



Event related potentials (ERP) reveal a robust response to visual symmetry in unattended visual regions

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ABSTRACT

Visual symmetry at fixation generates a bilateral Event Related Potential (ERP) called the Sustained Posterior Negativity (SPN). Symmetry presented in the left visual hemifield generates a contralateral SPN over the right hemisphere and vice versa. The current study examined whether the contralateral SPN is modulated by the focus of spatial attention. On each trial there were two dot patterns, one to the left of fixation, and one to the right of fixation. A central arrow cue pointed to one of the patterns and participants discriminated its regularity (symmetry or random). We compared contralateral SPN amplitude generated by symmetry at attended and unattended spatial locations. While the response to attended symmetry was slightly enhanced, the response to unattended symmetry was still substantial. Although visual symmetry detection is a computational challenge, we conclude that the brain processes visual symmetry in unattended parts of the visual field.

1. Introduction

Visual symmetry perception is remarkable. Within the Gestalt tradition symmetry has been discussed as a grouping principle (Koffka, 1935) with a key role in perceptual organisation and image segmentation (Bertamini, 2010; Machilsen et al., 2009; Mojica and Peterson, 2014). People can detect bilateral mirror symmetry with brief presentations (Barlow and Reeves, 1979; Julesz, 1971; Locher and Wagemans, 1993). Reflectional symmetry is particularly salient for human observers (Mach, 1886) and can be seen “at a glance” (Blaise Pascal as cited in Wolfe and Friedman-Hill 1992). This suggests symmetry can be detected automatically and preattentively (Wagemans, 1995), however the exact role of attention requires further research (Treder, 2010).

In recent years, there has been a focus on investigating the neural basis of symmetry perception (Bertamini et al., 2018; Bertamini and Makin, 2014; Cattaneo, 2017). Symmetry activations have been found with fMRI, primarily in the lateral occipital complex (LOC) and other extrastriate regions, but not in V1 or V2 (Keefe et al., 2018; Kohler et al., 2016; Sasaki et al., 2005; Tyler et al., 2005; Van Meel et al., 2019). Using TMS, Bona et al. (2014) found that the LOC is causally involved in symmetry perception.

EEG research has shown that visual symmetry generates an Event Related Potential (ERP) known as the *Sustained Posterior Negativity* (SPN). Amplitude at posterior electrodes is more negative for symmetrical than for asymmetrical images after the P1 and N1 components of the visual evoked potential (Jacobsen and Höfel, 2003; Makin et al., 2012). SPN amplitude scales with the salience of different kinds of symmetry over a range of around 3.5 microvolts (Makin et al., 2016). The SPN can be generated independently in each cerebral hemisphere: Wright et al. (2017) presented patterns to either the right or left of fixation and recorded independent SPNs over the contralateral hemisphere

Moreover, the SPN is robust to experimental manipulations of task. Early studies found that an SPN is present when participants attend to objective regularity or subjective beauty (Höfel and Jacobsen, 2007a), and that the SPN is unchanged when participants deliberately misreport responses (Höfel and Jacobsen, 2007b). More recently, we have compiled data from 41 SPN projects conducted at the University of Liverpool into a public database (<https://osf.io/2snkj/>). Combined analysis suggests that stimulus properties are the main determinant of SPN amplitude, and task is less important (Makin et al., 2022). The SPN response is reduced, but not abolished, when participants attend to other stimulus dimensions (Makin et al., 2020). In this sense, perceptual

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organization is automatic and does not require attention.

Behavioral studies have specifically tested the role of spatial attention in symmetry perception. [Olivers and van der Helm \(1998\)](#) investigated this with a classic visual search paradigm ([Treisman and Gelade, 1980](#)). Participants were presented with arrays of 1 to 4 patterns. Their task was to discriminate whether one of the patterns was symmetrical or all were random. If symmetry is processed pre-attentively and in parallel, response time should be independent of the number of distractors. However, [Olivers and van der Helm \(1998\)](#) found that response times increased with the number of distractors, indicating serial visual search of pattern locations. They concluded that symmetry does not pop out and could not be detected in unattended regions of the visual field. In their words, “symmetry detection per se requires selective attention” (p. 1101). In a subsequent visual search study [Hulleman et al. \(2000\)](#) found

parallel search for concave cusps, but again serial search for symmetry in simple shapes.

While [van der Helm \(2010\)](#) developed an alternative explanation for the visual search results, other methods support the original conclusions. [Roddy and Gurnsey \(2011\)](#) found that mirror symmetry does not serve as an alerting function and is subject to crowding when presented in the periphery. They concluded that symmetry is not special to the early visual system and might often go unnoticed. This is consistent with results of [Kimchi et al. \(2016\)](#), who found that symmetry does not capture visual attention.

On the other hand, there is evidence in favour of automatic symmetry detection in unattended regions. [Van der Helm and Treder \(2009\)](#) found that symmetry of unattended (outer) contours influenced processing of attended (inner) contours. Meanwhile, [Driver et al. \(1992\)](#)

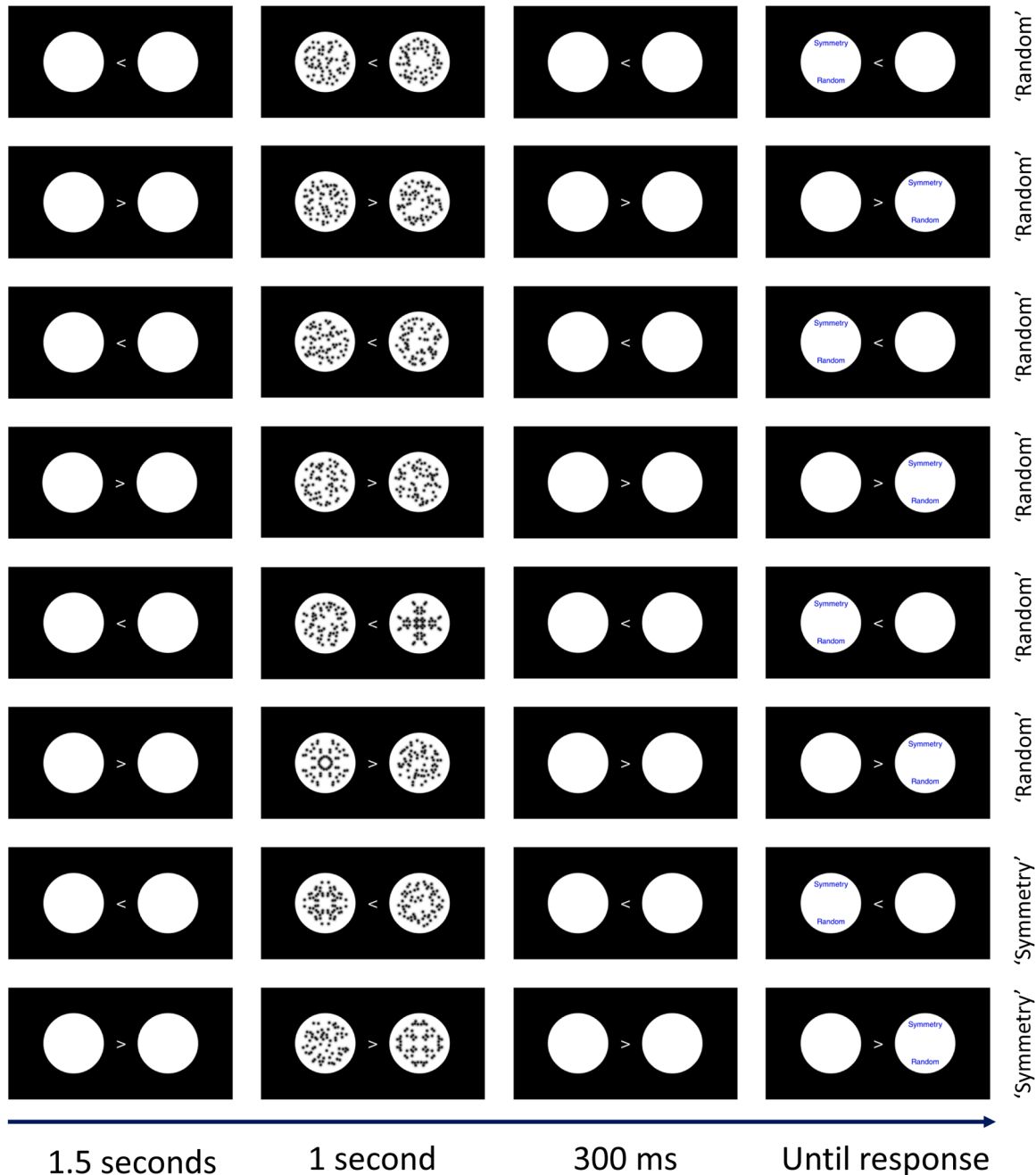


Fig. 1. Trial structure common to experiments A and B. Rows show all 8 trials presented in one experimental block; columns show different intervals on the trial timeline. The correct response (“Random” or “Symmetry”) is indicated far right. The participants understood the central cues (i.e., < or >) served as arrows pointing to the task relevant pattern.

found that symmetry still had typical effects on figure-ground organization in hemispatial neglect patients who ignored one side of objects (although brain responses to symmetry may be plastic and adjust to visual impairment, according to Casco et al. (2016). In sum, whilst symmetry is detected effortlessly and automatically when it is presented in attended regions of the visual field, there is uncertainty about whether symmetry is processed automatically in unattended regions.

We therefore conducted an EEG experiment to measure the contralateral SPN response to symmetry in covertly attended and unattended visual hemifields. On each trial, participants were presented with patterns to the left and right of fixation. In some trials, both patterns were random, in other trials one pattern was random and the other had four-fold reflectional symmetry (Fig. 1). A central arrow cue was presented before stimulus onset and through the presentation interval. This arrow cue informed participants which side was task relevant, and they then judged whether the cued pattern was symmetrical or random. We used an eye tracker to monitor central fixation, and excluded trials where participants moved their eyes.

We predicted that symmetry would generate a stronger contralateral SPN when presented in the attended hemifield (<https://aspredicted.org/9uz4b.pdf>). This is consistent with the visual search results from Olivers and van der Helm (1998), who suggested that symmetry is only discriminated once the location is attended. We were also interested in the size of the contralateral SPN response generated by symmetry in the unattended hemifield. Would unattended symmetry generate a weaker SPN, or no SPN at all?

The experiment was divided into two parts (termed experiment A and B) with 24 participants in each. Experiments A and B were identical, except that in B we included additional trials with a dot-probe manipulation. This was designed to assess whether covert spatial attention was biased towards the cued hemifield, as assumed. A blue dot probe appeared at the centre of peripheral patterns at some unpredictable time between 300 and 800 ms after stimulus onset (Fig. 2). The ERP response to the dot probe should be altered if covert attention is focused on its location (Doherty et al., 2005).

The data, analysis and experiment codes are publicly available on Open Science Framework (<https://osf.io/vmy5n/>). The EEG data is also

available at various levels of granularity as Project 24 in the SPN catalogue (<https://osf.io/2sncj/>)

2. Method

2.1. Participants

There were 48 participants (41 females, 4 left-handed, age 16–37, mean age =22.5). Half the participants completed Experiment A and half completed Experiment B. The experiment had local ethics committee approval and was completed in accordance with the 2008 declaration of Helsinki. The participants provided written informed consent before participating in the experiment.

2.2. Apparatus

EEG data was recorded continuously using a BioSemi Active-2 system. Data was collected from 64 scalp electrodes arranged according to the extended international 10–20 system. Stimuli were presented on a 53 × 30 cm LCD monitor with a refresh rate of 60HZ. The participants were held 57 cm from the monitor with a chin rest. The experiment was programmed in PsychoPy (Peirce, 2007). A 60 Hz Gazepoint infrared eye tracker was used to monitor fixation.

2.3. Stimuli

Example stimuli can be seen in Figs. 1 and 2. There were always 2 patterns, one to the left of central fixation and one to the right. Both patterns contained 64 dot elements in a white circular region with a diameter of approximately 4.4° of visual angle (dva). The rest of the screen was black. Each dot element had a Gaussian luminance mask and was approximately 0.2° in diameter. Dot position was constrained so the dots could not overlap and minimum distance between dots was 0.15°. There was an additional constraint which prevented dots falling in the very centre of the pattern.

The distance of the pattern from the central arrow cue was approximately 3.5°. Stimulus size parameters were chosen to be like those in

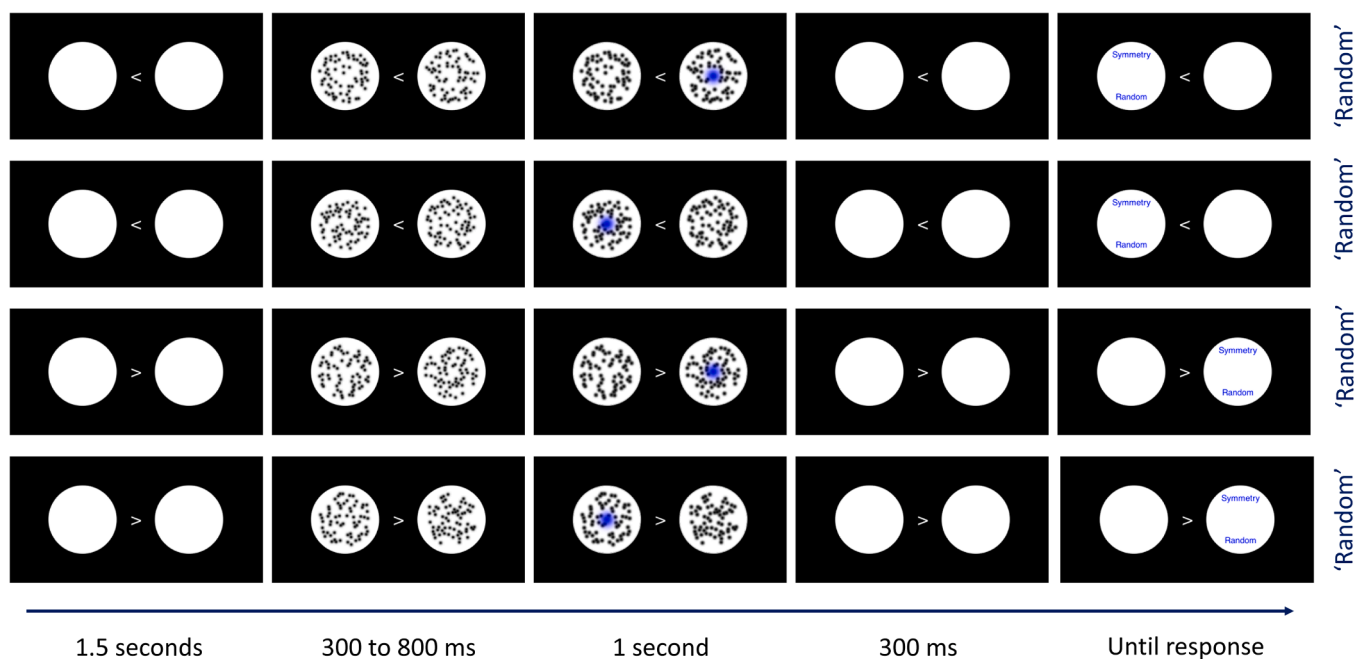


Fig. 2. Trials structure from additional dot probe trials in Experiment B. Patterns on the left and right were both random, so the correct response was always “Random”. The task irrelevant blue dot could appear in either the unattended or attended location at any time from 300 to 800 ms after stimulus onset. It then remained present for 1 s.

Wright et al. (2017). Novel images were generated for each trial, and participants were all presented with different exemplars.

2.4. Trial structure

First, we describe aspects of trial structure common to both Experiments A and B (Fig. 1). Every trial began with a 1.5 s baseline period where the empty two white disks and the arrow cue were presented. This was followed by a 1 s pattern presentation, during which the central arrow cue was still present, and then by a 300 ms second blank interval. Finally, the participant was prompted to enter judgement about whether the cued pattern was symmetrical or random. Participants entered their responses with the Y or B buttons of a standard computer keyboard: Y was used to report symmetry, B was used to report random. It is unlikely that the motor responses would have substantially altered EEG activity on the subsequent trial, and given the random trial order, there is no way this could explain systematic ERP effects.

In the dot probe trials in Experiment B, the trial structure was slightly different (Fig. 2). A blue gaussian masked dot appeared in the centre of one pattern. The blue dot probe had a visible diameter of approximately 1 dva. On dot probe trials background patterns were both random. The blue probe appeared equally in the attended or unattended locations and at a randomized interval between 300 and 800 ms after pattern onset. The blue dot was then present for another 1 s before the end of the trial. Dot probe trials thus lasted longer than other trials. These dot probe trials were not included in SPN analysis. Crucially, probes on symmetry trials were not included because the ERP response to the probe may interact with stimulus regularity, and systematic investigation of this would have increased the number of required trials to an impractical level. We therefore only presented probes on double random trials.

2.5. Procedure

The experiment began with a nine-point calibration of the Gazepoint eye-tracker and set up of the electrode cap. Experiment A consisted of 480 trials. The 8 basic trial types are shown in Fig. 4A. Half were double random trials, whilst the other half had one symmetrical and one random pattern. In half the trials the cue pointed left; in the other half the cue pointed right. These factors were fully crossed, giving 60 trials in each of the crucial conditions.

Participants first completed an eight-trial practice block, and then 60 experimental blocks. The 8 trial types shown in Fig. 1 were presented in a randomized order in each experimental block. The use of many short experimental blocks was designed to prevent long sequences of the same trial types. This encouraged participants to use the central arrow cue rather than habitually orientating covert spatial attention to the left or right. There were breaks in the experiment every two blocks (16 trials). This allowed participants to rest and the experimenter to check the electrodes and eye tracker.

In Experiment B, the same basic trials were used again, but there were an additional 240 dot probe trials, giving 720 trials in total. Thus, there were 12 trials in each block, (the same 8 trials as in Experiment A, but with 4 additional probes). Participants were told that the blue dot probe was not task relevant. They again had a break every two blocks (24 trials).

2.6. EEG recording and analysis

EEG data was recorded continuously and then processed offline using EEGLAB toolbox for MATLAB (Delorme and Makeig, 2004). In Experiment B, A faulty F5 electrode was interpolated before any further EEG data pre-processing. Data was first referenced to the scalp average, low pass filtered at 25 Hz, and then broken into epochs from -0.5 to +1 s around stimulus onset, with a -200 ms pre-stimulus baseline. Epoched data was then cleaned with Independent Components Analysis (Jung et al., 2000). The number of ICA components removed ranged from 2 to

20 in Experiment A (mean = 8.75), and 3 to 12 in Experiment B (mean = 6.5).

ERPs evoked by the dot probe in Experiment B were examined with a different analysis pipeline, starting from the same raw data files. Here we analyzed the probe trials only, with -0.5 to +0.5 epochs time locked to probe onset, with a -200 ms pre-probe baseline. ICA was again used to remove EEG artifacts and the number of components removed ranged from 2 to 8 (mean = 4.42).

The contralateral SPN was defined as mean amplitude at posterior electrodes on the opposite side to the symmetrical pattern. The posterior clusters used were (P7 PO3 PO7 O1) on the left side of the head, and (P8 PO4 PO8 O2) on the right side of the head. For each condition, amplitudes were averaged over the four electrodes in a cluster, and all time-points in an interval. The contralateral SPN was then calculated as the amplitude difference from the equivalent double random condition. The contralateral SPNs had clear early (250–350) and late sub-intervals (500–1000), so we examined these post-hoc.

Contralateral SPN amplitude was analyzed with mixed ANOVA. There were three within-subjects factors [Interval (early, late) X Attention (attend random, attend symmetry) X Hemisphere (left, right)] and one between-subjects factor [Experiment (A, B)]. There were 24 participants in each experiment.

We acknowledge that our electrode clusters and time windows were not selected a priori (<https://aspredicted.org/9uz4b.pdf>). This is admittedly not ideal, but using spatiotemporal clusters that are not centred on effects of interest is also problematic. Therefore, we focus on the post-hoc clusters, but also report the pre-registered analysis for the sake of transparency.

In Experiment B, the dot probe generated an evoked potential. We expected this to be enhanced when the probe appeared in the attended location. This was examined using a 180–220 ms post probe time window (where the positive component peaked) at the OZ electrode (where the effect was maximal).

2.7. Fixation control and trial exclusion

It is important to ensure that EEG analysis was based on trials where participants maintained central fixation. If they move their eyes to the cued pattern, we would merely be comparing neural responses to foveal and peripheral symmetry, rather than covertly attended and unattended symmetry. We therefore excluded all trials from EEG analysis where eye position shifted by more than 2.5° during the 1 s interval when stimulus was on the screen. The 2.5° criterion was chosen because it approximates the width of the gap between left and right stimuli (Fig. 4A).

Fig. 3A shows grand average eye position over time without trial exclusion. Eye position was attracted to the cued pattern, particularly around 400 ms from stimulus onset. Fig. 3B shows p values from *t*-tests comparing attend left vs attend right conditions at each time point. The tendency to move the eyes to the cued location was significant for many successive timepoints between around 200 and 600 ms. Fig. 3C and D shows that these unwanted fixation breaks were successfully removed from trials used in our EEG analysis. There were now no time points where attend left and attend right conditions differed significantly.

After excluding these trials, we also excluded any other trials where amplitude was more than +/- 100 microvolts at any electrode. We then excluded 11 participants for whom more than 50 % of trials were excluded. This left 48 participants for data analysis. An average of 21–24 % trials were excluded from each condition (Experiment A: average 26 %, min 3 %, max 48 %; Experiment B: average 19 %, min 0 %, max 45 %). Trial exclusion rate was higher than many previous SPN experiments, where it is typically around 10 %. However, we can be confident that we are only analysing EEG from trials where participants did not break fixation.

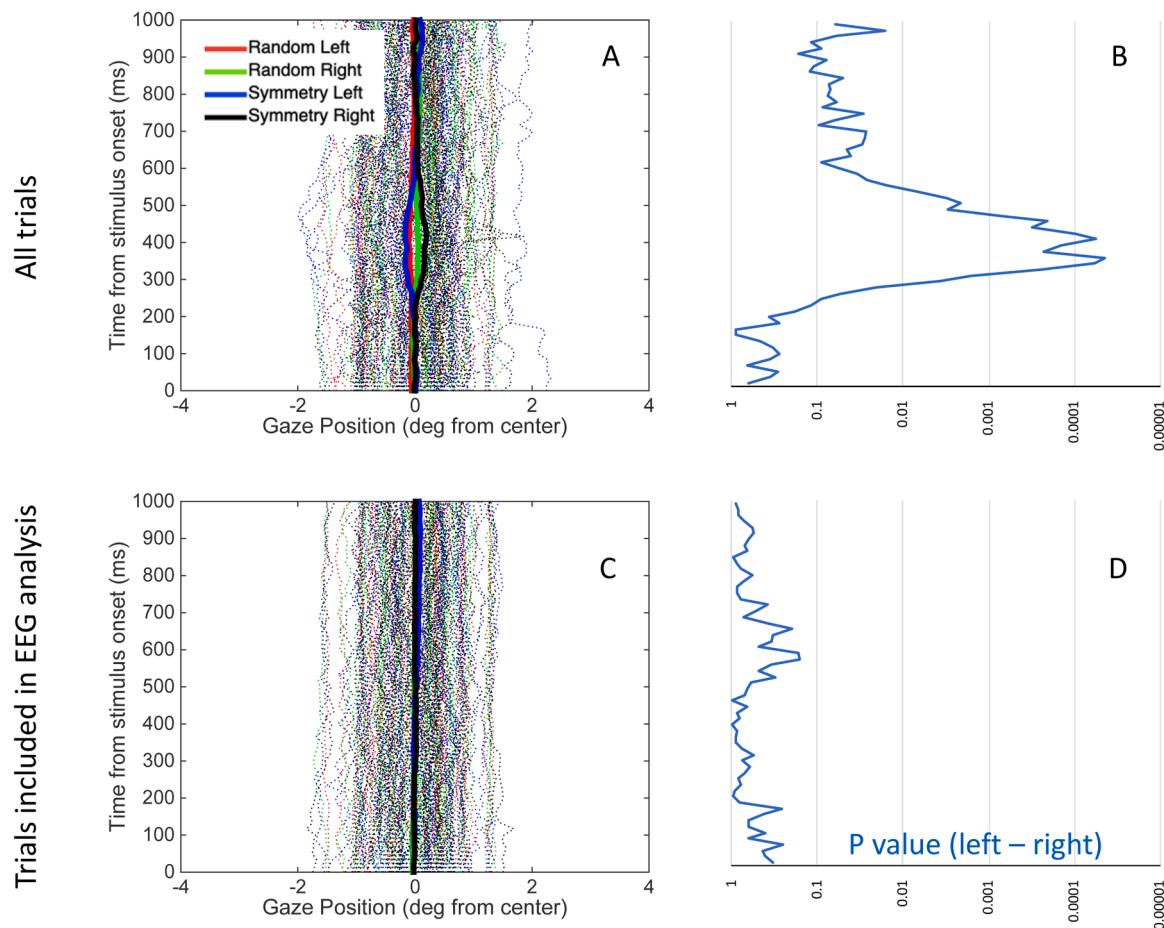


Fig. 3. Oculomotor behavior in all trials (a, b) and oculomotor behavior in the trials included in EEG analysis after fixation breaks were excluded (c, d). Left panels show grand average eye position over the 1000 ms presentation interval, superimposed on individual subject traces. Right panels show p values on a logarithmic scale from t tests comparing attend left and attend right conditions. Note that participants did sometimes break fixation and move their eyes towards the attended pattern, but these trials were removed from EEG analysis.

3. Results

Participants successfully discriminated symmetrical from random patterns at the cued location. They gave the correct answer on 88–100 % of the trials (mean = 97 %).

Symmetrical patterns generated a contralateral SPN (Fig. 4B). The contralateral SPN was slightly stronger when the symmetrical pattern was in the attended hemifield, but still substantial when it was in the unattended hemifield. The contralateral SPN waves had clear early peak (250–350 ms) and longer late interval (500–1000 ms).

The critical contralateral SPN means are shown in Fig. 5. One sample *t*-tests confirmed a significant negativity in both early and late windows, in both hemispheres, and both when symmetry was attended and unattended (minimum effect: right hemisphere, late window, attend to random, $t(47) = -2.071$, $p = .044$, $d_z = -0.299$).

A mixed ANOVA was conducted to test the SPN effects. The three within-subjects factors were Interval (early, late), Hemisphere (left, right) and Attention (attend symmetry, attend random). The between-subjects factor was Experiment (A, B). The DV was mean SPN amplitude. This revealed significant main effects of Interval ($F(1,46) = 70.818$, $p < .001$, partial $\eta^2 = 0.606$) and Attention ($F(1,46) = 5.907$, $p = .019$, partial $\eta^2 = 0.114$). The SPN was larger in Experiment B ($F(1,46) = 5.227$, $p = .027$, partial $\eta^2 = 0.102$). The only significant interaction was Hemisphere X Experiment ($F(1,46) = 4.174$, $p = .047$, partial $\eta^2 = 0.083$). This interaction is small, and difficult to interpret. There were no other effects or interactions (the largest non-significant effect was the main effect of Hemisphere ($F(1,46) = 2.064$, $p = .158$)).

Covert attention increased SPN amplitude by 0.22 microvolts in the early interval (11.2 % increase) and 0.41 microvolts in the later interval (70 % increase). When averaging across other Interval and other factors, the attentional effect was present in 31/48 participants, while the SPN itself was presented in 46/48 participants. This highlights the fact that the contralateral SPN was primarily stimulus driven, and only weakly altered by spatial attention. This is also illustrated in the topoplots in Fig. 6: The contralateral SPN is similar whether symmetry is attended or unattended.

The attentional effect was supported by an analysis that departed from the pre-registered pipeline (<https://aspredicted.org/9uz4b.pdf>). Following Wright et al. (2017), we pre-registered Experiment A, and planned to analyze different electrode clusters [P1, P3, P5, P7, PO3 and PO7 and P2, P4, P6, P8, PO4 and PO8] and time windows [200–600 ms]. This pre-registered analysis on Experiment A confirmed a significant contralateral SPNs when symmetry was in attended locations ($M = -0.59$ microvolts: $t(23) = -3.718$, $p = .001$, $d_z = -0.759$) and unattended locations ($M = -0.55$ microvolts: $t(23) = -3.264$, $p = .003$, $d_z = -0.666$). However, there was no difference between the two conditions ($t(23) = 0.572$, $p = .573$). The response to symmetry at unattended locations was thus confirmed by two analysis pipelines. However, the attentional effect is not supported by the pre-registered pipeline, although it is evident in post hoc pipeline. Given the resulting uncertainty about this effect, we replicated it in a new control experiment (described below).

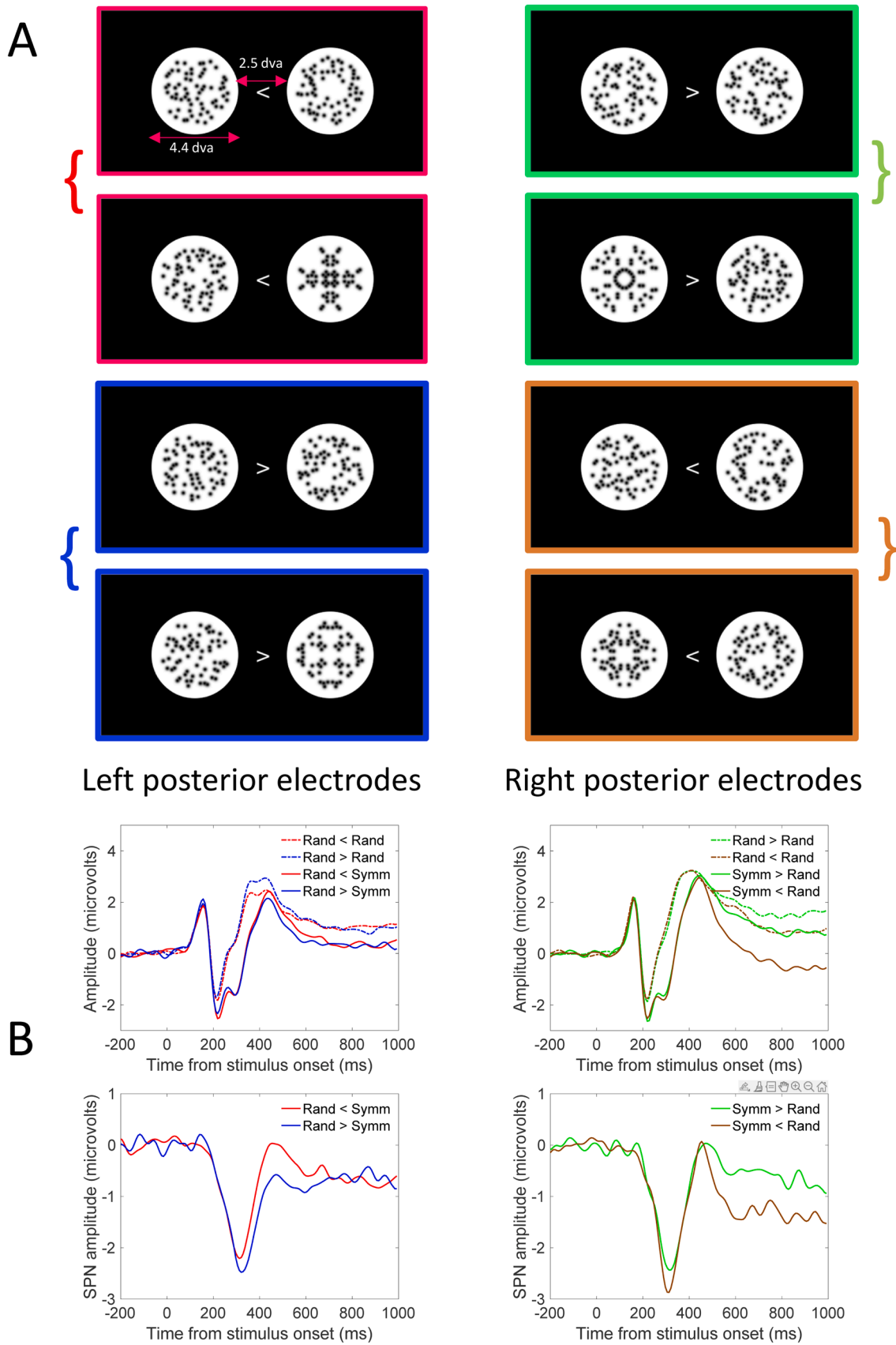


Fig. 4. (A) Stimuli used in Experiments A and B. Color coded borders were not part of the stimuli but correspond to the SPN waves in panel B. (B) ERP waves (top) and SPNs (bottom). Waves from left hemisphere cluster are shown in the left column, and waves from the right hemisphere cluster are shown in the right column. SPNs are differences from the double random condition with the same cue direction. The colored brackets in A show the comparisons used when computing the SPNs in B.

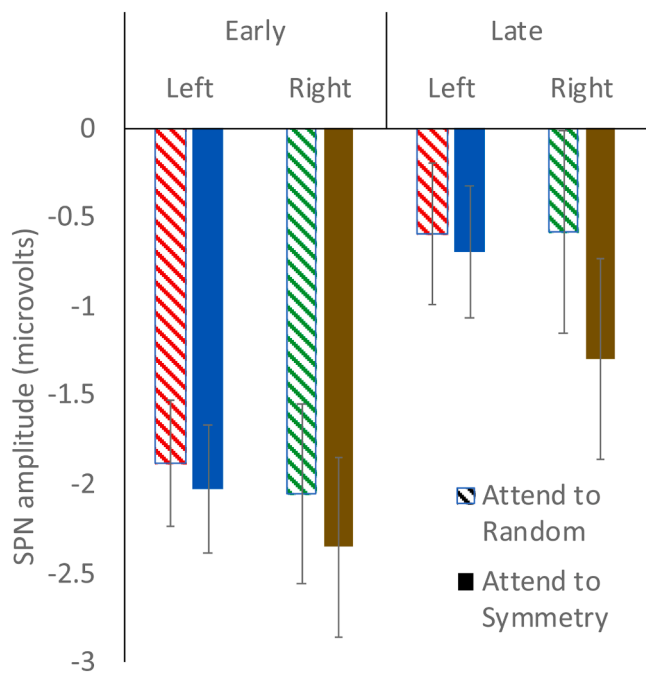


Fig. 5. Contralateral SPN amplitude in early (250–350) and late (500–1000 ms) windows, over left and right hemispheres. SPNs are differences from the double random condition with the same cue direction. The SPN was much larger in the early random window than the late window and was slightly larger when participants were attending to symmetry. color coding is matched to Fig. 4. Error bars = 95 % CI.

3.1. Dot probe response

We assume that participants moved covert spatial attention to the cued location. The dot probe manipulation in Experiment B was designed to test this assumption. We would not expect the probe to activate the visual brain regions as visual symmetry does, so there was no reason to use the same electrodes as the SPN analysis.

The probe generated a P1-like response at electrode OZ, peaking around 200 ms (Fig. 7). This peak was larger when the probe was presented at the attended location ($t(23) = 2.091, p = .048, d_z = -0.427$). This difference suggests that covert spatial attention was directed toward the cued location, as assumed. However, the marginal p value and use of post-hoc spatiotemporal parameters demand that we interpret this ERP with caution.

3.2. Control experiment

The results of Experiments A and B suggested that the brain responds to symmetry in unattended regions only slightly less than in attended regions. However, there were two weaknesses with these results. First, we used post-hoc electrodes and time windows to demonstrate attentional modulation. Second, when symmetry was unattended, participants were attending to a random pattern on the other side of the screen. It is interesting to compare these results with a baseline condition in which participants can ignore regularity of the peripheral patterns. We thus ran a control experiment with two blocks. One block was a repeat of Experiment A, which we called the ‘Attend peripheral regularity block’. In the other block, spatial attention was focused on the central region and participants discriminated the presence or absence of a blue background patch (Fig. 8). We called this the ‘Attend central color block’. The order of blocks was counterbalanced.

There were 480 trials in the Attend peripheral regularity block (as there were in Experiment A). There were also 480 analyzed trials in the Attend central color block, plus additional 240 blue oddball trials, which

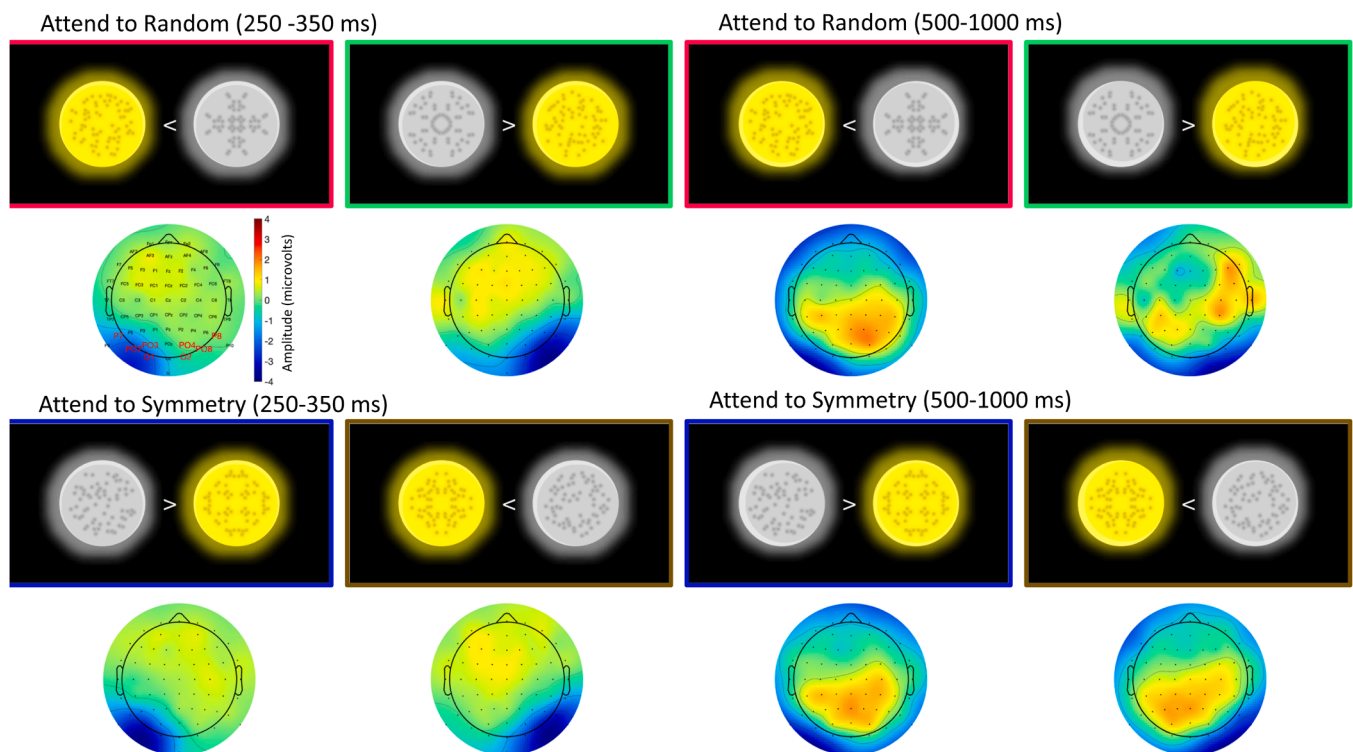


Fig. 6. Posterior SPN topography in early window (250–350 ms, left) and late window (500–1000 ms, right). The color-coded borders around the stimuli are the same as in Fig. 4A. The yellow and grey overlays illustrate the spotlight of spatial attention, focusing on the cued location. The electrodes used in analysis are highlighted top left.

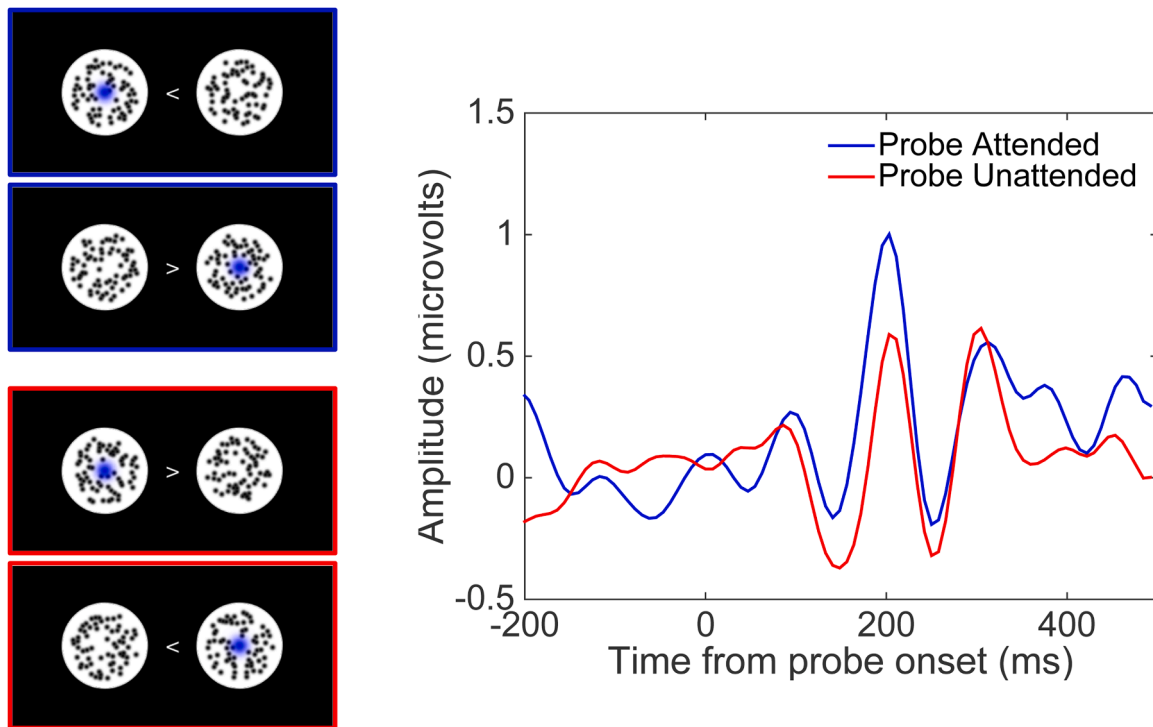


Fig. 7. VEP responses to the blue probe when it appears on top of an attended or unattended region. Zero represent probe onset, and ERPs are time-locked to probe onset.

were not analyzed. This meant that the number of analyzed trials was matched in the two blocks.

The contralateral SPN was computed in the same way as the original experiment. We now have contralateral SPN waves from three attentional conditions: (1) attend peripheral symmetry, (2) attend peripheral random, and (3) attend central color. Our predictions and analysis plan were pre-registered (<https://aspredicted.org/ec7mq.pdf>). We predicted that the contralateral SPN would be selectively enhanced in the attend peripheral symmetry condition, and the other two conditions would be reduced and similar (attend peripheral symmetry > attend peripheral random = attend central color).

Power analysis indicated that we needed 64 participants to replicate the original main effect of Attention (alpha 0.05, effect size partial $\eta^2 = 0.114$, power = 0.8). We then collected data from 75 participants, anticipating the need for replacement. However, many participants did not provide usable eye tracking and/or EEG data on the required 50 % of trials, so this control analysis was based on a sample of 39 participants, for whom at least 50 % of trials were retained.

Average trial exclusion rate was 23 % in the Attend peripheral regularity block (max = 49 %, min = 4 %) and 17 % in the attend central color block (max = 44 %, min = 3 %). On average, 9.231 ICA components were removed from the Attend peripheral regularity block (max = 17 min = 3) and 10.154 were removed from the Attend central color block (max = 20, min = 5).

Participants correctly discriminated regularity on 74.8–100 % of trials in the Attend peripheral regularity block (mean = 98.2 %), and correctly identified the presence or absence of the blue background on 97.9–100 % of trials in the Attend central color block (mean = 99.6 %).

ERP results from the control experiment are shown in Fig. 9. All six contralateral SPNs in the early window were significant (smallest effect = $t(38) = -7.155$, $p < .001$, $d_z = -1.146$). As expected, the contralateral SPN waves from the Attend peripheral regularity block were like those recorded in Experiment A. The contralateral SPN was thus larger when spatial attention was focus on the symmetrical pattern. However, the contralateral SPN was unexpectedly reduced in the Attend central color block compared to both these conditions.

Repeated measures ANOVA found a main effect of Interval ($F(1,38) = 99.660$, $p < .001$, partial $\eta^2 = 0.724$) and Attention ($F(2,76) = 10.685$, $p < .001$, partial $\eta^2 = 0.219$), and an Interval X Attention interaction ($F(2,76) = 5.232$, $p = .007$, partial $\eta^2 = 0.121$). There were no effects involving Hemisphere ($F(2,76) < 1.783$, $p > .174$). In the early 250–350 ms window, there was a large effect of Attention ($F(2,76) = 19.161$, $p < .001$, partial $\eta^2 = 0.335$), which was reduced in the later 500–1000 ms window ($F(2,76) = 2.730$, $p = .072$, partial $\eta^2 = 0.067$). In the early window, all pairwise differences were significant ($t(38) > 2.123$, $p < .041$, $d_z > 0.339$).

This analysis used 39 participants instead of the pre-registered 64 participants, because an unexpectedly high number did not meet the pre-registered 50 % trial retention threshold. An alternative approach is to compromise on the trial retention threshold rather than sample size and retain 64 participants. This is possible if we include all participants for whom more than 23 % of trials were retained. This approach is described in supplementary materials and produces very similar results.

In summary, the control experiment replicated the effect of Attention on contralateral SPN amplitude with an a priori spatiotemporal cluster. It also provides a baseline comparison condition where participants are not engaging with the regularity of peripheral patterns at all. Compared to this baseline, the contralateral SPN was always enhanced. Specifically, it was enhanced when participants directed spatial attention to a peripheral symmetrical pattern (not surprising), and it was also enhanced when they directed spatial attention to a peripheral random pattern on the opposite side of the screen (more surprising).

4. Discussion

We studied the role of spatial attention in perception of symmetry. It has been suggested that symmetry can only be detected once its location is attended (Olivers and van der Helm, 1998). In our study, we tested whether the neural response to symmetry is altered by the current focus of covert spatial attention. Results from three new experiments showed that there was a response to symmetry (SPN) in attended and unattended hemifields. In addition to this main finding, this SPN was modulated by

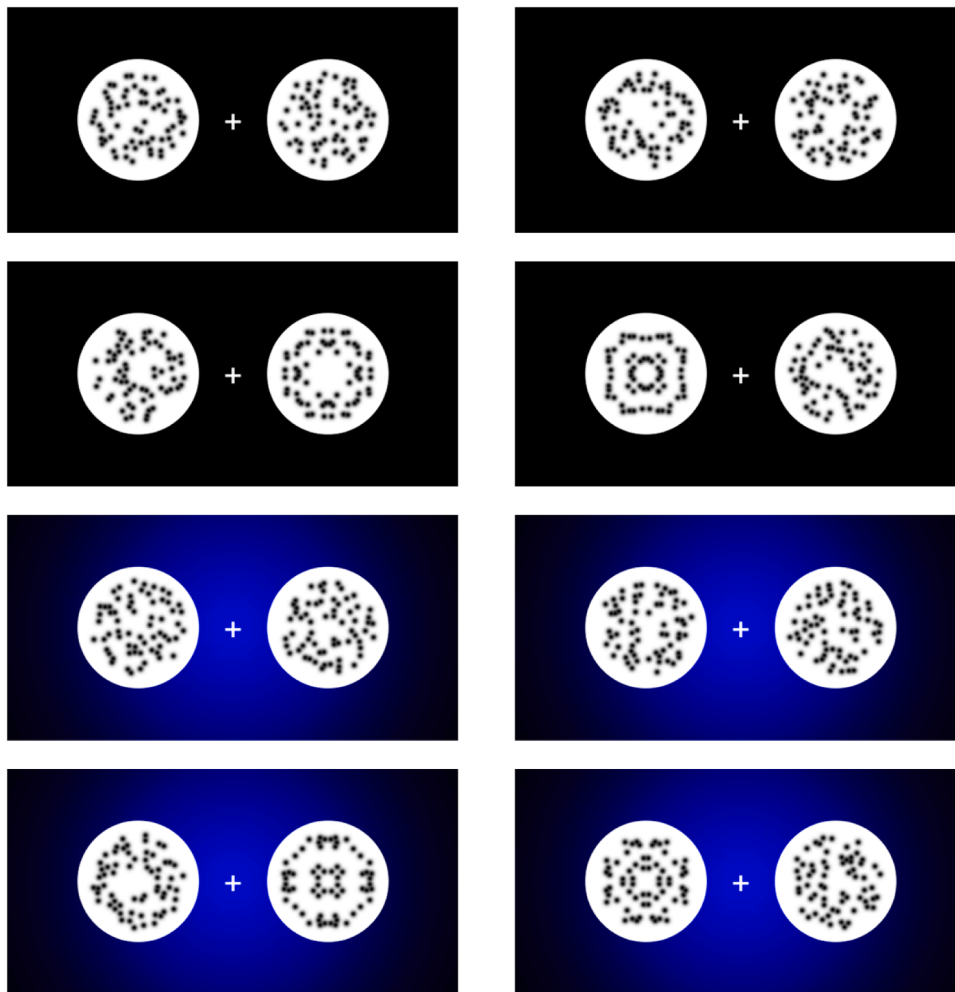


Fig. 8. Control experiment stimuli in the attend central color block. Participants completed two blocks, the *Attend peripheral regularity block* (which was the same as Experiment A) and the *Attend central color block*, where the task was to respond to a blue patch in the central region. Stimuli from the Attend central color block are shown here.

attention, and it was slightly larger when symmetry was in the attended hemifield.

The contralateral SPN was stronger in the early time window (250–350 ms) than in the late time window (500 to 1000 ms). Attention increased the SPN amplitude by 11 % in the early interval and 70 % in the later interval. Although the later effect seems large in percentage terms, its absolute magnitude (0.41 microvolts) was small when compared with other stimulus driven SPN modulations (Makin et al., 2022). Many visual features, such as motion, produce a larger neural response when presented in attended regions (Treue and Maunsell, 1996). This is apparently true of symmetry as well.

Subjective stimulus energy is often increased in attended regions, so stimuli appear brighter, faster, or more perceptually organised (Barbot et al., 2018; Carrasco and Barbot, 2019). In one study, Barbot et al. (2018) found that dot matrices appeared more organised when presented in the attended hemifield (13 % difference). This closely parallels our findings, where the SPN was larger for patterns in the attended hemifield (11 % difference in the early window).

Other research has examined the relationship between spatial attention and feature based attention. These may be partially dissociable mechanisms. For instance, Treue and Martinez-Trujillo (2007) reviewed evidence that feature attention can enhance neural responses, even when the features are located outside the spotlight of spatial attention. The relative importance of feature and spatial attention was further illustrated by our control experiment. The contralateral SPN was

weakest when participants were monitoring the presence of a blue patch at screen centre (no feature attention on regularity, no spatial attention on symmetrical region). The contralateral SPN was larger when feature attention was focused on regularity, but spatial attention was directed at the random pattern on the opposite side of the screen (feature attention on regularity, no spatial attention on symmetrical region). Finally, the contralateral SPN was largest of all when feature attention was focused on regularity and spatial attention was directed at the symmetrical pattern (feature attention on regularity, spatial attention on symmetry). This suggests feature attention does not simply enhance brain responses to features at attended spatial locations but enhances responses to these features at other locations as well.

Olivers and van der Helm (1998) claimed that symmetry can be discriminated only when its spatial location is attended. Their visual search results suggested that symmetry is not processed preattentively and in parallel across the whole visual field. This conclusion seems at least superficially inconsistent with our large symmetry response in unattended locations. To explain this, we note that Olivers and van der Helm (1998) measured a behavioral response with reaction times above 400 ms, whilst our SPN began around 250 ms. We also note that visual search tasks tap the time needed to make a binary decision about the presence of symmetry. While the extrastriate cortex extracts symmetry from anywhere in the visual field, visual search participants may only report binary judgments only once they have scanned all item locations with spatial attention.

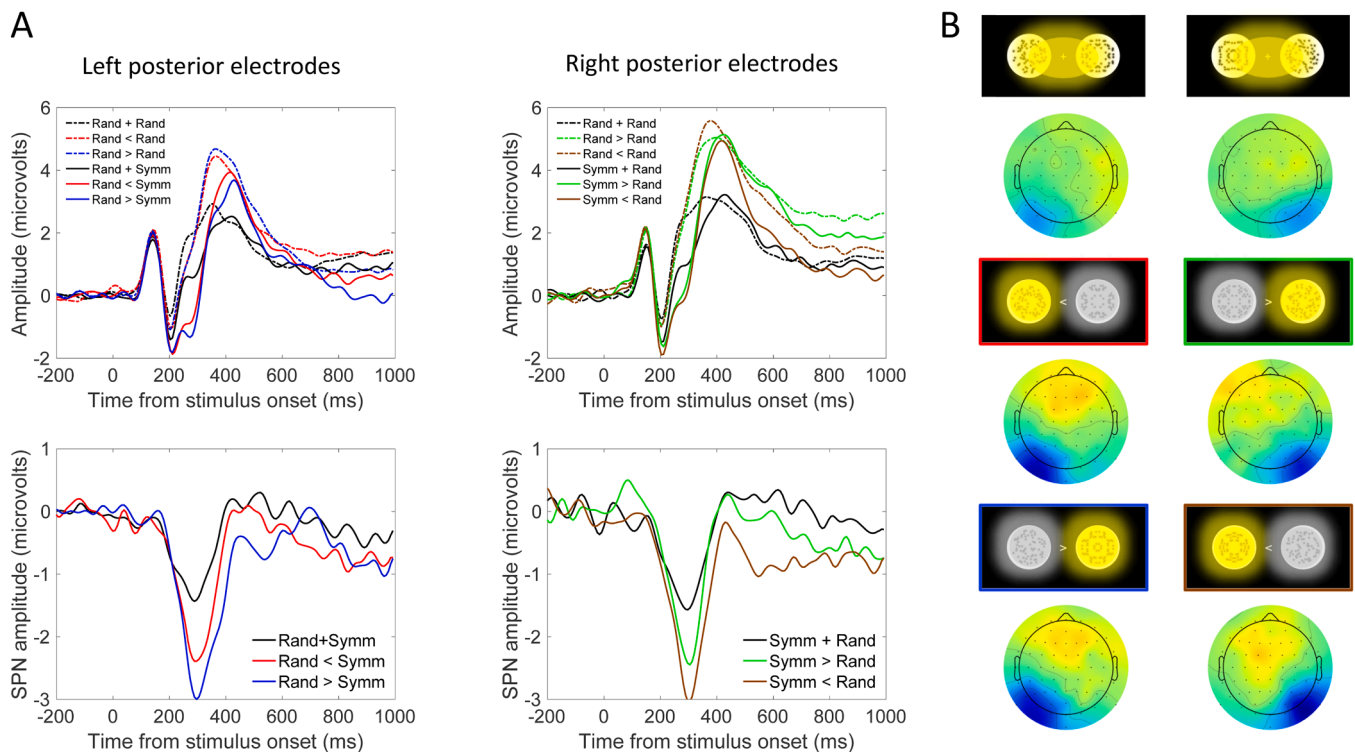


Fig. 9. Control experiment results. (A) ERP and SPN waves from left and right posterior electrode clusters. (B) Posterior SPN topography in early windows (250–350 ms). Conventions are the same as Figs. 4 and 6. The contralateral SPN was weakest when participants were attending to the presence/absence of a blue patch at screen centre (black *Rand + Symm* and *Symm + Rand* waves).

Others have also investigated the role of feature-based attention on symmetry processing. One type of study has investigated detection of minor departures from perfect symmetry in multi-color square displays. Participants apparently search for imperfections in one color at a time (e.g. no imperfections in green... check... no imperfections in red... check...). Response time thus increases with the number of colors in the display (Huang and Pashler, 2002; Morales and Pashler, 1999). Another type of study has investigated the ability to discriminate 50 % symmetry from 0 % symmetry in 2 interval forced choice tasks. Performance apparently improves when symmetry and noise dots are segregated by color (e.g. symmetry dots green and noise dots red), especially when the symmetry-carrying color is predictable (Gheorghiu et al., 2016; Wu and Chen, 2015, 2017). These studies show that symmetry detection is modulated by feature attention to color. Here we show something different: namely that feature attention to regularity can enhance brain responses to regularity, even when the regularity is at an unattended spatial location.

4.1. Alternative explanations and limitations

Finally, we consider alternative explanations for the results. First, some participants may have spontaneously moved covert attention to the task-irrelevant, uncued pattern on some trials. These spontaneous shifts probably happened but is impossible to assess their prevalence. Can spontaneous shifts explain the SPN generated by patterns in the ‘unattended’ visual hemifield? Would we have recorded an SPN to patterns in unattended regions without these unwanted spontaneous shifts?

We think this alternative explanation is unlikely because the time course of the SPN was so similar when symmetrical patterns were in the attended or unattended hemifields. Occasional redirecting of covert spatial attention to the un-cued pattern could happen at any time in the 1 s epoch, and would not produce a brain response with a precise onset. However, it is possible that attentional modulations of the SPN might be

larger if attention was more reliably fixed on the cued location.

Second, the VEP response to the dot probe was marginally significant and this analysis can only tell us something about double random trials. This manipulation alone would perhaps not be sufficient to confirm that covert attention was directed to the cued location. However, we also note that unwanted eye movements were strongly biased towards the cued location (Fig. 3). It is well known that eyes are attracted to covertly attended locations, leading to microsaccades and systematic fixation breaks (Gowen et al., 2007). This also strongly supports our assumption that participants attended to the task relevant, cued pattern more than the opposite side.

Finally, we do not know whether participants ever became conscious of the regularity of stimuli in the unattended hemifield. Given that these unattended stimuli generated a large contralateral SPN, it is likely that participants became aware of the regularity on some trials.

5. Conclusion

We predicted a stronger contralateral SPN when symmetry appeared in the attended location. This predicted effect was significant, but remarkably small. There was a large contralateral SPN generated by symmetry in both attended and unattended hemifields. Our study confirms that perceptual organisation processes still operate in unattended parts of the visual field. This is an important step forward in understanding the conditions under which perceptual organization happens. Although detection of visual symmetry is computationally challenging (Sundaram et al., 2022), it nevertheless occurs automatically outside the focus of spatial attention.

Data sharing

All ERP and behavioral data, and codes for analysis and stimulus presentation, are freely available on Open Science Framework (<https://osf.io/vmy5n/>). We are happy for other researchers to use this material.

This is also Project 24 in the SPN catalogue (<https://osf.io/2sncl/>).

CRediT authorship contribution statement

Yiovanna Derpsch: Writing – review & editing, Writing – original draft, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization. **John Tyson-Carr:** Visualization, Resources, Project administration, Investigation, Formal analysis, Data curation. **Giulia Rampone:** Data curation, Conceptualization. **Marco Bertamini:** Writing – review & editing, Resources, Conceptualization. **Alexis D.J. Makin:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

There are no conflicts of interest.

Data availability

Data is public as explained in data availability statement.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.neuroimage.2024.120568](https://doi.org/10.1016/j.neuroimage.2024.120568).

References

- Barbot, A., Liu, S., Kimchi, R., Carrasco, M., 2018. Attention enhances apparent perceptual organization. *Psychon. Bull. Rev.* 25 (5), 1824–1832. <https://doi.org/10.3758/s13423-017-1365-x>.
- Barlow, H.B., Reeves, B.C., 1979. Versatility and absolute efficiency of detecting mirror symmetry in random dot displays. *Vision Res.* 19 (7), 783–793. [https://doi.org/10.1016/0042-6989\(79\)90154-8](https://doi.org/10.1016/0042-6989(79)90154-8).
- Bertamini, M., 2010. Sensitivity to reflection and translation is modulated by objectness. *Perception* 39 (1), 27–40. <https://doi.org/10.1068/p6393>.
- Bertamini, M., Makin, A.D.J., 2014. Brain activity in response to visual symmetry. *Symmetry* 6, 975–996. <https://doi.org/10.3390/sym6040975> (Basel).
- Bertamini, M., Silvanto, J., Norcia, A.M., Makin, A.D.J., Wagemans, J., 2018. The neural basis of visual symmetry and its role in mid- and high-level visual processing. *Ann. N. Y. Acad. Sci.* 1426 (1), 111–126. <https://doi.org/10.1111/nyas.13667>.
- Bona, S., Herbert, A., Toneatto, C., Silvanto, J., Cattaneo, Z., 2014. The causal role of the lateral occipital complex in visual mirror symmetry detection and grouping: an fMRI-guided TMS study. *Cortex* 51, 46–55. <https://doi.org/10.1016/j.cortex.2013.11.004>.
- Carrasco, M., Barbot, A., 2019. Spatial attention alters visual appearance. *Curr. Opin. Psychol.* 29, 56–64. <https://doi.org/10.1016/J.COPSYC.2018.10.010>.
- Casco, C., Destefani, E., Pinello, L., Sato, G., Battaglini, L., 2016. Hyper-vision of mirror symmetry in patients with macular degeneration reflects parafoveal cortical reorganization. *Restor. Neurol. Neurosci.* 34 (1) <https://doi.org/10.3233/RNN-150562>.
- Cattaneo, Z., 2017. The neural basis of mirror symmetry detection: a review. *J. Cogn. Psychol.* 29 (3), 259–268. <https://doi.org/10.1080/20445911.2016.1271804>.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Methods* 134 (1), 9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>.
- Doherty, J.R., Rao, A.L., Mesulam, M.M., Nobre, A.C., 2005. Synergistic effect of combined temporal and spatial expectations on visual attention. *J. Neurosci.* 25 (36), 8259–8266. <https://doi.org/10.1523/jneurosci.1821-05.2005>.
- Driver, J., Baylis, G.C., Rafal, R.D., 1992. Preserved figure-ground segregation and symmetry perception in visual neglect. *Nature* 360 (6399), 73–75. <https://doi.org/10.1038/360073a0>.
- Gheorghiu, E., Kingdom, F.A.A., Remkes, A., Li, H.C.O., Rainville, S., 2016. The role of color and attention-to-color in mirror-symmetry perception. *Sci. Rep.* 6, 29287. <https://doi.org/10.1038/srep29287>.
- Gowen, E., Abadi, R.V., Poliakoff, E., Hansen, P.C., Miall, R.C., 2007. Modulation of saccadic intrusions by exogenous and endogenous attention. *Brain Res.* 1141, 154–167. <https://doi.org/10.1016/j.brainres.2007.01.047>.
- Höfel, L., Jacobsen, T., 2007a. Electrophysiological indices of processing aesthetics: spontaneous or intentional processes? *Int. J. Psychophysiol.* 65 (1), 20–31. <https://doi.org/10.1016/j.ijpsycho.2007.02.007>.
- Höfel, L., Jacobsen, T., 2007b. Electrophysiological indices of processing symmetry and aesthetics: a result of judgment categorization or judgment report? *J. Psychophysiol.* 21 (1), 9–21. <https://doi.org/10.1027/0269-8803.21.1.9>.
- Huang, L., Pashler, H., 2002. Symmetry detection and visual attention: a “binary-map” hypothesis. *Vision Res.* 42 (11), 1421–1430. [https://doi.org/10.1016/S0042-6989\(02\)00059-7](https://doi.org/10.1016/S0042-6989(02)00059-7).
- Hulleman, J., Te Winkel, W., Boselie, F., 2000. Concavities as basic features in visual search: evidence from search asymmetries. *Percept. Psychophys.* 62 (1) <https://doi.org/10.3758/BF03212069>.
- Jacobsen, T., Höfel, L., 2003. Descriptive and evaluative judgment processes: behavioral and electrophysiological indices of processing symmetry and aesthetics. *Cogn. Affect. Behav. Neurosci.* 3 (4), 289–299. <https://doi.org/10.3758/CABN.3.4.289>.
- Julesz, B., 1971. *Foundations of Cyclopean Perception*. University of Chicago Press.
- Jung, T.P., Makeig, S., Humphries, C., Lee, T.W., McKeown, M.J., Iragui, V., Sejnowski, T.J., 2000. Removing electroencephalographic artifacts by blind source separation. *Psychophysiology* 37 (2), 163–178. <https://doi.org/10.1006/000857091000003>.
- Keefe, B.D., Gouws, A.D., Sheldon, A.A., Vernon, R.J.W., Lawrence, S.J.D., McKee, D. J., Wade, A.R., Morland, A.B., 2018. Emergence of symmetry selectivity in the visual areas of the human brain: fMRI responses to symmetry presented in both frontoparallel and slanted planes. *Hum. Brain Mapp.* 39 (10), 3813–3826. <https://doi.org/10.1002/hbm.24211>.
- Kimchi, R., Yeshurun, Y., Spehar, B., Pirkner, Y., 2016. Perceptual organization, visual attention, and objecthood. *Vision Res.* <https://doi.org/10.1016/j.visres.2015.07.008>.
- Koffka, 1935. *Principles of Gestalt Psychology*. Harcourt, Brace & Company.
- Kohler, P.J., Clarke, A., Yakovleva, A., Liu, Y., Norcia, A.M., 2016. Representation of maximally regular textures in human visual cortex. *J. Neurosci.* 36 (3), 714–729. <https://doi.org/10.1523/JNEUROSCI.2962-15.2016>.
- Locher, P.J., Wagemans, J., 1993. Effects of element type and spatial grouping on symmetry detection. *Perception* 22 (5), 565–587. <https://doi.org/10.1068/p220565>.
- Mach, E., 1886. *The Analysis of Sensations and the Relation of the Physical to the Psychological*. Dover.
- Machilsen, B., Pauwels, M., Wagemans, J., 2009. The role of vertical mirror symmetry in visual shape detection. *J. Vis.* 9 (12), 1–11. [10.1167/9.12.11](https://doi.org/10.1167/9.12.11).
- Makin, A.D.J., Rampone, G., Morris, A., Bertamini, M., 2020. The formation of symmetrical gestalts is task independent, but can be enhanced by active regularity discrimination. *J. Cogn. Neurosci.* 32 (2), 353–366. https://doi.org/10.1162/jocn_a.01485.
- Makin, A.D.J., Tyson-Carr, J., Rampone, G., Derpsch, Y., Wright, D., Bertamini, M., 2022. Meta Research: lessons from a catalogue of 6674 brain recordings. *eLife* 11, e66388. <https://doi.org/10.7554/eLife.66388>.
- Makin, A.D.J., Wilton, M.M., Pecchinenda, A., Bertamini, M., 2012. Symmetry perception and affective responses: a combined EEG/EMG study. *Neuropsychologia* 50 (14), 3250–3261. <https://doi.org/10.1016/j.neuropsychologia.2012.10.003>.
- Makin, A.D.J., Wright, D., Rampone, G., Palumbo, L., Guest, M., Sheehan, R., Cleaver, H., Bertamini, M., 2016. An electrophysiological index of perceptual goodness. *Cereb. Cortex* 26, 4416–4434. <https://doi.org/10.1093/cercor/bhw255>.
- Mojica, A.J., Peterson, M.A., 2014. Display-wide influences on figure–ground perception: the case of symmetry. *Atten. Percept. Psychophys.* 76 (4), 1069–1084. <https://doi.org/10.3758/s13414-014-0646-y>.
- Morales, D., Pashler, H., 1999. No role for colour in symmetry perception. *Nature* 399 (6732), 115–116. <https://doi.org/10.1038/335700034>.
- Olivers, C.N.L., van der Helm, P.A., 1998. Symmetry and selective attention: a dissociation between effortless perception and serial search. *Percept. Psychophys.* 60 (7), 1101–1116. <https://doi.org/10.3758/bf03206161>.
- Peirce, J.W., 2007. PsychoPy – Psychophysics software in Python. *J. Neurosci. Methods* 162 (1–2), 8–13. <https://doi.org/10.1016/j.jneumeth.2006.11.017>.
- Roddy, G., Gurnsey, R., 2011. Mirror symmetry is subject to crowding. *Symmetry* 3 (4), 457–471. <https://doi.org/10.3390/sym3030457> (Basel).
- Sasaki, Y., Vanduffel, W., Knutsen, T., Tyler, C.W., Tootell, R., 2005. Symmetry activates extrastriate visual cortex in human and nonhuman primates. *Proc. Natl. Acad. Sci. U. S. A.* 102 (8), 3159–3163. <https://doi.org/10.1073/pnas.0500319102>.
- Sundaram, S., Sinha, D., Groth, M., Sasaki, T., Boix, X., 2022. Recurrent connections facilitate symmetry perception in deep networks. *Sci. Rep.* 12 (1) <https://doi.org/10.1038/s41598-022-25219-w>.
- Treder, M.S., 2010. Behind the looking glass: a review on human symmetry perception. *Symmetry* 2, 1510–1543. <https://doi.org/10.3390/sym2031510> (Basel).
- Treisman, A.M., Gelade, G., 1980. A feature-integration theory of attention. *Cogn. Psychol.* 12 (1), 97–136. [https://doi.org/10.1016/0010-0285\(80\)90005-5](https://doi.org/10.1016/0010-0285(80)90005-5).
- Truee, S., Martinez-Trujillo, J.C., 2007. Attending to features inside and outside the spotlight of attention. *Neuron* 55 (2). <https://doi.org/10.1016/j.neuron.2007.07.005>.
- Truee, S., Maunsell, J.H.R., 1996. Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 382 (6591), 539–541. <https://doi.org/10.1038/382539a0>.
- Tyler, C.W., Baseler, H.A., Kontsevich, L.L., Likova, L.T., Wade, A.R., Wandell, B.A., 2005. Predominantly extra-retinotopic cortical response to pattern symmetry. *NeuroImage* 24 (2), 306–314. <https://doi.org/10.1016/j.neuroimage.2004.09.018>.
- van der Helm, P.A., 2010. Weber-Fechner behavior in symmetry perception? *Atten. Percept. Psychophys.* 72 (7), 1854–1864. <https://doi.org/10.3758/app.72.7.1854>.

- van der Helm, P.A., Treder, M.S., 2009. Detection of (anti)symmetry and (anti)repetition: perceptual mechanisms versus cognitive strategies. *Vision Res.* 49 (23), 2754–2763. <https://doi.org/10.1016/j.visres.2009.08.015>.
- Van Meel, C., Baeck, A., Gillebert, C.R., Wagemans, J., Op de Beeck, H.P., 2019. The representation of symmetry in multi-voxel response patterns and functional connectivity throughout the ventral visual stream. *NeuroImage* 191, 216–224. <https://doi.org/10.1016/j.neuroimage.2019.02.030>.
- Wagemans, J., 1995. Detection of visual symmetries. *Spat. Vis.* 9 (1), 9–32. <https://doi.org/10.1163/156856895x00098>.
- Wolfe, J.M., Friedman-Hill, S.R., 1992. On the role of symmetry in visual search. *Psychol. Sci.* 3 (3) <https://doi.org/10.1111/j.1467-9280.1992.tb00026.x>.
- Wright, D., Makin, A.D.J., Bertamini, M., 2017. Electrophysiological responses to symmetry presented in the left or in the right visual hemifield. *Cortex* 86, 93–108. <https://doi.org/10.1016/j.cortex.2016.11.001>.
- Wu, C.C., Chen, C.C., 2015. The symmetry detection mechanisms are color selective. *Sci. Rep.* 4 (1), 3893. <https://doi.org/10.1038/srep03893>.
- Wu, C.C., Chen, C.C., 2017. The integration of color-selective mechanisms in symmetry detection. *Sci. Rep.* 7, 42972. <https://doi.org/10.1038/srep42972>.