The extrastriate symmetry response is robust to variation in visual memory load

Yiovanna Derpsch1,2 | Giulia Rampone1 | Andrea Piovesan1 | Marco Bertamini1,3 | Alexis D. J. Makin1

1Department of Psychological Sciences, University of Liverpool, Liverpool, UK
2School of Psychology, University of East Anglia, Norwich, UK
3Department of General Psychology, Università di Padova, Padova, Italy

Correspondence
Yiovanna Derpsch, School of Psychology, University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ, UK.
Email: Y.Derpsch@uea.ac.uk

Funding information
Economic and Social Research Council, Grant/Award Number: ES/S014691/1

Abstract
An Event Related Potential response to visual symmetry, known as the Sustained Posterior Negativity (SPN), is generated whether symmetry is task relevant or not, and whether symmetry is attended or not. However, no study has yet examined interference from concurrent memory tasks. To answer this fundamental question, we investigated whether the SPN is robust to variation in Visual Working Memory (VWM) load. In Experiment 1 (N = 24), each trial involved a sample display, a probe and a test display. Sample and test displays contained either four colors or four black shapes, and the probe was either a symmetrical or random pattern. We compared a memory task and a passive viewing task. In the memory task, participants held color or shape information in VWM when the probe was presented. In the passive viewing task, there were no memory demands. Contrary to our predictions, there was no evidence that VWM interfered with the symmetry response. Instead, there was a general SPN enhancement during both color and shape memory tasks compared to passive viewing. In Experiment 2 (N = 24), we used symmetrical patterns themselves as sample and test to maximize interference. Again, the SPN was enhanced in the memory task compared to passive viewing. We conclude that the visual symmetry response is not impaired by concurrent VWM tasks, even when these tasks involve remembering symmetry itself. It seems that the SPN is not only attention-proof, but also memory-proof. This adds to evidence that symmetry perception is robust and automatic.

KEYWORDS
EEG, memory, sustained posterior negativity, symmetry, visual working memory

1 | INTRODUCTION

A great deal is known about the neural response to visual symmetry. The symmetry response is robust to changes in task (Makin et al., 2020), changes in focus of spatial attention (Derpsch et al., 2019) and changes in focus of feature attention (Bertamini et al., 2020). Overall, the symmetry response is typically reduced, but not abolished, when
attention is directed away from symmetry. However, this apparent robustness has not been investigated in relation to memory. We tested whether the neural response to symmetry can be abolished when observers hold visual information in working memory. Starting from Baddeley and Hitch’s (1974) working memory model, we focused on Visual Working Memory (VWM), a term defined by Luck and Vogel (2013) “as the active maintenance of visual information to serve the needs of ongoing tasks” (p. 391).

2 | NEURAL RESPONSE TO SYMMETRY

Functional MRI work has shown that symmetrical dot patterns activate a network of extrastriate visual regions, including V4 and the LOC (Chen et al., 2007; Keefe et al., 2018; Kohler et al., 2016; Sasaki et al., 2005; Tyler et al., 2005), whereas symmetry response is not found in V1 or V2. More recently, van Meel et al. (2019) used multi-voxel pattern analysis to examine the strength of the symmetry code in different regions. They found that LOC voxels best captured the distinction between symmetrical and asymmetrical patterns.

This extrastriate symmetry response can also be measured with EEG. Symmetry generates an Event Related Potential (ERP) called the Sustained Posterior Negativity (SPN); amplitude is more negative at posterior electrodes when participants observe symmetrical compared to asymmetrical patterns (Jacobsen & Höfel, 2003; Makin et al., 2012; Norcia et al., 2002). SPN amplitude scales with the salience of different symmetries (Makin et al., 2016, 2020) as illustrated in Figure 1. For example, reflection produces the largest SPN, probably because it is more salient than rotation or translation (Mach, 1886/1959; Makin et al., 2013).

The SPN is generated by visual symmetry across a range of tasks (for reviews see Bertamini et al., 2018; Cattaneo, 2017). For example, SPN waves can be recorded when participants discriminate symmetry, but also when they are evaluating beauty (Jacobsen & Höfel, 2003), deliberately misreporting responses (Höfel & Jacobsen, 2007), discriminating word valence (Rampone et al., 2014), counting the number of objects (Makin et al., 2014) or discriminating color (Makin et al., 2015, 2020). This is consistent with behavioral work, which also suggests symmetry is processed preattentively. Indeed, it has long been thought that symmetry perception emerges effortlessly and automatically (Wagemans, 1995).

More evidence for automaticity comes from a recent experiment on covert spatial attention (Derpsch et al., 2019) that found a contralateral SPN when symmetry appeared to the left or right of fixation. This contralateral SPN was similar whether covert spatial attention was directed towards symmetry or not. Whilst the SPN can be enhanced by visuospatial attention, it is still present when symmetry is presented in unattended regions. This result was paralleled in the domain of feature attention by Bertamini et al. (2020). Participants observed clouds of white and black dots and only one color was task relevant. However, regularity in the unattended color had a systematic influence on SPN amplitude. Hence there is converging evidence that the extrastriate symmetry response is robust and automatic: it still occurs when processing resources are diverted away from the symmetrical stimulus (Figure 1). In the current work, we expand on these findings by testing whether the SPN generated by task-irrelevant symmetry is robust to changes in VWM load.

The claim that the SPN is robust and automatic, or “attention-proof”, requires some clarification. Attention enhances neural responses throughout the visual cortex, and few visual responses are purely stimulus-driven and completely indifferent to attentional state. A visual operation can nevertheless be properly classed as robust and automatic without meeting this strict criterion. A robust and automatic visual operation happens frequently and reliably even when the outcome is not task relevant (for more on automaticity, see Bargh & Ferguson, 2000), and the visual operations that generate the SPN are like this (Figure 1). A counterexample of a non-automatic operation may be the formation of view-invariant representations: this only happens when such representations are needed (Makin et al., 2015; Seth & Baars, 2005).

3 | GESTALT, SYMMETRY AND VWM

Gestalt laws (e.g., proximity, similarity, closure, symmetry) facilitate grouping of parts into a perceptual whole. Koffka (1935) suggested that structured gestalts create a more stable memory trace than chaotic arrays. Subsequently, Attneave (1955) argued that symmetrical patterns are more accurately remembered than random patterns and that this “may be taken to indicate that some perceptual mechanism is capable of organizing or encoding the redundant pattern into a simpler, more compact, less redundant form” (p. 220). More recently, gestalt effects on VWM have been demonstrated using diverse methods. Woodman et al. (2003) suggested that the visual system uses gestalt cues to bias the move of perceptual representations into working memory, based on the fact that objects that are grouped together tend to be stored together. And using a Corsi blocks test, Kemps (2001) demonstrated that recall was better when the sequence was spatially symmetrical than when it was random. These results were
replicated by Rossi-Arnaud et al. (2006) and then again with three different axes by Rossi-Arnaud et al. (2012). This literature suggests a close link between perception and memory: gestals, including symmetrical gestals, are encoded more efficiently. Such a close link indirectly suggests concurrent memory tasks could interfere with gestalt formation.

It is likely that VWM is mediated by persistent representation in the visual cortex after stimulus offset. This idea is articulated by proponents of the perceptual memory model (Pasternak & Greenlee, 2005), the sensory recruitment hypothesis (Rademaker et al., 2019; Serences et al., 2009) and other related accounts (Fuster, 2009). This persistent representation does not necessarily involve heightened neural activation. Using MVPA, Serences et al. (2009) found that information about color and orientation could be selectively decoded from V1 voxels during delay, even though the univariate BOLD response was not elevated. Likewise,
Harrison and Tong (2009) found representational similarity between visible and remembered gratings in cortical areas V1 to V4. Consequently, it seems that visual memory and visual perception tasks recruit corresponding visual regions, and potentially interfere with each other.

Neuroimaging studies have identified distinctive brain responses to colors and shapes (for reviews see Grill-Spector & Weiner, 2014; Mullen, 2019). Although color processing can be found in V1 and V2, it primarily activates V4 (Desimone et al., 1985; Kanwisher, 2010; Livingstone & Hubel, 1984). Conversely, shapes preferentially activate the LOC (Grill-Spector et al., 1999; Kraut et al., 1997; Malach et al., 1995). While V4 and LOC both respond to symmetry (Sasaki et al., 2005), the symmetry response is probably more akin to the LOC centered shape response than the V4 centered color response. We thus expected shape memory to interfere with symmetry perception more than color memory.

4  |  CURRENT STUDY

We investigated whether the SPN is robust to changes in VWM load. Experiment 1 measured the SPN under memory and passive view conditions with colors or shapes (Figure 2). Therefore, the IVs were Task (memory, passive) and Stimuli (color, shape), and the DV was SPN amplitude generated by the probe patterns in the delay. The SPN was defined as the amplitude difference between symmetrical and random probes. If memory load interferes with symmetry processing, the SPN would be reduced in the memory tasks compared to the passive tasks.

In the two memory tasks, participants stored 4 sample items, observed the symmetrical or random probe, then compared the sample with 4 test items. On 50% of trials, the sample and test items were the same; on the other 50% of the trials, 1 of the 4 items was different at test. Participants judged whether the sample and test were the Same or Different. Here shape or color information was stored in VWM when the probe was presented. We chose 4 items because this is often claimed to be the capacity limit of VWM (Luck & Vogel, 1997). In the two passive conditions, the participants made a very easy judgement about whether the perimeter of the test array was red or blue. Therefore, no information was stored in VWM when the probe pattern was presented (Figure 2).

Both memory tasks were informed by a pilot behavioral study in which performance was around 75% correct. Crucially, this indicated that the cognitive load of shape and color tasks was both comparable and below ceiling. Therefore, VWM was equally challenged by these tasks because participants were holding shape and color information in VWM during the delay when the probe was presented. We hypothesized that VWM load would affect concurrent symmetry processing, and thus the SPN should be reduced in memory tasks compared to passive viewing. We also tentatively predicted that the shape memory cost would be greater than the color memory cost. After all, visual object information is coded in LOC, which is also required to code symmetry. These hypotheses were pre-registered (https://aspredicted.org/9sh7k.pdf).

5  |  EXPERIMENT 1 METHOD

5.1  |  Participants

Twenty-four participants were recruited (19 female, 21 right-handed, average age 21.5, range 18 to 46). Participants had normal or corrected-to-normal vision and were not color blind. The study had local ethics committee approval (Ref 2122) and was conducted in accordance with the 2008 Declaration of Helsinki.

5.2  |  Design

We used a within-subjects design with 4 conditions: Task (memory, passive) and Stimuli (color, shape). The DV was the SPN amplitude generated by the probe patterns. The SPN is the amplitude difference between symmetrical and random probes. The study was pre-registered (https://aspredicted.org/9sh7k.pdf) and the results and experiment presentation scripts are available on Open Science Framework (https://osf.io/uzky9/).

5.3  |  Apparatus

The apparatus was the same as our recent SPN research (Derpsch et al., 2019). Participants were held 57 cm from a 51° × 29° 60 Hz LCD monitor. A chin rest was used for head stabilization. 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. The experiments were programmed in PsychoPy3 (Peirce et al., 2019).

5.4  |  Stimuli

5.4.1  |  Color stimuli

The color square items used in the color task are shown in Figure 2 (upper panel). The diameter of the grey background disk was 4°. The squares were 0.5° × 0.5°. The four
**FIGURE 2** All conditions used in memory and passive Tasks of Experiment 1. In the memory tasks, the participants compared the sample and test stimuli. In the passive tasks, the same conditions were presented but participants were asked to judge the border color of the test stimuli answering Red or Blue (see last rows). The probe patterns were not task relevant. We measured the SPN comparing waves generated by Symmetrical and Random probes (see left 4 and right 4 columns).
colored squares were ±0.75° from the center, arranged in a 1.5° wide global square. This global square was positioned in the foveal region to reduce unwanted saccades and covert shifts of attention. On the sample presentation, each square was selected at random from 7 blue/green colors chosen from a PsychoPy pre-set (Blue, Dark Blue, Royal Blue, Dark Green, Dark Olive Green, Forest Green and Teal) with no duplication. The colors were chosen exclusively from within a blue/green spectrum (approx. ~450–560 nm wavelength or 90° to 270° hue angle) to match task difficulty with the shape memory task (it is more difficult to differentiate and remember colors from a similar hue category; Bae et al., 2015). On same trials, the same colors were shown at test. On different trials, 1 of the 4 colored squares changed at test. The identity of the changed colored square was selected at random.

5.4.2 | Shape stimuli

Stimuli used in the shape task are shown in Figure 2 (lower panel). Stimulus sizes was similar to the color task, so the 7 shapes had approximately the same area (~0.5 deg²). On the sample presentation, four small black shapes were selected at random from a set of 7 (Cross, Club, Diamond, Disk, Moon, Star and Triangle) with no duplication. On same trials, the same shapes were shown at test. On different trials, 1 of the 4 shape items changed at test, and the identity of the changed shape was selected at random.

5.4.3 | Probe stimuli

Probe patterns contained 64 elements within a circle of 3.2° diameter. These elements were placed within a grey circular background 4° in diameter. Each element was a dot generated as a black circle with a 0.45° diameter. However, there was a Gaussian luminance mask with a standard deviation of 0.75°. Therefore, the Gabor appeared with a size of approximately half the original dot dimension (0.225° diameter). Element position was constrained so they could not overlap and the minimum distance between them was 0.14°. There was an additional constraint which prevented Gabor falling in the very center of the pattern (an 0.15° diameter exclusion zone). The symmetrical patterns had 4 axes of reflection to maximize SPN amplitude (Makin et al., 2016).

5.5 | Procedure

All participants completed two tasks with two stimulus types: memory shape, memory color, passive shape, and passive color (Figure 2). These were presented in separate blocks, and block order was balanced, so half completed the memory task first; half completed the passive task first. Within this, stimuli were balanced, so half the participants saw the shapes first and half saw the color first. In each task, there were 15 blocks of 8 trials (480 trials in total) and each trial type was shown once per block. Crucially, in the ISI there were 60 probe trials with a symmetrical pattern and 60 probe trials with a random pattern. This trial number is sufficient for a reliable SPN recording (see Boudewyn et al., 2018 for analysis of trial number and statistical power in ERP research). Before each task there was a single practice block with 8 trials.

Trial structure is shown in Figure 2. Each trial began with a 1000 ms baseline period where a central grey disk was presented. This was followed by a 500 ms stimulus presentation (4 shapes or 4 color items) and then a 750 ms blank interval. After this, the ISI consisted of a 750 ms pattern presentation (symmetrical or random). Then a 1000 ms test presentation showed either the same sample stimuli array again, or a different test array. Finally, the participant made a judgement. They pressed either the left (A) or right (L) key to report Same or Different in the memory tasks and pressed either the left (A) or right (L) key for Red or Blue perimeter in the passive viewing tasks. The meaning of left and right keys was counterbalanced across participants. One participant’s behavioral data was missing in Shape Memory task, so behavioral analysis was conducted on the remaining 23.

5.6 | EEG analysis

EEG data was processed in EEGLAB13.4.4b in Matlab 2014b (Delorme & McKeag, 2004). As in previous SPN research, data from 64 scalp electrodes was average referenced, was low pass filtered at 25 Hz, downsampled to 128 Hz, and segmented into epochs. Here epochs were time locked to the onset of the probe pattern (~500 to +750 ms, with a ~200 to 0 ms baseline). Data was cleaned with independent components analysis (ICA; Jung et al., 2000). The number of components removed ranged from 1 to 21 (mean = 4.43). After ICA cleaning, trials where amplitude exceeded ±100 microvolts at any electrode were removed. We extracted SPNs (symmetry – random) at a priori electrode cluster PO7, O1, O2 and PO8 from 250–750 ms after probe onset. After observing the ERP waves, we took a post-hoc decision to divide this into early (250–450) and late (450–750) windows.

As explained in Supplementary Material, ICA cleaning reduces the need for trial rejection by 24% on average,
although this varies greatly between participants. Between 4 and 7 of the 24 participants would need to be replaced without ICA cleaning, depending on condition. However, results were similar whether ICA cleaning is included in the pipeline or not. ICA cleaning removes the blink artifact, but then results in inclusion of blink trials where participants closed their eyes. It is likely that this did not alter ERPs substantially because blinks were concentrated before stimulus onset.

5.7 | Experiment 1 Results

5.7.1 | Behavioral results

Performance was at ceiling in both passive tasks (99% correct). By contrast, performance was similar in shape memory and color memory tasks, and much below ceiling (colour 74%, shape 75%, \(t(22) = 0.694, p = .495\)). These replicate the pilot behavioral study. We also note that memory performance was similar whether the probe was symmetrical or random (Colour memory task, 73% vs. 75%, \(t(22) = 1.199, p = .243\); Shape memory task 74% versus 76%, \(t(22) = 1.182, p = .250\)).

5.7.2 | EEG results

The SPN difference wave was present in all conditions (Figure 3). SPN amplitude was similar in color and shape conditions. Crucially, there was no evidence that holding information in VWM reduced SPN amplitude. In fact, the SPN was enhanced (i.e., more negative) in the memory tasks. However, this unexpected enhancement was only present in the early part of the SPN window (250–450 ms). The same effects are shown in topographic difference maps in Figure 4, and bar chart in Figure 5.

These impressions were confirmed with a three-factor repeated measures ANOVA [Window (250–450, 450–750) × Stimuli (Colour, Shape) × Task (Memory, Passive)]. There was no main effect of Stimuli (\(F(1,23) = 1.439, p = .242\)) and no interactions involving Stimuli (\(F < 1\)). The SPN was significantly stronger in the early window (\(F(1,23) = 106.397, p < .001\), partial \(\eta^2 = 0.822\)). There was also a Window × Task interaction (\(F(1,23) = 16.332, p = .001\), partial \(\eta^2 = 0.415\)). In the early window there was a main effect of Task (\(F(1,23) = 10.944, p = .003\), \(\eta^2 = 0.322\)). Conversely, in the late window there was no main effect of Task (\(F < 1\)). All 8 SPNs illustrated in Figure 5 constituted a significant response to symmetry (one sample t tests, symmetry – random < 0, \(p < .013\), see 95% CI).

5.7.3 | Potential interactions between SPN and other posterior negativities

Many studies have reported posterior negativities that scale with VWM load (e.g., Luria, 2016; Vogel & Machizawa, 2004). One of these is the Negative Slow Wave (NSW) which is bilateral with centrally presented stimuli. NSW amplitude increases with memory load and would be large when remembering 4 items in our memory tasks (Feldmann-Wüstefeld, 2021). There are various ways NSP and SPN could be interrelated. One possibility is that the NSW would summate with the SPN at the scalp level. This might explain the apparent SPN enhancement in the memory tasks. However, this possibility can be ruled out—baseline correction to the 200 ms pre-probe interval subtracts pre-existing NSW differences. However, to examine other possible interactions between NSP and SPN, we extracted −500 to 2000 ms epochs with 200 ms pre-sample baseline.

EEG pre-processing was based on our standard procedures. On average, 5,667 ICA components were removed from each participant (min = 0, max = 16). After ICA cleaning, an average of 28.4% of trials were removed due to high amplitude artifacts (±100 microvolts at any of the 64 scalp electrodes). For this analysis, three participants were removed because less than 50% of trials remained. Analysis was thus based on 21 participants.

ERPs from electrode cluster [PO7 O1 O2 and PO8] are shown in Figure 6. Results from tasks with color stimuli are shown on the left and from tasks with shape stimuli are shown on the right. Grand average ERP waves are shown on the top row (with Sample, Delay and Probe intervals highlighted).

The NSW was calculated as the difference between memory and passive tasks. This subtraction removes purely stimulus-driven responses to the sample array. NSW waves are shown in the middle row of Figure 6. When color stimuli were used, the NSW was generated in the 200–1000 ms interval (\(t(20) = −3.328, p = .003\)). Conversely, there was no such NSW for shape stimuli (\(t(20) = 0.150, p = .882\)). This difference between color and shape conditions was significant (\(t(20) = 2.989, p = .007\)). The absent NSW in the shape task is surprising. It could be explained if participants grouped the 4 items into a single gestalt, effectively reducing VWM load from 4 to 1. However, performance was similar in the color and shape memory tasks (74% vs. 75% correct), suggesting they were cognitively similar, and no special strategies were available for encoding shapes.

The SPN was calculated as the difference between symmetrical and random probes in the 1500 to 1700 ms interval (corresponding to the 250 to 450 intervals reported in the original analysis). The SPN enhancement in the memory
tasks is evident again (Figure 6, bottom row). This was confirmed with repeated measures ANOVA [2 Task, (memory, passive) × 2 Stimuli (colour, shape)]. There was a main effect of Task ($F(1,20) = 7.351, p = .013, \eta^2 = 0.269$), but no main effect of Stimuli ($F < 1$) and no interaction ($F < 1$). It is noteworthy that no aspect of the SPN results was dependent on the presence or absence of a previous NSW, which emphasizes the independence of the SPN and the NSW.

Next, we tested the significance of the 4 SPNs with one sample $t$ tests (Symmetry – Random difference wave $<0$). The exception was the SPN in the passive task with color stimuli ($p = .173$). The other three SPNs were significant ($p < .015$). It is not surprising that SPN effects are weaker compared to the original analysis. We are now baseline correcting to an interval $−1700$ to $−1500$ ms before probe onset, rather than $−200$ to $0$ ms before probe onset. This allows substantial amplitude drift to accumulate, causing noisy individual differences to emerge. On top of this, increased trial and participant removal decreases signal to noise ratio.

Finally, in tasks with color stimuli, individual subject NSW amplitude ranged from $−4.237$ to $+3.198$ microvolts. There was no indication that participants with a larger NSW had a larger SPN enhancement in the memory task ($r = .340, p = .132$). This suggests that the observed SPN enhancement has little to do with the earlier NSW.

5.8 | Experiment 1 Discussion

Experiment 1 found no evidence that holding color or shape information in VWM interferes with SPN generation. This is consistent with other work showing concurrent memory demands do not interfere with visual processing (Vickery et al., 2010), but inconsistent with our a priori predictions. In fact, SPN amplitude was larger in the memory task, particularly in the early part of the probe presentation interval ($250–450$ ms). This unexpected early enhancement could be due to increased visual alertness.

We also conducted exploratory analysis of memory related components time locked to sample onset (Luria et al., 2016). We focused on the NSW, which is bilateral for centrally presented stimuli and scales with set size (Feldmann-Wüstefeld, 2021; Fukuda et al., 2015). The NSW
was apparent in the color memory task, but not in the shape memory task. This suggests tasks were not cognitively equivalent, although performance was similar. Despite this, the SPN enhancement was very similar in both color and shape memory tasks. We elaborate more on similarities and differences between SPN and NSW in the general discussion.

To maximize chances of detecting any interference from memory, we designed Experiment 1 so that the symmetrical and random probes were never task relevant. There was nothing to be gained from processing the probe regularity. If anything, this would distract from the primary goal of remembering the four sample items. Nevertheless, despite the potential distractor costs, the brain not only processed the symmetrical pattern, but it actually generated a greater SPN compared to the passive viewing conditions.

6 | EXPERIMENT 2

Experiment 1 suggested that the SPN is robust to interference from concurrent color and shape memory tasks. However, this could be because color and shape processing mechanisms do not overlap with symmetry processing mechanisms. Experiment 2 tested a stronger form of interference: participants held green symmetrical patterns in VWM when the black probes were presented. They judged whether the green sample and test symmetrical patterns were the same or different (Figure 7). We reasoned that
this would maximize memory-based interference with probe symmetry processing. Experiment 2 was also pre-registered (https://aspredicted.org/9sh7k.pdf).

6.1 | Experiment 2 method

Twenty-four participants were involved (20 females, 21 right-handed, mean age 21.75, range 18 to 43). The results and experiment presentation scripts can be found on Open Science Framework (https://osf.io/uzky9/). The apparatus was the same as in Experiment 1. Stimuli and trial structure are shown in Figure 7. The probe stimuli were the same as Experiment 1. The sample and test symmetries were generated by the same algorithm as the probes, although the Gabor elements were green instead of black. On same trials, the same green symmetrical pattern was shown at sample and test. On different trials, 8 of the 64 green Gabor elements changed position (so 12.5% of the pattern was different).

This made the change quite subtle, as substructures of the green sample pattern were similar at test. Earlier pilot work showed that this gave a performance at around 75% correct, thus matching Experiment 1. In contrast, performance was near ceiling if all elements changed position.

As in Experiment 1, tasks were presented in blocks and order was balanced. There were 15 blocks of 8 trials (240 trials in total) and each trial type was shown once per block. In the ISI there were 60 probe trials with a black symmetrical pattern and 60 probe trials with a black random pattern. Before each task there was a single practice block with 8 trials. Temporal parameters were identical to Experiment 1 (Figure 7).

6.2 | EEG analysis

EEG pre-processing procedures were the same as Experiment 1. In the memory task, an average of 6.375
components were removed from each participant (min 2, max 14). In the passive task, an average of 6.875 were removed (min 2, max 14). Trial exclusion rates were around 2%–3% in all conditions. As explained in Supporting Information, ICA cleaning reduces the need for trial removal by 15% on average. Furthermore one participant would need to be replaced without ICA cleaning. However, results were similar whether ICA cleaning is included in the pipeline or not.

6.3 | Experiment 2 results

Participants were 99% correct when discriminating test perimeter color in the passive task and 78% correct when judging changes in the memory task. Memory performance was unaffected by regularity of the probe ($t(23) = 0.106, p = .917$).

ERP results are shown in Figure 8. We included a Time window factor for consistency with Experiment 1, although the differential effect of Task in early and late windows was not so clear in Experiment 2. The SPN was significantly larger in the memory task than in the passive task ($F(1,23) = 11.330, p = .003, \eta^2_p = 0.330$). There was a main effect of Window ($F(1,23) = 27.399, p < .001, \eta^2_p = 0.544$). Unlike Experiment 1, there was no Window × Task interaction ($F < 1$). There were significant SPNs in all conditions (one sample t tests, $p < .001$, Figure 8d).

FIGURE 7 | Stimuli examples for all conditions in Experiment 2. As in Figure 2, in the memory tasks, the participants compared the sample and test stimuli. In the passive tasks, the same conditions were presented but participants were asked to simply judge the border color of the test stimuli answering Red or Blue (see last rows). The probe patterns were not task relevant. We measured the SPN comparing waves generated by symmetrical (4 left columns) and random probes (4 right columns).
of Experiment ($F(1,46) = 2.981, p = .091$) and again the only interaction involving Experiment was the Task × Window × Experiment interaction ($F(1,46) = 4.383, p = .042$, partial $\eta^2 = 0.087$). These interactions support the impression that the task effect was more persistent in Experiment 2.

Next, NSW signals in Experiment 2 were analyzed in the same way as Experiment 1. On average, 7.563 components were removed from each participant (min 2, max = 14). After ICA cleaning, 17.8% of trials were removed due to 100 microvolt artifacts. All 24 participants were retained. Results are shown in Figure 9. The NSW (memory − passive waves) was evident again, but it was contained within the 500–1250 ms delay period ($t(23) = -3.026, p = .006$). This differs from Experiment 1 with Colour stimuli, where the NSW fell between 200 and 1000 ms.

The SPN (symmetrical probe − random probe, 1500 to 1700 ms) was significant in both memory and passive tasks ($p < .005$, one sample $t$ tests). The apparent enhancement in the memory task did not reach significance with a two tailed test ($t(23) = 1.830, p = .080$). As with Experiment 1, there was no correlation between NSW and magnitude of SPN enhancement in the memory task ($r = .146, p = .496$).

### 6.4 Experiment 2 Discussion

The hypothesis that a memory task involving symmetry would interfere with symmetry perception was not supported in Experiment 2. On the contrary, as with Experiment 1, SPN amplitude was larger in the memory task than in the passive task. This enhancement was slightly more persistent in Experiment 2, although we do not wish to overinterpret this minor and unexpected difference between the experiments. The NSW was found in Experiment 2, although the onset was later than in Experiment 1 Colour task.

We assume that participants stored the symmetrical gestalt in VWM during the delay. However, it is possible that they performed the task by attending to one subsection and noticing whether a change occurred in that section or not. However, encoding of gestalts is superior, and the best available gestalt was the whole pattern. Furthermore, it is effortful to move covert attention to a subregion when...
the task demands central fixation. We think it is unlikely many participants used a parts-only strategy for the memory task in Experiment 2, but we cannot rule this out without further experiments.

7 | GENERAL DISCUSSION

In the present study, we hypothesized that maintaining any information in VWM should interfere with visual symmetry processing, resulting in a reduced SPN. This was not supported. We found no evidence that holding color and shape information in VWM impaired SPN amplitude (Experiment 1). Furthermore, we found no evidence for SPN reduction when holding similar symmetrical patterns in VWM (Experiment 2). Overall, in both experiments, the SPN was larger in the memory task than in the passive task. This unexpected enhancement was stronger in the early part of the probe interval (250–450 ms), particularly during Experiment 1.

These novel results emphasize the automaticity of symmetry processing. Previous work has shown that the SPN is attention-proof (Bertamini et al., 2020; Derpsch et al., 2019; Makin et al., 2020) and the evidence presented here shows that the SPN is also memory-proof. All these results provide converging evidence for automaticity of symmetry processing.

We also note that performance on the memory tasks was always around 75% correct, and not affected by probe regularity. There was no evidence that symmetrical probes selectively impaired performance on the concurrent memory task. This is most remarkable in Experiment 2 because one might expect symmetrical probes to selectively interfere with the already-stored symmetrical patterns. Consequently, it seems visual symmetry response is independent from VWM.

The unexpected aspect of our results was the enhanced SPN in the memory tasks. This could be due to increased visual alertness. Participants were probably prepared, more ready to see and attend to something during the ISI of the memory tasks. The fact that the enhancement was very similar in color, shape, and symmetry memory tasks points to a general explanation of this kind. Nevertheless, future experiments with more engaging alternatives to the passive viewing tasks are required to establish this conclusion. This putative effect of alertness may seem inconsistent with the claim that the SPN is attention-proof, which we used to frame the current research. However, that claim only means the SPN survives most experimental manipulations of task; amplitude still depends on attentional state to some extent.

There is substantial evidence that memory and perception overlap. Perceptual organization clearly

FIGURE 9 Experiment 2 ERP waves with extended epoch. Results from Experiment 2. Conventions are the same as Figure 6.
allows for efficient VWM (Attneave, 1955; Kemps, 2001; Woodman, 2003). Indeed, Morey (2019) has suggested that the effect of perceptual organization on visual memory is a robust boost on memory performance. This all suggests that determinants of gestalt formation are also determinants of successful encoding. Our results do not challenge this conclusion. Nor do our results challenge the perceptual memory model (Pasternak & Greenlee, 2005) or the sensory recruitment hypothesis (Harrison & Tong, 2009; Serences et al., 2009): it is plausible that the same neural populations mediate visual perception and visual memory. However, these neural populations may have adequate capacity for simultaneous memory and perceptual operations without them interfering with each other. Indeed, Rademaker et al. (2019) found that sensory and mnemonic information could coexist in the visual cortex: visual areas may be capable of multiplexing, so novel visual information need not wipe out stored information. One possibility is that layer 4 codes new visual symmetry inputs whilst layer 5 codes information held in VWM (e.g., Van Kerkoerle et al., 2017), which could facilitate rapid comparison without interference.

Classic work by Mack and Rock (1998), Moore and Egeth (1997) and recently Wood and Simons (2019) has demonstrated that subliminal gestalt grouping induces visual illusions. The current study goes a step beyond that: it shows that the brain responds to symmetry even when it is potentially disruptive to the primary task, not just when it is irrelevant to the primary task.

7.1 SPN and other posterior negativities

The SPN generated by symmetry resembles other known ERPs that are related to VWM processes. For instance, the Contralateral Delay Activity (CDA) measured at electrodes PO7/8 is an index of VWM. A typical task is like our memory tasks, but with cue indicating that participants should remember items presented in the left or right hemifield. Amplitude is more negative on the contralateral hemisphere (Vogel & Machizawa, 2004; Vogel et al., 2005). The contralateral-ipsilateral difference wave is the CDA, and its amplitude scales with the number of items held in working memory, reaching an asymptote at individual VWM capacity (for review see Luria et al., 2016). Although the CDA is sometimes called the Sustained Posterior Contralateral Negativity (SPCN; Jolicoeur et al., 2008), it is quite different to the SPN. The CDA/SPCN is the contralateral-ipsilateral difference wave (e.g., PO7–PO8) whilst the SPN is the bilateral symmetry-random difference wave (e.g., average of PO7 and PO8).

The SPN is more like a VWM related component called the NSW which is also bilateral. NSW scales with set size for centrally presented stimuli, and also asymptotes at VWM capacity (Feldmann-Wüstefeld, 2021; Fukuda et al., 2015). Should the SPN be reinterpreted as a symmetry-induced modulation of the NSW? Perhaps symmetrical patterns are spontaneously encoded in VWM whilst random patterns are not, so symmetrical conditions generate an NSW? Consideration of NSW and SPN amplitudes makes this implausible. The SPN scales with the amount of regularity in the image (Makin et al., 2016) and reaches −3.5 microvolts (as shown in Figure 1; Makin et al., 2020). In contrast, NSW scales with the number of encoded items, with −1 microvolt difference between 1 item and the asymptote (Fukuda et al., 2015). The SPN is simply too large to be an incidental NSW caused by spontaneous VWM processing.

This was investigated in additional analysis (Figures 6 and 9). We extracted longer epochs, including the ERP activity following the sample as well as probe. The difference between memory and passive tasks isolates VWM activity following the sample. Indeed, these difference waves can be interpreted as an NSW with set size 4 in Experiment 1, or NSW generated by storage of a green symmetrical pattern in Experiment 2. Experiment 2 provides the most interesting comparison here. The NSW following the green symmetrical sample was −1.04 microvolts, whilst the subsequent SPN generated by the probe (computed from exactly the same ERP data) was −2.85 microvolts. If the SPN was actually an NSW caused by differential VWM processing, relative effect sizes would be reversed. It is unlikely that spontaneous encoding of symmetry would generate an NSW nearly 3 times larger than active encoding of similar symmetry.

While we do not think the SPN should be universally reinterpreted as a symmetry induced change in VWM processes, it is possible that the preceding NSW activity contributed specifically to the observed SPN enhancement in the memory task. We found an NSW (memory-passive) in the color stimuli conditions of Experiment 1 (200–1000 ms following sample onset) and again in Experiment 2 (500–1250 ms following sample onset). Surprisingly, there was no NSW in the shape stimuli conditions of Experiment 1. Crucially, the subsequent SPN effects were similar in all tasks, despite various differences in the preceding NSW. Furthermore, there was no correlation between participant’s NSW and magnitude of the SPN enhancement. We conclude that the SPN can be most parsimoniously understood as a response to symmetrical probes which was
enhanced by a general increase in visual alertness during the memory tasks. Other interpretations of the SPN are incompatible with one or more aspects of these results or the wider literature.

8 | CONCLUSION

Recent work has shown that the SPN is robust to variation in task (Makin et al., 2020), feature attention (Bertamini et al., 2020) and spatial attention (Derpsch et al., 2019). In the current study we found the SPN is also robust to variations in memory load. Contrary to our predictions, there was no evidence that VWM interfered with the symmetry response. Instead, there was a general enhancement in all memory conditions (colour and shape memory in Experiment 1, and symmetry memory in Experiment 2). This is probably due to non-specific increases in visual alertness during the memory tasks. We conclude that the symmetry network is not disrupted by concurrent visual memory tasks, even when these tasks involve remembering symmetry itself. These findings are a novel demonstration of the automatic nature of symmetry perception.

ACKNOWLEDGEMENTS

This project was funded by an ESRC grant award (ES/S014691/1). We thank Kezia Finch, Chloe Finlinson, Katie Hardiman, Maya Huelin, Jack Poynton, Anna Southward and Grace Stewart for assisting with data collection.

CONFLICT OF INTEREST

We declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Yiovanna Derpsch: Conceptualization; Formal analysis; Investigation; Methodology; Project administration; Visualization; Writing-original draft; Writing-review & editing. Giulia Rampone: Data curation; Formal analysis; Investigation. Andrea Piovesan: Investigation; Writing-review & editing. Marco Bertamini: Conceptualization; Methodology; Supervision; Writing-review & editing. Alexis D. J. Makin: Conceptualization; Formal analysis; Funding acquisition; Investigation; Methodology; Software; Supervision; Visualization; Writing-original draft; Writing-review & editing.

DATA AVAILABILITY STATEMENT

All ERP and behavioral data, and codes for analysis and stimulus presentation, are freely available on Open Science Framework. We are happy for other researchers to use this material.

ORCID

Yiovanna Derpsch https://orcid.org/0000-0002-4380-5058

REFERENCES


**Supporting Information**

Additional supporting information may be found in the online version of the article at the publisher’s website.

---

**How to cite this article:** Derpsch, Y., Rampone, G., Piovesan, A., Bertamini, M., & Makin, A. D. J. (2021). The extrastriate symmetry response is robust to variation in visual memory load. *Psychophysiology*, 58, e13941. https://doi.org/10.1111/psyp.13941