The extrastriate symmetry response can be elicited by flowers and landscapes as well as abstract shapes

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Previous research has investigated the neural response to visual symmetry. It is well established that symmetry activates a network of extrastriate visual regions, including V4 and the Lateral Occipital Complex. This symmetry response generates an event-related potential called the sustained posterior negativity (SPN). However, previous work has used abstract stimuli, typically dot patterns or shapes. We tested the generality of the SPN. We confirmed that the SPN wave was present and of similar amplitude for symmetrical shapes, flowers and landscapes, whether participants were responding either to image symmetry or to image color. We conclude that the extrastriate symmetry response can be generated by any two-dimensional image and is similar in different stimulus domains.

Introduction

Visual symmetry can be detected rapidly and efficiently (Barlow & Reeves, 1979; Treder, 2010; Tyler, 1995; Wagemans, 1995). Psychophysical work has confirmed that vertical reflection is particularly salient (Wenderoth, 1994), and that reflection is more salient than rotation or translation (Palmer & Hemenway, 1978; Royer, 1981; van der Helm & Leeuwenberg, 1996; Wagemans, Van Gool, Swinnen, & Vanhorebeek, 1993), as first noted by Ernst Mach (Mach, 1886).

Recent research has focused on the neural responses to visual symmetry (Bertamini & Makin, 2014; Bertamini, Silvanto, Norcia, Makin, & Wagemans, 2018; Cattaneo, 2017). Functional magnetic resonance imaging (fMRI) has shown that symmetry activates a network of areas in the extrastriate cortex, with the strongest responses in area V4 and in the shape-sensitive Lateral Occipital Complex (LOC). Moreover, there is no symmetry response in V1 or V2 (Chen, Kao, & Tyler, 2007; Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005; Tyler et al., 2005). The extrastriate symmetry response increases with the degree of regularity in wallpaper patterns (Kohler, Clarke, Yakovleva, Liu, & Norcia, 2016) and the proportion of symmetry in symmetry + noise displays (Keefe et al., 2018; Sasaki et al., 2005). Recently, van Meel, Baeck, Gillebert, Wagemans and Op de Beeck (2019) found that the distinction between symmetrical and asymmetrical dot patterns can be reliably decoded from patterns of voxel activations in LOC. Transcranial magnetic stimulation work provides converging evidence: For example, Bona, Herbert, Toneatto, Silvanto and Cattaneo (2014) found that disruption of LOC selectively impairs symmetry discrimination (see also Bona, Cattaneo, & Silvanto, 2015; Cattaneo, Mattavelli, Papagno, Herbert, & Silvanto, 2011).

Electroencephalographic (EEG) studies have found that symmetry generates an event-related potential (ERP) called the sustained posterior negativity (SPN).
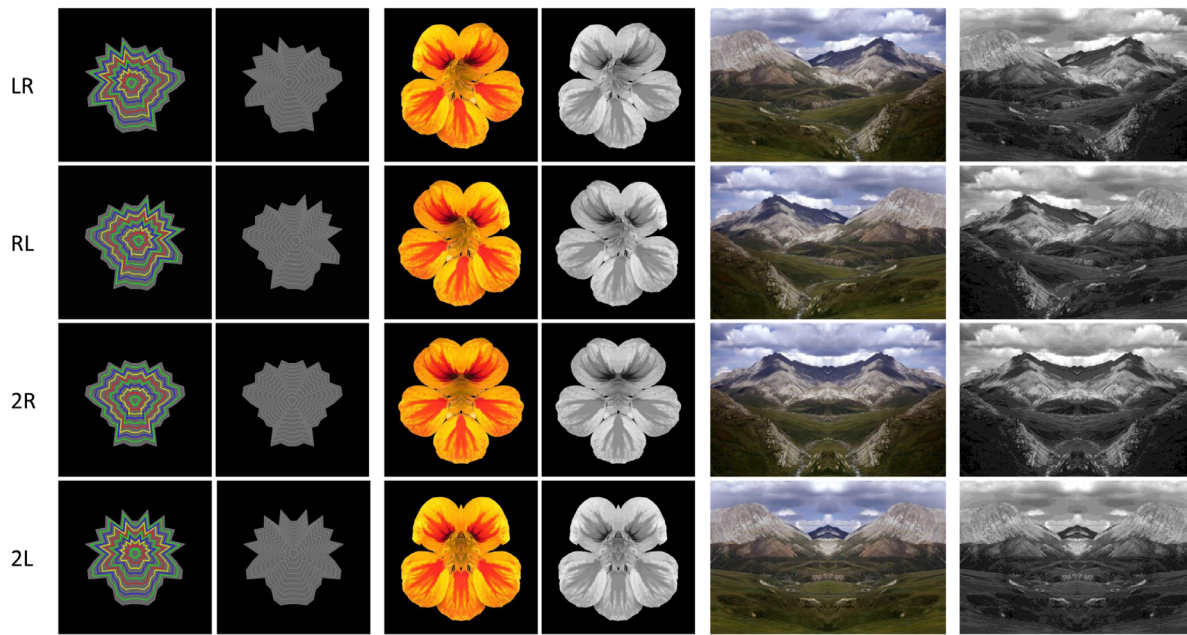
Figure 1. Stimulus shapes, flowers and landscapes. The experiment used 10 images from each of the 24 categories shown here. Rows show how our images were generated (LR = Left Right, RL = Right Left, 2R = symmetry made from mirroring two right sides, 2L = symmetry made from mirroring two left sides).

Amplitude is more negative at posterior electrodes when participants view symmetrical compared to asymmetrical images (Höfel & Jacobsen, 2007a; Jacobsen & Höfel, 2003; Makin, Wilton, Pecchinenda, & Bertamini, 2012; Martinovic, Jennings, Makin, Bertamini, & Angelescu, 2018; Wright, Mitchell, Dering, & Gheorghiu, 2018). SPN amplitude scales with the salience of different regularities, and is closely correlated with theoretical and behavioral measures of perceptual goodness (Makin et al., 2016; Palumbo, Bertamini, & Makin, 2015). Furthermore, the SPN can be recorded when participants are engaged in either active symmetry discrimination or in some secondary task (Höfel & Jacobsen, 2007a, 2007b; Makin, Rampone, Pecchinenda, & Bertamini, 2013). Other SPN work has shown that the extrastriate symmetry network always responds to symmetry in the image, but can sometimes go beyond this and recover symmetry in the object, independent of changes in virtual view angle (Makin, Rampone, & Bertamini, 2015) and despite partial occlusion (Rampone, Makin, Tatlidil, & Bertamini, 2019). Finally, the steady-state visual evoked potential approach can be used to isolate the symmetry response in the odd harmonic frequencies (Alp, Kohler, Kogo, Wagemans, & Norcia, 2018; Kohler et al., 2016; Norcia, Candy, Pettet, Vildavski, & Tyler, 2002) and the amplitude of this signal also scales with symmetry salience (Oka, Victor, Conte, & Yanagida, 2007).

As this brief review shows, modern neuroimaging techniques have been employed to characterize the extrastriate symmetry response; However, nearly all of this work has used *abstract* symmetrical stimuli - typically dot patterns or polygons. Of course, this has advantages and allows careful control of stimulus parameters, but it remains unclear how the brain responds to symmetry in realistic images. We therefore compared the SPN waves generated by vertical reflectional symmetry in abstract shapes, flowers and landscapes (Figure 1). Are the brain responses to symmetrical flowers and landscapes similar to symmetrical abstract shapes? This question is important for establishing the ecological validity and generality of previous neuroimaging work on symmetry perception. Because this was an exploratory study aimed at elucidating the boundary conditions for SPN generation, we could have used other classes of non-abstract stimuli. However, there were three advantages to using flowers and landscapes, as explained next.

First, the same flowers and landscapes had been used in recent work on preference (Bertamini, Rampone, Makin, & Jessop, 2019; Hůla & Flegr, 2016) and it is valuable to maintain stimulus consistency across studies even if research questions are completely different: unforeseen and instructive relationships might then emerge.

Second, landscapes may shed light on some known gestalt formation processes. It is known that symmetry and objecthood interact (Kimchi, Yeshurun, Spehar, & Pirkner, 2016; Koning & Wagemans, 2009; Machilsen, Pauwels, & Wagemans, 2009), and that people are

quicker to detect reflectional symmetry when it is the property of a single object rather than the property of the gap between two objects (Baylis & Driver, 2001; Bertamini, Friedenberg, & Argyle, 2002; Bertamini, Friedenberg, & Kubovy, 1997; Koning & Wagemans, 2009). Such considerations suggest that symmetry in landscapes, which are collections of many objects, might be processed by a different visual pipeline, and thus NOT generate an SPN.

Furthermore, while preference for symmetry in abstract patterns and shapes is a near universal law of aesthetics (Palmer, Schloss, & Sammartino, 2013), many people prefer *asymmetrical* landscapes (Bertamini et al., 2019), possibly because they look more familiar and less artificial (Figure 1). It is also known that people often prefer asymmetrical compositions in paintings (McManus, 2005). Therefore preference data again suggests that symmetry in landscapes is visually different to symmetry in single objects. But does it generate a different neural response?

Third, flowers are real, biologically significant single objects. Unlike symmetrical landscapes, symmetrical flowers have some natural aesthetic appeal, but are not socially significant like faces, and are not processed by dedicated visual regions like the occipital and fusiform face areas. It is thus interesting to compare SPN results from shapes, flowers and landscapes.

As in previous work (Makin et al., 2015), we compared SPN waves when participants were either classifying images according to their symmetry (symmetrical vs. asymmetrical) or according to their color (color vs. grayscale). We reasoned that participants might be able to treat landscapes as 2D symmetrical images if forced to do so by task demands, but they might not do so spontaneously. We thus speculated that the landscape SPN would be disproportionately reduced in the Color task.

To summarize, the main aim of our exploratory study was to establish the boundary conditions for the SPN generation. However, we did venture some speculative a-priori predictions. For abstract shapes, we predicted that SPN amplitude will be large and task independent. For landscapes, we predicted a reduced SPN, particularly in the Color task. All our preliminary hypotheses were logged on aspredicted.org, along with plans for EEG data pre-processing (https://aspredicted.org/3jv3y.pdf).

We made no attempt to control all low-level differences across the three domains. Amongst other things, luminance, contrast, spatial frequency, number of elements, number of edges, and overall size were not matched. These confounds limit what we can say about the differential brain response to shapes, flowers and landscapes. However, in this study the aim was to measure 1) the response to symmetry compared to asymmetry within each domain, then 2) compare the magnitude of this difference across domains. We

made the assumption that low-level differences between domains can be subtracted away, because such low-level factors will equally affect both symmetrical and asymmetrical stimuli within a domain. This assumption has its limitations and can be debated, but it is justifiable in light of previous SPN work. SPN amplitude is systematically affected by the number of axes and proportion of symmetry in the image, but is relatively unaffected by low-level visual variables (Makin et al., 2016). Therefore, if landscapes did not generate an SPN (as we tentatively predicted) it would probably not be due to the existence of low-level features which distinguished the landscapes from the other domains.

Before the Symmetry and Color tasks, we ran a speeded response time experiment on the same participants. In this RT experiment they discriminated symmetry from asymmetry in the images as quickly and accurately as possible. The RT experiment allowed us to compare SPN amplitude with behavioral measures of symmetry salience in each domain. However, SPNs in the Color task could be enhanced by prior training with symmetry discrimination in the RT experiment. We thus ran another *Color control task* on a different group of 20 participants, but without the prior behavioral RT experiment. We predicted (and found) that SPN waves were similar in this Color control task (https://aspredicted.org/pb7sx.pdf).

Methods

Participants

Sixty participants were involved. All had normal or corrected-to-normal vision, and most participated for course credit. There were 20 participants in the Symmetry task (age 18–47, mean age 21.4, 4 male, 2 left handed), 20 in the Color task (age 18–36, mean age 21.5, 6 male, 2 left handed) and 20 in the Color control task (age 18–50, mean age 20.9, 4 male, 2 left handed). The study had local ethics committee approval and was carried out in accordance with the declaration of Helsinki (2008).

Apparatus

EEG data was collected using a Biosemi ActiveTwo system (Amsterdam, Netherlands) from 64 scalp electrodes arranged according to the international 10–20 system. Band pass filters were set at 0.16 and 100 Hz. Stimuli were presented to participants on a 51 × 29 cm LCD monitor with a nominal 60 Hz refresh rate. HEOG and VEOG were monitored online to check for unwanted blinks and eye movements. The participants were held 57 cm from the monitor with a

chin rest. The experiment was programmed in Python using open-source PsychoPy libraries (Peirce, 2007).

Stimuli

Our stimulus generation procedure is illustrated in the four rows of Figure 1. We began with an asymmetrical image (top row, LR = LeftRight) and mirror reversed it to produce another asymmetrical exemplar (second row, RL). We then took the right side of the first asymmetrical image, and mirrored it on the left (third row, 2R), and the left side of the first asymmetrical image, and mirrored it on the right (forth row, 2L) and. Therefore, half the images were asymmetrical (rows 1 and 2) and half symmetrical (rows 3 and 4). These images were produced once in color, and once in greyscale. This process was repeated for 10 different images of each type, so our experiments used 240 different images in total. Exactly the same stimuli were used in the Symmetry, Color and Color control tasks.

Shapes and flowers were approximately 10° wide and landscapes were a 21.2 × 13.2° rectangle. The images were presented on a black background, so there was no rectangular frame for shapes and flowers, as there was for landscapes. These parameters were chosen for consistency with previous work using the same images (Bertamini et al., 2019).

Flowers were taken from Hůla & Flegr (2016), and modified to obtain perfect bilateral reflectional symmetry. We selected the following species: Epipactis palustris; Euphrasia rostkoviana; Impatiens noli-tangere; Lathyrus tuberosus; Limodorum abortivum; Melittis melissophyllum; Mimulus moschatus; Ophrys apifera; Pisum sativum; Tropaeolum majus; Veronica beccabunga; Viola biflora and Viola reichenbachiana. The landscapes were the same as those used in Bertamini et al. (2019). They were obtained using the keyword "landscape" for a Google image search with a setting of "free to use, share or modify".

Procedure

Before the Symmetry and Color tasks, participants first completed a 15-minute response time experiment (called the RT experiment). Importantly, there was no RT experiment before the Color control task.

In the RT experiment, participants classified the stimuli as Asymmetrical (left key) or Symmetrical (right key) as quickly and accurately as possible. Images were preceded by a 1.5 second blank screen with a central blue fixation cross. Cues above the images indicated the response mapping. A warning tone sounded if participants entered the wrong response. All 240 images were used once in the RT experiment. The RT experiment was divided into 10 blocks of 24 trials, and

participants could have a break between each block. Before this, there was a 24-trial practice block, based on a representative subset of images.

In the EEG experiments, each trial began with a 1.5 s baseline interval, followed by a 1.5 s image presentation interval. The blue fixation cross was presented centrally throughout both intervals. After the image disappeared, participants entered their responses using the left or right keys of the keyboard. Unlike the RT experiment, key mapping switched unpredictably on each trial, and responses were not speeded. There were 80 trials in each critical condition [3 Stimulus domain (Shape, Flower, Landscape) X 2 Symmetry (Symmetrical, Asymmetry)]. The sequence of 240 images was presented twice in the EEG experiment, giving 480 trials in total. The sequences were presented in a different randomized order to each participant. However, each individual image appeared once in the first half of the experiment, and once in the second half.

Analysis

Mean response times from the RT experiment were obtained from each participant (excluding a minority of trials where an incorrect judgment was entered). These were analyzed with repeated measures ANOVA [3 Stimulus domain (Shape, Flower, Landscape) X 2 Symmetry (Symmetrical, Asymmetry)]. For all ANOVA analysis, the Greenhouse-Geisser correction factor was used whenever the assumption of sphericity was violated (Mauchly's W, $p < 0.05$). For proportion correct data, non-parametric Freidman's ANOVA used because many data points were 1, indicating perfect performance.

EEG analysis and pre-processing was based on previous SPN work in our lab (e.g. Makin et al., 2016). EEG data was recorded continuously and then processed offline using eeglab 13.4.4b (Delorme & Makeig, 2004) in Matlab 2014b (MathWorks, Natick, MA). Data were first referenced to the scalp average, low-pass filtered at 25Hz with the IIRFILT function, downsampled to 128 Hz and then broken into epochs from −0.5 to +1.5 seconds around stimulus onset, with a −200 ms pre-stimulus baseline. The epoched data was cleaned with Independent Components Analysis (Jung et al., 2000). This was used to remove blink, eye movement and other gross artifacts. In the Symmetry task, an average of 11 components were removed per participant (min = 2, max = 18). In the Color task, an average of 10.55 components were removed per participant (min = 3, max = 20). In the Color control task, an average of 7.85 components were removed (min = 3, max = 16). Next, trials with amplitude more extreme than +/− 100 microvolts at any scalp electrode were excluded (7–11% mean exclusion rate, very similar in all conditions and tasks).

SPN was defined a priori as the amplitude difference between symmetrical and asymmetrical conditions at posterior electrode cluster [PO7, O1, O2 PO8] from 300–1000 ms post stimulus onset. SPN amplitude was then analyzed with mixed ANOVA [3 Stimulus Domain (Shape, Flower, Landscape) × 3 Task (Symmetry, Color, Color control)].

We also examined split half reliability of our ERP signals, and found that ERPs were similar for first and second presentation of each stimulus, which happened in the first and second halves of the experiment respectively. See Supplementary Materials on OSF (osf.io/ycqr3/). This suggests that there were no strong fatigue, practice or familiarity effects (an interesting methodological point for SPN researchers).

We also examined amplitude of flower and landscape SPNs in the context of many previously published SPNs generated by different regular abstract stimuli. Grand-average SPN amplitude varies between around 0 and 4 microvolts, and more than 80% of this variance can be explained by a theoretical measures of perceptual goodness called the 'W-load' (Makin et al., 2016). We re-ran the regression analysis again and confirmed that flower and landscape SPNs were not statistical outliers. For consistency with Makin et al. (2016), we calculated all SPNs from PO7/8 in the 300–400 ms window (where amplitude is typically maximal), and we only use published SPNs from experiments where participants were explicitly discriminating regularity (Makin et al., 2015; Makin, Rampone, Morris, & Bertamini, 2019; Makin et al., 2013, 2012, 2016; Palumbo et al., 2015). Therefore, we used only SPNs from the Symmetry task in the current study, not the Color or Color control tasks. These criteria limited us to 36 grand-average SPNs. To assess significance of this W vs. SPN relationship (without assuming independence or non-aggregated data) we used the linear mixed-effects model toolbox in R (Bates, Mächler, Bolker, & Walker, 2015). The DV was 780 individual-participant SPN mean amplitudes. Experiment and Participant were entered as random factors.

Open science policy

All codes for experimental presentation, stimulus, and EEG and behavioral analysis are freely available on Open Science Framework, along with pre-processed EEG data (osf.io/ycqr3/).

Results

Behavioral RT experiment

Results for the RT experiment are shown in Figure 2. For response time data, repeated measures ANOVA revealed a main effect of Stimulus domain (F $(2,78) = 17.955$, $p < 0.001$, partial $\eta^2 = 0.315$). There was no main effect of Symmetry (F $(1, 39) = 1.295$, $p = 0.262$), however, there was a Stimulus domain X Symmetry interaction (F $(1.534, 59.827) = 25.142$, $p < 0.001$, partial $\eta^2 = 0.392$), partly because participants were quicker to classify shapes as asymmetrical $(t(39) = -4.686, p < 0.001)$, but quicker to classify landscapes as symmetrical $(t(39) = 2.780, p = 0.008)$. It is noteworthy that *symmetrical* landscapes were discriminated quicker than symmetrical flowers (t $(39) = 4.663$, $p < 0.001$) or symmetrical shapes (t $(39) = 2.765$, $p = 0.009$), which did not differ from each other (t (39) 1.114, $p = 0.272$). This particular aspect of the behavioral results suggests symmetry was most salient in landscapes. For proportion correct data, asymmetrical flowers were less likely to be classified correctly compared to the other five conditions $(\chi(5) = 53.663, p < 0.001)$.

EEG experiment

In the EEG experiment, participants gave the correct answer on nearly every trial in the Symmetry task (mean P correct $= 0.93$ to 0.96) the Color task (mean P correct $= 0.94$ to 0.98) and in the Color control task (mean P correct $= 0.96$ to 0.98).

Figure 3 shows grand average ERPs from the shape, flower and landscape domains of each task (left panels). The theoretically interesting finding was that amplitude was lower for symmetrical than asymmetrical conditions *within* each domain. These SPN difference waves (symmetry – asymmetry) can be seen in the right panels of Figure 3. The SPN was evident across all three domains but slightly larger (i.e. more negative) for landscapes. The SPN was similar in all three tasks. These effects can also be seen in the nine topographic difference plots in Figure 4 (where the SPN appears as blue at posterior electrodes).

Other unexpected effects can be seen in the grand average ERP waves (Figure 3). The evident early modulations of P1 and N1 were systematic but not of central interest here. See Supplementary Materials on OSF (osf.io/ycqr3/). After P1 and N1, there were overall amplitude differences between domains (Landscape > Flower > Shape). Indeed, these between-domain differences were much larger than the difference between symmetry and asymmetry within each domain. However, these are difficult to interpret because shapes, flowers and landscapes differed on so many visual dimensions.

These apparent SPN effects were confirmed with mixed ANOVA (DV = SPN amplitude defined as symmetry – asymmetry, at the posterior electrode cluster [PO7 O1 O2 PO8] in the 300–1000 ms. window). The nine means corresponding to this ANOVA
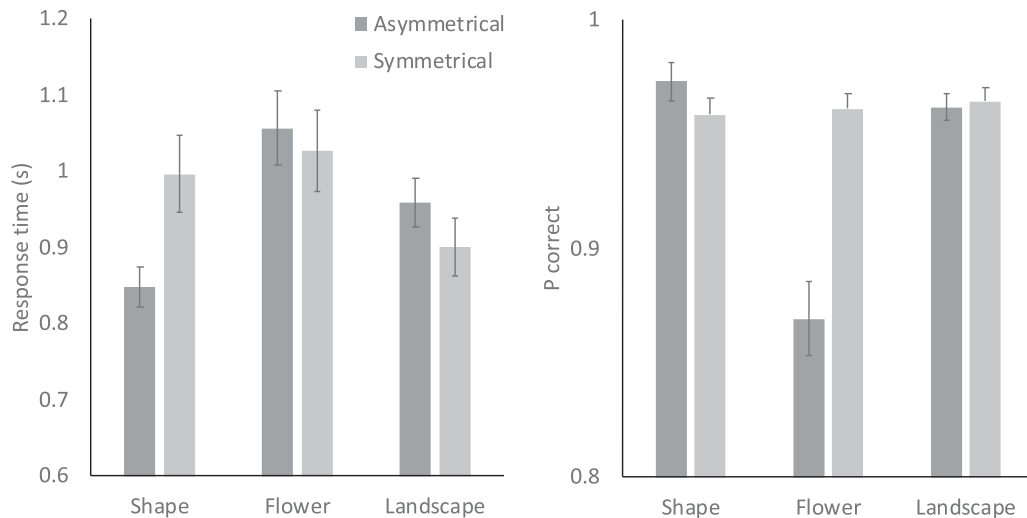
Figure 2. Behavioral RT experiment results. Left panel shows mean response times, and the right panel shows proportion of correct responses. Error bars = +/− 1 S.E.M.

are shown in Figure 5. There was no effect of the between-subjects factor Task (F $(2,57)$ = 1.476, p = 0.237) and no Stimulus domain X Task interaction (F $(4,114)$ < 1, N.S). However, there was a main effect Stimulus domain (F $(2,114)$ = 4.910, p = 0.009, partial η^2 = 0.079). The landscape SPN was significantly larger than the flower SPN (t (59) = 2.457, p = 0.017) and shape SPN (t (59) = 2.982, p = 0.004). The shape and flower SPNs were similar (t (59) = 0.715, p = 0.477).

The SPN itself was significant in 8/9 conditions (amplitude less than 0, one sample t tests, p < 0.004). The exception was the marginal shape SPN in the Color control task (p = 0.058). The SPN was present in 46/60 participants in the shape domain, 52/60 in the flower domain, and 55/60 in the landscape domain (all p < 0.001, binomial test). In contrast, the SPN was stronger in the landscape domain (compared to the average of the other two domains) in just 39/60 participants (p = 0.027)[1]. Additional analysis found no interactions involving stimulus Color (largest effect, F $(2,57)$ = 2.293, p = 0.110). Finally, there were no interactions involving Hemisphere (largest effect, F $(2,57)$ = 2.094, p = 0.133), although the topoplots in Figure 4 indicate some hemispheric asymmetries.

SPNs for flowers and landscapes in the context of previous research

Although there was a main effect of Domain, the flower and landscape SPNs were typical of abstract 1-fold reflection stimuli seen in previous research. To illustrate this, we re-analyzed SPNs from multiple published experiments with SPN amplitude ranged from ~0 to 4 microvolts.

To understand this analysis, we need to briefly cover previous work on the topic of 'perceptual goodness'. This a term from the Gestalt school, and it refers to salience, obviousness or perceptual strength of a visual configuration. Goodness is closely related to the law of Prägnanz: Given an image, the visual brain tends to construct the *simplest* perceptual interpretation it can. Some visual configurations readily afford simple perceptual interpretation, others do not. This difference determines perceptual goodness of the visual configuration. These gestalt concepts are intuitive, but difficult to precisely define and quantify. Some have suggested that a good gestalt is one that can coded by a small number of parameters (Hochberg & McAlister, 1953; Wagemans et al., 2012). Despite these conceptual challenges, perceptual goodness can be estimated for different types of regularity using the *holographic weight of evidence model,* which is based on Structural Information Theory. The holographic model assigns a W-load to different regularities (van der Helm & Leeuwenberg, 1996)[2], and Makin et al. (2016) found a strong linear relationship between W-load and SPN amplitude (R^2 = 0.81 to 0.86).

We extended the analysis in Makin et al. (2016) with new SPNs recorded more recently. We then included the flower and landscape SPNs from the current study. Arguably, the holographic model cannot be directly used compute W-load for flowers and landscapes because the definition of a single element is necessarily ambiguous in these domains. Nevertheless, however one defines an element, there are always twice as many elements as there are symmetrically positioned pairs of elements. According to the holographic model, this means W = 0.5 for flowers and landscapes, just as W = 0.5 for one-fold reflection dot patterns. Given this, we can then test whether the flower and landscape
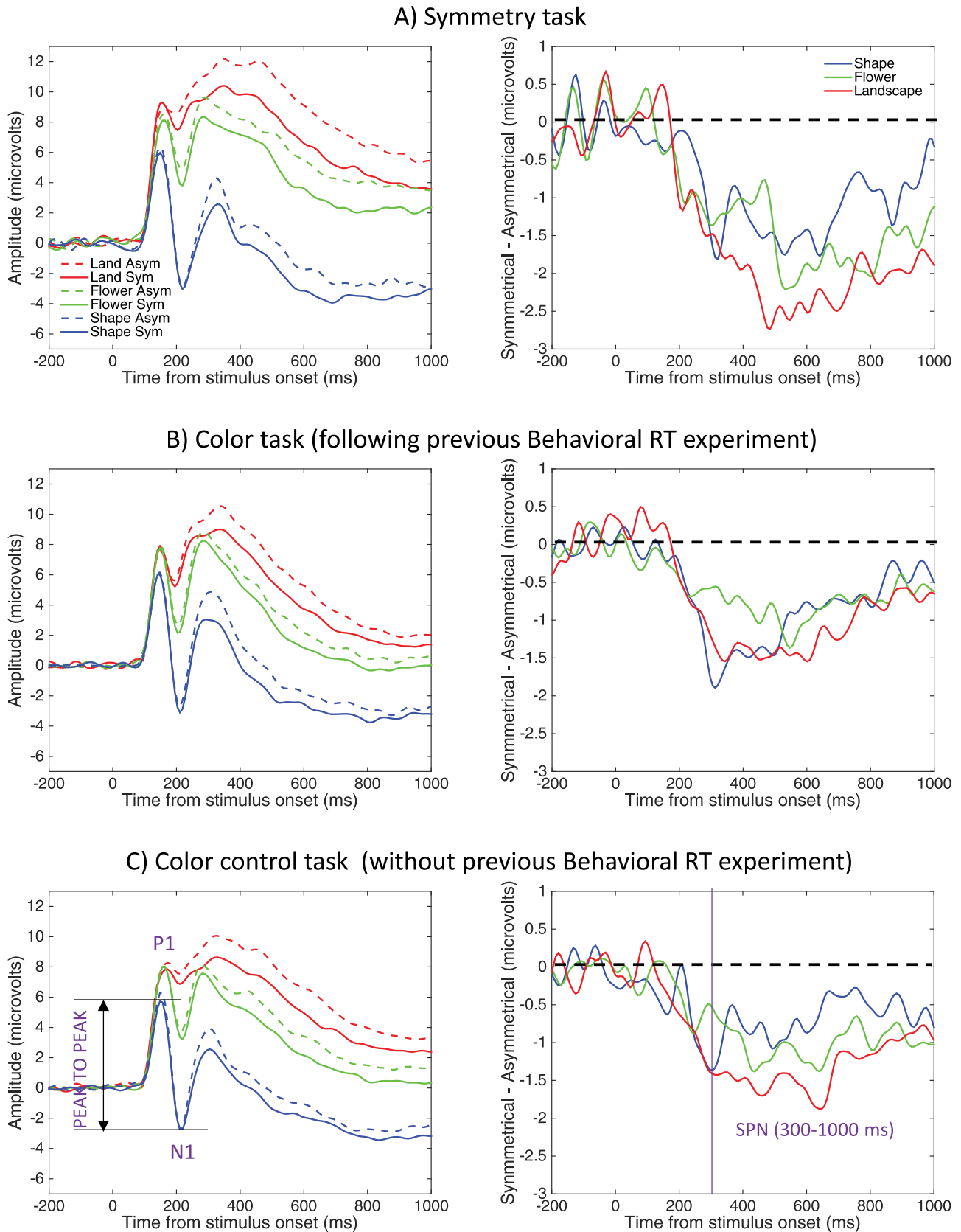
Figure 3. Grand-average ERPs and SPN difference waves. Waves were taken from electrode cluster PO7, O1, O2 and PO8 (see red circles in Figure 4 for locations). Results from the Symmetry task are in upper panels (A), results from Color task are in middle panels (B), and results from Color control task are in the lower panels (C). P1, N1, the SPN window and peak-to-peak metric are all annotated in C. The VEP metrics are analyzed in the Supplementary Materials on OSF (osf.io/ycqr3/).
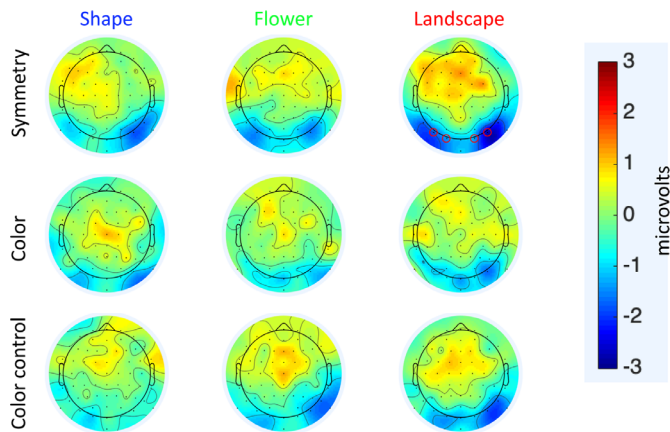
Figure 4. Topographic difference maps. These topoplots illustrate the difference between symmetrical and asymmetrical conditions (300 to 1000 ms). Columns show shape, flower and landscape domains. Rows show Symmetry, Color and Color control tasks. The SPN appears as blue at posterior electrodes. The electrode cluster used for SPN analysis is highlighted with red circles (top right).
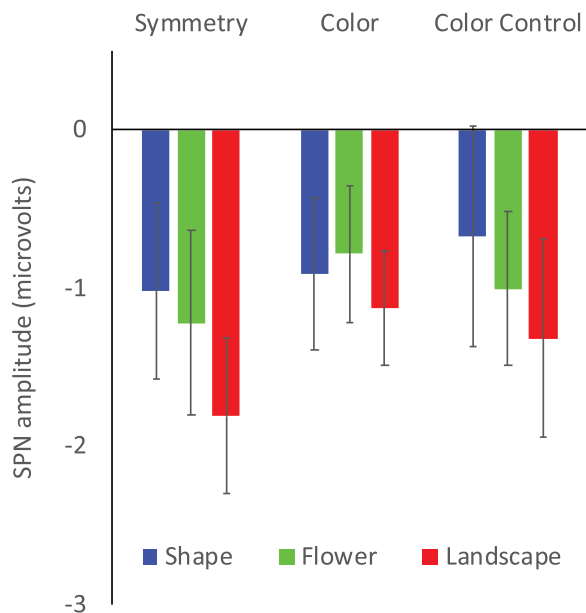

Figure 5. SPN amplitudes. Bars show difference from asymmetry (300 to 1000 ms) in the three tasks and three stimulus domains. Error bars = 95% confidence intervals. The fact that error bars do not cross zero indicates a significant SPNs in 8/9 conditions (p < 0.05).

SPNs were typical other SPNs generated by abstract regularities.

As can be seen in Figure 6A, W explained 81% of variance in grand-average SPN ($\chi^2(1) = 304.75$, p <0.001, linear mixed effects model). Crucially, the flower and landscape SPNs were not outliers here. We confirmed this statistically by measuring the residual

for each grand-average SPN, then converting the residuals to Z scores (Figure 6B). The Z residuals for flowers and landscapes were less than 1.96 (so p > 0.05; see red lines in Figure 6B). In sum, the flowers and landscapes generated the SPNs to be expected if they were processed as abstract stimuli with a single axis of reflection.

Discussion

Although there has been some work recording EEG responses to symmetry in photographs of cars (Sambul, Murayama, & Igasaki, 2013), this was the first attempt to compare SPNs generated by symmetry across abstract and non-abstract domains. There was a similar SPN wave for abstract shapes, flowers and landscapes. The SPN was also similar in the Symmetry, Color and Color control tasks.

The relationship between behavioral RT and SPN was straightforward if we consider the RT for symmetrical stimuli only. Participants were fastest to report symmetry in the landscape domain, and slower to report symmetry in the shape and flower domains. Likewise, the SPN was larger in the landscape domain, and smaller in the shape and flower domains. This is consistent with previous research, where RT for symmetrical stimuli and SPN amplitude were correlated (Makin et al., 2016). However, we note that other aspects of the behavioral RT experiment did not align with SPN results, so we do not wish to over interpret this.

It seems that symmetry in landscapes was more salient than symmetry in other domains (resulting larger SPNs and faster RTs). One obvious explanation is that landscapes were larger images – It could be that the additional size increased symmetry salience for landscapes. Another possibility is that landscapes had more substructures on each side of the axis, and these supported extraction of global symmetry (Locher & Wagemans, 1993). However, these are speculations which require further work with controlled stimuli, for now we can say that landscapes, flowers and shapes all generated an SPN.

Although landscapes generated a significantly larger SPN than flowers or shapes, we do not want to overstate this relatively small difference. Indeed, additional analysis comparing 36 grand average SPNs showed the landscape SPNs *were not high amplitude anomalies*. For abstract stimuli, SPN amplitude can be predicted using the W-load from the holographic model (Makin et al., 2016; van der Helm & Leeuwenberg, 1996), and the landscape SPNs fall close to the W vs. SPN regression line (Figure 6B). This suggests that symmetry in landscapes is processed in the usual way by the extrastriate symmetry network.
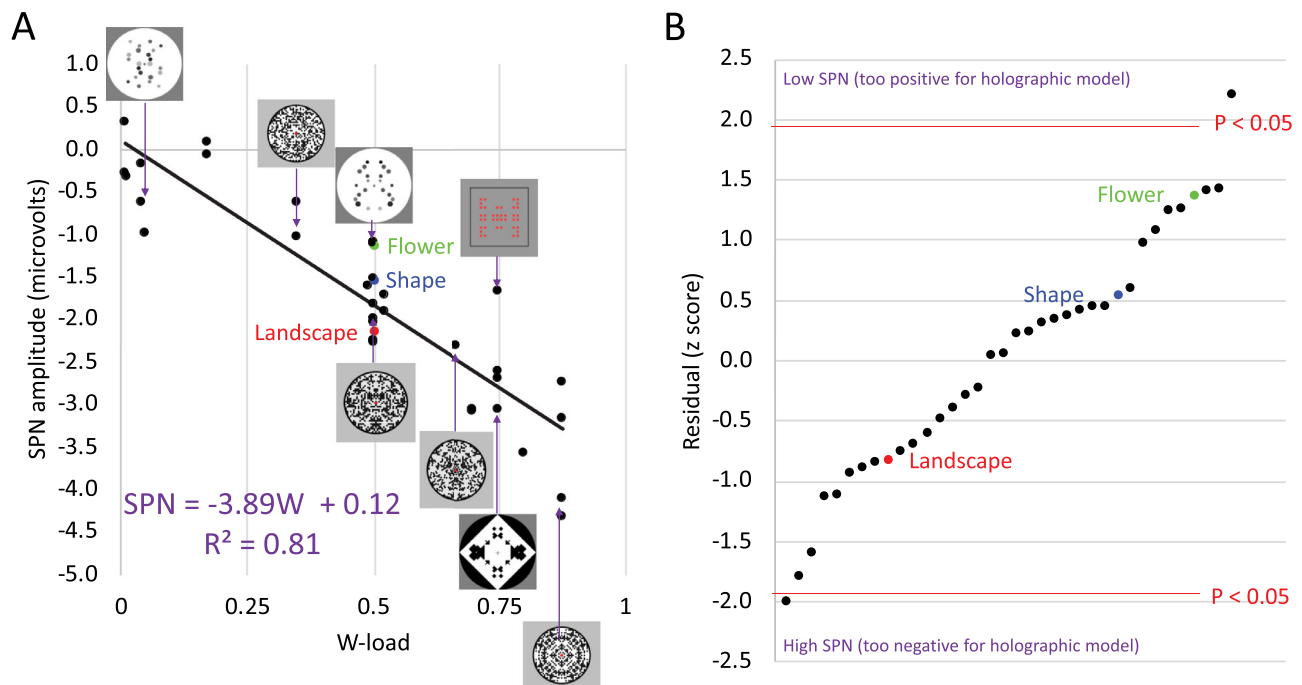
Figure 6. SPNs from previous research as context. (A) Grand-average SPN (electrode cluster PO7/8, 300 to 400 ms) is shown as a function of W-load. Example stimuli from selected experiments are included in insets (not to scale). The example stimuli were merely chosen because the regularity is visible when reproduced in small images. (B) Residuals analysis; Landscape and flower SPNs were not statistical outliers from the regression line in A (see red line boundaries).

Before the study began, we tentatively predicted that landscapes would generate a weak SPN, particularly in the Color task. After all, landscapes are collections of objects, and symmetry in landscapes looks artificial. We reasoned that the SPN-generators in the extrastriate cortex might engage with individual objects, such as trees or mountains, rather than the vista as a whole, and would therefore be indifferent to symmetry in the vista. This links to previous work where reflectional symmetry is more efficiently detected when it is the property of a single object, rather than a gap between two objects (Bertamini et al., 1997). However, there was no evidence for this.

The landscape SPN helps characterize mid-level vision more generally. It could be that the extrastriate networks are tuned to properties of single objects (Kourtzi & Kanwisher, 2001; Vinberg & Grill-Spector, 2008) and thus they do not code non-accidental spatial relations *between* multiple objects distributed over large areas. However, landscapes were evidently processed as unified symmetrical images, even when symmetry was not task relevant. While more research is needed, this preliminary result suggests that the extrastriate symmetry response is not gated by scene segmentation and prior extraction of single objects.

Although most neuroimaging work has used abstract stimuli, there has been some attempt to compare the symmetry perception between abstract and biological

stimuli with psychophysical methods. Evans, Wenderoth and Cheng (2000) found that people were significantly better at detecting symmetry in top-down pictures of crabs and insects than abstract dot patterns. However, the well-known vertical orientation advantage was apparent with all stimuli domains, again demonstrating that the results obtained from abstract stimuli generalize to real-world objects.

There is a linear relationship between proportion of symmetrical dots in the image and SPN amplitude (Palumbo et al., 2015). It remains to be seen if this kind of scaling can be demonstrated for landscapes or other realistic images. It could be more complicated than this if symmetry matters more in some parts of the landscape image than other parts of the landscape image. For example, the SPN may only index symmetrical arrangements of foreground, not background objects. Again, this is a topic for future work.

Summary

We compared the neural response to symmetry in abstract shapes, flowers and landscapes. Although symmetry in landscapes is visually different, the SPN response to symmetry was similar across all three

domains. This held true whether participants were actively discriminating symmetry or color. We conclude that the neural response to symmetry is both domain general and task independent.

Keywords: Regularity, EEG, ERP, SPN, LOC

Acknowledgments

Footnotes

[1] We also checked whether SPN amplitude correlated with the symmetry classification speed, as measured by the previous behavioral RT experiment. This analysis used 40 participants from the Symmetry and Color tasks (because there was no previous behavioral RT experiment before the Color control task). It could be that participants who are quick to classify symmetry (within a domain) also generated a large SPN (within the same domain). However, this was not confirmed (largest correlation $r = 0.024$, $p = 0.884$).

[2] We sadly note that Peter van der Helm is very ill at the moment, and his research and insights have been a huge benefit to our lab. We would like to acknowledge his great contribution to symmetry perception research.

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