



The response to symmetry in extrastriate areas and its time course are modulated by selective attention



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ABSTRACT

Neurophysiological studies have shown a strong activation in visual areas in response to symmetry. Electrophysiological (EEG) studies, in particular, have confirmed that amplitude at posterior electrodes is more negative for symmetrical compared to asymmetrical patterns. This response is present even when observers perform tasks that do not require processing of symmetry. In this sense the activation is automatic. In this study we test this automaticity more directly by presenting stimuli that contain both symmetry and asymmetry, as overlapping patterns of dots of different colour (black and white). Observers were asked to respond to symmetry in only one of the two colours. If feature-based attention has no role the response should depend on properties of the image. If attention fully filters only the relevant colour the response should depend on properties of the relevant colour only. Neither of these models fully explained the data. We conclude that selective attention does modulate the neural response to symmetry, however we also found a significant contribution from the irrelevant pattern.

1. Introduction

The human visual system is sensitive to image regularity, and in particular 2D patterns of symmetry. Neurophysiological studies using different methodologies have shown symmetry activations in ventral, lateral and dorsal occipital cortex, including the Lateral Occipital Complex (LOC) (for recent reviews see Bertamini et al., 2018; Cattaneo, 2017). In this study we use a well-established event related potential (ERP) procedure to test the role of selective attention. Stimuli were dot patterns divided in two sets, one white and one black. Observers were asked to detect the presence of symmetry within one set. That is, only dots of one colour were relevant for the task. In the next part of the introduction we review the literature, and then set out specific hypotheses about how attention to colour modulates the neural response to symmetry.

In fMRI studies, the symmetry response has been defined as a contrast between activation when symmetry is present in the image, and activation when symmetry is absent. For example, in Sasaki et al. (2005) a symmetry response was detected using fMRI in extrastriate regions including V3A, V4, V7 and in the LOC. Moreover, the LOC activation scaled with the proportion of symmetric dots in the image. TMS studies have found that disruption of the LOC slows symmetry

perception (Bona et al., 2014, 2015). Electrophysiological studies have reported a difference in posterior event-related potentials (ERP) when symmetry is present in the image and when symmetry is absent. The ERP is more negative for symmetry, this negativity starts after the P1 and N1 components and is sustained over several hundred milliseconds. This component has been called Sustained Posterior Negativity or SPN (Bertamini & Makin, 2014; Jacobsen & Höfel, 2003; Norcia, Candy, Pettet, Vildavski, & Tyler, 2002; Wright, Mitchell, Dering, & Gheorghiu, 2018). Supporting the claim that the SPN is an index of symmetry processing, Palumbo et al. (2015) confirmed that its amplitude scales with the relative amount of symmetry to noise in the stimulus. SPN amplitude also correlates with salience of different symmetry types (Makin et al., 2016). Moreover, Wright et al. (2018) have documented that the activation is highly sensitive to the luminance matching of the elements across the symmetry axis.

Therefore, converging evidence from studies using fMRI, EEG, and TMS has identified an extended network of extrastriate areas that are active in response to image symmetry. Importantly for our study, Sasaki et al. (2005) reported that the response was automatic in the sense that was present also when participants did not have to respond to symmetry. A more recent fMRI study by Keefe et al. (2018) has confirmed this finding. In other words, the symmetry activation is present even if

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observers are performing a task in which symmetry is not relevant. This automatic activation has been documented also in a series of SPN studies (Höfel & Jacobsen, 2007; Jacobsen & Höfel, 2003; Makin, Rampone, Pecchinenda, & Bertamini, 2013; Makin, Rampone, Wright, Martinovic, & Bertamini, 2014; Makin et al., 2020; Kohler et al., 2016; Wright et al., 2017).

Makin et al. (2013) compared SPN when participants were discriminating regularity type or looking out for rare oddball trials, and they found them to be similar. The same result has been found when observers judged the symmetry of the pattern and when they judged its colour (Makin et al., 2015). Moreover, Höfel and Jacobsen (2007) found the SPN even when participants deliberately misreported their responses to symmetry.

Recently, Jacobsen et al. (2018) reanalysed data from Jacobsen and Höfel (2003). Observers engaged in either a beauty evaluation task or a symmetry task. In the original study no significant SPN activation was present when participants responded to beauty. This is an interesting case because symmetry is relevant for both tasks, and the comparison is between a detection and an evaluation. The reanalysis confirmed the presence of a symmetry-driven SPN to symmetric patterns in both tasks. However, this SPN was modulated by task and was stronger during symmetry detection. This study also highlights that settings and parameters of the data analysis, such as choice of electrodes and reference, can affect results.

Kohler et al. (2016) used a steady-state visual evoke potential (SSVEP) paradigm to study perception of symmetry. These studies confirmed that the extrastriate symmetry response can be isolated (in the amplitude of odd harmonics) and that this response is present even during passive viewing (see also Alp, Kohler, Kogo, Wagemans, & Norcia, 2018; Norcia et al., 2002; Oka, Victor, Conte, & Yanagida, 2007).

In their review in 2014, Bertamini and Makin (2014) summarised the evidence and concluded that the neural response to symmetry is automatic. This means that when symmetry is present in the image a neural response (and an SPN) is *always* generated. The converse is not necessarily true. Images that imply symmetry, for example when symmetry is distorted by perspective, *can* generate the symmetry-specific neural response. This second case, however, is not automatic and depends on an active engagement by the observer. That is, the SPN is generated for slanted images if the task requires a classification of the stimulus as symmetric or asymmetric (Makin et al., 2015) and a similar principle applies for fMRI activation (Keefe et al., 2018). Another case of symmetry implied but not present in the image is when parts of the patterns are presented at different points in time. The visual system can, when observers attend to symmetry, respond to the regularity specified in the integrated whole (Rampone et al., 2019).

So far, therefore, the automaticity aspect has been studied by comparing different tasks, or with passive viewing. However, observers could spontaneously notice and classify symmetry even when the task does not mention symmetry explicitly. In other words, when responding to another dimension, such as colour, there is no need to ignore symmetry. A more direct approach is to present relevant and irrelevant pattern information within the same image. If attention acts like a filter, the neural response to symmetry will be determined only by the symmetry of the relevant pattern. Conversely if the neural response is entirely stimulus driven, both the relevant and the irrelevant patterns will determine the neural response.

Early theories proposed that attention acts as a filter for incoming information (Broadbent, 1958). Although we now know the limits of the filter metaphor, selection is still a defining aspect of attention. Moreover, it is now well established that attention affects fairly basic visual processes, such as contrast discrimination and visual acuity (Carrasco, 2011). These findings are consistent with evidence of attention modulation of activity at many levels, including V1. In turn, early visual areas are likely to be affected by feedback from other extrastriate areas (Reynolds et al., 1999). One mechanism that can explain

increased acuity is a change in receptive field size: Neurophysiological studies with monkeys have shown that endogenous attention can shrink the size of receptive fields in areas V4 and MT (Anton-Erxleben, Stephan, & Treue, 2009; Connor, Preddie, Gallant, & Van Essen, 1997).

In addition to selection of regions of space, attention can also be feature-based or object-based. For example, in a classic paper on object-based attention Duncan (1984) presented images of a box and a line on top of each other. Judgments concerning the same object were possible simultaneously without loss of accuracy, whereas judgments concerning different objects were not. To study feature attention many studies have manipulated colour. Moran and Desimone (1985) for example demonstrated that firing rate in area V4 is driven mainly by the task-relevant stimulus colour. The stimuli were two bars of different colours. The selective nature of visual attention for objects and features has been confirmed in human electrophysiological studies (e.g., Valdes-Sosa et al., 1998). Müller et al. (2006) used steady-state visual evoked potentials and presented intermingled red and blue dots that flickered at different frequencies. An enhanced amplitude of the corresponding SSVEP was recorded when observers attended to the red or to the blue set.

Selectivity to colour has been studied in the case of perception of bilateral symmetry. Morales and Pashler (1999) compared patterns with two versus four colours and described a cost in accuracy when there were more colours. Symmetry in these multi-colour patterns is detected by switching attention from one colour to another, extracting separate signals. Gheorghiu et al. (2016) tested additional conditions, and in particular the role of segregation by colour or luminance. They concluded that matching colour or luminance of elements in reflected positions is important, with a cost for mismatches, but segregation in colour sets was beneficial only when observers could direct their attention to the relevant colour. This again demonstrates the important role of feature-selective attention in perception of symmetry.

Wright et al. (2018) used stimuli with a mix of elements of different colours, or different luminance. They confirmed that the SPN response is related to the amount of symmetry matches, independently of how many different colours were present. This response, however, was reduced in the case of a mismatch in colour or luminance (anti-symmetry). They concluded that for symmetry (matching elements), detection mechanisms pool signals that originate from different colours/luminance into a single channel.

2. Posterior negativity and symmetry

Starting from the work by Jacobsen & Höfel, 2003; Norcia et al., 2002, the sustained negativity is a well-documented ERP component associated with symmetry. There are other components that are negative and posterior. Some also are known to play a role in deployment of attention. In particular there is a sustained posterior contralateral negativity (SPCN) and an N2 posterior contralateral negativity (N2pc) (Girelli & Luck, 1997; Jolicoeur, Brisson, & Robitaille, 2008; Klaver et al., 1999). These are not directly comparable with the SPN in that they are computed as difference between the signals in the two hemispheres. Therefore, they specifically relate to the deployment of visual-spatial attention to one location. A similar consideration applies to the early directing attention negativity (EDAN) (Nobre, Sebestyen, & Miniussi, 2000).

Another negative component is sensitive to a change in stimulus category and is called the mismatch negativity (MMN), in cases of visual stimuli visual MMN or vMMN) (Näätänen et al., 2005; Czigler, 2007, 2014). This mismatch negativity emerges when there is a violation of a regularity. The paradigm relies on presentation of a stream of stimuli belonging to a category, placed outside the focus of attention. After the pattern is established, deviant stimuli are presented that do not belong to the category. In a study by Kecskés-Kovács et al. (2013) the stimuli were symmetric or random black and white matrices. Random deviant stimuli within a stream of symmetric stimuli elicited the vMMN.

However, the vMMN was not present for symmetric deviant stimuli within a stream of random stimuli. The authors suggest that random stimuli do not create a perceptual category, and therefore the symmetric deviant did not break such category. The vMMN is a difference computed between similar stimuli (e.g. standard symmetry - deviant symmetry). This avoid problems of comparing physically different stimuli. However, this makes a direct comparison with the SPN impossible as the SPN is by definition a difference between physically different stimuli (symmetry-random). We will return to the issue of attention modulation as indexed by different ERP components in the final discussion.

3. A study with overlapping patterns

To study the role of feature-based attention on the neural response to symmetry we developed the following procedure. A configuration of 124 dots was presented for 1000 ms on a grey background. Half of the dots were white and the other half black. Either of these two sets could form a symmetrical pattern. For some observers the task was to pay attention and report whether the white pattern was symmetrical, ignoring the black pattern. For other observers the task was to pay attention and report whether the black pattern was symmetrical, ignoring the white pattern. This task of reporting symmetry was designed to be easy. We use labels in which the first and second letters specify the symmetry (S) or asymmetry (A) in the attended and unattended patterns respectively. Therefore, we have four conditions: SS, SA, AS, and AA. However, as the SPN is defined as a difference wave with respect to the response to asymmetry, the AA condition will be the baseline against which we evaluate the other three conditions Figs. 1 and 2.

In terms of the recorded ERP, there should be an SPN when symmetry is in the attended colour. If symmetry is processed automatically, there should also be an SPN when symmetry is in the unattended colour. Conversely, if symmetry is only processed in the attended colour, SS should equal SA, and there should be no SPN at all for AS. As perception of regularity is affected by contrast effects (Sun et al., 2019) SS and SA may diverge also for reasons that do not relate exclusively to attention. However, a particularly interesting comparison is that between the two conditions in which half of the dots are placed in a symmetrical configuration: SA and AS. Here if we ignore the task the

information in the image is the same.

In this task symmetry is always relevant, it is therefore unlike a procedure in which observers are responding to an orthogonal dimension (e.g., Makin et al., 2015; Keefe et al., 2018). It would be possible to device also a task in which observers are presented with these overlapping stimuli and are asked to respond only to the pattern of one colour with respect to another dimension. This manipulation is not included in the present study. With the current procedure we focus only on the issue of whether visual attention to symmetry can select information based on a feature (colour), and on the effect of this selection on the neural response to symmetry.

We predict a modulation of the SPN in which the largest amplitude is present for SS, a reduced amplitude is present for SA, and a much-reduced response is present for the AS condition. This follows from the hypothesis that some activation in response to symmetry in the image is generated automatically. We defined and registered a relevant time window based on previous studies (<https://aspredicted.org/ix72a.pdf>). This window extends between 300 and 1000 ms. This analysis focuses on the SPN, we predict that there will not be significant effects for other early visually evoked components.

4. Methods

4.1. Participants

Twenty-two participants took part in the study (17 females, 5 males, mean age 24, age range 18–48). They had normal or corrected to normal vision and were naive with respect to the experimental hypothesis. The study had local ethics committee approval (Health and Life Sciences Research Ethics Committee N4813) and was conducted in accordance with the principles of the 2008 Declaration of Helsinki. For eleven participants the attended colour was white, for the other eleven it was black.

5. Stimuli

The stimuli were generated and presented using Python and PsychoPy (Peirce, 2009), and presented on a LCD monitor, at 60 Hz frame rate and 1920 × 1080 resolution. All stimuli were presented in

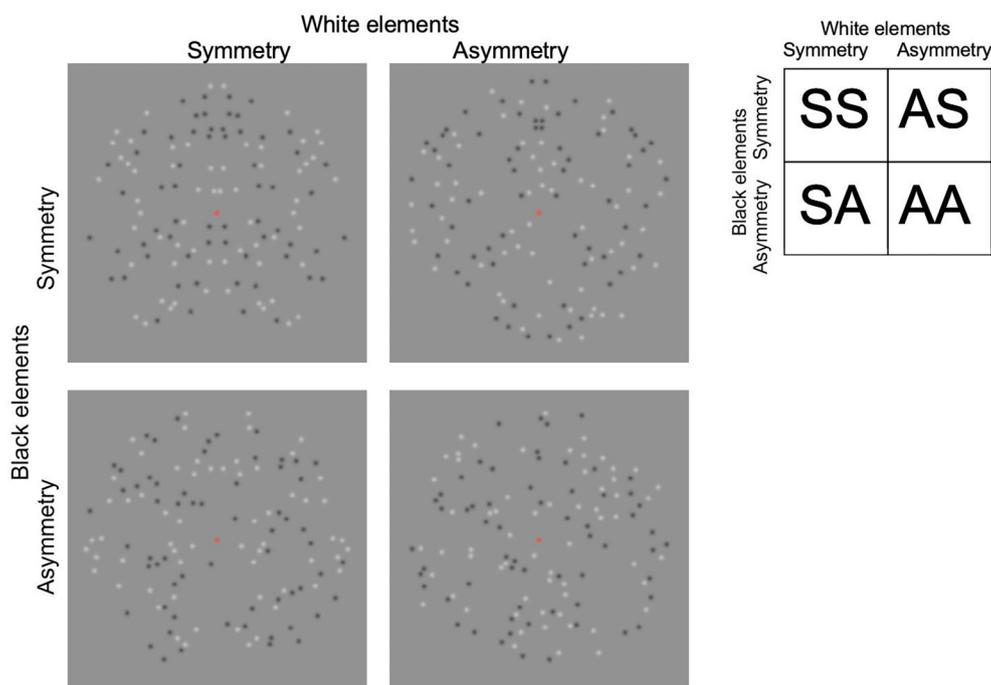


Fig. 1. Combination of symmetry and asymmetry for the two sets of elements. Symmetry could be present in both sets (top left), in only one of the colour sets, or in neither (bottom right). The table on the right shows the conditions for a participant who is attending to white. For a participant attending to black, AS and SA would be reversed.

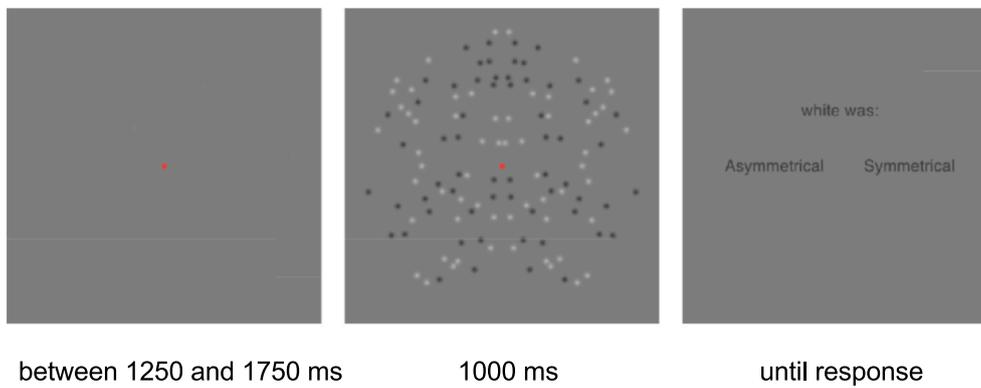


Fig. 2. Trial structure. A fixation mark was on the screen for a variable interval (between 1250 and 1750 ms). This was followed by the stimulus. After 1000 ms the stimulus was replaced by a response screen. The left and right location of the keys that corresponded to symmetry and asymmetry was randomly varied between trials to avoid early motor responses.

the centre of the monitor on a mid-gray background with mean luminance of 39 cd/m^2 .

There were always 124 Gaussian dots within a circular region with a diameter of 11.4 degrees. The size of each dot was 0.46 degrees (diameter), with a gaussian luminance mask with a standard deviation of 1/6 of the diameter. Dot position was constrained so the dots could not overlap using a minimum distance between centres of 0.5 degrees. White dot had a maximum luminance of approximately 84 cd/m^2 and black dots of 14 cd/m^2 .

6. Apparatus and procedure

Participants were tested individually. The experiment was conducted in an electrically shielded room, participants used a chinrest positioned at 57 cm from the monitor. EEG data were recorded continuously from 64 scalp electrodes arranged by the international 10–20 system. We used the BioSemi active-two system EEG system, sampling at 512 Hz, with 0.16 to 100 Hz bandpass filter.

Participants received instructions and started the task with 16 practice trials. After that, there were 272 experimental trials. The four conditions were balanced (68 trials for SS, SA, AS, and AA) and there was also a balanced presentation of instructions about which key to press to report the presence of symmetry. After the disappearance of the stimulus a message on the screen informed the participant to press the key on the right (using the right hand) to say symmetry and to press the key on the left (using the left hand) to say asymmetry. The message had the left and right positions reversed on an equal number of trials. During the experiment there were sixteen breaks. They provided an opportunity for the participant to rest and for the experimenter to check any electrode if necessary.

7. Analysis

Data were analysed offline using the eeglab 14.1.2b toolbox (Delorme and Makeig, 2004) in Matlab 2019b. Pre-processing was designed to be as similar as possible to previous EEG studies with visual symmetry (Makin, Wilton, Pecchinenda, & Bertamini, 2012). EEG data were re-referenced to a scalp average, and downsampled to 128 Hz. We then segmented the data into -0.5 to 1 s epochs. Independent Components Analysis (ICA) was used to remove oculomotor and other artefacts (Jung et al., 2000). After ICA, trials where amplitude exceeded ± 100 μV at any electrode were excluded. We defined and registered a relevant time window based on previous studies of the SPN (<https://aspredicted.org/ix72a.pdf>). This window extends between 300 and 1000 ms. We did not make predictions for other early visually evoked components.

8. Results

8.1. Behavioural results

Responses were coded as correct or incorrect. Overall level of performance was high (94% correct) and consistent across participants (range from 85% to 98%). Differences between the four conditions were small: 98% for SS, 87% for SA, 94% for AS, and 96% for AA. In the ERP analysis error trials were excluded.

9. ERP analysis

Based on the pre-registration methods, we performed the planned analysis on the following cluster of electrodes: PO7, PO8, O1 and O2. Fig. 3 shows that the event related potential for the entire interval (1000 ms), separately for the four conditions. It also shows the SPN for the three conditions tested, as the difference wave after subtracting the case in which there was no symmetry (AA).

We performed an ANOVA with the following within-subjects factors: Symmetry (SS, AS, SA), and Hemisphere (Left, Right) and one between-subjects factor: Colour attended (White, Black). The SPN amplitude was different in different Symmetry conditions ($F(2,40) = 5.13$, $p = 0.010$, $\eta_p^2 = 0.20$) but it was not affected by any other factor (Hemisphere: $F(1,20) = 3.09$, $p = 0.094$, $\eta_p^2 = 0.13$; Colour attended: $F(1,20) = 0.33$, $p = 0.567$, $\eta_p^2 = 0.01$) or interactions. If one colour had captured attention more than the other, this would have produced an interaction between Symmetry and Colour attended. However, there was no evidence of such interaction ($F(2,40) = 0.19$, $p = 0.831$, $\eta_p^2 < 0.01$).

The ANOVA does not test whether SPN amplitude is greater than zero. Therefore, we tested this difference to establish the presence of the SPN in each condition. This difference was confirmed for SS ($t(21) = -3.91$, $p = 0.001$) and for SA ($t(21) = -3.42$, $p = 0.003$) but not for AS ($t(21) = 1.74$, $p = 0.097$).

10. Mass univariate analysis

Although ERP responses were consistent with our predictions, this analysis is spatiotemporally restricted. We therefore carried out an analysis across all electrodes and time points (Martinovic et al., 2018; Pernet et al., 2015). The analysis was conducted using permutation-based t-tests implemented in the eeglab toolbox with 5000 permutations.

Fig. 4 shows a statistical map with all electrodes and the three conditions. A criterion p value of 0.05 was used, so all areas in grey correspond to $p > 0.05$. This visualization of the SPN suggests that it was present but not to the same extent in the three conditions. It also shows that our a priori electrode choice was not ideal. The posterior activity appears to involve a larger area. Because of this reason we performed a new detailed analysis with a larger cluster of electrodes

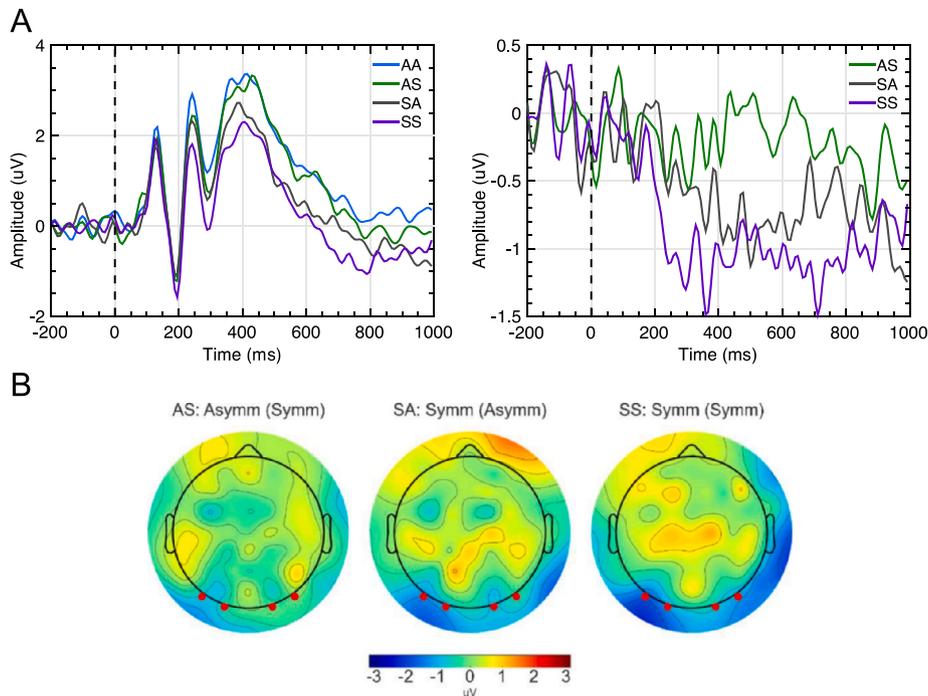


Fig. 3. (A) (Left) Grand Average ERPs for the four conditions. The time is shown with respect to stimulus onset (at zero). (Right) Sustained posterior negativity (SPN) for SS, SA, and AS. (B) Scalp maps for the three conditions.

(16). This is available in [Supplementary materials](#). Overall, it confirmed the presence of the SPN and the same pattern of results reported here.

11. Time course analysis

As planned, our analysis was limited to posterior electrodes and to the window of time between 300 and 1000 ms. We decided to further investigate the onset and the time course of the SPN and to compare the conditions. The existing literature has found that the SPN is always present following the N1 component, from approximately 250 ms. There are different levels of symmetry salience, for example in the case of different types (rotation vs. reflection) or when the proportion of symmetry elements vary. Salience typically affects the amplitude but not the onset of the SPN (Bertamini et al, 2018). However, this study is the first to test active selection of one of two subset of the elements in the image. We therefore decided to test differences in SPN onset between SS, SA and AS conditions.

We used a jackknife-based method (Miller et al., 1998) and latency estimates were retrieved using the procedure described in Smulders (2010). This was implemented using the protocol outlined by Liesefeld et al. (2016). The estimates for the onset are plotted in Fig. 5A for the conditions in which there was a significant SPN. We computed estimates for onset for each participant and condition. An amplitude threshold of 30% of the peak amplitude was used in the 300 to 1000 ms latency interval. On average the onset for the SS condition was 179 ms (SD 77) and for the SA condition it was 233 ms (SD 924). Given the amount of variability (see confidence intervals in Fig. 5) these results are consistent with our selection of 300 ms in our preregistered analysis choice. Nevertheless, we repeated the analyses with the new computed, rather than arbitrary, choice for the temporal window, and further explored the possible existence of separate components.

As a first step we carried out the statistical analysis on the data obtained from the jackknife method, based on a single window that started from 203 ms. This window was based on a 30% amplitude

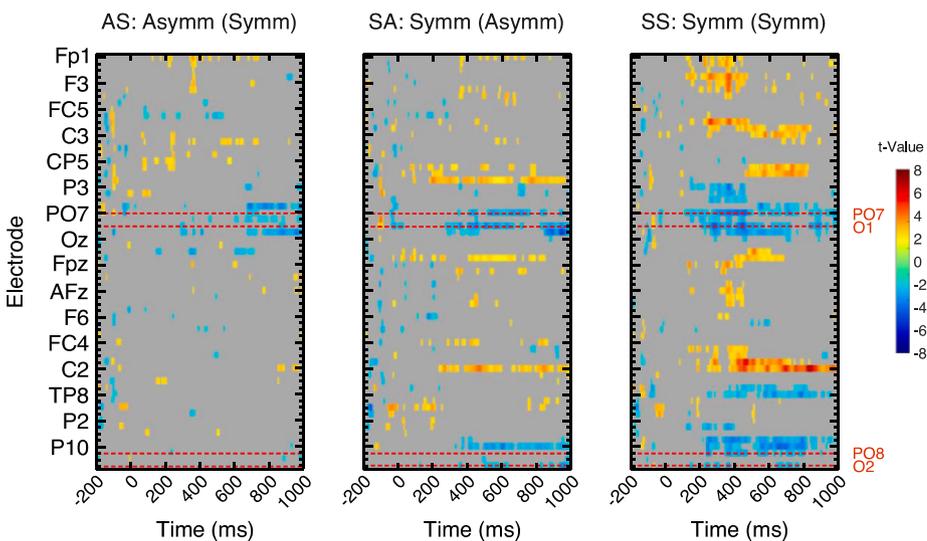


Fig. 4. Mass univariate analysis. Permutation-based one-sample t-tests for each difference wave. Positive t-values (red) indicate a change in the direction opposite the SPN pattern and negative t-values (blue) indicate a change consistent with the SPN. Time from stimulus onset is shown on the x-axis and electrodes on the y-axis. Electrodes of interest (PO7, PO8, O1, O2) are highlighted. Non-significant t-values ($p > 0.05$) are masked in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

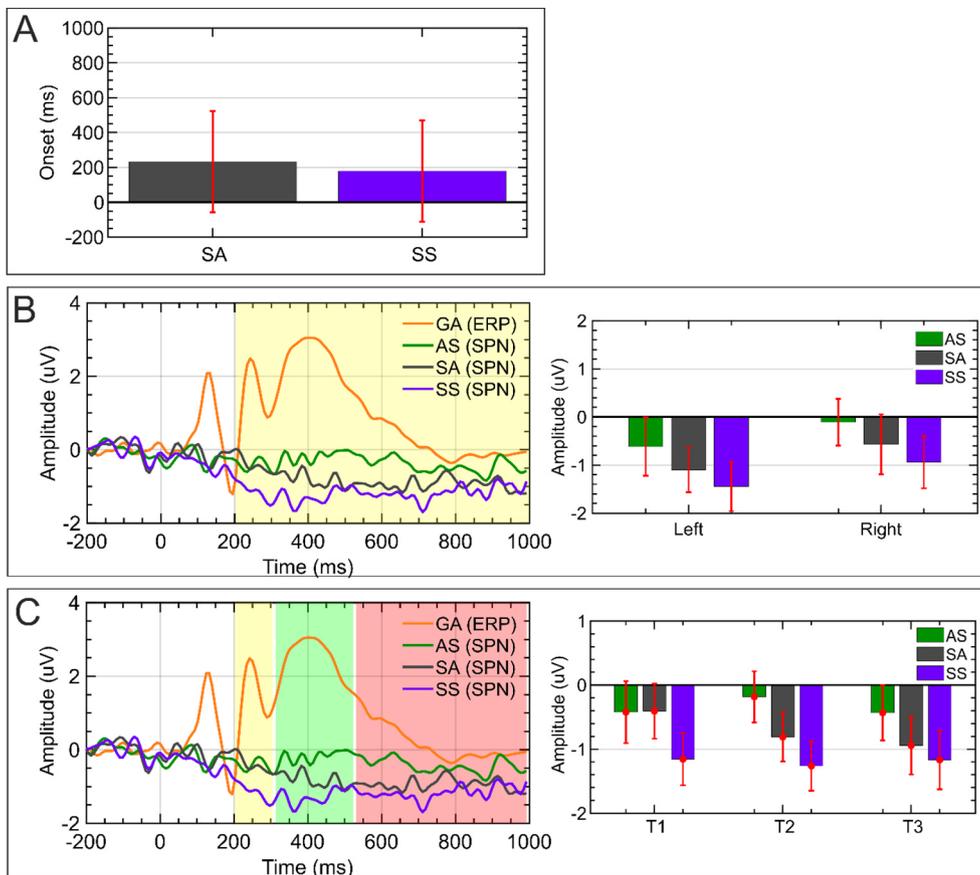


Fig. 5. (A) Mean onset of activity across subjects using an amplitude threshold of 30%. This is the onset of the SPN for conditions in which there was an SPN. (B) Onset of the SPN wave calculated using the grand average ERP. An amplitude threshold of 30% of the peak amplitude between 300 and 1000 ms was used, anchored to the peak of the N1 component. Mean activity between the onset of the SPN and the end of the epoch was calculated for each condition, as well as for each hemisphere (right). (C) The SPN interval was split into three windows. The first window was defined as the onset of the SPN, as described in (B), spanning the length of the P2 until the onset of the next component. The onset and offset of the second window were defined using a threshold of 30% of the peak amplitude between 300 and 500 ms, encapsulating the positive component occurring in this window. The third window was the interval spanning from the offset of the second window to the end of the epoch, capturing the sustained activity towards the end of the epoch. Mean activity for the difference waves is shown for each time window (right). Error bars indicate 95% within-subject confidence intervals.

threshold on the grand average ERP waveform across all conditions given this had the largest signal-to-noise ratio (see Fig. 5B). The peak of the N2 was used as an anchor for the onset of the SPN wave. A mixed ANOVA had following factors: Symmetry (SS, AS, SA), Hemisphere (Left, Right) and Colour attended (White, Black). The SPN amplitude was different in different Symmetry conditions ($F(2,40) = 5.18$, $p = 0.010$, $\eta_p^2 = 0.21$) but it was not affected by other factors (Hemisphere: $F(1,20) = 2.91$, $p = 0.103$, $\eta_p^2 = 0.13$; Colour attended: $F(1,20) = 0.27$, $p = 0.607$, $\eta_p^2 = 0.01$) or interactions. When we tested the SPN amplitude against zero we confirmed that the SPN for SS and SA were significant ($t(21) = -3.66$, $p = 0.001$) and ($t(21) = -2.93$, $p = 0.008$) but AS was not ($t(21) = 1.96$, $p = 0.063$).

Next we used the same methods to locate early, middle and late SPN components (see Fig. 5C). The onset of the early window was defined using a 30% peak amplitude threshold of the P2 component, occurring at approximately 240 ms, anchored to the peak of the preceding N2 peak. Since this P2 component did not return to baseline, the offset of the early window was defined as the onset of the middle window. The onset of the middle window was anchored to the trough occurring at approximately 280 ms and defined using a 30% amplitude threshold with respect to the peak at approximately 400 ms. The offset of the middle window was the point at which the amplitude returned to the same threshold used to define the onset. The late window was the interval between the offset of the middle window until the end of the epoch. This late window aimed to capture the sustained activation occurring toward the end of the epoch. We carried out the statistical analysis with a new factor for the three windows. A mixed ANOVA had following factors: Symmetry (SS, AS, SA), Hemisphere (Left, Right) Time Window (Early, Middle, Late) and Colour attended (White, Black). The SPN amplitude was different in different Symmetry conditions ($F(2,40) = 5.73$, $p = 0.006$, $\eta_p^2 = 0.22$) but it was not affected by other factors or interactions.

As before we tested when the SPN amplitude was greater than zero.

This time we did it for three separate windows. Early: The SPN for SS was significant ($t(21) = -3.65$, $p = 0.002$) but not for SA ($t(21) = -1.30$, $p = 0.207$) or AS ($t(21) = 1.40$, $p = 0.176$). Middle: The SPN for SS and SA were significant ($t(21) = -3.79$, $p = 0.001$) and ($t(21) = -2.96$, $p = 0.008$) but not for AS ($t(21) = 0.67$, $p = 0.508$). Late: The SPN was significant for SS ($t(21) = -3.56$, $p = 0.002$) for SA ($t(21) = -3.38$, $p = 0.003$) and for AS ($t(21) = -2.18$, $p = 0.041$).

Therefore, when we divided the epoch into three windows, we see evidence that the SPN is strongest for SS (where it emerges early) and we discovered also something interesting about the AS condition. An SPN emerged for this condition in the last window. We need to be cautious about this result for two reasons. The first is the exploratory nature of our time course analysis. These time windows were extracted from the data but are not well-established ERP components. Second, the long presentation time may imply that after participants attended to the relevant colour and were confident about the correct response their attention could move to the other colour even before the response was manually entered.

12. Discussion

We used patterns with two colours, and asked participants to focus on just one of the two and report whether the pattern was symmetrical. The target pattern was symmetrical half of the times, and the irrelevant pattern was also symmetrical half of the times. This is a typical feature attention task and therefore it allows us to compare neural responses to the target when a irrelevant pattern was present which was either symmetric or asymmetric. In particular we compare three conditions where relevant and irrelevant stimuli were: Symmetry/Symmetry (SS) Symmetry/Asymmetry (SA) and Asymmetry/Symmetry (AS). Note that in the SA and AS cases the amount of symmetry in the image is the same. An efficient selection based on feature differences would predict

similar responses in the two conditions with symmetry present in the target colour (SS and SA). It would also predict no activation when symmetry is only present in the non-target colour (AS). By contrast an automatic response to properties of the image would predict a stronger response to SS and equivalent responses to AS and SA.

We compared the sustained posterior negativity (SPN) and found that the strongest activation was in response to SS, and a weaker response was present for SA. For AS the signal was not significantly different from AA. This suggests a strong modulation from feature attention (a clear difference between SA and AS), but also an effect from the irrelevant pattern (a clear difference between SS and SA).

It was already known that feature attention affects symmetry perception. In particular, Gheorghiu et al. (2016) have shown that segregation by colour is beneficial when observers could direct their attention to the relevant colour. More generally, attention to symmetry may be critical for the presence of an SPN when symmetry is implied by the information in the image (e.g. a symmetry pattern seen in perspective) (Makin et al., 2015). Here, we shown how a task requiring observers to focus on only one colour/luminance modulated the neural response.

Our time course analysis shows an early onset of the SPN for both an image in which only symmetry was present but also for an image in which the relevant pattern was symmetrical (even though the irrelevant pattern was asymmetrical). Moreover, a weaker negativity emerged also for the condition in which symmetry was only in the irrelevant pattern. As our stimuli were on the screen for 1 s there are two possible explanations. It may be the result of a shift of attention to the irrelevant colour, or it may show that when a response to symmetry is suppressed (selected out) the response will emerge, but it will be delayed. A third possible explanation relates to the findings in Wright et al. (2018). They observed a series of general EEG microstates comparable between symmetrical and noisy patterns. These microstates, likely responsible for general shape perception, are followed by a symmetry-specific EEG microstate occurring at ~ 550 ms. Hence, the lack of symmetry in the attended pattern may imply that symmetry could not be used to facilitate shape perception within the first two windows, but the presence of symmetry in the irrelevant pattern elicited the symmetry-specific microstate only in the late window after ~ 550 ms. The timing of the microstates broadly corresponds to the three time windows identified in the current analysis. Furthermore, the comparable ERPs – as well as microstate presence, duration and variance explained – in unsegregated and segregated patterns (equivalent to our SS and SA/AS patterns), highlight the importance of attention in influencing neural processing. We plan to conduct direct tests of these possibilities in the near future.

Brain responses as measured by ERPs are modulated by attention. This applies also to early components such as N1 and P1, and when attention is directed to one of two spatially overlapping surfaces (for a review see, Luck et al., 2000). With respect to symmetry, it is known that symmetry produces a specific response, and that this response is automatic. The evidence of automatic processing relies mainly on a comparison between a task in which symmetry is relevant and one in which it is not (Bertamini et al., 2018), or between symmetry detection and symmetry evaluation (Jacobsen et al., 2018). Additionally, a deviation from symmetry can produce a mismatch negativity (MMN) even when the stimuli are outside the focus of attention (Kecskés-Kovács et al., 2013). In the current study automatic processing is shown for attended or unattended overlapping patterns. Feature-based selection changes but does not eliminate the typical SPN response to symmetry.

In summary, in this study observers examined and judged the spatial properties of one set of dots having a particular colour (black or white) while ignoring another set of dots of a different colour. The two patterns of dots were presented together, thus attention could not be confined to one region of space. The aim was to test to what extent a neural response to symmetry was directly a function of image properties, and to what extent it was instead a function of the attended colour. We found a clear effect of attention, visible when we compare stimuli with the same amount of symmetry carried by either the attended or the

ignored set. However, attention did not completely remove an effect of the unattended set, with the strongest response to the configuration in which symmetry was present in both attended and ignored sets. Models of symmetry processing must integrate the automatic response and the attention modulation. These may be mediated by different neural circuits although from our data we could not identify a difference in the onset or topology. Other techniques, combined with brief and masked presentation, may contribute to our understanding of the interplay of these processes.

CRediT authorship contribution statement

Marco Bertamini: Conceptualization, Methodology, Investigation, Writing - original draft. **Giulia Rampone:** Methodology, Investigation, Formal analysis. **John Tyson-Carr:** Methodology, Investigation, Formal analysis. **Alexis D.J. Makin:** Methodology, Investigation, Formal analysis.

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Author contributions statement

M.B., A.D.J.M., conceived the experiment, A.D.J.M., G.R., J.T., M.B. conducted the experiments and analysed the results. M.B. led the writing and all authors contributed to the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.visres.2020.09.003>.

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