection symmetry is presented, not when random or translation patterns are presented. This is different from the right-lateralized ERD response found by Makin, Wilton et al. (2012), which was equivalent during symmetrical and random presentations. What was critical in the ERD work was that observers were engaged in a symmetry discrimination task.

In this study, participants saw reflection or translation patterns, while EEG responses were recorded. The orientation of the pattern was either horizontal or vertical (Figure 3.1). In the case of reflection, this means a vertical or horizontal axis of symmetry, but in both cases (reflection and translation) a rigid transformation matches elements in one half of the stimulus to elements in the other half. Therefore, vertical and horizontal orientation refers to the separation between these two halves.

A “look left” strategy predicts that ERD lateralization should only occur in the vertical condition. In the horizontal condition, the same strategy would involve moving attention up and down, rather than left and right, and this would not result in systematically right-lateralized ERD. Conversely the right hemisphere specialization hypothesis predicts comparable lateralized ERD in horizontal and vertical conditions. There is potential for confusion here: To reiterate a point made above, posterior ERD is expected to be equivalent

on reflection and translation trials (as found by Makin et al., 2014). The novel question in this work was whether this ubiquitous right lateralization during regularity discrimination would be observed when the patterns are horizontally orientated.

A secondary aim of this study was to investigate the role of orientation on the symmetry-related ERPs, which has not been studied extensively. Some psychophysical experiments have found that the vertical axis of reflectional symmetry is more salient than the horizontal axis (e.g., Friedenberg & Bertamini, 2000). It is expected that there will be a larger SPN in the vertical condition than the horizontal condition. This would be consistent with the findings of Makin et al. (2013), who found a relationship between visual salience and SPN amplitude.

3.3. Method

3.3.1. Participants

Twenty-four participants took part in the study (age 18–44, mean age 22, 6 males, 1 left-handed). Participants had normal or corrected-to-normal vision, and some received course credit upon completion of the study. The study was approved by the Ethics Committee of the University of Liverpool and conducted in accordance with the Declaration of Helsinki (revised 2008).

3.3.2. Apparatus

Participants sat 100 cm from the monitor (1,280 × 1,024; 60 Hz, Mitsubishi, Tokyo, Japan) with their head stabilized with a chin rest. Participants used the A and L buttons of the computer keyboard to enter their responses. Stimuli were presented on a CRT monitor and controlled with open source PsychoPy software (Peirce, 2007). EEG activity was recorded using a BioSemi (Amsterdam, The Netherlands) Active-Two amplifier in an electrically

shielded and darkened room. EEG was sampled continuously at 512 Hz from 64 scalp electrodes arranged according to the standard International 10-20 system. Common mode sense (CMS) and driven right leg (DRL) were used as reference and ground electrodes. 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. These were used to detect blinks and eye movements.

3.3.3. Design

The study had a within-subjects design: Regularity (reflection, translation) \times Orientation (horizontal, vertical) with 72 trials per condition. The trials were presented in a randomized sequence for each participant.

3.3.4. Stimuli

Stimuli consisted of filled gray circles that varied in brightness (Figure 3.1). In each half of the patterns there were 11 elements, which varied in radius between 0.5° and 1° . There were 0.9° between the centers of the dots. The patterns were presented either with a vertical or a horizontal orientation with a line going through the center of the pattern indicating the orientation. A black fixation cross also appeared at the center of each pattern. The background consisted of a white circle, which had a diameter of 14.4° . Vertical patterns were very similar to those used by Makin et al. (2013).

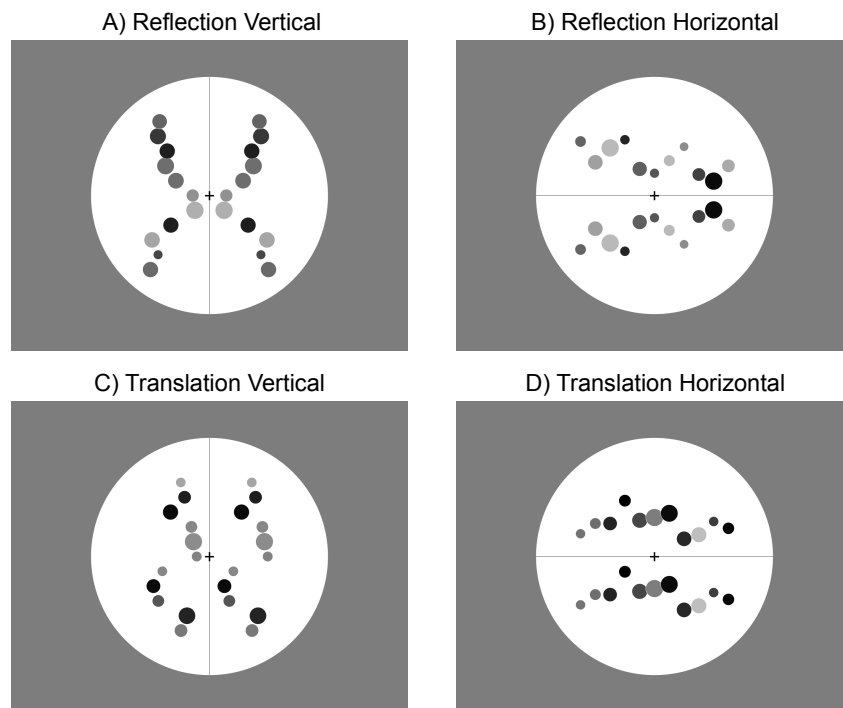


Figure 3.1. Example stimuli from the four conditions (vertical reflection, horizontal reflection, vertical translation, and horizontal translation). Actual stimuli were generated so as to be different in each trial. Participants discriminated reflection from translation.

3.3.5. Procedure

Participants sat in front of a CRT monitor in a darkened and electrically shielded room. The experiment consisted of a total of 288 trials. Each trial began with a 1.5-s baseline period, when the screen showed the background circle, the central fixation cross, and the oriented line. The dot elements then appeared reflected or translated on either side of the midline. The stimuli stayed on screen for 2 s. This design ensured that axis orientation was predictable before presentation, and thus participants did not have to compute this while making reflection-translation judgments. This ensured a cleaner measure of the neural response to the different regularities than would have been possible if orientation was unpredictable before stimulus onset. With this design, it made sure that the time to perceive the orientation did not vary between the reflection and the translation conditions.

After each trial, participants were presented with a response screen, and they had to report whether the observed pattern was a reflection or a translation. The response screen informed them to press the button on the left for “reflection” and on the right for “translation” or vice versa. The two orders varied between the trials and were counterbalanced across conditions so that no motor planning was possible before the response screen appeared (Makin, Wilton et al., 2012). Participants had up to 10 s to log a response. The experiment was divided into eight blocks, which allowed participants to have breaks in which they could rest their eyes. Prior to the start of the main experiment, participants completed a practice block. This consisted of eight trials, and its design reflected that of the main experiment.

3.3.6. EEG Analysis

EEG data was processed using the EEGLAB toolbox in MATLAB (Delorme & Makeig, 2004). The raw EEG signals from the 64 electrodes were re-referenced offline to a scalp average and low-pass filtered at 40 Hz. The data were then sampled at 128 Hz in order to reduce file size and segmented into -1-s to 2-s epochs with a baseline of -200 ms to 0 ms. Ocular and muscle artifacts were identified and removed using independent components analysis (ICA). The data were then re-formed as 64 independent components and an average of 11.4 components removed from each participant (min = 1, max = 18). After ICA, trials that had amplitude greater than $\pm 100 \mu\text{V}$ for any electrode were removed. The average proportion of excluded trials did not differ significantly between the four conditions (reflection vertical, 18%; translation vertical, 15%; reflection horizontal, 17%; translation horizontal, 14%, $F(3,69) = 2.475, p = .069, \eta^2 = .279$).

Time frequency analysis was performed on the same cleaned data that were used for the ERP analysis, using the FieldTrip toolbox for MATLAB (Oostenveld, Fries, Maris, & Schoffelen, 2011). Frequency bands from 5 to 20 Hz were explored, with a -500 to 0 ms

baseline. Raw data were convolved with a Hanning-tapered wavelet comprising four cycles at each frequency. Relative power was then computed as a proportion change from baseline. Wavelets were positioned at increments separated by 50 ms through the raw data. This means that low frequency wavelets overlapped to a greater degree than high frequency ones. The preprocessing steps were matched with Makin et al. (2014). We measured desynchronization in the 10–14 Hz frequency band from 400 to 1,000 ms post-stimulus onset. These parameters were similar, but not identical, to those used by Makin et al. (2014), that is, 400–700 ms, 8–13 Hz, where right lateralized alpha ERD was also measured during reflection translations. The time-frequency window used by Makin et al. (2014) was not centered on the effects here, so the parameters were adjusted. This decision did not substantially affect the results. Secondary analysis reported in the online supporting information showed essentially the same ERD effects when the same window as Makin et al. (2014) was used.

3.3.7. Electrooculogram Analysis

Although participants were instructed to fixate and eye movement artifacts were removed, these measures are not perfect. Therefore, it was important to establish whether eye movements and blinks contaminated some conditions more than others. To do this, the electrooculogram (EOG) analysis techniques used in our previous studies were improved (e.g., Makin et al., 2013; Makin, Wilton et al., 2012) by measuring EOG activity at the time window of the SPN or ERD, and only for trials included in the ERP and ERD analysis. For the selected EOG data, we computed the difference between maximum and minimum amplitude, then averaged this metric over all trials in each condition.

VEOG activity from the SPN window (250 to 1,000 ms) was analyzed with repeated measures analysis of variance (ANOVA): Regularity (Reflection, Translation) \times Orientation (Vertical, Horizontal). Ideally, there would have been no effects or interactions; however,

there was significantly more VEOG activity in the reflection trials than the translation trials, $F(1,23) = 10.03$, $p = .004$, $\eta_p^2 = .304$, and in the vertical trials than the horizontal trials, $F(1,23) = 5.77$, $p = .025$, $\eta_p^2 = .200$. There was no Regularity \times Orientation interaction, $F(1,23) < 1$, *n.s.* This pattern differs from SPN results reported below. Next, the same analysis was performed, but using VEOG activity from the time window used for posterior ERD (400 to 1,000 ms). There were main effects of Regularity, $F(1,23) = 11.43$, $p = .003$, $\eta_p^2 = .332$, and Orientation, $F(1,23) = 5.46$, $p = .029$, $\eta_p^2 = .192$, and no interaction, $F(1,23) < 1$, *n.s.* Again, this is a different pattern from the ERD results reported below.

To further establish that differential blinking was not responsible for posterior ERPs, potential correlations between the VEOG metric and amplitude at bilateral posterior electrode clusters were measured. There was no significant correlation in any of the four conditions (maximum $r = .24$, $p = .268$). Next, similar correlations between VEOG activity and bilateral occipital alpha ERD were examined, and there were no significant correlations here either (maximum $r = -.34$, $p = .105$). Finally, there were no correlations between right lateralization of posterior ERD and VEOG activity (maximum $r = .16$, $p = .442$). It can be concluded that the effects of interest recorded at posterior electrodes do not reflect differential blinking.

Next, the same analysis of HEOG data from the SPN window (250 to 1,000 ms) was conducted. There were no effects or interactions, $F(1,23) < 1$, *n.s.* Furthermore, there were no effects when the ERD window was examined (400 to 1,000 ms; $F(1,23) < 1$, *n.s.*). This shows that unwanted horizontal eye movements were equally distributed across conditions, and thus do not explain the effects of interest.

There were no correlations between posterior ERP amplitude and HEOG metric (maximum $r = -.32$, $p = .131$). There was no correlation between HEOG and the bilateral ERD response in any condition (maximum $r = -.12$, $p = .592$), and no correlations between HEOG and ERD lateralization (maximum $r = -.15$, $p = .470$).

In summary, there were some differences in VEOG activity between conditions, while unwanted HEOG activity was equally prevalent across conditions. Moreover, very little variance in the effects of interest was explained by individual variability of the EOG metrics. It can be concluded that the results reported below cannot be attributed to gross eye movement artifacts. Further examination of this issue is reported below.

3.4. Results

3.4.1. Behavioural Results

Participants discriminated patterns as reflection or translation. They made a correct discrimination on most of the trials (mean correct = 97.04%), with no differences between conditions (reflection, 97%; translation, 97%; horizontal, 97% vertical; 98%). Responses were entered after the patterns disappeared, and were unspeeded. Response times were not instructive in this study.

3.4.2. Event-Related Potentials

Figure 3.2 shows topographic maps of grand-average ERPs from 250 to 1,000 ms. It can be seen that distribution of scalp activity was broadly comparable in the four conditions; however, difference maps, shown in Figure 3.2B, highlight important effects. There was an unexpected difference between horizontal and vertical trials, shown in the top left map. There was a clear SPN (i.e., amplitude was lower in reflection than the translation conditions), shown in the top right map. The SPN was present in both vertical and horizontal trials, as shown in the topographic maps below. It can be seen that SPN was larger on the right. Based on these difference plots, electrodes were selected for statistical analysis. These were O1, PO3, and PO7 and right-sided homologues, O2, PO4, and PO8. These electrodes are highlighted in gray in Figure 3.2B, and ERP waves from these electrodes are shown in

Figures 3.2C, D (see supporting information for complementary analysis of SPN using different electrodes).

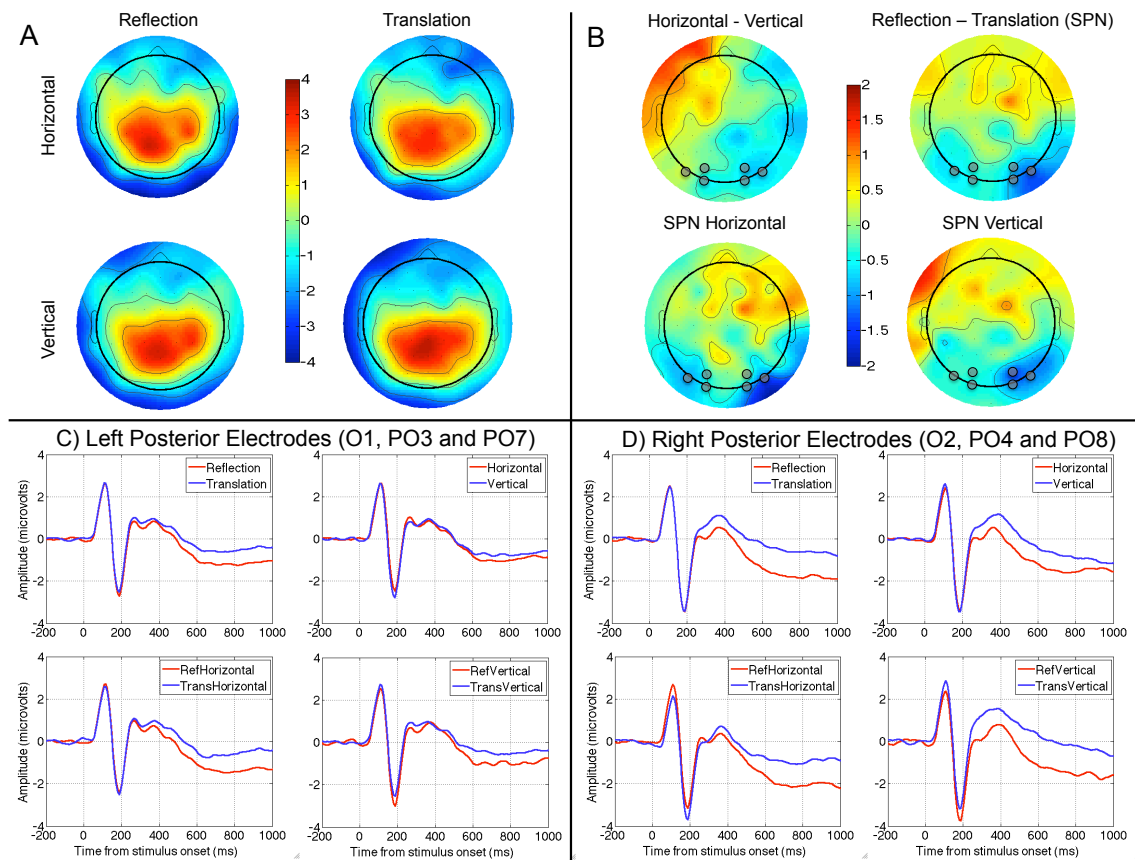


Figure 3.2. Event-related potentials. A: Grand-average topographic maps from the four conditions (vertical reflection, horizontal reflection, vertical translation, and horizontal translation) averaged over the 250–1,000 ms time window. B: Difference plots derived from this data. Electrodes used for analysis are highlighted with a gray dot. C: Grand-average ERP waves from left posterior electrodes (O1, PO3, and PO7) in different conditions. D: Equivalent data from right posterior electrodes (O2, PO4, and PO8).

Amplitude in the 250 to 1,000 ms window was explored with repeated measures ANOVA: Hemisphere (left, right), \times Regularity (reflection, translation) \times Orientation (horizontal, vertical). As expected, there was a main effect for regularity, $F(1,23) = 18.85, p < .001, \eta_p^2 = .450$, because amplitude was lower in reflection than translation trials. The only other significant effect was Regularity \times Hemisphere interaction, $F(1,23) = 5.26, p = .031, \eta_p^2 = .186$. To explore this interaction, we analyzed left and right electrode clusters separately. The effect of regularity was significant in both clusters, but smaller on the left (left

electrodes, $F(1,23) = 9.47$, $p = .005$, $\eta_p^2 = .292$; right electrodes, $F(1,23) = 17.63$, $p < .001$, $\eta_p^2 = .434$. There were no significant effects involving orientation in the main analysis, although there was a borderline Hemisphere \times Orientation interaction, $F(1,23) = 3.98$, $p = .058$, $\eta_p^2 = .148$. As suggested by Figure 3.2, there was an effect of orientation on the right, $F(1,23) = 7.43$, $p = .012$, $\eta_p^2 = .244$, but not on the left, $F(1,23) < 1$, *n.s.*

3.4.3. Time Frequency Analysis

Time frequency analysis is shown in Figure 3.3. The results were straightforward. At posterior electrodes, there was clear desynchronization in the 10–14 Hz band from around 400 ms onwards in all conditions (see supporting information for complementary analysis of different time windows and frequency bands). This ERD was more pronounced on the right hemisphere than the left in all conditions, and also stronger in horizontal than vertical trials. Baseline-relative alpha power was obtained in a set of left and right posterior electrodes where the effect was most pronounced (O1, PO3, and PO7 and right-sided homologues). Power was explored with three-factor repeated measures ANOVA: Hemisphere (left, right) \times Regularity (reflection, translation) \times Orientation (horizontal, vertical). There was a main effect of hemisphere, $F(1,23) = 8.08$, $p = .009$, $\eta_p^2 = .260$, and orientation, $F(1,23) = 12.434$, $p = .002$, $\eta_p^2 = .351$, but no other effects or interactions (next largest effect regularity, $F(1,23) = 3.289$, $p = .083$, $\eta_p^2 = .125$, because posterior ERD was marginally larger for translation).

To get a sense of whether the right lateralization was driven by a small subgroup of participants, we tested the presence or absence of the effect in each participant (averaged across all four conditions). Seventeen of the 24 participants showed more alpha ERD in the right posterior electrodes (71%, $p = .032$, one-tailed binomial test).

Topographic plots (400 to 1000 ms, 10-14 Hz)

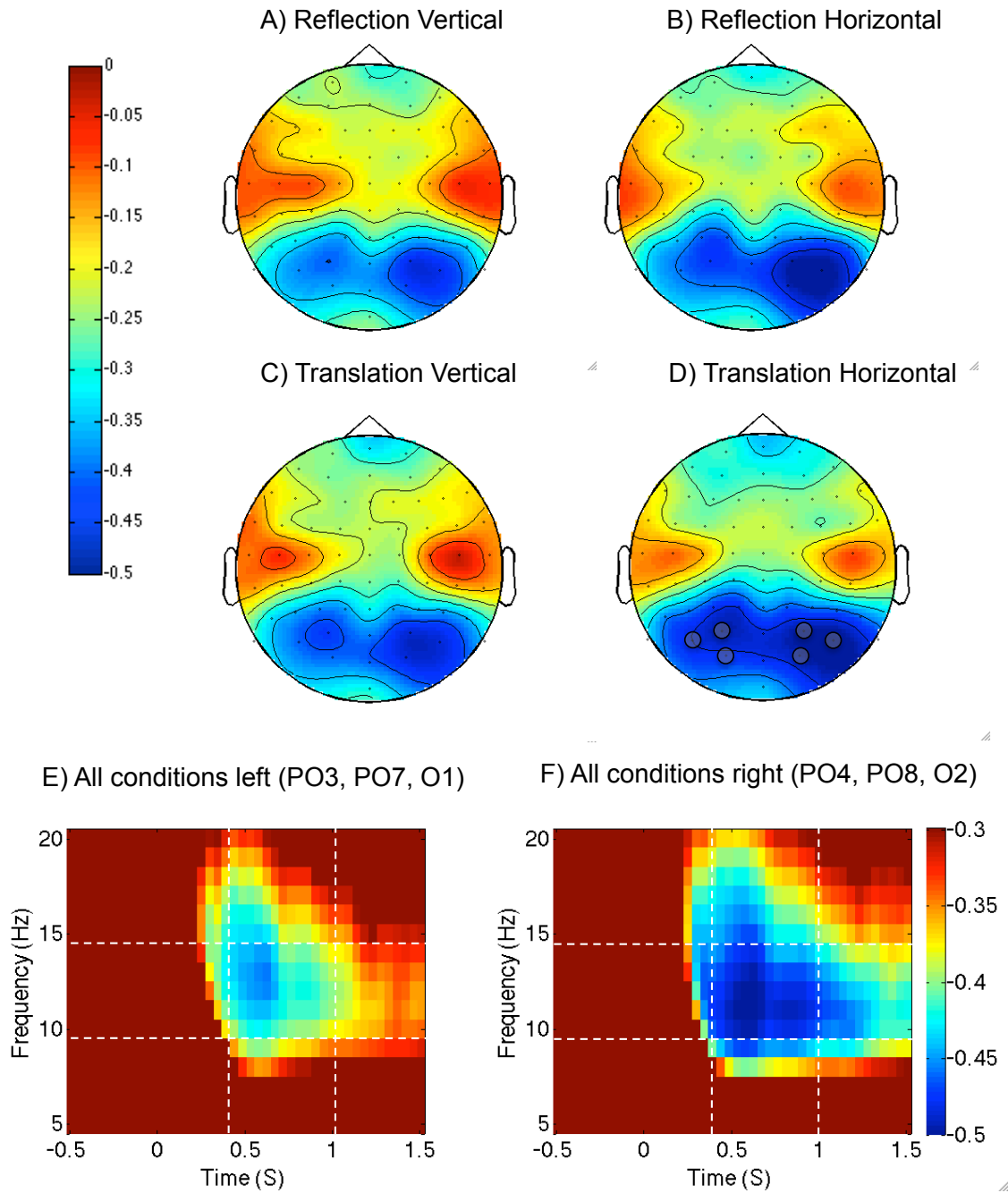


Figure 3.3. Event-related desynchronization. A–D: Scalp distribution of 10–14 Hz powers from 400 to 1,000 ms poststimulus onset. The analysis focused on posterior desynchronization (blue on these figures). Note that this response is bilateral, but stronger in

the right hemisphere in all conditions. Electrodes used for analysis are highlighted with a gray dot. E, F: Time frequency spectrograms from left and right posterior electrode clusters, respectively (collapsed across all conditions). Note that ERD is greater on the right. Power is shown as proportion of power in the baseline interval (-500 to 0 ms). Dashed white lines indicate the time and frequency bands that were used to produce the topographic plots above and for statistical analysis.

3.5. General Discussion

In previous work, Makin, Wilton et al. (2012) recorded posterior alpha desynchronization when people discriminated pattern regularity. This ubiquitous neural response to visual onsets indicates cortical excitation in posterior regions (Buzsáki, 2006; Klimesch et al., 2007). This ERD is evident over both hemispheres, but it was consistently stronger in right posterior electrodes (Makin et al., 2014; Makin, Wilton et al., 2012). However, this right lateralization in our previous work was inconclusive. It could result from either (a) a transitory shift of spatial attention to the left side of the patterns, enhancing contralateral inputs; or (b) a functional and anatomical specialization whereby the right posterior regions are more active during regularity discrimination.

In the current work, equivalent right lateralization of posterior alpha ERD was found when patterns were either vertically or horizontally oriented. Moving attention across the midline axis in the horizontal condition would involve moving attention upwards or downwards, which would not alter the balance of activity between left and right hemispheres. Therefore, right lateralization in the horizontal condition may have a different explanation. It is proposed that the right posterior regions are specialized for regularity discrimination, and are thus more active than the equivalent left hemisphere regions.

Despite the robust results, one cannot fully discard the look left hypothesis. It could be that participants visually explore the patterns by moving covert attention to the left hemifield, even in the horizontal condition. A leftward perceptual bias is commonly reported in judgments of magnitude, numerosity, and grayscale discrimination (Nicholls, Bradshaw, &

Mattingley, 1999); this has been reported to be the consequence of an attentional bias (Nicholls & Roberts, 2002). It remains possible that this ubiquitous shift of spatial attention to the left could explain our current results. However, it is unlikely that the effect that we have measured results from a generic scanning bias because it was not present when observers did not engage in a symmetry discrimination task (Makin et al., 2014).

There may be functions of the right hemisphere that are activated during all tasks, and have nothing to do with the processing of reflection/translation. For example, the simple need to maintain fixation and generally engage attention may produce greater right hemisphere activation. To counter this, we refer again to Makin et al. (2014), who included a matched control condition where right lateralization was not apparent. Although further control experiments are required, there is important converging evidence from Bona et al. (2014), who found that TMS disruption of the right LOC had a greater effect on symmetry discrimination than the TMS disruption of the left LOC. We thus think it is likely that dedicated symmetry discrimination networks are right lateralized, and alpha ERD indexes this.

The current work can be related to previous findings on hemispheric specialization. The two best-replicated findings on hemispheric specialization in humans are left lateralization for language, and right lateralization for spatial tasks. These biases may be causally related, and can be mutually reversed in some people (often left-handers, Cai et al., 2013). Regularity discrimination may be one kind of right hemisphere spatial task. Wilkinson and Halligan (2002) note that line bisection tasks require placing a mark at the center of a line, thus producing a symmetrical image. This ability is dramatically disrupted by right hemisphere damage compared to left hemisphere damage. These authors suggest that, while both hemispheres are sensitive to symmetry, there is right hemisphere specialization. In their Experiment 2, participants were faster and more accurate to detect symmetry when stimuli

were flashed in the left visual field (i.e., processed by the right hemisphere). Moreover, in a recent study, Verma et al. (2013) found a similar left visual field advantage for reflection symmetry detection in participants who were left lateralized for language (irrespective of handedness).

Although it is tempting to conclude that ERD lateralization is a simple manifestation of this apparent right brain specialization for symmetry perception, it is important to note that the ERD lateralization was comparable for both reflection and translation in this study, and in the findings of Makin et al. (2014). Moreover, in previous work right lateralization of alpha ERD was found for both reflection and random patterns (Makin, Wilton et al., 2012). Right-lateralized ERD is not a neural response to the presence of symmetry, but a signature of engagement with regularity discrimination tasks. The ERD in this study thus differs in an important way from the results of Wilkinson and Halligan (2002) and Verma et al. (2013), who found no hemispheric advantages when people responded to random stimuli.

Which right-lateralized brain networks display reduced alpha rhythm during all trials of a regularity discrimination task? It is thought that the occipital alpha rhythm is generated by excitation–inhibition cycles between visual cortical regions and the thalamus (e.g., Buzsáki, 2006). It is likely that the current work measured changes in oscillatory activity in visual areas, although these are, of course, subject to influences from higher brain regions (Laufs et al., 2006). However, there is some ambiguity here, which should not be glossed over: Most classic “right hemisphere dominant” functions, such as mental object rotation and spatial attention, are mediated by the parietal lobes, that is, well beyond the early visual maps that supposedly produce the posterior alpha rhythm. It could be that this experiment recorded ERD in the parietal regions rather than earlier visual regions, which is not so well documented. Alternatively, the posterior ERD could occur in early visual areas, but this could have been affected by ipsilateral top-down connections from functionally asymmetrical

parietal areas. The current work cannot resolve such questions about the source of the scalp recordings.

If regularity discrimination mechanisms are right lateralized, one might expect to see converging evidence from fMRI studies. Jacobsen, Schubotz, Höfel, and Crammon (2006) compared activations produced by a discriminate symmetry task (collapsing over symmetry or random trials) with all conditions of an aesthetic judgment task (beautiful or ugly) and a control condition where participants made a trivial visual discrimination (arrow pointing left or right). Our results imply that there would be right-lateralized activity in the posterior regions during the discriminate symmetry task; however, Jacobsen et al. (2006) did not find this. As well as various frontal and parietal activations, the extrastriate visual cortex was found to be more active in the discriminate symmetry than in the control condition, while the left extrastriate visual cortex was more active during the discriminate symmetry task than the aesthetic judgment task. However, these fMRI results depend on the nature of the comparison tasks as much as the nature of the symmetry discrimination task. Right lateralization of alpha ERD is a reliable signature of regularity discrimination, although it is currently difficult to relate this to existing neuroimaging work on this topic, which has not reliably shown greater right hemisphere activation (Chen et al., 2007; Jacobsen et al., 2006; Sasaki et al., 2005; Tyler et al., 2005). Previous studies that have examined EEG and fMRI activity have shown that decreased alpha power correlates with increase blood-oxygen-level dependent (BOLD) signals in occipital regions (e.g., Goldman et al., 2002), so right lateralization of the BOLD signal would be expected. This has not been reported, although this may reflect differences in the nature of the signal and the tasks used. TMS studies have also failed to find consistent right lateralization; with one study finding a right hemisphere lateralization (Bona et al., 2014) while another did not (Cattaneo et al., 2011).

We found that horizontal patterns resulted in more occipital alpha ERD than vertical patterns. This effect was bilateral, implying more activation of both left and right posterior regions during horizontal trials. Previous symmetry perception research has shown that vertical orientations are detected faster (Friedenberg & Bertamini, 2000; Julesz, 1971). However, it is not clear whether the vertical advantage survives when axis orientation can be anticipated (Wenderoth, 1994; Wenderoth & Welsh, 1998). In this study, the orientation of the axis was reliably cued before the stimulus appeared, so it is unlikely that regularity discrimination was more difficult in the horizontal condition. It is thus unlikely that task difficulty explains the effect of orientation on alpha ERD. Incidentally, the fact that behavioral discrimination performance was near perfect in all conditions is not relevant here. This was an unspeeded judgment: participants may be correct every time, but still find the discrimination more difficult in one condition than another.

Julesz (1971) suggested that the reflectional symmetry of the visual system made processing vertical symmetric patterns easier than other orientations. Each half of a vertically presented symmetrical pattern is processed via the contralateral cortical hemisphere, with this activation then matched across the vertical midline. This suggests that the corpus callosum mediates the putative advantage of vertical symmetry detection at fixation. Herbert and Humphrey (1996) found support for this callosal hypothesis because two subjects born without a corpus callosum did not detect vertically presented symmetrical patterns quicker than horizontal ones. The effect of orientation on ERD is consistent with the callosal hypothesis in so much as it shows a different neural response when communication across the callosum is required. It is interesting that within-hemisphere connections activated in the horizontal condition produced more alpha ERD than between-hemispheric ones, because shorter connections lead to higher frequency coupling, and greater desynchronization at lower frequencies (Buzsáki, 2006). However, the effect of orientation on ERD should be treated

cautiously, because it was highly dependent on pre-processing stages. (There was no ERD difference between horizontal and vertical conditions when the analysis was run without ICA, see Appendix 2 Figure 2.2).

The SPN was also present in this EEG data: Amplitude was lower in the reflection conditions than the translation conditions from around 250 ms until the end of the epoch. This is similar to what was reported in Makin et al. (2013, 2014). However, the current work makes the novel contribution of showing that the SPN is comparable whether patterns are oriented vertically or horizontally. Previous work by Beh and Latimer (1997) also compared ERPs for horizontal and vertical symmetry; however, they did not show a clear SPN component and their experiment only had a small number of participants, so it is difficult to relate these results to the growing SPN literature on symmetry perception (Höfel & Jacobsen, 2007a; Jacobsen & Höfel, 2003; Makin, Wilton et al., 2012; Norcia et al., 2002).

Another novel finding was that the SPN was more pronounced in right hemisphere electrode clusters. However, this result should be treated cautiously because the crucial Hemisphere \times Regularity interaction was eliminated when we adopted different data preprocessing procedures (See Appendix 2). Nevertheless, the SPN and ERD are both potentially generated by right-lateralized networks, and these signals reflect different aspects of the same or overlapping systems.

The topography and latency of the SPN may be familiar to ERP researchers. Specifically, there are links with the negative-deflection mask, reported by Verleger, Gorgen, and Jaskowski (2005), but more generally, many ERPs are characterized by a sustained, late wave following the high frequency visual evoked potential (Luck, 2005). For instance, a sustained posterior contralateral negativity is found when people attend to the right or left side of space (Lefebvre, Dell'acqua, Roelfsema, & Jolicoeur, 2011), or when people hold multiple items in visual working memory (Vogel & Machazawa, 2004). Furthermore,

presentation of recognizable objects compared to scrambled objects produces a negative late component at posterior electrodes, beginning around 230 ms (Gruber & Müller, 2005; Martinovic, Mordal, & Wuerger, 2011). Of course, different neurocognitive processes generate these ERPs, despite some crude waveform similarity. In summary, the regularity-related SPN is partly defined by the stimuli that produce it, not just latency and topography, which are partly shared with other slow negatives related to visual, motor, attentional, and working memory processes.

3.6. Conclusions

This study has confirmed the presence of a right-lateralized posterior alpha desynchronization during a regularity discrimination task. Previous work has shown that this ERD response is present across all trials. We tested whether the right lateralization was due to a temporary shift of spatial attention to the left, prioritizing contralateral inputs, or to a functional specialization of the right hemisphere for regularity discrimination. If ERD lateralization was produced by participants shifting spatial attention to one side of the pattern, it would disappear when the pattern was oriented horizontally (as moving attention to the right or left would serve no purpose in comparing the two halves). It was found that right lateralization of ERD was equivalent for both orientations. The right bias may therefore reflect specialization of the right hemisphere for regularity discrimination, possibly because the task requires the processing of complex spatial information.

Let us summarize the mixed evidence for right lateralization during regularity discrimination: (a) Psychophysical and neuropsychological work has shown that symmetrical patterns presented to the right hemisphere are detected more quickly. (b) Right hemisphere brain damage has a more profound effect on line bisection. (c) There is no evidence for right lateralization from fMRI. (d) TMS work shows that the right LOC plays a greater role than

the left in symmetry discrimination. (e) Alpha ERD is often right lateralized, in all conditions (reflection, random, or translation) and independently of orientation. This response usually occurs when the task is to classify regularity, but not during figure-ground discrimination. (f) The symmetry-related SPN is sometimes weakly right lateralized. (g) There is no comparable evidence for left lateralization. What firm conclusions can be drawn from this mixed evidence? We propose that symmetry perception is bilateral, mediated by extrastriate areas and the LOC, but that the right LOC plays a more prominent role. Although the right lateralization of symmetry discrimination networks is not detected with all neuroimaging techniques under all circumstances, it is likely to be a real phenomenon.

4. Does visual crowding influence the SPN?

4.1. Abstract

The human visual system is efficient at processing symmetry in central vision. However, symmetry detection can be impaired when it is in the periphery and when other objects flank it (Roddy & Gurnsey, 2011). Electrophysiological symmetry studies have identified a difference wave where amplitude is lower for reflection than random patterns 200ms after stimulus onset. This component has been termed the Sustained Posterior Negativity (SPN). Previously, we have demonstrated that this response can be produced to reflection in peripheral vision (Wright, Makin, & Bertamini, 2016). Here, we investigated how visual crowding modulates this response. In Experiment 1, reflection and random patterns were presented in periphery (4.5° from fixation). These were either presented in isolation or flanked by other random patterns positioned either side or above and below the target. Participants had to discriminate whether the target was reflection or random. In an early time window (200-600ms after stimulus onset) the SPN was present. The size of the SPN in this time window reflected the strength of crowding, with stronger crowding producing a smaller SPN. Target-flanker similarity can also influence crowding strength; this was examined in Experiment 2 and Experiment 3. In Experiment 2, the targets and flankers could be either all reflection, all random or the target and flankers could be different in shape. It was found that crowding abolished the SPN. In Experiment 3, black targets were presented amongst white flankers with the target and flankers either all reflection, all random or the target and flankers could be different in shape. The SPN was present in the early time window with the size of this response scaling with the strength of crowding. We conclude that although the SPN is a response to symmetry in the image it is subject to interference from flanking objects.

4.2. Introduction

An important function of the visual system is image segmentation and object identification. Symmetry is a salient visual property that may play a fundamental role in these visual processes (Machilsen, Pauwels, & Wagemans, 2009; Pizlo & Stevenson, 1999; See Wagemans, 1995 for a review). For example, the visual system processes symmetry in central vision efficiently and rapidly, particularly when the axis is vertical compared to other orientations (Bertamini, Friedenber, & Kubovy, 1997; Mach 1886/1959; Julesz, 1971). Symmetrical regions are also perceived as figures when presented in ambiguous figure-ground displays (Kanizsa & Gerbino, 1976). However, both peripheral presentation and flanking objects can compromise successful symmetry perception.

In peripheral vision, symmetry detection is still possible but it is reduced. Reflection symmetry is detected most accurately at fixation but as it is moved away from fixation, therefore increasing eccentricity, sensitivity decreases (Barrett, Whitaker, McGraw, & Herbert, 1999; Gurnsey, Herbert & Kenemy, 1998; Saarinen, 1988; Sally & Gurnsey, 2001). However, this drop in performance can be reduced with stimulus magnification so that as eccentricity increases so does the size of the stimuli (Tyler & Hardage, 1996).

Flanking objects in the periphery can also impair symmetry perception. For example, when random distractors flank reflection, successful discrimination of symmetry decreases (Roddy & Gurnsey, 2011). This impairment to detect a target among flankers in the periphery has been explained by visual crowding. Visual crowding has been extensively studied since it was first described by Korte (1923) and it has been found to apply to a range of different stimuli (i.e. lines, Gabor stimuli, and faces) in peripheral vision but diminished at fixation (See Levi, 2008 for a review). Crowding is dependent on the eccentricity of the target alongside the position and how densely spaced the flankers are to the target (Bouma, 1970;

Toet & Levi, 1992; Whitney & Levi, 2011). The ability to recognize the identity of an object increases as the critical spacing between target and flankers increases.

Currently, there is no single agreed upon model of crowding. In recent years a ‘pooling’ explanation has received much popularity with it suggested that crowding results from the integration of feature information leading to the generation of an inaccurate percept (Greenwood, Bex, & Dakin, 2009, 2010; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). Pooling of features can result from feature averaging (Parkes et al., 2001), positioning averaging (e.g. Dakin et al., 2010; Greenwood et al., 2009) or pixel averaging/blurring. Pooling could occur in a more complicated manner through the measuring of a set of summary statistics. For example, a model proposed by Balas et al. (2009) measured a number of statistics from a given image including position, phase, orientation, and scale. They suggested that stimuli in the periphery are represented in the visual system by these. The basic premise of all of these models is that for each percept global statistics are preserved but access to local features is blocked. Alternatively, a ‘substitution’ model suggests that due to spatial uncertainty participants mistake or swap the features of the target with the features of the distractor (Ester, Klee, & Awh 2014; Ester, Zilber & Serences, 2015). Grouping may also play an important role, whereby crowding is increased when target and flankers group together (Manassi, Lonchampt, Clarke & Herzog, 2016; Pachai, Doerig, & Herzog, 2015). In relation to the neural basis of crowding numerous areas have been proposed including V1 (Millin, Arman, Chung, & Tjan, 2013), V2 (Bi et al., 2009), and V4 (Motter, 2006).

4.2.1. Brain responses to symmetry

Electrophysiological work in symmetry perception has identified a symmetry specific late component known as the *Sustained Posterior Negativity* (SPN). This is exhibited as a difference in amplitude between reflection and random (or occasionally another regularity)

patterns from around 200ms after stimulus onset (Bertamini & Makin, 2014; Norcia et al., 2002). The SPN is greatest for reflection (Makin et al., 2012), with this response scaling with the amount of Gestalt ‘goodness’ or symmetry in the image (Makin et al., 2015; Palumbo et al., 2015). It can be produced to stimuli in the periphery with each hemisphere being able to independently produce this response (Wright, Makin & Bertamini, 2016) whilst a comparable response is produced regardless of whether reflection is vertically or horizontally orientated (Wright, Makin & Bertamini, 2015). For the SPN to be produced, participants do not need to actively discriminate symmetry; it has been recorded when participants misreport their answers, when reflection or random required a ‘yes’ response in a 2AFC task and when the colour of the symmetry had to be reported (Höfel & Jacobsen, 2007a; Höfel & Jacobsen, 2007b; Makin, Wilton, Pecchinenda & Bertamini, 2012).

Neuroimaging and TMS studies have localized the neural generators responsible for the SPN to the posterior visual areas (Lateral Occipital Complex (LOC), V3a, V4 and V5), with symmetry processing occurring in a bottom-up fashion whereby activity in V3 and V4 takes place prior to LOC activation (Bona et al., 2014; Cattaneo, Mattavelli, Papagno, Herbert & Silvanto, 2011; Chen, Kao & Tyler, 2007; Kohler et al., 2016; Sasaki, Vanduffel, Knutsen, Tyler & Tootell, 2005; Tyler et al., 2005). In conjunction, EEG source localization has suggested the extrastriate visual areas are involved in the production of the SPN (Makin et al., 2012).

4.2.2. Investigation of visual crowding and the SPN

Typically, the SPN has been examined for symmetry in central vision. The one exception, Wright, Makin & Bertamini (2016), demonstrated that the SPN could be produced for reflectional patterns in peripheral vision. However, it is still to be determined how flanking

objects specifically modulate the SPN. Behaviourally, reflection is subject to visual crowding (Roddy & Gurnsey, 2011).

We conducted three experiments to investigate how visual crowding influences the SPN. In all three experiments, participants were presented with a reflection or random target (4.5° from fixation) flanked by other objects in the left or in the right visual field. They were required to judge whether the target was reflectional or random. In Experiment 1, the target could either be presented in isolation or with two random flankers positioned above and below or either side of it. There are two hypotheses. The first hypothesis would predict that as the SPN is a response to symmetry in the image, this response would be present when reflection is present as the target, regardless of the position of the flankers in relation to the target. However, when on a horizontal meridian, crowding is stronger when the flankers are arranged horizontally than vertically (Fen, Jiang, & He, 2007). Consequently, a second hypothesis would predict that crowding will reduce the ability to perceive the target therefore the SPN should be reduced when the flankers are organized horizontally compared to vertically. Target-flanker similarity can also influence the strength of crowding (Kooi, Toet, Tripathy, & Levi, 1994; Levi et al., 2002; Pöder, 2007). In Experiment 2, the target and flankers were either all reflection, all random or different (the target could be reflection whilst the flankers were random or vice versa) in shape. When the target and flankers have dissimilar features, crowding is reduced as a result of pop out or attention. In Experiment 3, the target and flankers could be all reflection, all random or different (the target could be reflection whilst the flankers were random or vice versa), however the distractors and flankers had opposite contrast polarity. These experiments will firstly show whether a response to reflection is produced when other objects flank it, and secondly how the features and position of the flanking objects impact on this response.

4.3 Experiment 1

4.3.1. Method

4.3.1.1. Participants

Twenty-four participants took part in the study (age 18-28, mean age 19.4 (SD= 2.4), 1 male, 2 left handed) all of which had normal or corrected-to-normal vision. They received course credit upon completion of the study. The study was approved by the Ethics Committee of the University of Liverpool and conducted in accordance with the Declaration of Helsinki (revised 2008).

4.3.1.2. Apparatus

Participants were positioned in a chin rest 100cm from a 60Hz CRT monitor (40 x 30 cm) in an electronically shielded and darkened room. Electroencephalogram (EEG) data was recorded from 64 scalp electrodes using the BioSemi Active-Two system at 512 Hz. Common Mode Sense and Driven Right Leg electrodes were used as a reference and ground. Four external channels recorded bipolar horizontal and vertical electro-oculograph (EOG) signals. Apparatus are the same as those used in our previous ERP symmetry experiments and the other chapters of this thesis (Bertamini & Makin, 2014).

4.3.1.3. Design

The study had a single within-subjects factor (Arrangement [Reflection-NoFlankers, Random-NoFlankers, Reflection-FlankersVertical, Random-FlankersVertical, Reflection-FlankersHorizontal, Random-FlankersHorizontal]) with 80 trials per condition. The experiment consisted of 10 blocks with a total of 480 trials.

4.3.1.4. Stimuli

Examples of the stimuli can be seen in Figure 4.1. Stimuli were generated using the open-source PsychoPy software (Peirce, 2007). They consisted of a reflection or random pattern presented in isolation or flanked by two random flankers. Targets were positioned 4.5° either to the left or right of fixation. The patterns were 1.3° in diameter. The center-to-center distance between the target and the flanker was fixed at 1.8° which is well within the critical spacing required to induce crowding. Flankers were positioned above and below (Reflection-FlankersVertical, Random-FlankersVertical) or either side (Reflection-FlankersHorizontal, Random-FlankersHorizontal) of the target. Reflection patterns consisted of two axis of symmetry (horizontal and vertical). All patterns were black in colour and presented on a grey background.

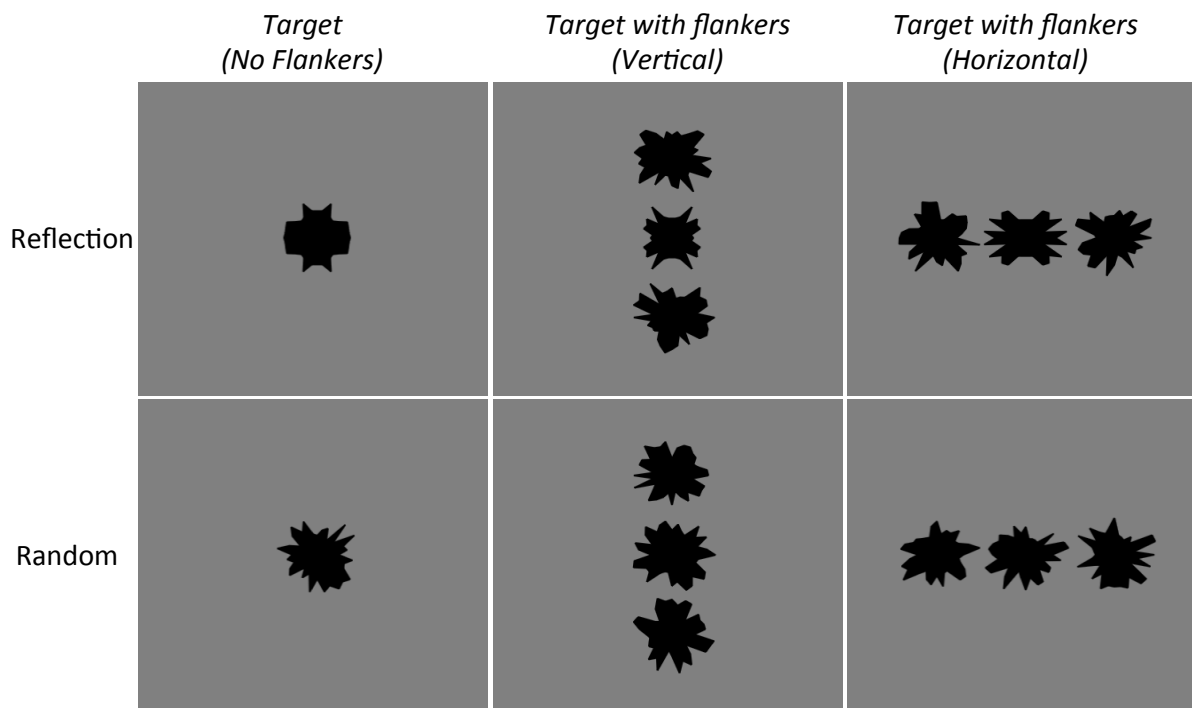


Figure 4.1. Examples of the stimuli used in Experiment 1. Targets were presented 4.5° from fixation in either the left or right visual field. Targets could be presented either unflanked (left panels) or flanked with two random patterns. Targets could be presented with the flankers positioned either above and below (middle panels) or either side of the target (right panels). The top row the target is reflection whilst the bottom row it is random. Participants had to

judge whether the target (the single pattern or the centre pattern when in a group of three) was reflection or random.

4.3.1.5. Procedure

Prior to the start of the experiment, participants performed a practise block in order to familiarise themselves with the task and to allow the electrodes to be checked. Participants were required to fixate centrally throughout the experiment. Each trial began with a baseline period of between 1.5-2 seconds, which consisted of a centrally positioned fixation cross. Stimuli were presented on screen for 216ms. Following stimulus presentation there was a blank screen for 1.5 seconds and then a response screen where they had up to 10 seconds to log a response. Using the 'A' and 'L' keys on a standard computer keyboard participants were required to discriminate whether the target pattern was reflection or random. The target pattern was defined as either the pattern in isolation or the centre pattern when accompanied by flankers.

4.3.1.6. EEG Analysis

The same EEG analysis was performed as in our previous symmetry ERP studies (Bertamini & Makin, 2014). EEG data was processed using the EEGLAB toolbox in MATLAB (Delorme & Makeig, 2004). Sixty-four electrodes recorded the raw EEG signal, which was re-referenced offline to a scalp average and low pass filtered at 40Hz. The data was sampled at 128Hz and segmented into epochs (-1s to 1.5s) with a baseline of -200ms to 0ms. 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. For each participant an average of 8.4 components were removed (min = 3, max = 14). Following ICA, trials that had amplitude greater than $\pm 100 \mu\text{V}$ for any electrode were removed. A comparable number of trials were removed from each condition (Reflection-

NoFlankers 13.6%; Random-NoFlankers 12.8%; Reflection-FlankersHorizontal 12.7%; Random-FlankersHorizontal 13.8%; Reflection-FlankersVertical 14.3%; Random-FlankersVertical 13.7%). The main analysis was conducted on the combined signal from electrodes P1, P3, P5, P7, PO3, PO7 from the left hemisphere and P2, P4, P6, P8, PO4, and PO8 from the right hemisphere in separate time windows (early: 200-600ms; late: 600-1000ms). Previous research has highlighted that the SPN may consist of an early and late time window (Makin et al., 2016). Electrodes were chosen as we were interested in the response in posterior regions and this selection had been used in our previous research (e.g. Wright, Makin & Bertamini, 2016). The SPN was defined as a difference in ERP amplitude between reflection and random.

4.3.2. Results

4.3.2.1. Behavioural

Participants discriminated the target pattern as either reflection or random. They correctly discriminated the target when it was presented without any flankers ($d' = 2.227$, criterion $c = -0.013$). Performance was greater in detecting the target when the flankers were above and below ($d' = 1.563$, criterion $c = 0.142$) compared to when the flankers were positioned either side of the target ($d' = 0.932$, criterion $c = 0.273$). These behavioural results show that the positioning of the flankers affected the ability of the participants to correctly identify the target.

4.3.2.2. Event-Related Potentials

Figure 4.2A shows the grand average amplitudes for all conditions. The SPN was present in only the early time window between 200-600ms after stimulus onset. This can be seen in the ERP plots and differences waves in Figure 4.2B, C and D. These show that the size of the

SPN response in this early time window reduced as the strength of crowding increased (i.e. the stronger the effect of crowding, the smaller the SPN).

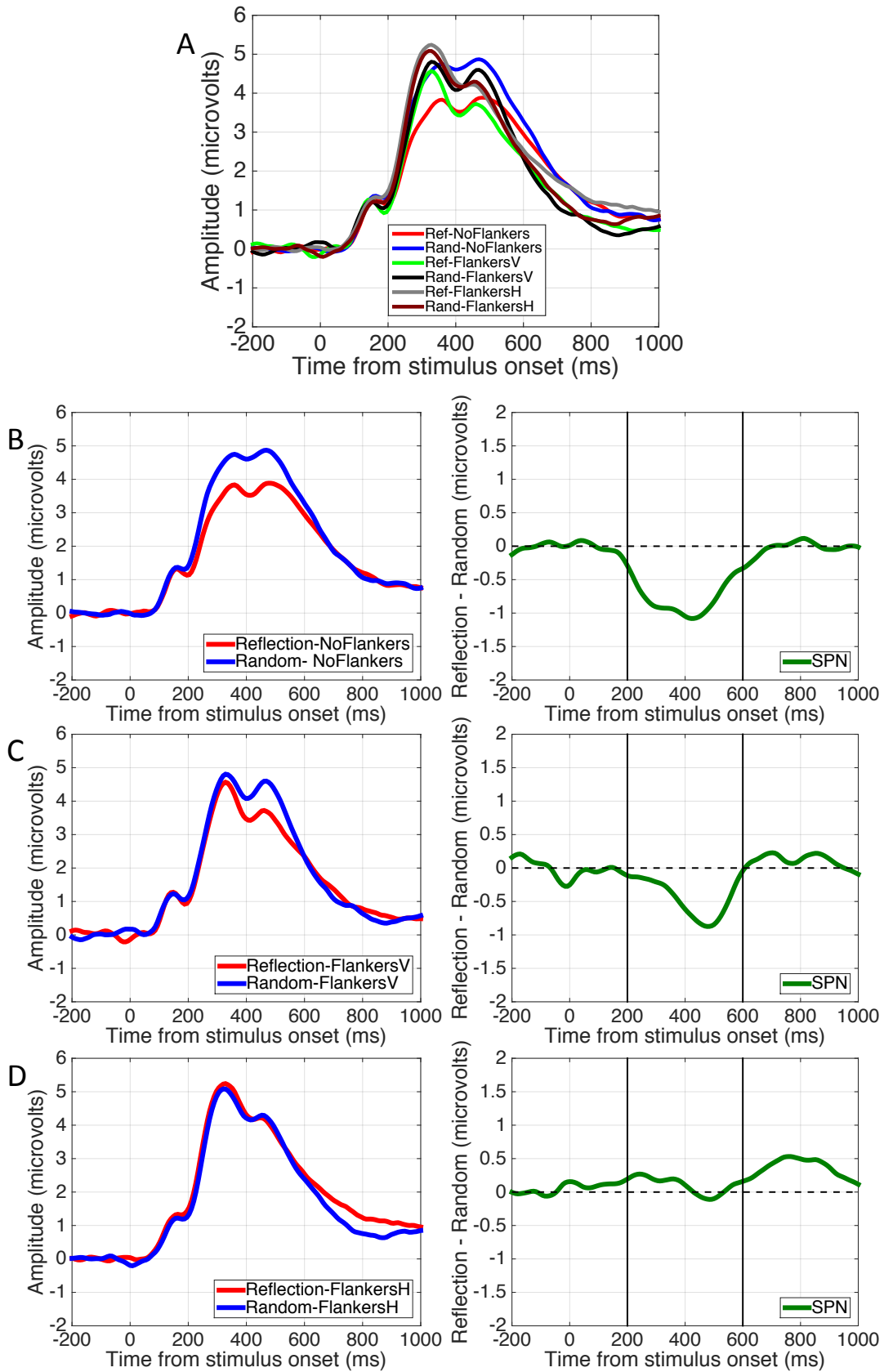


Figure 4.2. Grand-average ERPs for each condition collapsed across the left and right hemisphere in Experiment 1. A) Grand-average ERPs for all conditions over both

hemispheres. B) ERPs and difference wave when the targets are unflanked. C) ERPs and difference wave when the targets are flanked vertically. D) ERPs and difference wave when the targets are flanked horizontally.

A repeated measures ANOVA was performed [Hemisphere (Left, Right) x Time Window (200-600, 600-1000) x Arrangement (Reflection-NoFlankers, Random-NoFlankers, Reflection-FlankersVertical, Random-FlankersVertical, Reflection-FlankersHorizontal, Random-FlankersHorizontal)]. ERPs were affected by the Arrangement configuration ($F(5,115) = 4.161$, $p = 0.002$, partial $\eta^2 = 0.153$) and Time Window ($F(1,33) = 67.317$, $p = 0.001$, partial $\eta^2 = 0.745$). There was no main effect of Hemisphere. In terms of interactions, there was a Arrangement x Time interaction ($F(5,115) = 8.342$, $p = 0.001$, partial $\eta^2 = 0.266$). There was other interaction.

We then conducted a series of paired t-tests to further examine the Arrangement x Time interaction. When collapsed across both hemispheres for the early time window (200-600ms) there was a significant difference between Reflection-NoFlankers and Random-NoFlankers ($t(23) = -3.164$, $p = 0.004$, $d = -0.360$) as well as between Reflection-FlankersVertical and Random-FlankersVertical ($t(23) = -2.091$, $p = 0.048$, $d = -0.240$). There was no difference between Reflection-FlankersHorizontal and Random-FlankersHorizontal. In the late time window there were no differences between conditions.

4.3.3. Discussion

Experiment 1 has two clear findings. Firstly, the SPN was observed in the early time window (200-600ms after stimulus onset). This is the first study to show that the SPN can be produced when other objects in the periphery flank reflection. Secondly, the size of the SPN reduced as the strength of crowding increased. In this early time window the SPN was least pronounced when the flankers were positioned either side of the target. It was slightly more pronounced

when the flankers were above and below the target. Moreover, this result is in-line with behavioural findings showing that reflection is subject to crowding, along with vertical flankers inducing a stronger crowding effect than horizontal ones (Fen, Jiang, & He, 2007; Roddy & Gurnsey, 2011).

4.4. Experiment 2

Experiment 1 showed that in an early time window (200-600ms) the strength of crowding reduced the size of the SPN. Crowding is also influenced by target-flanker similarity (Baptiste-Bernard & Chung, 2011; Kooi, Toet, Tripathy, & Levi, 1994). When target and flankers share a similar feature (e.g. colour or shape) crowding is increased. Alternatively, when the target and flankers are dissimilar from each other, crowding is reduced due to increased attention or pop out of the target. This has been found with various stimuli features including colour, shape (Kooi, Toet, Tripathy, & Levi, 1994), size (Levi & Carney, 2009; Saarela, Sayim, Westheimer, & Herzog, 2009) and contrast polarity (Chakravarthi & Cavanagh, 2007).

We conducted a second experiment that investigated the influence of target-flanker similarity on the SPN. In this experiment the target and flankers could either be all reflection, all non-reflection or different in shape (Figure 4.3). As the SPN is a response to visual symmetry the SPN may scale with the number of symmetrical objects presented. It would be most pronounced when reflection flanks reflection, and least pronounced when the target and flankers are both random. Alternatively, as seen in Experiment 1 the amplitude of the SPN may reflect the strength of crowding. When the target and flankers are all reflection we would expect a greater SPN response than when the targets and flankers are different (reflection flanked by random or vice versa).

4.4.1. Method

Twenty-four participants took part in the study (age 19-43, mean age 24 (SD = 4.4), 15 males, 4 left handed). The apparatus were the same as in Experiment 1. There was a single within subjects design (Arrangement [Reflection-NoFlankers, Random-NoFlankers, Reflection-FlankersReflection, Reflection-FlankersRandom, Random-FlankersReflection, Random-FlankersRandom]) with 80 trials per condition. On each trial, participants were presented with a target (reflection or random) in either the left or right visual field. The target could be presented either in isolation (Reflection-NoFlankers, Random-NoFlankers) or flanked by either two reflection (Reflection-FlankersReflection, Random-FlankersReflection) or two random flankers (Reflection-FlankersRandom, Random-FlankersRandom) positioned to the left and right of the target. The stimuli and procedure were otherwise the same as in Experiment 1.

EEG analysis was the same as in Experiment 1. An average of 4.1 components were removed from each participant (min = 2, max = 11). For Reflection-NoFlankers 20.7% of trials were removed, for Random-NoFlankers 20.2%, Reflection-FlankersReflection 20.1%, Reflection-FlankersRandom 21.9%, Random-FlankersReflection 21.5% and for Random-FlankersRandom 20.7%.

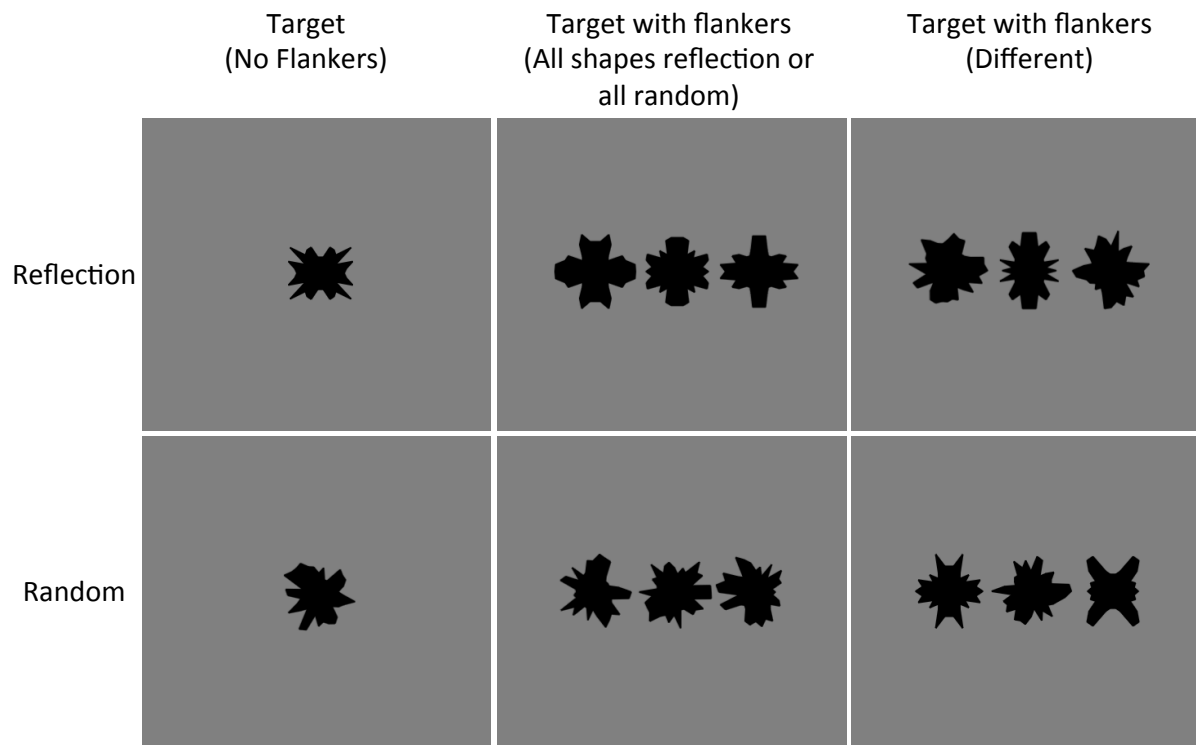


Figure 4.3. Examples of the stimuli used in Experiment 2. Targets were presented 4.5° from fixation either in the left or right visual field. Targets could be presented either in isolation (left panels) or flanked by other objects. The targets and flankers could either be all reflection (middle top panel), all random (middle bottom panel) or different in shape (right panels). The top row the target is reflection whilst the bottom row it is random. Participants had to judge whether the target (the single pattern or the centre pattern when in a group of three) was reflection or random.

4.4.2. Results

4.4.2.1. Behavioural

Participants discriminated the target pattern as either reflection or random. They were able to successfully discriminate the target ($d' = 2.310$, criterion $c = 0.061$) when it was not flanked. Performance dropped when the target and flankers were either all reflection or all random ($d' = 2.078$, criterion $c = -0.203$) and was lowest when the target and flankers were different ($d' = 0.706$, criterion $c = -0.148$). These results show that the ability to discriminate the target was affected by crowding.

4.4.2.2. Event-Related Potentials

Figure 4.4 shows the ERPs from Experiment 2. The SPN response was only present for the unflanked targets with reflection lower in amplitude than random between 200-600ms after stimulus onset. There were no differences in amplitude when the target and flankers were all reflection or all random (Figure 4.4C) or when they were different in shape (Figure 4.4D).

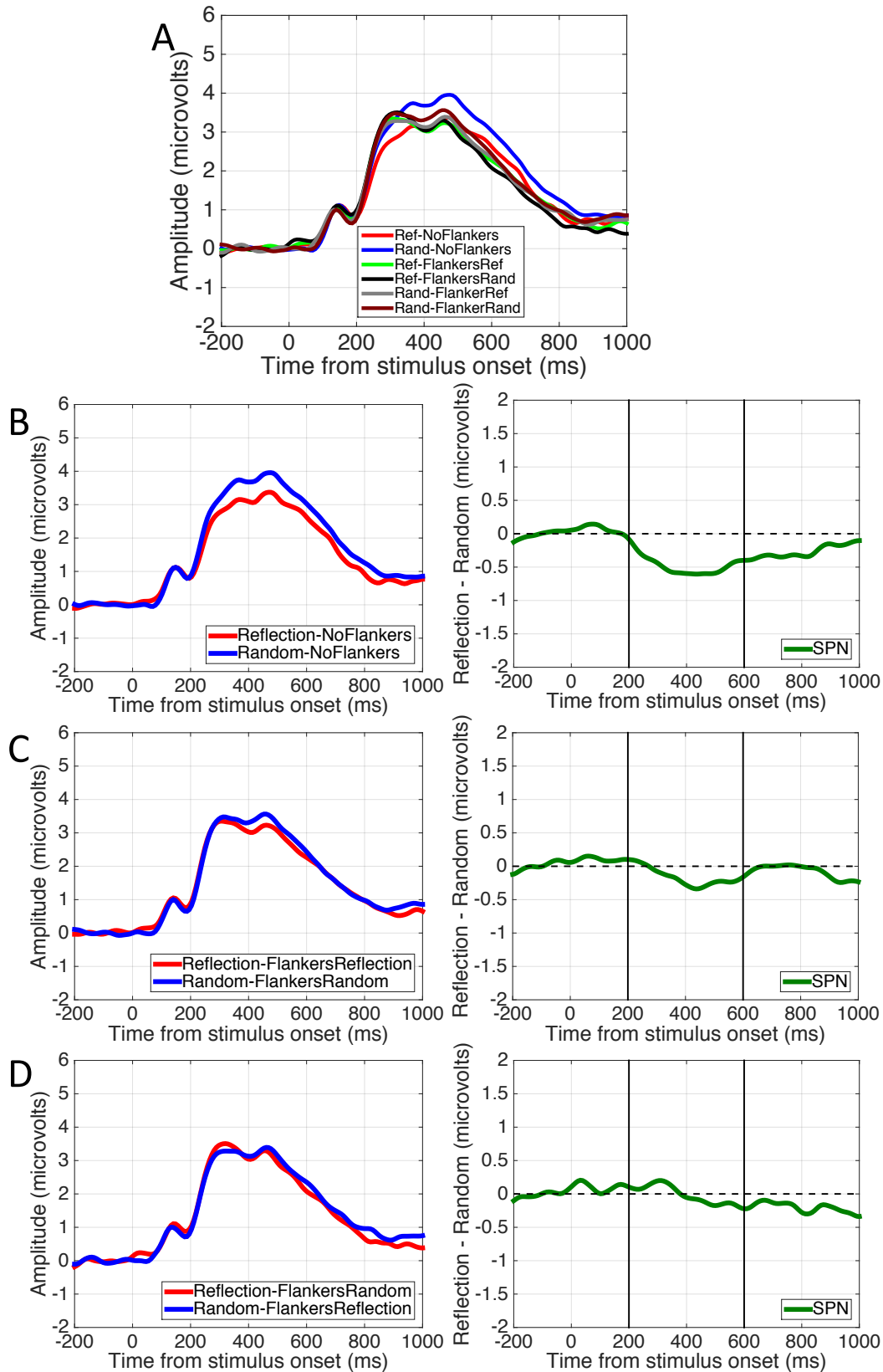


Figure 4.4. Grand-average ERPs for each condition collapsed across the left and right hemisphere in Experiment 2. A) ERPs for all conditions. B) ERPs and difference wave when

the targets are unflanked. C) ERPs and difference wave when the targets and flankers were all reflection or all random. D) ERPs and difference wave when the target and flankers were different.

A repeated measures ANOVA was performed [Hemisphere (Left, Right) x Time Window (200-600, 600-1000) x Arrangement (Reflection-NoFlankers, Random-NoFlankers, Reflection-FlankersReflection, Random-FlankersReflection, Reflection-FlankersRandom, Random-FlankersRandom)]. There was a main effect of Arrangement $F(5, 115) = 5.411$, $p = 0.001$, partial $\eta^2 = 0.190$ and Time $F(1, 23) = 41.509$, $p = 0.001$, partial $\eta^2 = 0.643$. There was a Arrangement x Time Window interaction $F(5, 115) = 3.861$, $p = 0.001$, partial $\eta^2 = 0.144$. There was no main effect of Hemisphere or any interactions.

When collapsed across hemispheres, paired samples t-tests showed there was a significant difference in the early time window between Reflection-NoFlankers and Random-NoFlankers ($t(23) = -4.059$, $p = 0.001$, $d = -0.355$). There were no other significant differences between conditions in either of the time windows.

4.4.3. Discussion

Experiment 2 showed that visual crowding eliminated the SPN response. The SPN was only present when the targets were unflanked. This is consistent with Experiment 1. However, although our stimuli produced crowding, the SPN response did not scale in size with it. When the targets were flanked the SPN response was no longer present.

Behavioural performance was reduced when the targets were flanked. It has been found that when target and flankers share similar features (e.g. colour, contrast polarity, shape or depth) crowding is increased (Kooi, Toet, Tripathy, & Levi, 1994). However we found the reverse with crowding stronger when the target and flankers differed in their shape features. This will be discussed later on.

We conducted a third experiment in which we manipulated the contrast polarity and shape of the flankers. For this experiment the target and flankers could either be all reflection, all random or different (target could be reflection whilst the flankers were random or vice versa) in shape whilst the target was always black and the flankers white. In Experiment 2 crowding abolished the SPN. When a target and flankers share similar features, the target loses its individuality and becomes hard to distinguish from the flankers. Consequently, the more the target is segregated from the flanker, the more crowding is reduced. By manipulating both contrast polarity and shape, this should make the target stand out and its features more accessible compared to the flankers therefore inducing the SPN.

4.5. Experiment 3

4.5.1. Method

Twenty-four participants took part in the study (age 18-25, mean age 19 (SD = 1.6), 5 males, 2 left handed). The apparatus were the same as in Experiment 1. There was a single within subjects design (Arrangement [Reflection-NoFlankers, Random-NoFlankers, Reflection-FlankersReflection, Reflection-FlankersRandom, Random-FlankersReflection, Random-FlankersRandom]) with 80 trials per condition. On each trial, participants were presented with a black target (reflection or random) in either the left or in the right visual field. The target could be presented either in isolation (Reflection-NoFlankers, Random-NoFlankers) or flanked by either two white reflection (Reflection-FlankersReflection, Random-FlankersReflection) or random flankers (Reflection-FlankersRandom, Random-FlankersRandom) positioned to the left and right of the target (Figure 4.5). The stimuli and procedure were otherwise the same as in Experiment 1.

EEG analysis was the same as in Experiment 1. An average of 4.9 components were removed from each participant (min = 2, max = 11). For Reflection-NoFlankers 18.5% of

trials were removed, for Random-NoFlankers 18.3%, Reflection-FlankersReflection 18.8%, Reflection-FlankersRandom 19.1%, Random-FlankersReflection 18.1% and for Random-FlankersRandom 19.1%.

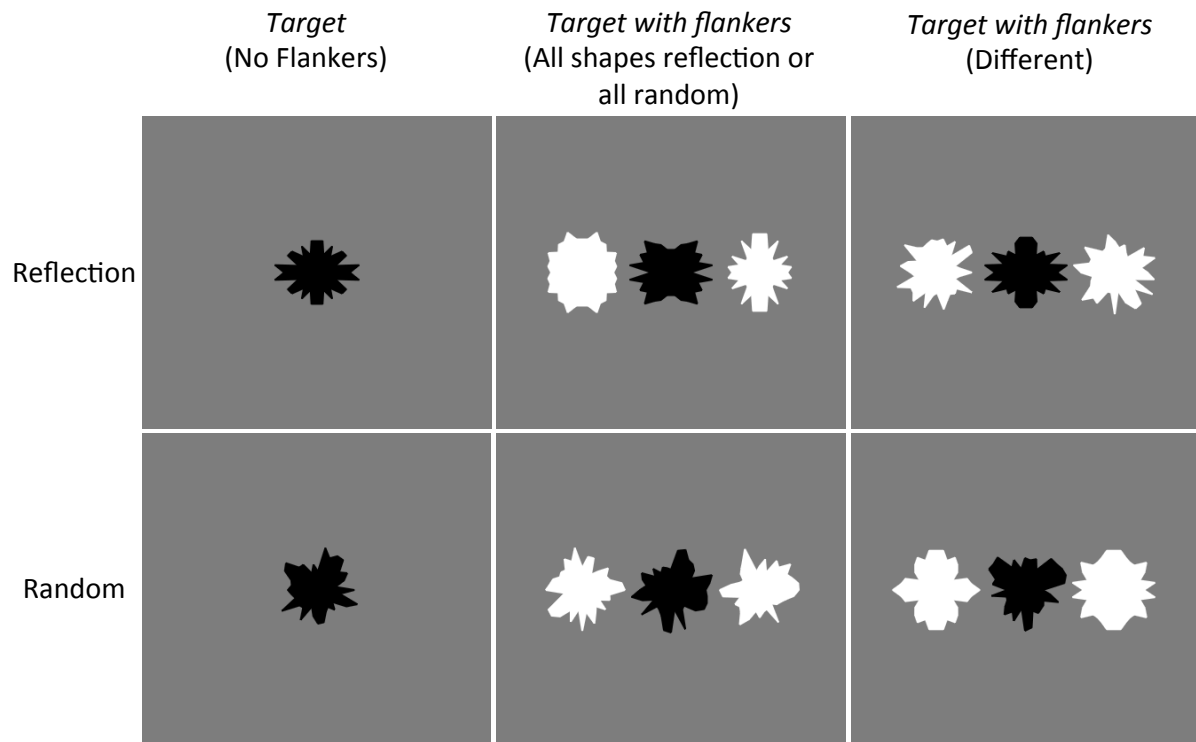


Figure 4.5. Examples of the stimuli used in Experiment 3. Targets were presented 4.5° from fixation either in the left or right visual field. Targets could be presented either in isolation (left panels) or flanked by other objects. The targets and flankers could either be all reflection (middle top panel), all random (middle bottom panel) or different in shape (right panels). The top row the target is reflection whilst the bottom row is random. Participants had to judge whether the target (the single pattern or the centre pattern when in a group of three) was reflection or random.

4.5.2. Results

4.5.2.1. Behavioural

Participants were required to judge whether the target was reflection or random. They were successfully able to discriminate the target when it was unflanked ($d' = 1.9$, criterion $c = 0.05$). Crowding was strongest when the target and flankers were different ($d' = 0.8$, criterion $c = 0.2$) in shape compared to when the target and flankers were either all reflection or all random ($d' = 1.5$, criterion $c = 0.19$).

4.5.2.2. Event-Related Potentials

Figure 4.6 shows the ERPs for Experiment 3. When the targets were unflanked reflection was lower in amplitude than random between 200-600ms after stimulus onset. This was also true when the target and flankers were all reflection or all random. There was no difference in amplitude between reflection and random when the target and flankers were different.

A repeated measures ANOVA was performed [Hemisphere (Left, Right) x Time Window (200-600, 600-1000) x Arrangement (Reflection-NoFlankers, Random-NoFlankers, Reflection-FlankersReflection, Random-FlankersReflection, Reflection-FlankersRandom, Random-FlankersRandom)]. The between-subjects factor was Experiment (Experiment 2, Experiment 3).

There was a main effect of Arrangement $F(5, 230) = 5.705$, $p = 0.001$, partial $\eta^2 = 0.110$ and Time $F(1,46) = 90.898$, $p = 0.001$, partial $\eta^2 = 0.664$. There was an Arrangement x Time Window interaction $F(5,230) = 5.258$, $p = 0.001$, partial $\eta^2 = 0.103$. There were no other main effects or interactions.

When collapsed over hemispheres for the early time window paired samples t-tests showed that there was a significant difference between Reflection-NoFlanker and Random-NoFlanker ($t(23) = -4.695$, $p = 0.001$, $d = -0.388$). There was a significant difference between Reflection- FlankersReflection and Random-FlankersRandom ($t(23) = -2.708$, $p = 0.013$, $d = -0.198$). In the late time window there were no significant differences between conditions.

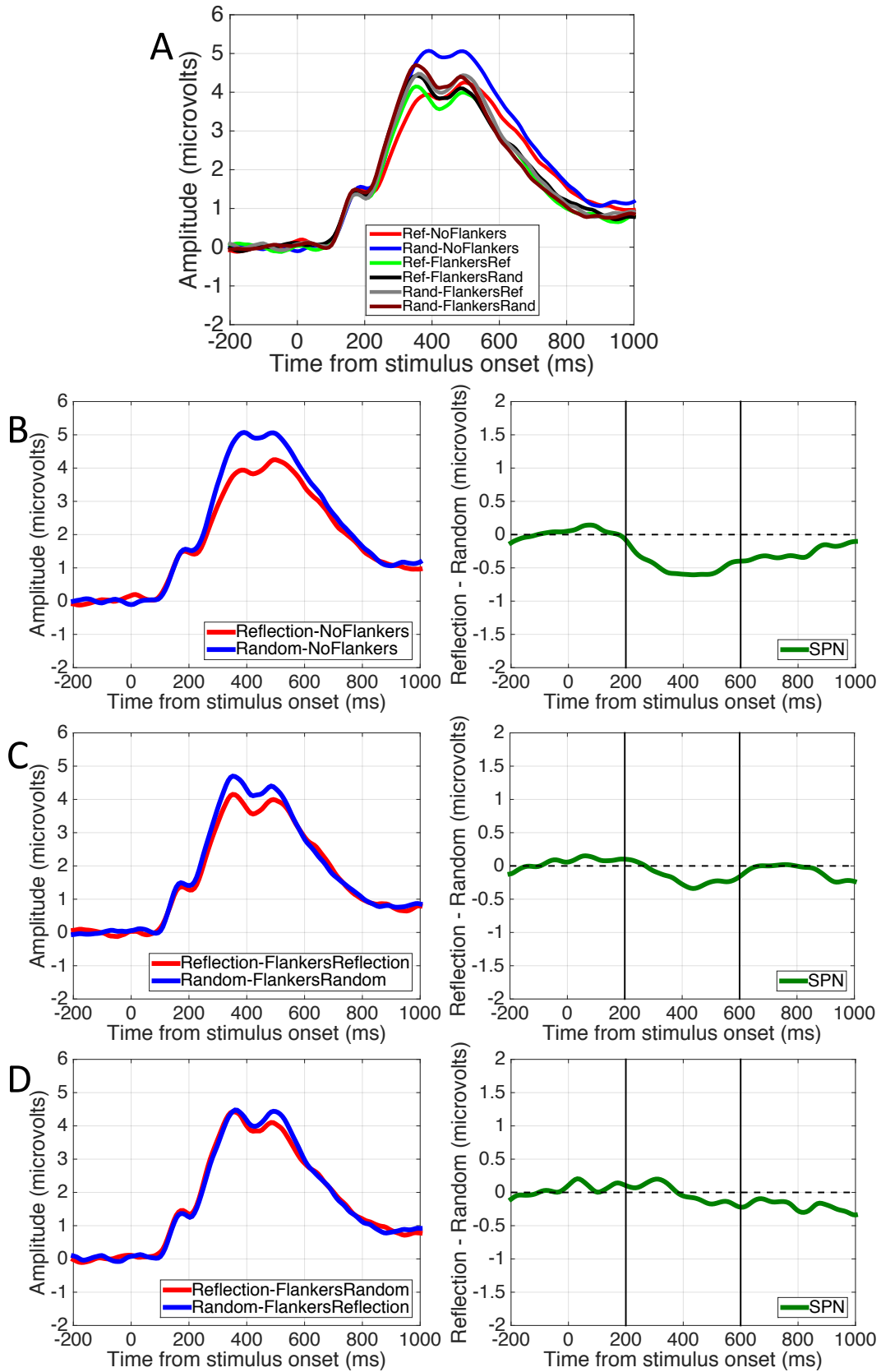


Figure 4.6. Grand-average ERPs for each condition collapsed across the left and right hemisphere in Experiment 3. A) ERPs for all conditions collapsed across both hemispheres. B) ERPs and difference wave when the targets are unflanked. C) ERPs and difference wave

when the targets and flankers were all reflection or all random. D) ERPs and difference wave when the target and flankers were different.

4.6. General Discussion

Symmetry plays a key role in object recognition. Nevertheless, object recognition can be hindered when targets are placed amongst other flanking objects. Electrophysiological research has identified a symmetry specific ERP component known as the Sustained Posterior Negativity where reflection is lower in amplitude compared to random from around 200ms after stimulus onset. However, it is not known how flanking objects modulate this response. Across three experiments, reflection and random were presented in the periphery either in isolation or flanked by other objects. In Experiment 1, flankers were positioned both above and below the target or either side of it. In Experiment 2 and 3, we examined target-flanker similarity with target and flankers either being the same or different in terms of their features. These experiments allowed us to examine how flanking objects in the periphery influence the SPN.

The results demonstrate that visual crowding reduces the SPN response. In Experiment 1, the size of this response in an early time window (200-600ms after stimulus onset) was found to reflect the strength of crowding (i.e., the stronger the effect of crowding, the smaller the SPN). In Experiment 2, crowding eliminated the SPN in the early and late time windows both when the target was all reflection, all random and when the target and flankers were different. In Experiment 3, the SPN was present in the early time window when target and flankers were matching in shape (although they had opposite contrast polarity). This is the first time that visual crowding has been shown to influence the SPN response. Moreover, these experiments reproduce and advance the findings of Wright, Makin and Bertamini (2016) who showed that the SPN could be produced to patterns in the periphery. Firstly, we confirm that the SPN can be generated to stimuli in peripheral vision. Secondly, we show that the SPN

can be produced to stimuli positioned at an even greater eccentricity (4.5°) from fixation than Wright, Makin and Bertamini (2016) demonstrated.

Why is there an SPN in Experiment 3 but not in Experiment 2 despite both demonstrating crowding? One possible explanation is that the target and flankers may group together. In Experiment 2 grouping may be strongest. Here the target and the flankers were always positioned on a horizontal orientation and had the same luminance. Experiment 1 contained a comparable condition in terms of feature and position similarity to those in Experiment 2. For this condition, flankers were positioned to the left and right of the target and similarly to Experiment 2 no SPN was observed. For Experiment 3, the difference in luminance should isolate the target from the flanker, reduce crowding and produce an SPN. Although it could be argued that a masking mechanism is being employed here instead of crowding as the visibility of the target is reduced by the high luminance of the flankers. When the targets and flankers are all reflection, the symmetry sensitive networks may be registering the symmetry in the image but this is not reflected in behavioural performance that should be on a par with the no flanked condition. This finding was not expected and so this is only a post hoc explanation, which will require further investigation.

The contextual effect of surround suppression may also operate in the stimuli used in these experiments, to either enhance or suppress the detectability of the target. Crowding and surround suppression are similar phenomena that both make it difficult to perceive the target (Petrov & McKee, 2006). The results of Experiments 2 and 3 may in fact reflect surround suppression. When flankers and target are different, surround suppression may enhance the detectability of the target. Alternatively, surround suppression may suppress the target when the target and flankers are similar (all reflection or all random) in shape. This would explain the behavioural findings. In Experiments 2 and 3 when the target and the flankers were either all reflection or all random crowding was weaker than when target and flankers were different

in shape. Previously, it has been found that crowding is reduced when targets and flankers are dissimilar to one another as they likely group together (Kooi et al., 1994; Manassi et al., 2012; Sayim et al., 2008). However, an alternative explanation for the behavioural findings is that in Experiment 2 participants are utilizing a substitution mechanism whereby the flankers are mistaken or ‘swapped’ for the target. Likewise, in Experiment 3 despite changing the luminance of the flankers to make the target more individual it may have masked the target causing the participants to report the flankers.

Past experiments have found that the SPN is a response to symmetry (Bertamini & Makin, 2014). This response scales with the amount of symmetry in the image with it greatest for reflection patterns 100% symmetrical and parametrically reducing as the amount of symmetry decreased (Palumbo, Makin, & Bertamini, 2015). These experiments allowed us to examine whether the SPN also scaled with the *number* of symmetrical objects in the image. However we found that the number of objects did not influence the size of the SPN response. This finding is consistent with chapter 4 of this thesis, which demonstrates that the SPN response in central vision is not increased to an ensemble of three reflectional objects compared to a single reflectional object.

The present work suggests that the size of the SPN in an early time window may reflect the strength of visual crowding. Still it could be argued that the response seen in these experiments is similar to other attention related ERPs such as the Sustained Posterior Contralateral Negativity (SPCN) or the N2pc. Both of these attention-related ERPs are recorded (around 200-350ms after stimulus onset) from posterior brain regions contralateral to the side of the presented stimuli (Lefebvre, Dell’acqua, Roelfsema & Jolicoeur, 2011). We think that it is unlikely that the response recorded in our experiments can be attributed to the SPCN, the N2pc or any other attention-related ERP. Firstly, the presentation of the stimuli in the left or right visual fields was randomized. This would prevent participants from allocating

their spatial attention to a single visual hemifield or switching between the left and the right. Secondly, the size of the SPN response in Experiments 1 and 3 scaled with crowding strength. The SPN was greatest for the unflanked conditions compared to the flanked conditions. As stimulus location was unpredictable, participants would shift attention to the pattern irrespective of whether it was flanked or unflanked. If the ERPs observed were due to attention a similar response would have been produced regardless of the stimulus arrangement.

4.7. Conclusion

Crowding is ubiquitous in everyday life, as objects are rarely perceived in isolation. Symmetry is deemed as an important feature that enables the detection of an object, however its detection can be hindered by peripheral presentation and flanking objects. Across three experiments that used different stimulus configurations, we found that visual crowding modulated the SPN response. In an early time window (200-600ms after stimulus onset) this response scaled with the strength of crowding. In conclusion we have provided evidence that surrounding objects influence the neural response to symmetry.

5. How does figure-ground assignment influence the neural response to visual symmetry?

5.1. Abstract

Figure-ground assignment is important in segmenting objects from their background. Both convexity and reflectional symmetry are strong cues in determining which objects are perceived as the figure. Electrophysiological research has identified a symmetry specific response: the Sustained Posterior Negativity (SPN). Amplitude is lower for symmetrical than random patterns from around 200ms after stimulus onset. We examined how figure-ground assignment affected the SPN. Participants were presented with stimuli adapted from Gerbino and Kanisza (1976) that contained alternating foreground and background regions in which reflectional symmetry and convexity were placed in competition. Stimuli consisted of three types of configurations: Reflection in the figure (foreground regions were convex and reflection), reflection in ground (background regions were concave and reflection) and random (no reflection in foreground or background). In Experiment 1, there was a significant difference in ERP amplitude between reflection in the figure and reflection in the ground. There was no difference between reflection in the ground and random. However, in Experiment 1 when reflection was the figure this region was convex and when reflection was in the background this region was concave. Reflection and convexity were therefore confounded. To address this, in a control experiment we examined the response to shapes that were either reflection or random with contours that were either convex or concave. An SPN response to reflection was observed for convex shapes, thus discounting the confound from Experiment 1. These results demonstrate that the neural response to symmetry is dependent on figure-ground assignment.

5.2. Introduction

When presented with a scene containing multiple objects the visual system effortlessly segments objects from their backgrounds through figure-ground assignment. Without this process, object recognition would not be possible. Gestalt psychologists have identified a number of cues that determine which regions are perceived as figures and which appear as ground these include reflectional symmetry, convexity, enclosure and size (Bahnsen, 1928; Koffka, 1935; Rubin, 1915/1958; Pomerantz & Kubovy, 1986). Regions that are reflectional symmetric, convex, open and small are more likely to be perceived as figures (Kubovy & Pomerantz, 1986; Hochberg, 1972; Palmer, 1999). Figure-ground assignment has been proposed to involve inhibitory competition and occurs when two regions share a border. The border is perceived as belonging to the region that wins this competition and is thus considered the figure whilst the other region becomes the ground.

5.2.1. Symmetry and figure-ground assignment

Symmetry is a prevalent object feature that plays a key role in object representation (For a recent review, see Treder, 2010). It has been reported that reflectional symmetric regions are perceived as the figure above chance (90% in Bahnsen, 1928; 80% in Driver, Baylis, & Rafel, 1992; and 62% in Peterson & Gibson, 1994). Although reflection symmetry is deemed an important cue in figure-ground perception, the difference in behavioural reports suggest it may not always be enough to determine what is perceived as the figure, particularly when combined with another cue such as convexity (Arnheim, 1954). Kanizsa and Gerbino (1976) put reflectional symmetry and convexity into direct competition with one another. They presented participants with alternating regions where concave regions were reflectional whilst the convex regions were less reflectional. Observers were required to judge which region they perceived as the figure. Both convexity and symmetry affected figure-ground assignment, but

convexity was a more powerful factor. Vecera, Flevaris and Filapek (2004) and Peterson and Salvagio (2008) have both replicated these findings.

However, the effectiveness of convexity as a figural cue varies depending on context. Peterson and Salvagio (2008) found that convexity was weak for displays that had just two regions but increased as the number of alternating black and white regions increased. In support of this, Mojica & Peterson (2014) found that reflectional symmetry and convexity are equally effective as figural cues. When presented with black-and-white displays with alternating symmetrical and asymmetric regions (either two or six), participants perceived the symmetrical regions as the figures, with this effect being as strong as for convexity.

5.2.2. Brain responses to symmetry

Neuroimaging experiments have highlighted that a number of areas are active during reflection symmetry perception including V3a, V4d, V7 and the Lateral Occipital Cortex (LOC). However, there was no activation in either V1 or V2 (Tyler et al., 2005; Chen, Kao, & Tyler, 2007). Recently, Kohler et al. (2016) documented parametric activations to rotational symmetry in V3, V4, VO1 and LOC. High density EEG showed that symmetry perception along the ventral stream occurred in a feed-forward fashion with responses in V3 and V4 occurring before LOC.

Electrophysiological symmetry research has identified a late component termed the *Sustained Posterior Negativity* (SPN). ERP amplitude is lower for symmetrical patterns than random patterns from around 200ms after stimulus onset. The SPN is present for reflection, translation, and rotation, whilst it is largest for reflection (Makin et al., 2013). The SPN originates from the LOC and extrastriate visual areas (Makin et al., 2012). The SPN is task independent with it being produced (although reduced) even when participants are not explicitly required to attend to it. Rampone, Makin and Bertamini (2015) showed that the

SPN was reduced when participants performed a colour compared to a regularity discrimination for slanted reflectional and random stimuli.

5.2.3. Investigation of figure-ground assignment on the SPN

We were interested in examining how figure-ground assignment influences the neural response to symmetry. Participants were presented with displays inspired by the stimuli used by Kanizsa and Gerbino (1976) that had alternating coloured regions. The displays contained three arrangements: reflectional figure regions that are convex (Reflection in figure), reflectional background regions that are concave (Reflection in ground) and random, which contained no reflection (Figure 5.1). Note that by design the figural regions are always convex and slightly smaller. By combining the factor convexity, size, and continuity with the outside background we assumed that there was little ambiguity in terms of which regions were perceived as figures. Participants were simply instructed to judge which region (red or green) they perceived as being in the foreground. If their responses are consistent with our assumption they will be able to report the colour of the region we have specified as figure (through convexity, size, and background colour).

As both arrangements contain reflection and due to the SPN responding to symmetrical representations, we may get a similar SPN for reflectional regions that are convex and reflectional regions that are concave. However, the random configuration and reflection in ground both contain concave shapes in the background. As convexity is a stronger figure-ground cue than symmetry, these conditions should produce similar ERPs. Note, in this experiment reflection is confounded with convexity. We therefore conducted a series of control experiments to address this.

In Experiment 2 we modified the stimuli by removing the black border and the half occluded shape. Moreover, to reduce the impression of figure-ground when presenting convex

shapes the ground region was black. Alternatively when presenting concave shapes the figure regions were black. We compared the SPN in a group of 32 participants who judged the patterns according to colour (red or green) while ignoring symmetry and another group of 32 participants who judged symmetry (reflection or random) whilst ignoring colour. In Experiment 3, we centred the stimuli so that the fixation cross was no longer situated along a border. Previous SPN experiments had always presented the fixation cross on the axis of symmetry (e.g. Makin et al., 2013; Wright et al., 2015). In Experiment 4, the stimuli used in Experiments 2 and 3 were modified to further ensure that any bi-stability in figure-ground perception was reduced. The black figure (for the convex shapes) and the ground (for the concave shapes) were changed to grey so that it matched the rest of the screen. On half of the trials participants were presented with a single shape (reflection or random) whilst on the other half three shapes were presented (all reflection or all random). The shapes (the single shape or three shapes) were matched for curvature polarity (convex or concave).

5.3. Method

5.3.1. Participants

Thirty-two participants took part in the study (age 16-41, mean age 24.28 (SD= 6.2), 12 males, 0 left handed). All participants had normal or corrected to normal vision, and received either course credit for participating or a monetary reimbursement. The study was conducted in accordance with the declaration of Helsinki and had approval of the University ethics committee.

5.3.2. Apparatus

Participants sat in an electrically shielded and darkened room, at a distance of 100 cm from a 60 Hz CRT monitor (1280 x 1024). EEG data was recorded from 64 scalp electrodes at 512

Hz using the BioSemi Active-Two system. Additional Common Mode Sense (CMS) and Driven Right Leg (DRL) electrodes served as reference and ground. Bipolar horizontal and vertical electro-oculograph (EOG) signals were recorded from four external channels. The apparatus were the same as used by Makin et al. (2013) and in previous chapters of this thesis.

5.3.3. Stimuli

Figure 5.1 shows examples of the stimuli used in Experiment 1. Stimuli were produced using the experiment generator software, PsychoPy (Peirce, 2007). The black frame was 10.7° in width and 7.1° in height. The shapes consisted of seven ovals on a vertical axis. These ovals varied in size, shape, orientation and position on each trial. There were eight alternating regions (4 foreground; 4 background). In half of the trials the foreground was red (RGB = 128,0,0; $\text{cd/m}^2 = 4$) whilst in the other half it was green (RGB = 0,128,0; $\text{cd/m}^2 = 11$). All stimuli were unique on each trial thus avoiding familiarity.

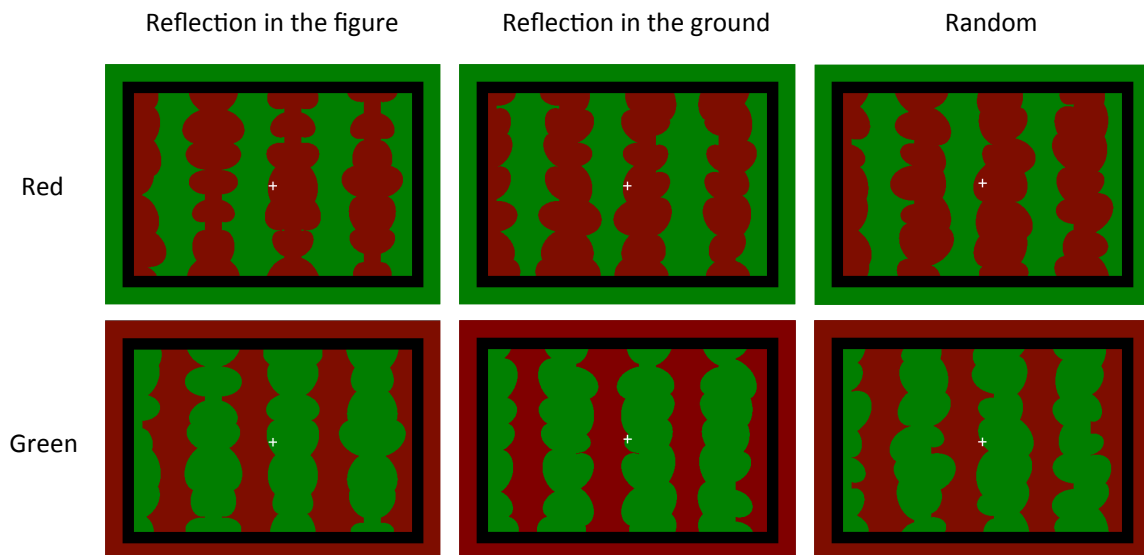


Figure 5.1. Examples of the stimuli used in Experiment 1. Left panels: Reflection in the figure – the figure regions were convex and reflectional in shape. Middle panels: Reflection in the ground -figure regions were convex whilst the ground contained reflectional concave regions. Right panels: Random - reflection was not present in either the ground or figure region. The top row the figure is red, whilst for the bottom row the figure is green. Participants had to judge whether the figure regions were red or green.

5.3.4. Design

The study had a two factor within subjects design (Arrangement [Reflection in figure, Reflection in ground, Random] x Colour [Red, Green]) with 40 trials per condition. This gave a total of 240 trials.

5.3.5. Procedure

Each trial began with a baseline period of 1.5 seconds, which consisted of a centrally positioned fixation cross. Stimuli were present for 1.5 seconds whilst participants fixated centrally. They had to report whether they perceived the foreground region as either red or green by pressing either the 'A' or 'L' buttons on the computer keyboard. Prior to the start of the experiment to familiarise the participants with the task a practise block was completed. The experiment was divided into 10 blocks to allow the participants to have regular breaks and for the electrodes to be checked.

5.3.6. EEG analysis

EEG data from 64 scalp electrodes was processed using the EEGLAB toolbox in MATLAB (Delorme & Makeig, 2004). Data was re-referenced to a scalp average and low-pass filtered at 40Hz. To reduce file size, this was downsampled to 128Hz. Epochs were extracted from -1 to 2 s, with a -200 to 0ms baseline. A behavioural filter was applied to the EEG data so that only the correct responses that the participants gave were used in the analysis. Artifacts such as eye blinks and movements were removed from the epochs using Independent Components Analysis (ICA; Jung et al., 2000). Data was reformed as 64 independent components. After ICA, epochs were removed which had amplitudes exceeding $\pm 100 \mu\text{V}$. Trials for each condition were averaged for each participant and grand-average ERPs were produced.

The SPN was defined as lower amplitude for reflectional than random patterns from 350 to 1000ms, averaged across left and right posterior electrodes (O1, PO7, PO3 on the left,

and O2, PO8 and PO4 on the right). This time window was chosen as although it is later than previous SPN studies (e.g. Makin et al., 2013) it ensured that the effects shown in Figure 4.2 were captured. N1 was defined as mean amplitude from 180 to 200ms after stimulus onset and was measured from the same electrodes as the SPN.

Only correct responses were analysed. On average, 9.5 components were removed from each of the participants' data (minimum: 2, maximum 16). For Reflection in figure 21.1%, Reflection in ground 20.4% and Random 20.5% trials were removed.

5.4. Experiment 1

5.4.1. Results

5.4.1.1. Behavioural

Participants reported whether they saw the foreground regions as red or green. Participants were equally accurate in reporting the convex region as the figure regardless of whether reflection was the figure (88%) or the ground (88%). For random, participants were correct for 89% of the trials.

Overall, performance was similar whether the figure was red (88%) or green (89%). There was no significant difference in accuracy when reflection in figure was red (87%) or green (90%). This was also true for reflection in ground (red 87%; green 88%) and random (red 89%; green 89%).

5.4.1.2. Event-Related Potentials

The amplitude of the SPN in posterior electrodes was sensitive as to whether reflection was perceived as being the figure or the ground. Figure 5.2A shows the ERPs collapsed by curvature (Reflection in figure, Reflection in ground and Random). There is a clear SPN where amplitude is lower for reflection in figure than reflection in ground and random (Figure 5.2B and C).

The SPN was analysed with two within-subject factors (Curvature [Convex, Concave] x Colour [Red, Green]). There was a main effect of Curvature ($F(2,62) = 3.733$, $p = 0.029$, partial $\eta^2 = 0.107$) and Colour ($F(1,31) = 10.873$, $p = 0.002$, partial $\eta^2 = 0.260$). There was no interaction between curvature and colour showing that these two factors produced unrelated neural responses. Paired samples t-tests showed that there was a significant difference between reflection in the figure and reflection in the ground ($t(31) = -2.669$, $p = 0.012$, $d = -0.124$) and a significant difference in the SPN between reflection in the figure and random ($t(31) = -2.124$, $p = 0.042$, $d = -1.192$). There was no difference between reflection in the ground and random.

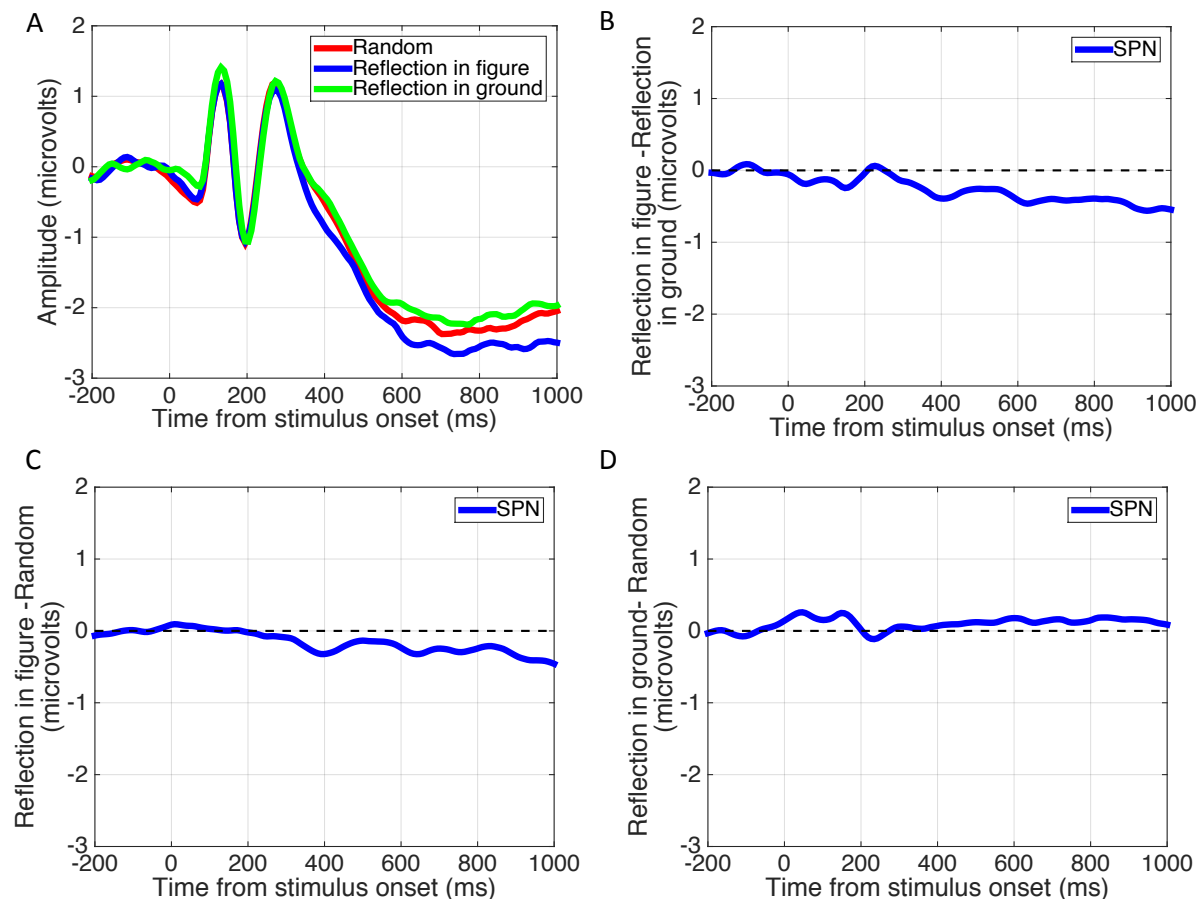


Figure 5.2. Grand-average ERPs for Experiment 1. A) Grand-average ERPs for each condition collapsed by curvature. B) Difference plot for Reflection in the figure - Reflection in the ground. C) Difference plot for Reflection in the figure - Random. D) Difference plot for Reflection in the ground - Random.

5.4.2. Discussion

Experiment 1 showed that when the reflection was perceived as being in the figure it produced lower amplitude ERP compared to when reflection was perceived as the ground. Reflection in the ground and random were also found to be similar in amplitude to one another. However, in this experiment reflection is presented as a convex shape (Reflection in the figure) and also as a concave shape (Reflection in the ground). The observed SPN could be the result of reflection or convexity. Experiment 2 set out to address this confound. In this experiment we modified the stimuli that were shown in Experiment 1 in three ways. Firstly, we removed the black border surrounding the alternating regions. Secondly, we removed the half occluded region. Thirdly, when convex shapes were present the ground was presented as black, whilst for the concave shapes the figure was presented as black. This ensured that any figure-ground ambiguity was reduced. If the SPN seen in Experiment 1 is a result of symmetry, we should find an SPN response for convex shapes in Experiment 2. Half of the participants performed a colour discrimination (red or green) whilst the other half performed a regularity discrimination (reflection or random). In Experiment 1, participants judged which colour was the figure, however in Experiment 2 performing a colour discrimination could be completed without attending fully to the stimuli. We therefore had another group of participants perform a regularity discrimination.

5.5. Experiment 2

5.5.1. Method

In Experiment 2, thirty-two participants (age 18-30, mean age 20.4 (SD = 3.4), 13 males, 5 left handed) were required to judge whether the presented shapes were red or green in colour. Another thirty-two participants (age 18-49, mean age 21.3 (SD = 6.8), 7 males, 7 left handed) were required to judge whether the shapes were reflection or random in shape. All participants

had normal or corrected to normal vision, and received course credit for participating or a monetary reimbursement. The study was approved by the University's ethics committee and adhered to the declaration of Helsinki. The apparatus were the same as in Experiment 1. There was a single within-subjects factor (Curvature [Reflection Convex, Reflection Concave, Random Convex, Random Concave]) with 80 trials per condition and a between-subjects factor (Task [Colour, Regularity]). The stimuli were modified from those used in Experiment 1 in order to reduce any figure ground ambiguity, with the black border and the half-occluded shape being removed (Figure 4.3). This resulted in three shapes being presented on screen simultaneously. For reflection convex the shapes were reflection and convex, whilst for reflection concave the shapes were reflection and concave in their shape. For random convex the shapes were convex and random, whilst for random concave the shapes were concave and random. Each shape was individually reflection or random (non-symmetrical) in shape. These four conditions allowed us to examine whether the SPN observed in the first experiment was the result of reflection or convexity. Convex shapes were presented with the ground as black, whilst concave shapes were presented with the figure as black.

EEG analysis was the same as Experiment 1, with only correct responses analysed. An average of 5.4 components were removed from each participant (min = 3, max = 14). For Reflection Convex 19.8%, Reflection Concave 19.3%, Random Convex 18.1% and Random Concave 18.3% of trials were removed.

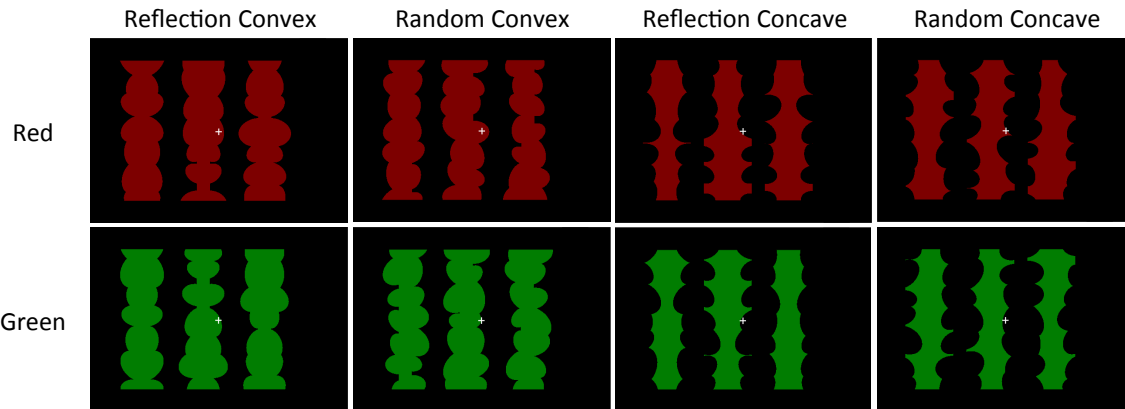


Figure 5.3. Examples of the stimuli used in Experiment 2. The group of three shapes were either all individually symmetrical or all individually random. Participants had to judge whether the coloured shapes were reflection or random. The top row the shapes were red whilst the bottom row the shapes were green.

5.5.2. Results

5.5.2.1. Behavioural

When participants had to report whether the displays contained red or green shapes performance was similar across the four conditions: Reflection Convex (97%), Reflection Concave (97%), Random Convex (97%) and Random Concave (97%). Performance was equivalent regardless of shape colour for Reflection Convex (red 97.3%; green 97.2%). This was also true for Reflection Concave (red 97.1%; green 97.4%), Random Convex (red 96.9%; green 97.5%), and Random Concave (red 97%; green 97.4%).

Moreover, when participants judged whether the shapes were reflection or random performance was also equally accurate across the four conditions: Reflection Convex (89.35%), Reflection Concave (90.7%), Random Convex (93.6%) and Random Concave (93.3%). The colour of the shapes made no difference to performance for this task. For Reflection Convex there was no difference whether it was red (89.6%) or green (89.1%). This was also true for Reflection Concave (Red 91.7%; Green 89.6%). Likewise, there were no

difference for Random Convex whether it was red (93.3%) or green (93.5%) or for Random Concave (Red 92.8%; Green 93.9%).

5.5.2.2. Event-Related Potentials

5.5.2.2.1. N1

Figure 5.4A and 5.4C suggest that ERP contour curvature differences exist as early as N1 both when participants performed a regularity and when they performed a colour discrimination as amplitude was lower for concave than convex. N1 was examined with a within subjects two factor ANOVA (Curvature [Convex, Concave] x Shape [Reflection, Random] x Colour [Red, Green]). The between-subjects factor was Task [Colour, Regularity]. There was a main effect of Curvature $F(1, 62) = 54.109$, $p = 0.001$, partial $\eta^2 = 0.466$ as concave was lower in amplitude than convex. There was a Colour x Task interaction $F(1, 62) = 7.866$, $p = 0.007$, partial $\eta^2 = 0.113$ and a Curvature x Colour x Task $F(1, 62) = 4.250$, $p = 0.043$, partial $\eta^2 = 0.064$.

5.5.2.2.2. SPN

Figure 5.4A shows that when participants performed a colour discrimination ERPs were lower for the convex shapes than for the concave ones. This was also the case for the regularity discrimination (Figure 5.4C). Figures 5.4B and 5.4D show the difference waves for convex and concave for the two tasks. There was no difference between Reflection Convex and Random Convex or between Reflection Concave and Random Concave regardless of task.

The SPN was examined with a three factor within subjects ANOVA (Shape [Reflection, Random] x Curvature [Convex, Concave] x Colour [Red, Green]). The between subjects factor was Task [Colour, Regularity]. There was a main effect of Curvature $F(1, 62)$

= 35.892, $p = 0.001$, partial $\eta^2 = 0.367$ and Task $F(1,62) = 11.487$, $p = 0.001$, partial $\eta^2 = 0.156$. There were no other main effects or interactions.

Paired samples t-tests confirmed that there were no significant differences between Reflection Convex and Random Convex or between Random Concave and Random Concave. This was the case for both the colour and regularity discrimination.

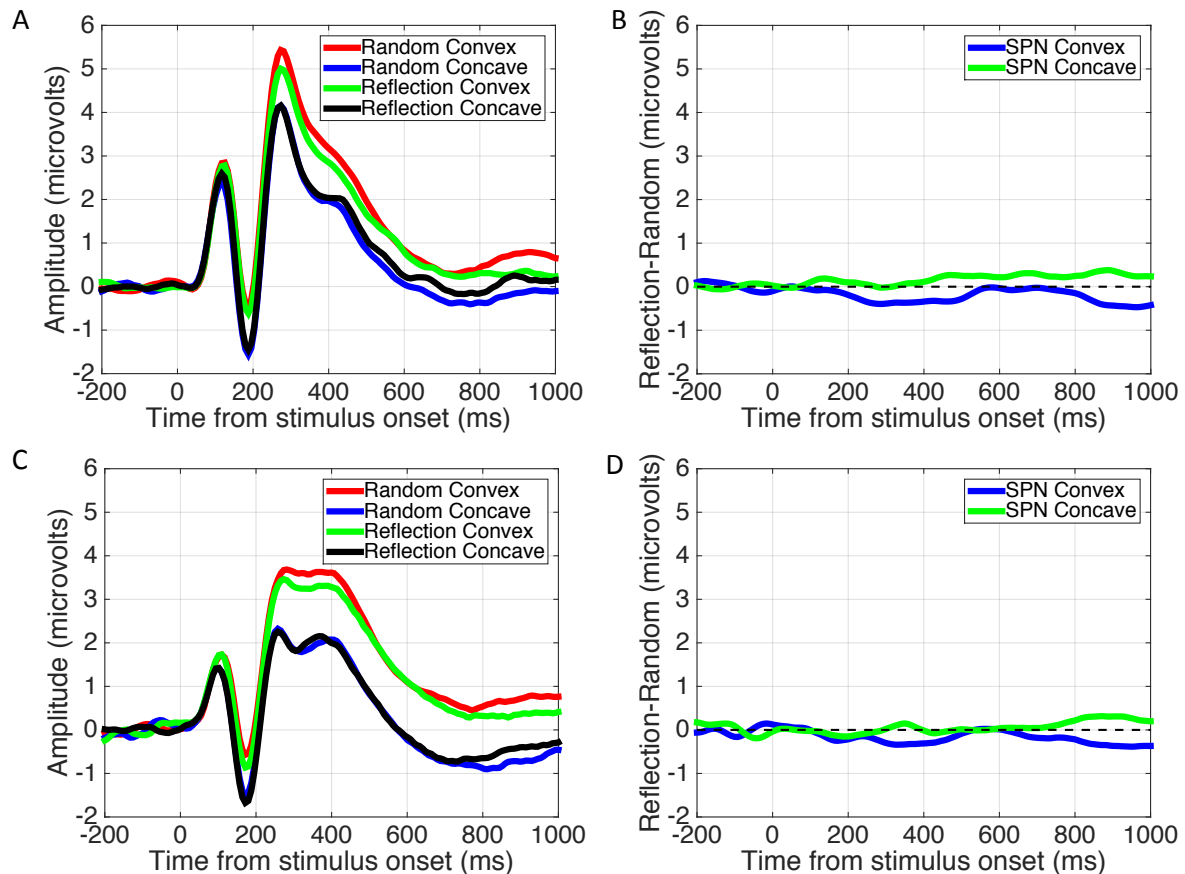


Figure 5.4. Grand-average ERPs for Experiment 2. A) Grand-average ERPs for each condition when participants performed a colour discrimination. B) Difference plot (Reflection-Random) for the convex and concave shapes when participants performed a colour discrimination. C) Grand-average ERPs for each condition when participants performed a regularity discrimination. D) Difference plot (Reflection-Random) for convex and concave shapes when participants performed a regularity discrimination.

5.5.3. Discussion

Experiment 2 found that when collapsed over symmetry, concave was lower in amplitude than convex. However, there was no SPN response for either convex or concave. This was

regardless of whether participants judged the colour or the regularity of the shapes. The lack of an SPN here was unexpected.

In Experiment 2 the fixation cross was positioned on a border between the figure and the ground. Previous SPN experiments had always presented the fixation cross on the axis of symmetry (e.g. Makin et al., 2013). The lack of an SPN response could therefore be a result of the position of the fixation cross. In Experiment 3, we repositioned the stimuli so that the fixation cross was on the axis of the central shape. The new black background may have also been a factor by producing figure-ground ambiguity. I will come back to this aspect later in section 5.6.3.

5.6. Experiment 3

5.6.1. Method

Twenty-four participants took part in Experiment 3 (age 18-47, mean age 25.87 (SD = 7.3), 14 males, 6 left handed). All participants had normal or corrected to normal vision, and received course credit for participating or a monetary reimbursement. The study had local ethics committee approval and was conducted in accordance with the declaration of Helsinki.

The apparatus and procedure were the same as in Experiment 2. There was a single within-subjects factor Arrangement [Reflection Convex, Reflection Concave, Random Convex, Random Concave]) with 80 trials per condition. The fixation point was moved so that it was positioned on the axis of the central shape instead of being on a border between the figure and the ground.

EEG analysis was the same as Experiment 1. An average of 7.9 components were removed from each participant (min = 3, max = 15). For Reflection Convex 24.9% of trials were removed, Reflection Concave 21.7%, Random Convex 26%, whilst 22.1% of trials were removed from Random Concave.

5.6.2. Results

5.6.2.1. Behavioural

Participants judged whether the shapes were reflection or random. Performance was better for random (Random Concave 94%; Random Convex 94.5%) than reflection (Reflection Concave 90.6%; Reflection Convex 90.6%).

For each condition, the colour of the stimuli made no difference to performance. For Reflection Convex (Green 90.2%; Red 91.1%) and Reflection Concave (Green 90.3%; Red 90.9%) performance was similar regardless of whether the shapes were red or green. This was also true for Random Convex (Green 94.7%; Red 94.3%) and Random Concave (Green 93.1%; Red 95%).

5.6.2.2. Event-Related Potentials

5.6.2.2.1. N1

Figure 5.5A suggests that ERP contour curvature differences exist as early as N1, with concave lower in amplitude than convex. N1 was examined with a within subjects three factor ANOVA (Curvature [Convex, Concave] x Shape [Reflection, Random] x Colour [Red, Green]). There was a main effect of Curvature ($F(1,23) = 14.289$, $p = 0.001$, partial $\eta^2 = 0.383$) because amplitude was lower for concave than convex. There was no effect of Shape or any interactions.

5.6.2.2.2. SPN

Figure 5.5A shows that ERPs were lower in amplitude for the concave regions than convex. There was no difference between Reflection Convex and Random Convex or between Reflection Concave and Random Concave (Figure 5.5B).

The SPN was examined with a three factor repeated measures ANOVA (Shape [Reflection, Random] x Curvature [Convex, Concave] x Colour [Red, Green]). There was a main effect of Curvature $F(1,23) = 36.877$, $p = 0.001$, partial $\eta^2 = 0.616$. There were no other main effects or interactions.

Paired-samples t-tests confirmed that there was no significant difference between Reflection Convex and Random Convex or between Reflection Concave and Random Concave.

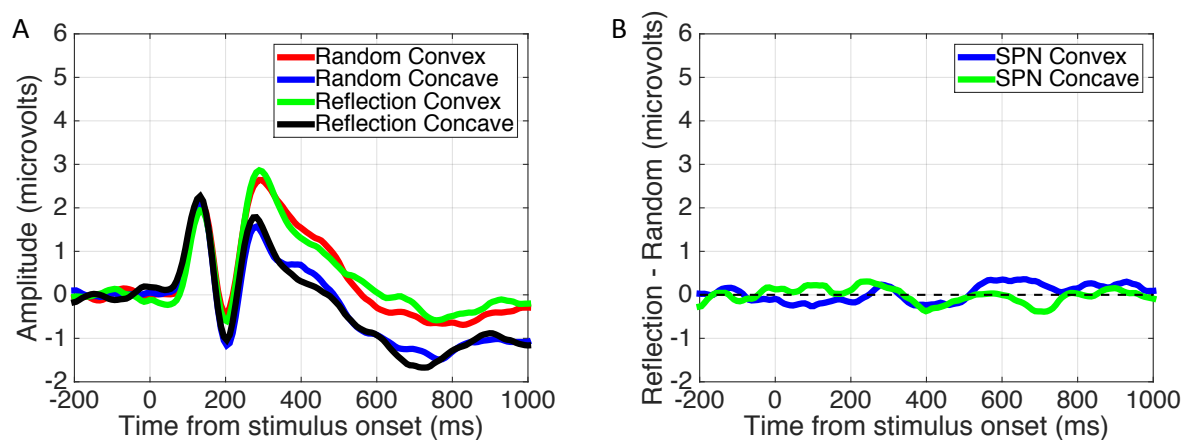


Figure 5.5. Grand-average ERPs for Experiment 3. A) Grand-average ERPs for each condition. B) Difference plot (Reflection-Random) for convex and concave shapes.

5.6.3. Discussion

For both Experiment 2 and Experiment 3 there was no difference between reflection and random for either contour curvature polarity. This may be due to the stimuli still having a degree of bi-stability with the black region not being sufficiently inhibited in order for the SPN to be produced. We therefore conducted Experiment 4 to address this. For this experiment the black region surrounding the convex or concave shapes was changed to grey to match the rest of the display (Figure 5.6).

To date, research has shown that the SPN is present for single objects in central vision with this response modulated by the amount of reflection symmetry in the image (Bertamini & Makin, 2014; Palumbo et al., 2015). Experiment 4 allowed us to investigate how the

number of symmetrical repeating shapes modulated the SPN response. For Experiment 4, participants were presented with either a single shape or three shapes. The group of three shapes were either all individually reflection or all individually random (Figure 5.6). Participants were required to judge whether the shapes were reflection or random.

5.7. Experiment 4

5.7.1. Method

Twenty-four participants took part in Experiment 4 (age 18-31, mean age 22.75 (SD = 3.8), 14 males, 3 left handed). All participants had normal or corrected to normal vision, and received course credit for participating or a monetary reimbursement. The study had local ethics committee approval and was conducted in accordance with the declaration of Helsinki. The apparatus and procedure were the same as in Experiment 2. There were two within-subjects factors (Arrangement [Reflection Convex, Reflection Concave, Random Convex, Random Concave] x Number [One, Three]) with 80 trials per condition.

EEG analysis was the same as Experiment 1. An average of 5.25 components were removed from each participant (min = 2, max =14). For Reflection Convex 16% of trials were removed, Reflection Concave 16.5%, Random Convex 16.3% whilst 17.8% of trials were removed from Random Concave.

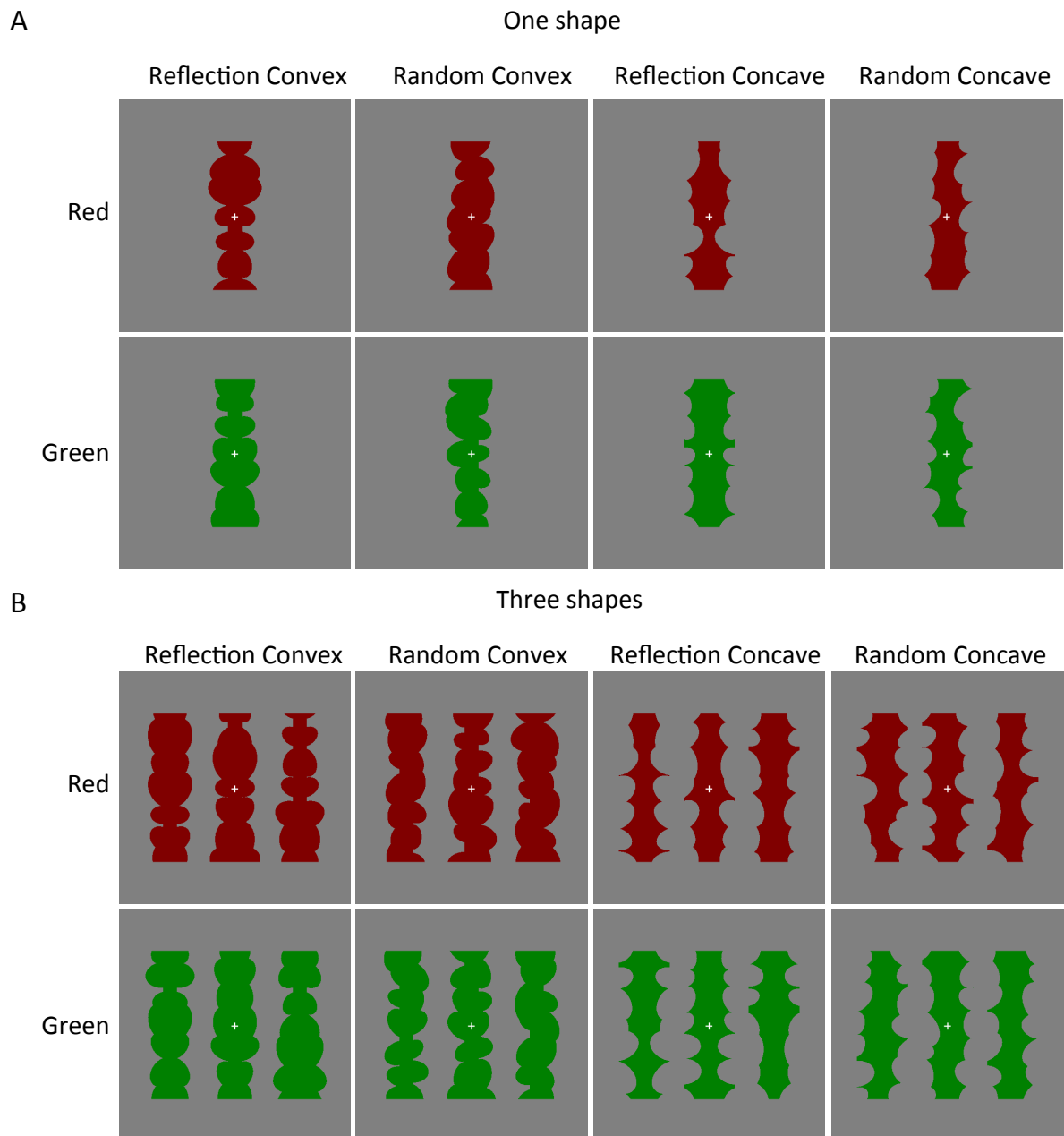


Figure 5.6. Examples of the stimuli used in Experiment 4. Participants were presented with either one (A) or three (B) shapes and had to judge whether they were reflection or random. For the three shapes, all were either uniquely reflection or random in shape. The shapes were either all red or all green in colour.

5.7.2. Results

5.7.2.1. Behavioural

Participants were required to judge whether the single shape or the group of three shapes were reflection or random. When participants were presented with one shape performance was

similar across all conditions (Reflection Convex 96.8%; Reflection Concave 96.3%; Random Convex 95.6%; Random Concave 95.8%). This was also the case when three shapes were presented (Reflection Convex 96.7%; Reflection Concave 95.8%; Random Convex 95.7%; Random Concave 96.7%).

Colour also made no difference to performance for either the one or the three shapes. For one shape performance for Reflection Convex was similar for both red (97.3%) and green (96.2%). This was also the case for Reflection Concave (Red 96.1%; Green 96.5%), Random Convex (Red 95.9% Green 95.3%) and Random Concave (Red 96.5% Green 95.1%). Performance for three shapes was also similar for Reflection Convex regardless of whether the shapes were red (97.1%) or green (96.3%). This was also true for Reflection Concave (Red 96%; Green 95.6%), Random Convex (Red 96.3%; Green 95.2%) and Random Concave (Red 97%; Green 96.3%).

5.7.2.2. Event-Related Potentials

5.7.2.2.1. N1

Figure 5.8A suggests that ERP contour curvature differences exist as early as N1, with concave lower in amplitude than convex (Figure 5.7). N1 was examined with a within subjects four factor ANOVA (Curvature [Convex, Concave] x Shape [Reflection, Random] x Colour [Red, Green] x Number [One, Three]). There was a main effect of Curvature $F(1,23) = 39.070$, $p = 0.001$, partial $\eta^2 = 0.629$ and Colour $F(1,23) = 12.694$, $p = 0.002$, partial $\eta^2 = 0.356$. There were no other main effects or interactions.

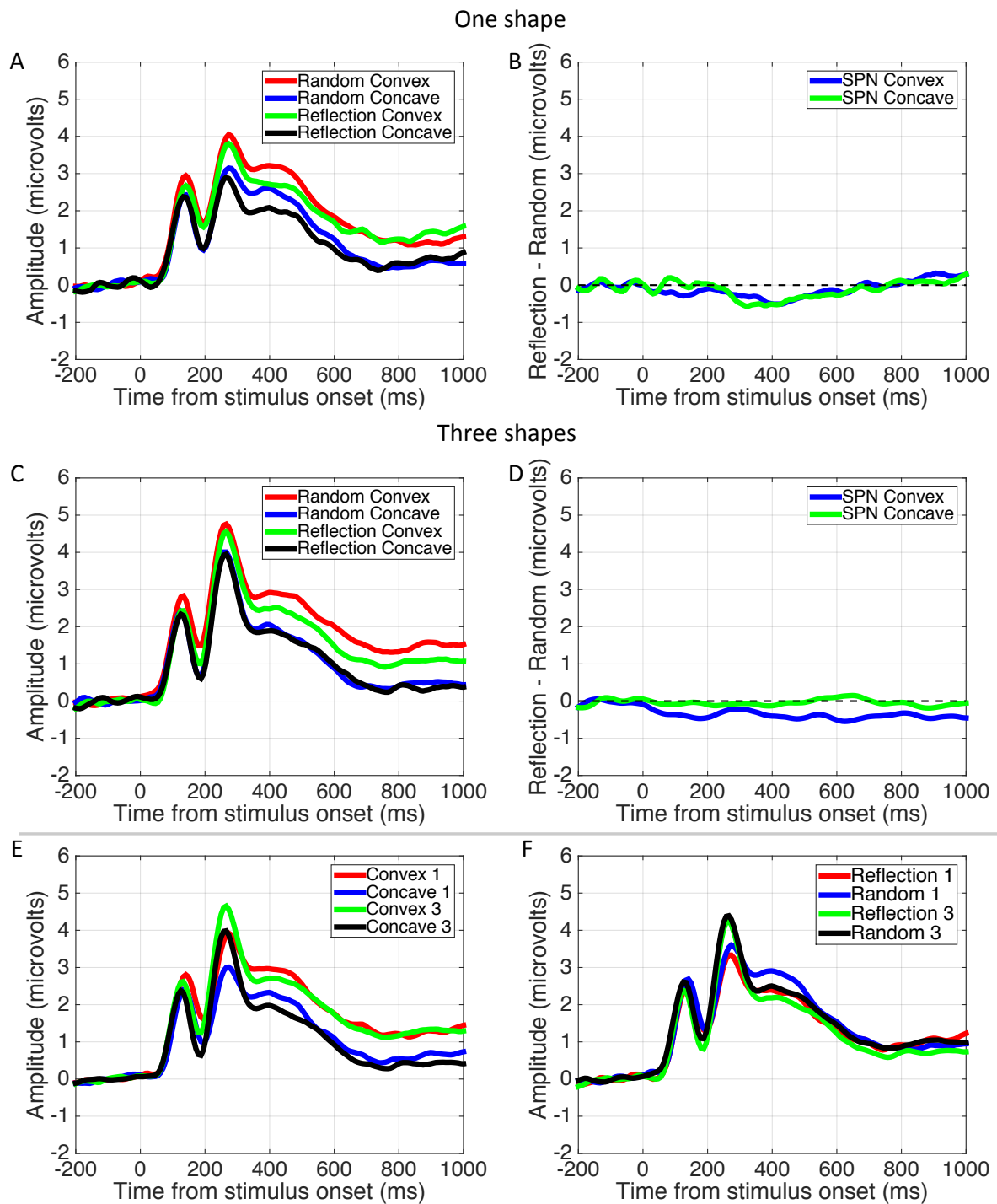
5.7.2.2.2. SPN

Figure 5.7A and 5.7C shows that ERPs were sensitive to convexity for both one and three shapes. Reflection Concave and Random Concave were both lower in amplitude than

Reflection Convex and Random Convex. There was a clear SPN for the convex shapes with Reflection Convex being lower in amplitude than Random Convex for three shapes (Figure 5.7B). For one shape there was no difference between reflection and random for either contour curvature polarity.

The SPN was examined with a four factor repeated measures ANOVA (Shape [Reflection, Random] x Curvature [Convex, Concave] x Colour [Red, Green] x Number [One, Three]). There was a main effect of Curvature $F(1,23) = 26.545$, $p = 0.001$, partial $\eta^2 = 0.536$. There was no main effect of Shape or Number and no interactions. This lack of an interaction with Number demonstrates that the SPN is not influenced by the multiple repetition of symmetry in central vision.

Paired samples t-tests for three shapes showed that there was a significant difference between Reflection Convex and Random Convex $t(23) = -2.218$, $p = 0.037$, $d = -0.17$. There was no difference between Reflection Concave and Random Concave. For one shape, paired samples t-tests revealed that there were no significant differences between either reflection or random for either contour curvature.



5.8. General Discussion

The visual system effortlessly organises visual scenes into coherent objects. Figure-ground assignment plays a key role in this process by ensuring that when two regions share a border one region is perceived as the figure whilst the other becomes the ground. Both convexity and reflectional symmetry are cues that play an important function in determining which region is deemed the figure (Bahnsen, 1928). We examined how figure-ground assignment influences the neural response to symmetry.

In Experiment 1, ERP amplitude was lower for reflection in the figure than for both reflection in the ground and random; both of which produced similar ERPs. However, interpreting this experiment is difficult due to the deliberate confound of comparing reflection as convex (Reflection in the figure) and concave (Reflection in the ground). The lower amplitude observed for reflection in figure may be the result of either symmetry or convexity. Experiments 2-4 addressed this confound. For Experiment 4, an SPN response (reflection lower in amplitude than random) was produced for convex. This established that the SPN response was dependent on figure-ground assignment, with it being present when reflection is considered the figure.

To date, the SPN has been considered to be a response to symmetry in the image with amplitude mapping onto the saliency of the symmetry (Bertamini & Makin, 2014; Makin, Rampone, Pecchinenda, & Bertamini, 2013). We demonstrate, for the first time, that figure-ground assignment plays a key role in the production of the SPN. Symmetry is an important cue in figure-ground assignment whilst figures are deemed more salient than grounds. It is therefore logical that the response of the visual system depends on whether symmetry is perceived as being the figure or ground.

Although an SPN was observed for Experiment 4 for multiple convex shapes, why was it not seen consistently across all the experiments? It is likely that the SPN was not

always observed due to how the stimuli were designed. Although reflection is a salient feature, in these experiments there may still have been some figure-ground ambiguity. The regions may have competed for border ownership causing a perceptual shift between them. Moreover, as mentioned above, the amplitude of the SPN maps onto the visual saliency of the symmetry. Reflectional symmetry with a single axis is less salient and produces a smaller SPN than symmetry with two axes (Makin et al., 2016). The single axis reflection in these experiments along with the bi-stable nature of the stimuli may have consequently reduced the size of the SPN.

5.8.1. Contour Curvature ERP Negativity

For Experiments 2-4 contour curvature differences were present as early as N1 with amplitude lower for concave than convex. N1 is sensitive to visual parameters (e.g. size, luminance). Both the convex and concave shapes were presented as either all red or green, so luminance differences between conditions were unlikely. However, the size of the shapes, although they randomly varied within a defined set of parameters, was always different so may have been a contributing factor.

ERPs in the N1 time window have also been linked to visual attention and selective perceptual amplification (Luck et al., 1990). In accordance, Kanizsa figures produced enhanced N1 negativity compared with fragmented illusory contours suggesting that this component reflects attention and perceptual grouping (Herrmann & Bosch, 2001). The contour curvature negativity may have resulted from the concave shapes engaging more top-down attention than the convex shapes. Thus, suggesting that concave is detected more rapidly. Evidence for a perceptual advantage of concavity over convexity in the shape perception literature is mixed. Concavities have been found to be both more salient and more easily detected in visual search and change detection than convexities (Barenholtz, Cohen,

Feldman, & Singh, 2003; Hulleman, Te Winkel, & Boselie, 2000). However, the converse is also true with convex shapes detected faster than concave shapes (Bertamini, 2001; Bertamini & Freidenberg, 2001; Gibson, 1994; Hoffman & Singh, 1997). These contradictory results have been suggested to be due to convexities being perceived as parts with positional information, whilst concave regions are boundaries between parts (Bertamini, 2001). Unfortunately, the responses in our experiments were unspeeded so it is difficult to offer much support as to whether concave is inherently more salient.

Concave was also lower in amplitude than convex from around 350ms after stimulus onset. This is the first time that this convexity negativity has been documented. Previously, Mathes, Trenner and Fahle (2006) documented that concave produced higher N2 (190-330ms after stimulus onset) amplitude than convex. The discrepancy in latencies between our sets of experiments may be due to methodological differences. Mathes, Trenner and Fahle (2006) presented participants with open and closed contours defined by Gabor elements embedded in a background of randomly orientated distractors. Despite these differences it is logical that the visual system has convexity sensitive networks; with this network likely to involve the LOC, a region that has been implicated in object perception (Haushofer, Baker, Livingstone & Kanwisher, 2008).

5.8.2. Repetition of multiple symmetries

Past ERP research has found an SPN for single patterns in central vision (Bertamini & Makin, 2014; Höfel & Jacobsen, 2007; Makin, Wilton et al., 2012). Importantly, SPN amplitude has been found to increase as the proportion of reflection symmetry in the image increases (Palumbo, Makin & Bertamini, 2015). However, no previous work has explored the neural correlates of the differences between the number of symmetrical patterns presented in central vision. Experiment 4 allowed us to examine this. We found that ERPs did not differ between

single and multiple reflectional patterns. This result suggests that the neural generators of the SPN are not sensitive to the number of symmetrical objects. This is perhaps surprising given that the LOC, which has been suggested to be the major symmetry area, has been found to be sensitive to the total number of visual elements (Sasaki et al., 2005; Tyler et al., 2005; Xu & Chun, 2006). It may be that in Experiment 4 as all three patterns were the same regularity (despite individual local differences between the shapes) participants might have simply deployed attention to just one of the shapes instead of all three.

Previous work has argued that there are two distinctive stages of visual processing when multiple objects are encoded: individuation and identification. The LOC has been proposed to be involved with object identification, whereby multiple identical objects are processed as a single unique object (Xu, 2009). It is interesting to note that if the three objects had been processed by the LOC as a single object, reflection would have been lost. This was not the case so the three objects were processed separately.

5.9. Conclusion

In conclusion, figure-ground assignment is fundamental in visual perception in order for objects to be separated from the background. We placed reflection and convexity in direct competition to examine the influence of figure-ground assignment on the neural response to symmetry. Here, we show that the visual cortex processes reflectional symmetry efficiently and automatically with this response reliant on figure-ground assignment.

6. General Discussion

6.1. Introduction

Symmetry is an important feature in object recognition and image segmentation. Although human symmetry perception has a long history, it has only been in recent years that neuroimaging and electrophysiological research has provided a greater understanding of the brain processes that are involved. Electrophysiological research has identified a symmetry specific component (the Sustained Posterior Negativity; SPN) where ERP amplitude is lower for symmetrical than random shapes from around 200ms after stimulus onset (Bertamini & Makin, 2014; Norcia et al., 2002). The SPN has been reliably replicated across a number of experiments and several questions have already been addressed in the literature, however many still remain. Each chapter of this thesis has addressed one question: (1) Can the SPN be produced independently within each hemisphere? (2) Is right lateralised alpha desynchronisation during regularity discrimination the result of directed spatial attention or hemisphere specialisation? (3) Does crowding influence the SPN? and (4) How does figure-ground assignment influence the neural response to symmetry? In this final chapter, the main findings of this body of work will be outlined and discussed. Lastly, I will highlight directions for future research based on the findings of this thesis.

6.2. Review of the main findings

6.2.1. Chapter 2: Can the SPN be produced independently within each hemisphere?

To date, the SPN has only been examined for single objects in central vision. By presenting reflection in the left and right visual fields Chapter 1 demonstrated that the SPN could be produced to stimuli presented in the periphery. This provides confirming evidence that the SPN is a response to symmetry in the image. Moreover, the SPN was produced independently within each hemisphere, suggesting that symmetry perception could be achieved by just one

hemisphere. Consequently, inter-hemispheric connections do not play much of a role in this process. This finding was supported by the results from Chapter 3. This highlighted that a similar SPN was produced regardless of whether the symmetry was on a vertical or horizontal orientation, despite interhemispheric integration being required for vertical symmetry. It is also consistent with work showing that patients born without a corpus callosum are still able to perceive reflection symmetry (Herbert & Humphreys, 1996). As the neural response to symmetry can be produced within each hemisphere, with little interaction between hemispheres it led on to whether one hemisphere plays a greater role in symmetry perception. Previously, evidence has suggested that reflection symmetry perception may be right lateralised (Verma et al., 2013; Wilkinson & Halligan, 2002; See also Chapter 3). However, this chapter did not offer much evidence for this. A right lateralised symmetry response was only observed in Experiment 1, but not in Experiments 2 and 3.

6.2.2. Chapter 3: Is right lateralised alpha desynchronisation during regularity discrimination the result of directed spatial attention or hemisphere specialisation?

Chapter 3 examined whether right lateralised alpha desynchronisation observed in previous experiments indicated hemisphere specialisation or directed spatial attention. Past EEG studies have found that during regularity discrimination greater alpha desynchronisation was present in the right hemisphere (Makin et al., 2013). Alpha desynchronisation was exhibited in both the left and right hemispheres regardless of whether symmetry was on a vertical or horizontal orientation. However, alpha desynchronisation was more pronounced in the right hemisphere. We concluded that right lateralisation alpha desynchronisation resulted from hemisphere specialisation. This was consistent with previous work on hemisphere specialisation, which also indicated that although both hemispheres are sensitive to reflection symmetry the right hemisphere is specialised (Verma et al., 2013; Wilkinson & Halligan,

2002). Nevertheless, the hypothesis that this lateralisation was the result of directed spatial attention cannot be completely ruled out as participants may still shift their attention to the left when presented with a pattern in central vision. Thus, generating a right lateralised alpha desynchronisation response.

6.2.3. Chapter 4: Does visual crowding influence the SPN?

As a result of the findings of Chapter 2, which demonstrated that the SPN could be produced to stimuli in periphery, Chapter 4 presented reflection in the peripheral but flanked by other objects. Behaviourally, reflection symmetry perception is not only reduced when in the periphery but also when flanked by other objects (Roddy & Gurnsey, 2011). This chapter had two key findings. First, across three experiments it was demonstrated that the SPN is produced to objects presented in the periphery. This finding is consistent with the results of Chapter 2. Second, it was found that crowding strength modulated the detectability of reflection symmetry along with activity in symmetry-sensitive networks (as the strength of crowding increased, the size of the SPN response reduced).

6.2.4. Chapter 5: How does figure-ground assignment influence the neural response to symmetry?

Figure-ground assignment is important in visual perception in order to separate objects from their backgrounds. Both symmetry and convexity have been highlighted to be figural cues that determine this process. Chapter 5 presented participants with displays that had alternating coloured regions, which directly placed reflection and convexity in competition with one another. The SPN response was found to be dependent on figure-ground assignment. It was present when reflection was perceived as being the figure, but was absent when reflection was in the ground. This seems logical given the importance of symmetry in figure-ground

assignment and object recognition; an object does not matter as an object unless it is also figural.

Moreover, the number of reflection patterns in central vision did not influence the SPN response. Experiment 4 allowed for a comparison of the SPN when there were either one or three reflectional patterns presented. It was found that the SPN was similar for both one and three reflectional patterns. This was consistent with the findings from Chapter 4, which demonstrated that the SPN response did not scale with the number of presented reflectional objects in the periphery.

6.3. Hemisphere lateralisation of the neural response to visual symmetry

Previous symmetry experiments have highlighted a lateralised response to symmetry (Verma et al., 2013; Wilkinson & Halligan, 2002). For example, Verma et al. (2013) found that behaviourally reflection symmetry detection was facilitated by left visual field (thus processed in the right hemisphere) presentation for participants who were left lateralised for language. TMS work has also found converging evidence of a right hemisphere specialisation for symmetry (Bona et al., 2014). However a lateralised response has not been observed for fMRI studies. This body of work offers some evidence for a right hemisphere specialisation for symmetry perception in chapter 2 and 3, although the support offered in chapter 2 is not particularly strong. Chapter 4 found no evidence for a lateralisation of the symmetry response. A right hemisphere specialisation is consistent with global processing being dominant in the right hemisphere (Van Kleeck, 1989). Symmetry can be considered a type of global processing and therefore right hemisphere dominance would be appropriate. The lack of strong evidence for a dominant hemisphere in symmetry processing in this body of work may result from each hemisphere being able to process symmetry independently as demonstrated for the first time in Chapter 2.

6.4. Neural responses to symmetry in visual clutter

The SPN is considered to be a response to symmetry in the image (Bertamini & Makin, 2014). To recap, the SPN is produced by reflection, rotation and translation whilst reflection produces the largest amplitude SPN (Makin, Rampone, Pecchinenda & Bertamini, 2013). These differences in amplitude reflect the saliency of symmetry with sensitivity to reflection highest compared to other regularities (Makin, Pecchinenda & Bertamini, 2012; Royer, 1981). Moreover, SPN amplitude scales with the amount of reflection symmetry in the image (Palumbo, Makin & Bertamini, 2016). The SPN is present when participants are engaged in tasks other than regularity discriminations (Höfel & Jacobsen, 2007; Makin, Rampone, & Bertamini, 2014). The current experiments are in agreement with those previously reported with the SPN found to be a robust response to symmetry in the image. This response was modulated by factors, which varied the salience of reflection symmetry such as other objects (Chapter 4) and figure-ground assignment (Chapter 5). In conclusion, the SPN is an automatic response to symmetry that is sensitive to bottom-up stimulus features.

6.5. Directions for future research

This work has further expanded our knowledge and deepened our understanding of the electrophysiological response to visual symmetry; in conjunction it has raised additional avenues for future research to explore. While Chapter 5 examined how figure-ground assignment modulated the SPN by presenting stimuli that were perceived to differ in depth despite being on a 2D plane, future studies could examine symmetry presented in 3D. With the exception of Makin, Rampone & Bertamini (2014) who demonstrated that an SPN could be produced for slanted reflection in depth, neural responses to 3D symmetry have been currently understudied. The world is a rich 3D environment and investigating how the brain responds to these stimuli would provide a more complete understanding of symmetry

perception. A 2D retinal image can be the infinite projection of a number of 3D objects. Symmetry is a prevalent object feature by assuming the object is symmetric can help recover the 3D shape from the 2D retinal image. It is therefore likely that mechanisms exist for processing 3D symmetry, which are similar to the areas used to process 2D symmetry. Moreover, there are a number of salient properties (e.g. shading and texture gradients) that provide information about 3D shape that could also be examined in relation to the neural response to symmetry.

Chapter 3 examined alpha oscillations but future studies could also examine synchronous oscillatory neural activity in the gamma range (30-80Hz). A growing body of evidence has suggested that synchronised gamma oscillatory activity plays an active role in bottom-up visual feature binding (Fries, 2005; Singer & Gray, 1995). However, to date high frequency oscillations have not been examined extensively for symmetry perception.

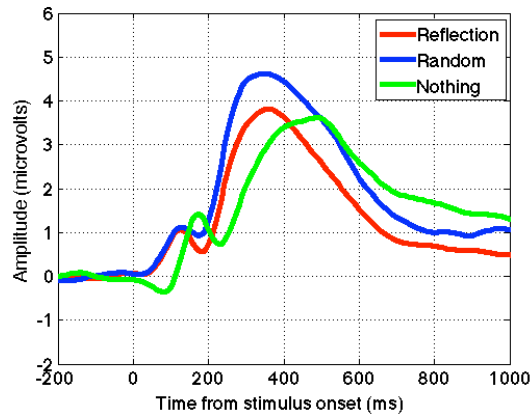
7. Appendix 1: Investigating whether the SPN is a neural response to symmetry

The SPN has always been analysed as a relative difference between reflection and either random or another regularity (Norcia et al., 2002; Wright, Makin, & Bertamini, 2015), with it being claimed that the difference observed is a neural response to symmetry. However, it could be fairly argued that the difference we see is the result of a neural response to random and not symmetry. Due to the novel paradigm used in Experiment 2 we are able to tease apart these competing arguments.

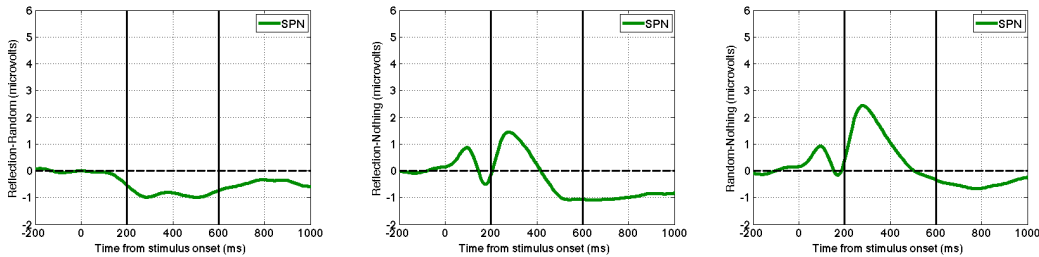
Firstly, we are able to compare reflection against nothing (no processed pattern). This comparison is important, as if we are able to show a difference between reflection and nothing it will allow us to make a second comparison between nothing and random. If we find that reflection and nothing are significantly different from one another but random and nothing do not differ from one another then it helps to strengthen the claim that the SPN is a neural response to symmetry.

The same electrodes (P1, P3, P5, P7, PO3 and PO7 and right side homologues) and time windows (early: 200-600ms; late 600-1000ms) were used as in Experiment 2. We performed a 2 x 2 Time Window (Early, Late) x Regularity (Reflection, Random, Nothing) ANOVA. Both Regularity ($F(2,46) = 4.973$, $p = 0.011$, partial $\eta^2 = 0.178$) and Time Window ($F(1,23) = 82.256$, $p = 0.001$, partial $\eta^2 = 0.781$) affected amplitude. An interaction confirmed that the amplitude of the regularities varied across the time windows ($F(2,46) = 50.491$, $p = 0.001$, partial $\eta^2 = 0.687$).

A. ERPs collapsed across hemispheres



B. Difference plots



Supplementary Figure 1.1. Grand-Average Event Related Potentials (ERPs) collapsed over the left and right hemisphere. Panel A shows the ERP waves for reflection, random and nothing. Panel B shows the difference plots for reflection, random and nothing.

We further explored this interaction with a series of paired t-tests. We first examined the *early* time window (200-600ms). As expected, amplitude was lower for reflection than random, $t(23) = -4.173$, $p = 0.001$, $d = -0.429$. There was however a significant difference between random and nothing ($t(23) = 4.649$, $p = 0.001$, $d = -0.575$).

Next, we looked at the *late* time window (600-1000ms). Again, reflection produced a lower amplitude wave compared with random ($t(23) = -2.162$, $p = 0.041$, $d = -0.298$). Importantly, a SPN was produced for reflection and nothing ($t(23) = -4.360$, $p = 0.001$, $d = -0.720$) with reflection producing a lower amplitude ERP waveform. Although nothing produced a lower amplitude compared with random wave these were not significantly different ($t(23) = -1.985$, $p = 0.059$, $d = -0.350$).

For the first time we show that the SPN can be produced as a relative difference between reflection and no pattern (although only in the later time window). We also show that the neural response to random does not differ from when no pattern was presented in the later time window. These comparisons allow us to conclude that the SPN is likely a neural response to symmetry.

An interesting feature was an early positive peak at around 180ms that was greater in amplitude (though slightly later in latency) for nothing compared to reflection or random (Supplementary Figure 1.1). Interhemispheric information transfer can account for the difference in latency. Amplitudes for the early components tend to be larger over contralateral than ipsilateral hemispheres (Gonzalez et al., 1994; Heinze et al., 1990). However the neural responses recorded were always from the contralateral hemisphere. The fact that this component is larger in the contralateral hemisphere in response to nothing than either reflection or random is puzzling.

8. Appendix 2: Consequences of different data selection procedures

In EEG research there is a potential problem with post hoc selection of channels, time windows and frequency bands. This can make statistical procedures invalid, or demand excessively strict multiple comparison correction procedures which would increase the chance of making a Type 2 error. To avoid this, it is advisable to choose parameters a-priori, and this approach is plausible when previous work provides clear effects that can be re examined.

This work replicated the findings of Makin et al. (2014), who also reported ERPs and ERD during a task where participants discriminated reflection from translation patterns. However, the parameters used in that analysis were not quite appropriate for the current data set. There is a tension between the desirability of a priori data selection criteria on the one hand, and capturing effects of interest on the other. This was resolved as follows: In the main manuscript, data was selected to capture the effects that were apparent in the Figures. However, to ensure that the results were not too dependent on these decisions, we re- ran the analysis using the same parameters as Makin et al. (2014).

The SPN results were very similar when PO7 and PO8 electrodes were used, as in Makin et al. (2014). Amplitude was explored in the 250 to 1000 ms window with repeated measures ANOVA (Regularity [Reflection, Translation] X Orientation [Horizontal, Vertical]). There was a main effect for Regularity ($F(1,23) = 27.50, p < 0.001, \text{partial } \eta^2 = 0.545$). There was no effect of Orientation ($F(1,23) = 1.64, p = 0.213, \text{partial } \eta^2 = 0.066$) or Regularity x Orientation interaction ($F(1,23) = 2.69, p = 0.114, \text{partial } \eta^2 = 0.105$). This replicates the main analysis, and confirms that the SPN was not too dependent on the choice of electrodes for analysis.

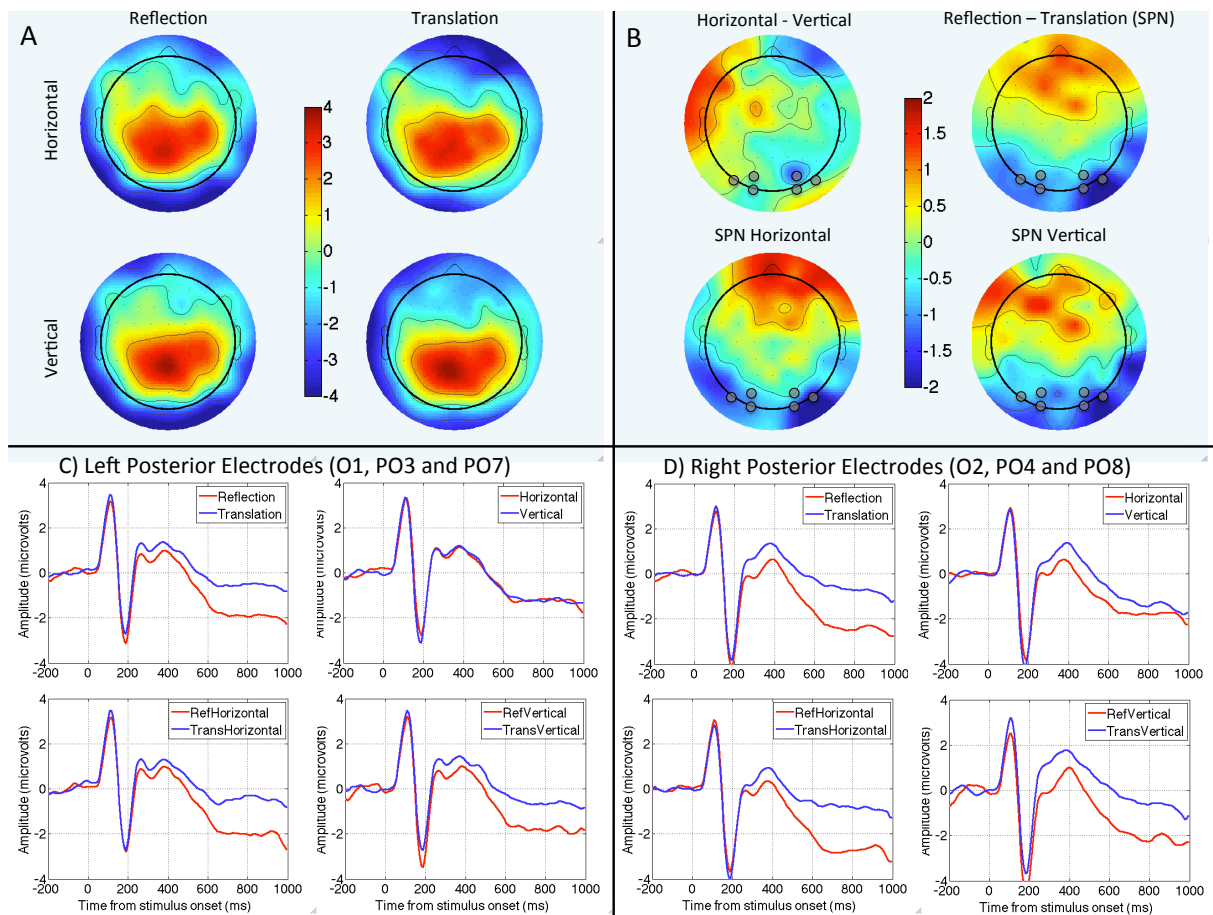
Next, the ERD analysis was re-run using the same time and frequency bands as Makin et al. (2014), that is, 400-700 ms, 8-13 Hz. There was main effect of Hemisphere ($F(1,23) =$

9.10, $p = 0.006$, partial $\eta^2 = 0.284$) and Orientation ($F(1,23) = 4.96$, $p = 0.036$, partial $\eta^2 = 0.177$). There were no other effects or interactions (next largest = Hemisphere X Regularity, $F(1,23) = 1.44$, $p = 0.243$, partial $\eta^2 = 0.059$). We note, however, that if the electrode clusters used here are different to those used by Makin et al. (2014). If the same electrodes were used, the main effect of Hemisphere was no longer significant.

8.1 Analysis without ICA

This study was designed to re-examine the electrophysiological responses during reflection/translation discrimination reported by Makin et al., (2014) and the ERPs reported by Makin et al. (2013). The pre-processing steps were designed to be as similar as possible to our previous work, to allow the most valid comparison. Nevertheless, it is important to examine potential distortions introduced by the ICA data cleaning procedures. ICA can be used to remove large, unwanted blink and eye movement artifacts, while retaining the cortical responses produced by the resulting visual field changes. To examine this issue, all analyses were rerun *without the ICA cleaning stage*. For SPN, trials were excluded when amplitude exceeded +/- 100 μV during the -200 to 1000 ms window (where all interesting effects were situated). Unsurprisingly, the mean number of excluded trials increased, from 16% to 30% in this case. For ERD analysis, the exclusion window was -500 to 1000, and 35% of trials were excluded.

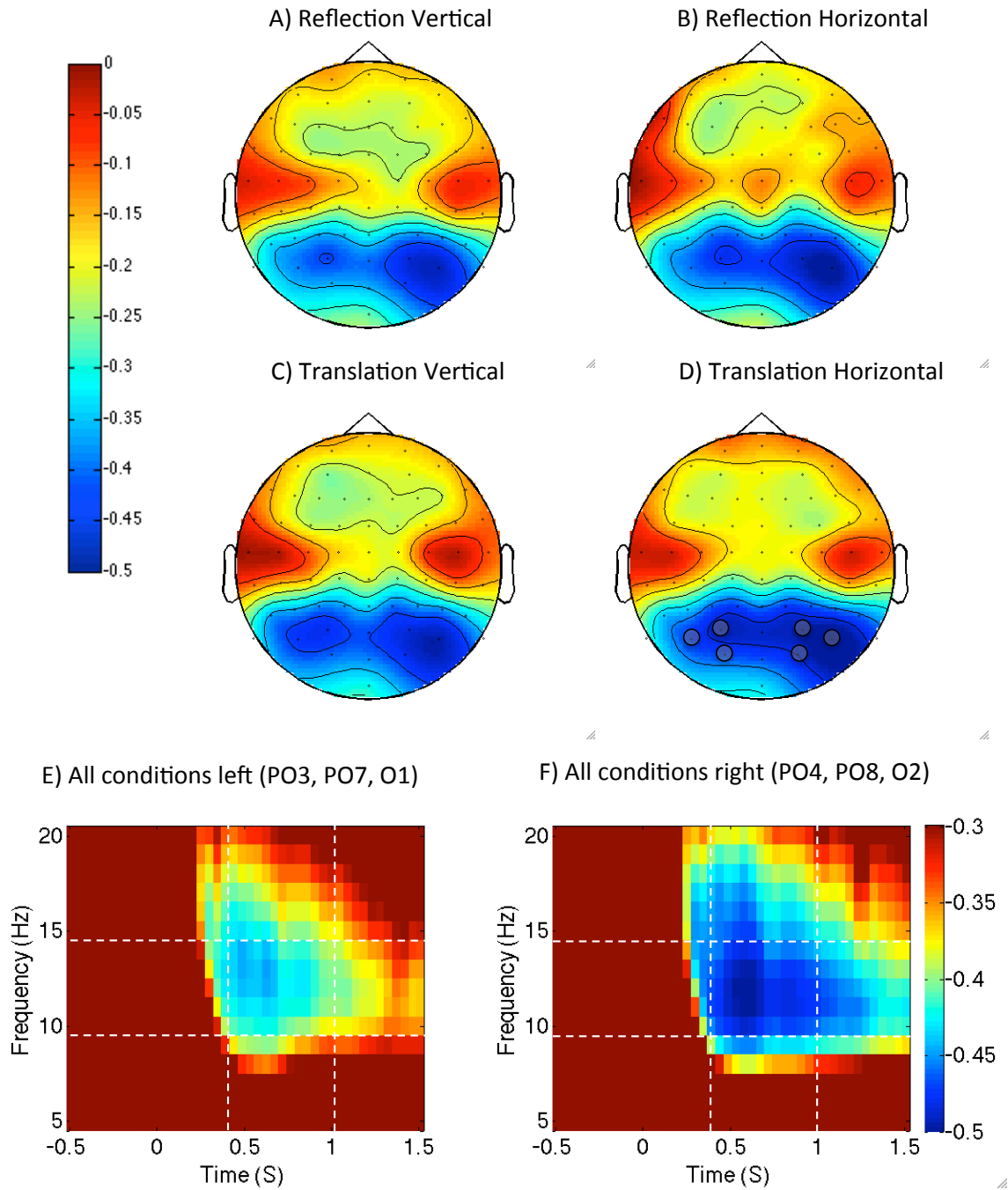
SPN amplitude was highly correlated between with and without-ICA versions of the data in every condition ($r = 0.82$ to 0.96). For SPN, there was still a main effect of regularity ($F(1,23) = 35.14$, $p < .001$, partial $\eta^2 = 0.604$), however the original Regularity X Hemisphere interaction was no longer significant ($F(1,23) = 3.28$, $p = 0.083$, partial $\eta^2 = 0.125$). Supplementary Figure 2.1 shows the results of the without-ICA analysis in the same format as Figure 3.2.



Supplementary Figure 2.1. Event-related potentials without ICA analysis. A: Grand-average topographic maps from the four conditions (vertical reflection, horizontal reflection, vertical translation, and horizontal translation) averaged over the 250–1,000 ms time window. B: Difference plots derived from this data. Electrodes used for analysis are highlighted with a gray dot. C: Grand-average ERP waves from left posterior electrodes (O1, PO3, and PO7) in different conditions. D: Equivalent data from right posterior electrodes (O2, PO4, and PO8).

For the ERD, there were again correlations between with and without-ICA versions of the data ($r = 0.86$ to 0.96). The original main effect of Hemisphere was still apparent in the no-ICA analysis ($F(1,23) = 5.93$, $p = 0.023$, $\text{partial } \eta^2 = 0.205$), however the main effect of orientation was considerably reduced ($F(1,23) = 2.24$, $p = 0.148$, $\text{partial } \eta^2 = 0.089$). This effect can thus be considered less robust than the other findings of this work. Supplementary Figure 2.2 parallels original Figure 3.3.

Topographic plots (400 to 1000 ms, 10-14 Hz)



Supplementary Figure 2.2. Event-related desynchronization without ICA analysis. A–D: Scalp distribution of 10–14 Hz powers from 400 to 1,000 ms poststimulus onset. The analysis focused on posterior desynchronization (blue on these figures). Electrodes used for analysis are highlighted with a gray dot. E, F: Time frequency spectrograms from left and right posterior electrode clusters.

9. References

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