

Electrophysiological responses to visuospatial regularity

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Abstract

Humans are quicker to detect reflectional than rotational or translational symmetry, despite the fact that these patterns are equally regular. We were interested in the neural correlates of these perceptual effects. Participants viewed random, reflection, rotation, and translation patterns while we recorded EEG from the scalp. Half the participants classified the pattern regularity overtly, the other half did not explicitly attend to pattern regularity but reported rare oddball trials, where two squares were embedded among the dots. The amplitude of a symmetry-related ERP known as the sustained posterior negativity was most pronounced for reflection, then rotation and translation. We suggest that reflectional symmetry, despite its biological significance, may not be processed by unique visual mechanisms, but instead it could be a preferred stimulus for a more general regularity-sensitive network in the extrastriate visual cortex.

Descriptors: Cognition, EEG/ERP, Sensation/Perception, Normal volunteers

The universe is full of symmetrical objects at all scales, and the visual systems of many animals are tuned to symmetry (Treder, 2010; Tyler, 1995; Wagemans, 1995). At a perceptual level, it could be that symmetry is an important cue for figure-ground segmentation (Machilsen, Pauwels, & Wagemans, 2009), but in addition it has also been suggested that symmetry is important because it signals reproductive fitness in other members of the species (Møller, 1992). When people use the word “symmetry,” they often mean bilateral reflectional symmetry; however, symmetry is present in any pattern that is identical after undergoing an isometric transformation. If we restrict ourselves to the two-dimensional (2D) plane, there are four possible symmetries: reflection, glide reflection, rotation, and translation (Palmer, 1991; Wagemans, 1995). The fact that people associate symmetry with reflection alone is probably not an accident—this is the regularity known to be most salient for the human visual system (Mach, 1886/1959; Makin, Pecchinenda, & Bertamini, 2012; Royer, 1981).

Many psychophysical studies have empirically confirmed and expanded Mach’s early observations. It is known that reflectional symmetry with a vertical axis is detected more rapidly than when the axis is horizontal or oblique (Bertamini, Friedenber, & Kubovy, 1997; Friedenber & Bertamini, 2000), unless a particular orientation is anticipated (Wenderoth, 1994). Moreover, reflectional symmetry is detected more quickly than rotation or translation, even when the patterns are equated in terms of mathematical regularity (Bertamini, 2010; Bertamini, Friedenber, & Argyle, 2002; Koning & Wagemans, 2009; Palmer & Hemenway, 1978;

Royer, 1981). The current study was designed to explore neural processing of images containing reflection, rotation, random, or translation configurations.

There have been several neuroimaging studies on symmetry perception (reviewed in Treder, 2010). Sasaki, Vanduffel, Knutsen, Tyler, and Tootell (2005) recorded cerebral blood flow with fMRI while participants viewed reflection or random patterns. V1 and V2 were not differentially activated, but reflection produced more activity in the areas V3–V7 and the lateral occipital complex (see also Chen, Kao, & Tyler, 2007; Tyler et al., 2005). Most recently, Cattaneo, Mattavelli, Papagno, Herbert, and Silvanto (2011) disrupted the bilateral dorsal lateral occipital complex with transcranial magnetic stimulation (TMS), and discovered that this altered perception of reflectional symmetry.

Most relevant to the current work, Jacobsen and Höfel (2003) recorded event-related potentials (ERPs) produced by symmetrical and random patterns. They reported an ERP component called the sustained posterior negativity (SPN). It should be noted that negativity is a relative term here, referring to the fact that amplitude was more negative for the symmetrical than random patterns between 600 and 1,100 ms poststimulus. The SPN was replicated in subsequent experiments when participants were not explicitly encouraged to categorize the patterns in terms of their symmetry (Höfel & Jacobsen, 2007a), when participants deliberately misreported their responses (Höfel & Jacobsen, 2007b), and when they were attending to symmetry in human faces (Royer, Höfel, & Jacobsen, 2008). More recently, Makin, Wilton, Pecchinenda and Bertamini (2012) again recorded the SPN and found that it was unaffected by whether participants processed the reflection or random patterns as targets.

Given the special status of reflectional symmetry for human observers, one important issue is whether reflection is processed in a way that is unique and different from other regularities. The neuroimaging literature has not directly compared neural responses

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to different types of symmetry (reflection, rotation, and translation) with random patterns on the same participants. We therefore recorded ERPs produced by these patterns.

We assume that there are networks in the visual cortex that are sensitive to regularity, and that these networks generate the SPN (indeed, Makin, Wilton, Pecchinenda, & Bertamini, 2012, identified extrastriate SPN generators with the LORETA source localization procedure). With this in mind, we next considered several explanations for the well-documented salience differences between the different regularities.

One possibility is that the SPN-generating networks are sensitive to reflectional symmetry, but not to rotation or translation. If this is the case, the SPN would only be present for reflection, and the waveforms in the random, rotation, and translation condition would be nearly identical. It is possible that specialized mechanisms would be dedicated to detection of reflectional symmetry, because reflection has a special evolutionary significance. For example, the body plan of animals has bilateral reflectional symmetry, and specialized systems are certainly involved in face perception (see Tyler, 1995, for more on the biological significance of reflectional symmetry).

A second possibility is that the SPN generators are equally sensitive to all regularities. If this is the case, the SPN waveform would be similar for each regularity type, and the detection speed differences between the regularity types must arise from differential processing elsewhere in the brain.

A third possibility is that the networks responsible for the SPN are most sensitive to reflection, but also respond to rotation and translation to some extent. In this case, the SPN would be most pronounced for reflection, but also present for rotation and translation. In this case, the networks that generate the SPN could explain the known detection speed differences. This would suggest that there are no special mechanisms dedicated uniquely to reflectional symmetry, contrary to hypothesis one.

We compared ERPs in two different tasks that required different levels of engagement with the patterns. In the *explicit discrimination task*, participants classified the patterns as reflection, rotation, random, or translation on every trial. Conversely, in the *oddball detection task*, participants did not have to classify patterns overtly, but instead responded to rare oddball trials where some pattern elements stood out from the rest. If the SPN is generated by relatively automatic, bottom-up visual processing, it would thus be comparable in both tasks despite different attentional requirements. However, the SPNs produced by different kinds of regularity might be affected by this manipulation in different ways.

Method

Participants

Forty-eight participants were involved in this study (16 male, 2 left-handed, age 18–45). Participants had normal or corrected-to-normal vision. The study had local ethics committee approval and was conducted in accordance with the Declaration of Helsinki (revised 2008).

Apparatus

Participants sat 140 cm from the 40 × 30 cm monitor and used the A, S, K, and L buttons of a computer keyboard to enter their responses. Stimuli were generated and presented on a CRT monitor using the PsychoPy software (Peirce, 2007). Electroencephalographic (EEG)

activity was recorded using a BioSemi Active-Two amplifier in an electrically shielded and darkened room. EEG was sampled continuously at 512 Hz from 64 AgCl scalp electrodes arranged according to the International 10-20 system. Two additional electrodes, called common mode sense (CMS) and driven right leg (DRL), were used as reference and ground. Bipolar vertical (VEOG) and horizontal (HEOG) electrooculogram electrodes were positioned above and below the right eye, and on the outer canthi of both eyes, respectively. The EOG data were obtained from four external channels of the same BioSemi amplifier.

Stimuli

The stimuli were carefully constructed, and examples are shown in Figure 1. All stimuli were composed of 22 dots, with 11 each side of the midline (i.e., 11 to the left of fixation, 11 to the right of fixation). Dots varied in size between approximately 0.4° and 0.8° of visual angle. Dots were presented on a gray background with a diameter of 10.2°. The average distance of the dots from the vertical midline was 1.5°; the maximum displacement from average was 1°. In the regular conditions, the dot pairs were presented in equally spaced rows on the Y dimension; the distance between rows was 0.6°. The dot color ranged from black to mid-gray. In the regular patterns, dot pairs on either side of the transformation were the same shade. This feature can be seen in Figure 1.

Two kinds of random patterns were used, which we call *unconstrained* and *constrained*. These were counterbalanced across explicit discrimination and oddball detection tasks (so 12 participants had explicit discrimination with constrained random patterns, 12 had explicit discrimination unconstrained, 12 had oddball detection constrained, 12 had oddball detection unconstrained). Unconstrained random patterns were comprised of dots that were allowed to fall anywhere on the Y dimension (within the spatial limits of the other patterns). Conversely, for participants in the constrained condition, random patterns still had uniform Y-dimension rows, so the random noise was entirely produced by positional variation on the X-dimension. Constrained and unconstrained random displays had different advantages. The constrained random patterns were better matched with the regular patterns in terms of low-level visual variables such as number of contours and amount of occlusion. However, the evenly spaced rows introduced some regularity into the random patterns, reducing the difference with the regular patterns. The unconstrained random patterns had less of this unwanted regularity, but free position on the Y dimension introduced low-level confounds: the average size and luminance of the unconstrained random patterns was less than the regular ones, and the number of occlusions was greater. We included both constrained and unconstrained random patterns in analysis as between-subjects factors to test these factors.

Manipulation Check

Before EEG recording started, all participants first completed a 10-min behavioral manipulation check experiment. This was a two-alternative forced choice task where they discriminated regular from random patterns as quickly and accurately as possible. They were instructed to press the A button if they saw a regular pattern (either reflection, rotation, or translation) and the L button if they saw a random pattern. Stimuli were constructed in the same way as those used in the subsequent EEG experiment, described above. There were 20 trials in each regularity condition, and 60 random trials. Patterns were presented for a maximum of 3 s, and were

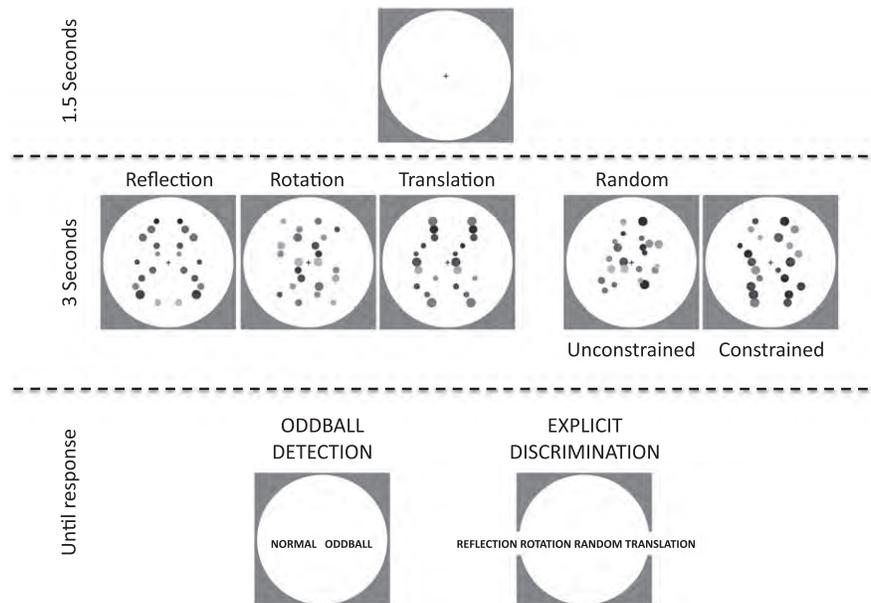


Figure 1. Stimuli used in this experiment. In the EEG recording, all participants were presented with 60 repeats of each regular pattern and 60 repeats of either the constrained or unconstrained random patterns. Patterns were visible for 3 s before participants entered their judgment. Half the participants explicitly discriminated between reflection, rotation, random, and translation patterns. For the other participants, the task was to judge whether it was a normal trial (all dots) or an oddball trial (two squares among the dots).

terminated upon button press. If participants pressed the wrong button, a beep sound was presented (800 Hz), and the pattern remained on the screen for a further 2 s. Before the manipulation check, participants were shown three examples of the different categories to ensure they understood the task.

Based on previous literature, we predicted that participants would be quicker to respond to reflectional symmetry compared to rotation or translation. This allowed us to confirm that the detection speed differences reported in earlier work (e.g., Royer, 1981) also applied to our participants.

EEG Experiment

We compared ERPs in two tasks that were completed by separate groups of 24 participants. One group were given an explicit discrimination task: They had to classify the patterns as reflection, rotation, random, or translation on each trial. The other group of 24 participants were given an oddball detection task: 16.6% of the trials were oddballs, in which two squares were added to patterns composed of circles. Therefore, observers did not have to attend to the different types of regularity and classify them. We were not interested in ERP responses to the oddball trials, although we expected to record a parietal P300 potential in these trials based on the large oddball-ERP literature (e.g., Luck, 2005).

In all experiments, there were 60 trials of each regularity type and 60 random trials. In the oddball detection task, there were an additional 12 oddball trials in each condition, which were not included in the analysis of the other ERPs. The patterns were presented in a unique random order for each participant, and could not be anticipated. Trials began with a 1.5-s fixation baseline, and then patterns were presented on the screen for 3 s (these parameters were chosen for consistency with previous symmetry-ERP literature, e.g., Jacobsen and Höfel, 2003, Makin, Wilton et al., 2012). Participants were instructed to fixate throughout the

period when the pattern was on the screen, as well as during the baseline period.

At the end of each trial, cue words appeared on the screen, with the positioning of the words indicating the response mapping for that trial (Figure 1). For example, in the explicit discrimination task, the cue words REFLECTION, ROTATION, RANDOM, and TRANSLATION appeared, with the position of the words arranged in an unpredictable way on each trial. Participants pressed left (A) and mid-left (S) keys with their left hand, and mid-right (K) and right (L) keys with their right hand. Participants understood that the keys corresponded to the positioning of the cue words, so if the cue REFLECTION was positioned on the far left side, and it was indeed a reflection trial, participants were required to press the far left (A) key. Alternatively, if the cue RANDOM was positioned on the far right, and it was a random trial, then participants were required to press the far right (L) key. In the oddball detection task, the words NORMAL and ODDBALL and the left (A) and right (L) buttons were used in the same way. The positioning of the cue words was counterbalanced with pattern types. The advantage of this protocol was that it was impossible to know which hand would be used to enter responses while the stimuli were on the screen, and therefore ERPs were not influenced by lateralized preparation of motor responses (Makin, Poliakoff, Ackerley, & El-Derey, 2012).

EEG Analysis

EEG data were processed using the EEGLAB toolbox in MATLAB. Raw signals from 64 scalp electrodes were referenced to an average reference, and low-pass filtered at 25 Hz. Data were resampled at 128 Hz to reduce file size, and segmented into -0.2 to $+2$ s epochs, with -200 to 0 ms baseline. After this, independent components analysis (ICA; Jung et al., 2000) was used to remove artifacts produced by blinks and eye movements. Data were reformed as 64 components, and an average of 7.85 components were removed

from each participant (min = 2, max = 16). After ICA, trials with amplitude beyond $\pm 100 \mu\text{V}$ at any electrode were excluded. The average proportion of excluded trials did not differ significantly between regularities (reflection 9%, rotation 9%, translation 10%, random 10%; $p = .505$), between participants in the explicit discrimination and oddball detection tasks (9% vs. 10%; $p = .561$), or between participants in constrained and unconstrained conditions (10% vs. 9%; $p = .603$). Finally, there was no difference between the proportion of excluded trials in the normal and oddball trials of the oddball detection task (9% vs. 8%; $p = .516$).

The participants were instructed to fixate centrally and avoid blinking throughout the trials, and we used ICA to eliminate eye movement artifacts. However, this procedure is imperfect, and it does not remove the cortical consequences of eye movements from the ERP signal. We therefore compared VEOG and HEOG activation in all conditions, without excluding any trials, in order to establish the prevalence of eye movements. We focused on EOG activity during the first 1 s of the presentations, where the ERPs of interest were recorded. Horizontal and vertical eye electrode channels were segmented into epochs (-0.2 to 1 s), and amplitude at each time point was converted to an absolute value before averaging across the interval.

Mean HEOG activity did not differ between regularity conditions (reflection $16.11 \mu\text{V}$, rotation $16.72 \mu\text{V}$, random $17.15 \mu\text{V}$, translation $16.37 \mu\text{V}$; $p = .100$) or between participants presented with constrained or unconstrained random patterns (17.28 vs. $15.90 \mu\text{V}$; $p = .419$). Although HEOG activity was significantly greater in the explicit discrimination task than the oddball detection task (18.88 vs. $14.29 \mu\text{V}$; $p = .01$), there were no interactions between regularity and task ($p = .214$) or regularity, task, and random constraints ($p = .503$). Finally, HEOG activity did not differ between normal and oddball trials (14.29 vs. $14.68 \mu\text{V}$; $p = .382$) in the oddball detection task.

Mean VEOG activity differed between regularities (reflection $30.68 \mu\text{V}$, rotation $28.07 \mu\text{V}$, random $28.61 \mu\text{V}$, translation $28.71 \mu\text{V}$; $p = .032$), but not between participants in the constrained and unconstrained conditions (28.34 vs. $29.70 \mu\text{V}$; $p = .737$). VEOG activity was greater in the explicit discrimination task than the oddball detection task (34.40 vs. $23.64 \mu\text{V}$; $p = .011$). There were no interactions between regularity and task ($p = .105$) or regularity, task, and random constraints ($p = .896$). VEOG activity did not differ between normal and oddball trials in the oddball detection task (23.64 vs. $24.28 \mu\text{V}$; $p = .516$).

Ideally, the HEOG and VEOG activity would be equal in all conditions. Nevertheless, we note that the distribution of EOG activity was fundamentally from the pattern of ERPs reported below, providing confidence that these patterns do not themselves result from unwanted EOG activity or artifact rejection procedures.

Statistical Analysis

Electrophysiological data were analyzed using mixed analysis of variance (ANOVA) techniques, where the within-subject factors were crossed with the between-subjects factors task and random constraints. The Greenhouse-Geisser correction factor was applied when the assumption of sphericity was violated. In the Results section, we report the epsilon value used to adjust degrees of freedom, the uncorrected F values, and the corrected p values. We report the exact p value from effects unless they are less than .001 (in which case we state that $p < .001$). Sometimes we summarize several statistics without reporting each individually. In this case,

we give the smallest or largest effect of those summarized, as appropriate.

For significant results, effect sizes were estimated with partial η^2 , which gives the proportion of variance attributable to factor. Important effects were explored further with paired samples t tests, and test effect sizes were estimated with Cohen's d , which gives the size of the effect in standard deviation units ((Mean1 - Mean2) / pooled SD). Most of the analyzed variables did not deviate significantly from the normal distribution shape according to Shapiro-Wilk test ($p > .05$, 3 out of 19 variables, none from the ERP analysis), and secondary nonparametric analysis confirmed all effects where the assumption of normality was violated.

Results

Manipulation Check

Before participants did the EEG experiment, they were presented with a short behavioral experiment, in which they had to discriminate regular from random patterns as quickly as possible. There were 60 random patterns, and there were 20 of each regularity type (reflection, rotation, and translation). Trials where participants pressed the wrong button were excluded (8.0%). Results are shown in Figure 2A. Reaction times in each condition were compared with mixed ANOVA, with one within-subjects factor, regularity (reflection, rotation, translation), and two between-subjects factors, Subsequent Task (explicit discrimination, oddball detection) \times Random Constraints (constrained, unconstrained). There was a main effect of regularity, $F(2,88) = 109.552$, $p < .001$, partial $\eta^2 = .713$, $\epsilon = .764$, because participants were quickest to detect reflection, then translation, then rotation, with the differences between all three being highly significant, $t(47) > 5.831$, $p < .001$, $d > 0.63$. There was also a between-subjects effect of random constraints, because people were quicker to respond when they were presented with unconstrained random patterns, $F(1,44) = 26.895$, $p < .001$, partial $\eta^2 = .379$. Finally, there was a significant Regularity \times Random Constraints interaction, $F(2,88) = 7.588$, $p = .003$, partial $\eta^2 = .147$, $\epsilon = .764$, partly because the reaction time (RT) difference between participants in the constrained and unconstrained groups was smaller for reflection than rotation or translation (although this difference was significant in all cases, $t(46) > 3.470$, $p < .002$, $d > 1.0$). The groups of participants involved in explicit discrimination and oddball detection performed in a similar way during the manipulation check experiment. There was no main effect of subsequent task, and no interactions involving this factor, $F(2,88) < 1$, ns .

EEG Experiment

Participants were presented with patterns of three different regularity types (reflection, rotation, and translation), along with random patterns (Figure 1). Half the participants explicitly classified the patterns according to regularity, and for these participants the proportion of correct answers were analyzed with a mixed ANOVA with one within-participants factor, regularity (reflection, rotation, random, translation) and one between-participants factor, random constraints (constrained, unconstrained). There was a main effect of regularity, $F(3,66) = 15.068$, $p < .001$, partial $\eta^2 = .407$, with best performance in the reflection condition, then random, translation, and worst performance for rotation (Figure 2B). With the exception of random and translation, the difference between all regularity conditions was significant, $t(23) > 2.247$, $p < .024$,

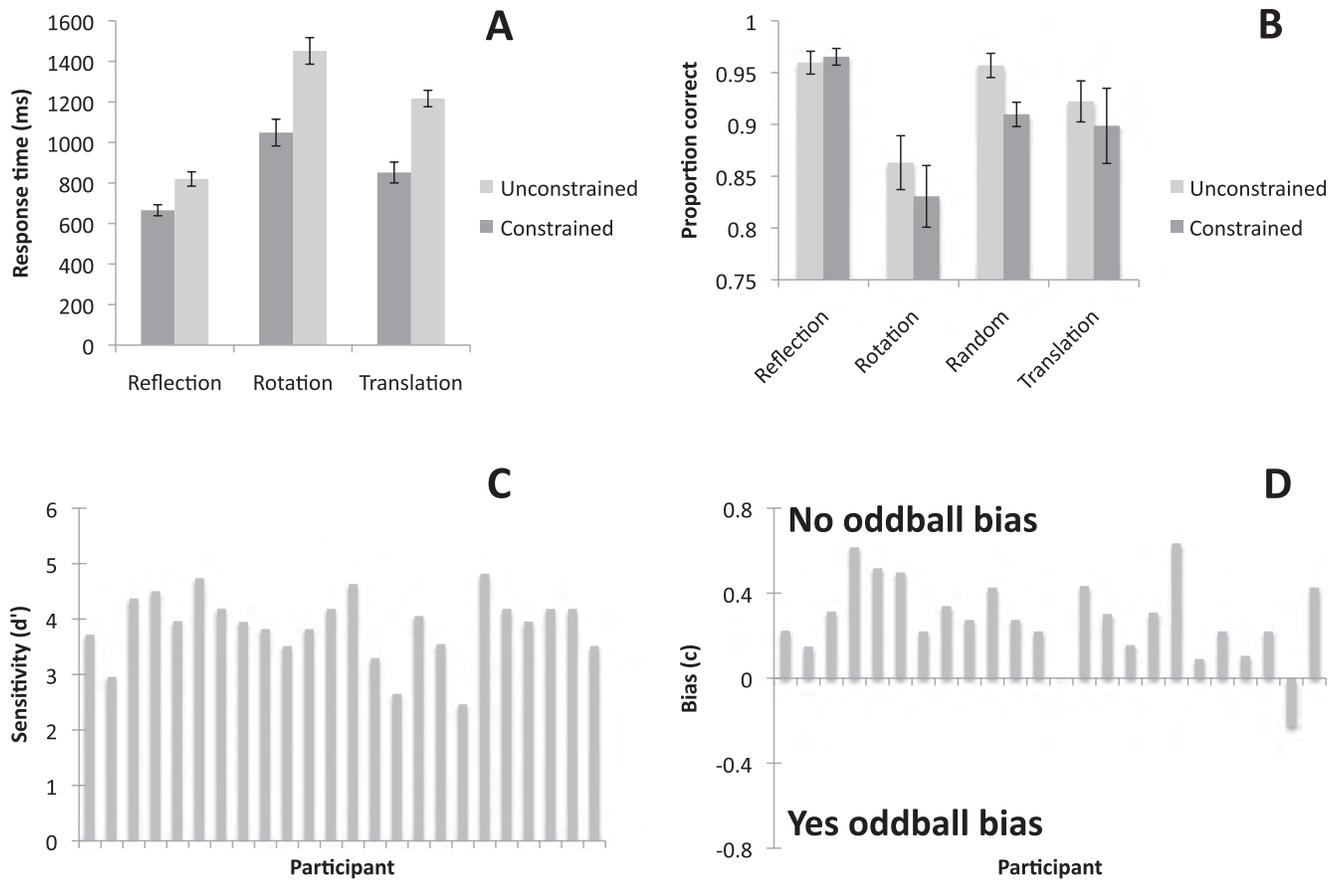


Figure 2. Behavioral results. A: Results of the manipulation check experiment. Mean response time is shown for each stimulus type. Separate bars show data for the groups of participants presented with constrained or unconstrained random patterns. B: Explicit discrimination performance as a function of regularity and random constraints. C: Sensitivity in the oddball detection task for each participant. Greater d' values reflect better performance. D: Response bias in the oddball detection task. Greater C values reflect bias towards reporting “no oddball.” Error bars = ± 1 S.E.M.

$d > 0.649$. Although it can be seen in Figure 2B that performance was slightly better for the group of participants with unconstrained random patterns, neither the effect of random constraints, $F(1,22) = 1.318$, $p = .263$, nor the Regularity \times Random Constraints interactions, $F(3,66) < 1$, ns , were significant.

Performance on the oddball detection task was measured with signal detection analysis. Oddball detection was extremely good for all participants, and mean d' was 3.883, significantly greater than the chance level, $t(23) = 31.378$, $p < .001$, $d = 6.405$; Figure 2C. Participants were biased to reporting “no oddball” (mean $C = 0.28$, $t(23) = 7.077$, $p < .001$, $d = 1.445$; Figure 2D). This is important because it suggests ERPs were not affected by the perception of nonexistent oddballs. Neither metric was significantly affected by the constraints of the random patterns, $t(22) < 1.517$, $p > .143$.

Sustained Posterior Negativity

In EEG research, there is an element of arbitrariness in choosing the electrodes and time points for statistical analysis from the large range of available options. We therefore examined the SPN using the same electrodes and time intervals as in Makin, Wilton et al. (2012). This was also the most appropriate interval for the current

data, and it allowed the best comparisons with previous work. SPN amplitude was measured at the PO7 and PO8 electrodes from 300 to 1,000 ms poststimuli. Figure 3 shows ERPs collapsed across the between-subjects factors task and random constraints. The SPN appears in Figure 3A as relatively lower amplitude in the regular conditions compared to the random condition from around 300 ms onwards. It can be seen that this component is present for all regularity types, but is more pronounced for reflection than rotation or translation.

The scalp distribution of the SPN is shown in Figure 3B, where the average voltage in the three regular conditions is subtracted from that of the random condition. In Figure 3B, there are three topographic plots: the left shows N1, which we discuss later. The middle and right plots show the SPN distribution for 300–650 ms and one for 650–1,000 ms windows. The similarity between these two demonstrates that the SPN remains stable across the whole period.

PO7 and PO8 amplitude in the 300 to 1,000 ms interval was analyzed with mixed ANOVA with a single within-subjects factor, regularity (reflection, rotation, random, translation), and two between-subjects factors, Task (explicit discrimination, oddball detection) \times Random Constraints (constrained, unconstrained).

The impressions in Figure 3A were confirmed by a strong main effect of regularity, $F(3,132) = 21.892$, $p < .001$, partial $\eta^2 = .332$.

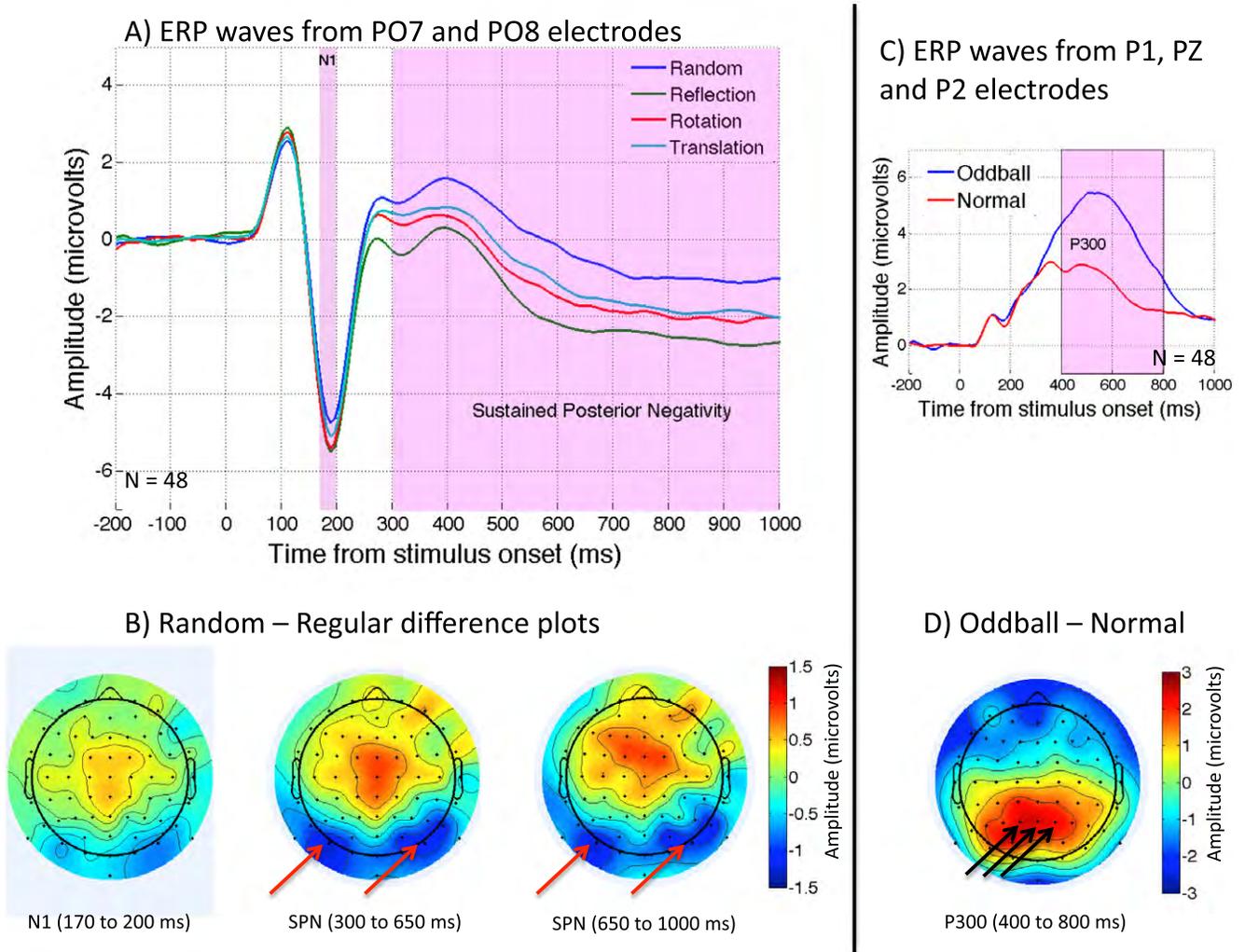


Figure 3. Grand average ERP waveforms ($N = 48$). A: Grand average ERPs from the PO7/PO8 electrodes in the four regularity conditions. N1 and SPN are highlighted in purple. B: Topographic plots of the difference between the average of the regular patterns and the random patterns at N1 and SPN latencies. The SPN is shown in two plots, demonstrating that it remains similar throughout. Here, red means higher amplitude in the regular patterns, blue means higher amplitude for the random patterns. C: Grand average ERP from the P1, PZ, and P2 electrodes. All ERPs were smoothed with a 10-point moving average filter, in addition to data preprocessing procedures described above (the same applies to other figures). D: Difference plot showing the parietal P300 component. Arrows on the topographic maps show the electrodes plotted in the corresponding ERP plots.

All three types of regularity produced significantly lower amplitude than random patterns (reflection, $t(47) = 5.928$, $p < .001$, $d = 0.478$; rotation $t(47) < 4.686$, $p < .001$, $d = 0.309$; translation $t(47) = 3.507$, $p = .001$, $d = 0.244$). The SPN wave produced by reflection was significantly more negative than that produced by rotation, $t(47) = 2.547$, $p = .014$, $d = 0.162$, or translation, $t(47) = 4.042$, $p < .001$, $d = 0.238$. There was no difference between the amplitude of the intermediate rotation and translation waves, $t(47) = 1.411$, $p = .165$.

There was no main effect of task, $F(1,44) = 2.931$, $p = .094$, or interactions between regularity and task, $F(3,132) < 1$, ns . This can be seen by comparing Figure 4A and B, which show the same ERP data in the explicit discrimination and oddball detection tasks separately. Indeed, there was a significant effect of regularity in both conditions (explicit discrimination, $F(3,69) = 8.525$, $p < .001$, partial $\eta^2 = 0.270$; oddball detection, $F(3,69) = 9.888$, $p < .001$, partial $\eta^2 = 0.301$). Insets in Figure 4 show further statistical analysis of the SPN. In these insets, the bars represent the

difference between random conditions and reflection, rotation, or translation from 300 to 1,000 ms (i.e., the size of the SPN for each regularity type). Asterisks give the p value from significant t -test comparisons.

There was a Regularity \times Random Constraints interaction, $F(3,132) = 6.994$, $p < .001$, partial $\eta^2 = .137$, which can be seen by comparing Figure 4C and D. The SPN was much less pronounced for the group of participants with the constrained random patterns (Figure 4C) than the unconstrained random patterns (Figure 4D), although there was a significant effect of regularity in both conditions: constrained, $F(3,69) = 4.567$, $p = .006$, partial $\eta^2 = 0.166$; unconstrained, $F(3,69) = 18.175$, $p < .001$, partial $\eta^2 = 0.441$.

Finally, there was a significant three-way interaction between regularity, task, and random constraints, $F(3,132) = 5.152$, $p = .002$, partial $\eta^2 = .105$. The nature of this interaction can be seen in Figure 5, which shows ERP plots for the 12 participants in each task and random constraints condition.

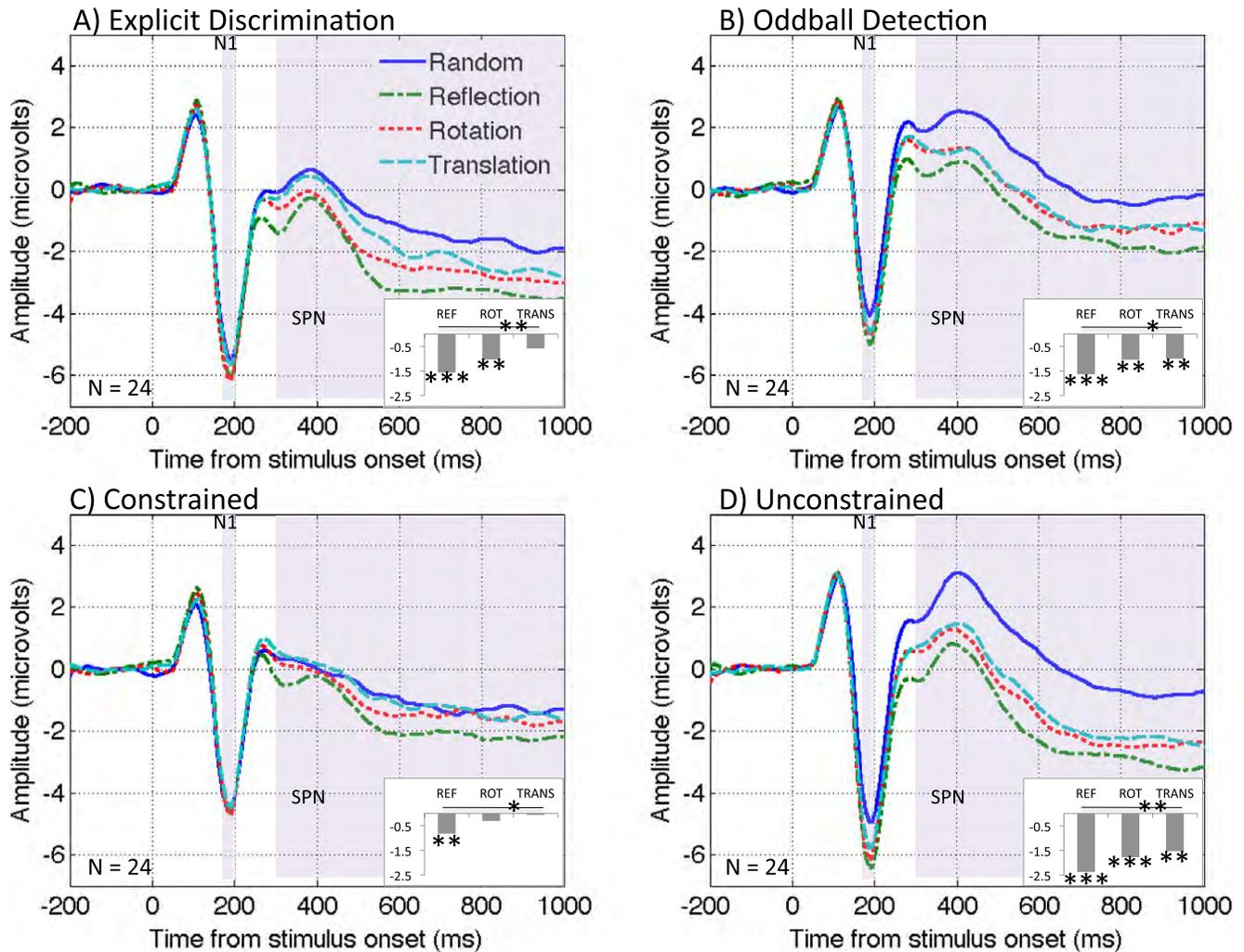


Figure 4. Grand average ERPs in each condition ($N = 24$). A: Explicit discrimination task. B: Oddball detection task. C: ERPs from participants presented with constrained random patterns. D: ERPs from participants presented with unconstrained random patterns. N1 and SPN windows are highlighted in purple. Insets show SPN amplitude for each regular pattern. Bars show the difference between the random wave and each regular wave from 300–1,000 ms poststimulus onset. Asterisks highlight significant differences, so that asterisks under the bars denote that the amplitude was less than random, while others show differences between regularities. * $p < .05$; ** $p < .01$; *** $p < .001$. (See online version for color figure.)

In the explicit discrimination task, the 12 participants presented with the constrained random patterns produced a similar ERP for rotation, translation, and random, while only reflection produced a clear SPN (Figure 5A). The SPN effects shown in Figure 5A were statistically significant. There was a main effect of regularity, $F(3,33) = 10.381$, $p < .001$, partial $\eta^2 = .486$. The reflection wave amplitude was significantly lower than rotation, random, or translation, $t(11) > 3.404$, $p < .0007$, $d > 0.349$. There were no differences between rotation, random, and translation waves, $t(11) < 1.932$, $p > .079$. The insets in Figure 5 summarize all SPN comparisons, with the same conventions as Figure 4.

Conversely, the 12 participants in the explicit discrimination task who were presented with unconstrained random patterns showed a unique wave for random patterns, but a similar SPN for the three types of regularity (Figure 5B). This resulted in a main effect of regularity, $F(3,33) = 7.191$, $p = .006$, partial $\eta^2 = .395$, $\varepsilon = 0.577$. The amplitude difference between each regularity type and random was significant, $t(11) > 2.748$, $p < .02$, $d > 0.434$, but there were no differences between the reflection, rotation, and translation waves, $t(11) < 1.084$, $p > .301$.

The 12 participants who completed the oddball detection task with constrained random patterns were the only group to show no effect of regularity, $F(3,33) = 1.334$, $p = .280$, Figure 5C.

Conversely, the 12 oddball detection participants with unconstrained random patterns had a strong main effect of regularity, $F(3,33) = 13.751$, $p < .001$, partial $\eta^2 = .556$, with significant differences between every pair of conditions, $t(11) > 3.012$, $p < .013$, $d > 0.353$, except rotation and translation, $t(11) < 1$, ns . The ERPs from this group most closely matched the pattern shown in Figure 3A, where ERPs from all participants were combined.

Given that the SPN wave seems very sensitive to visual salience and task parameters, we explored correlations between SPN amplitude for each regularity type (random wave–regular wave) and detection speed measured by the manipulation check experiment. There was no evidence that participants with larger SPN were quicker to detect the equivalent regularity in the earlier manipulation check ($r < .265$, $p > .068$). Likewise, in the explicit discrimination task, there were no correlations between SPN amplitude and the proportion of correct classifications ($r < .138$, $p > .523$).

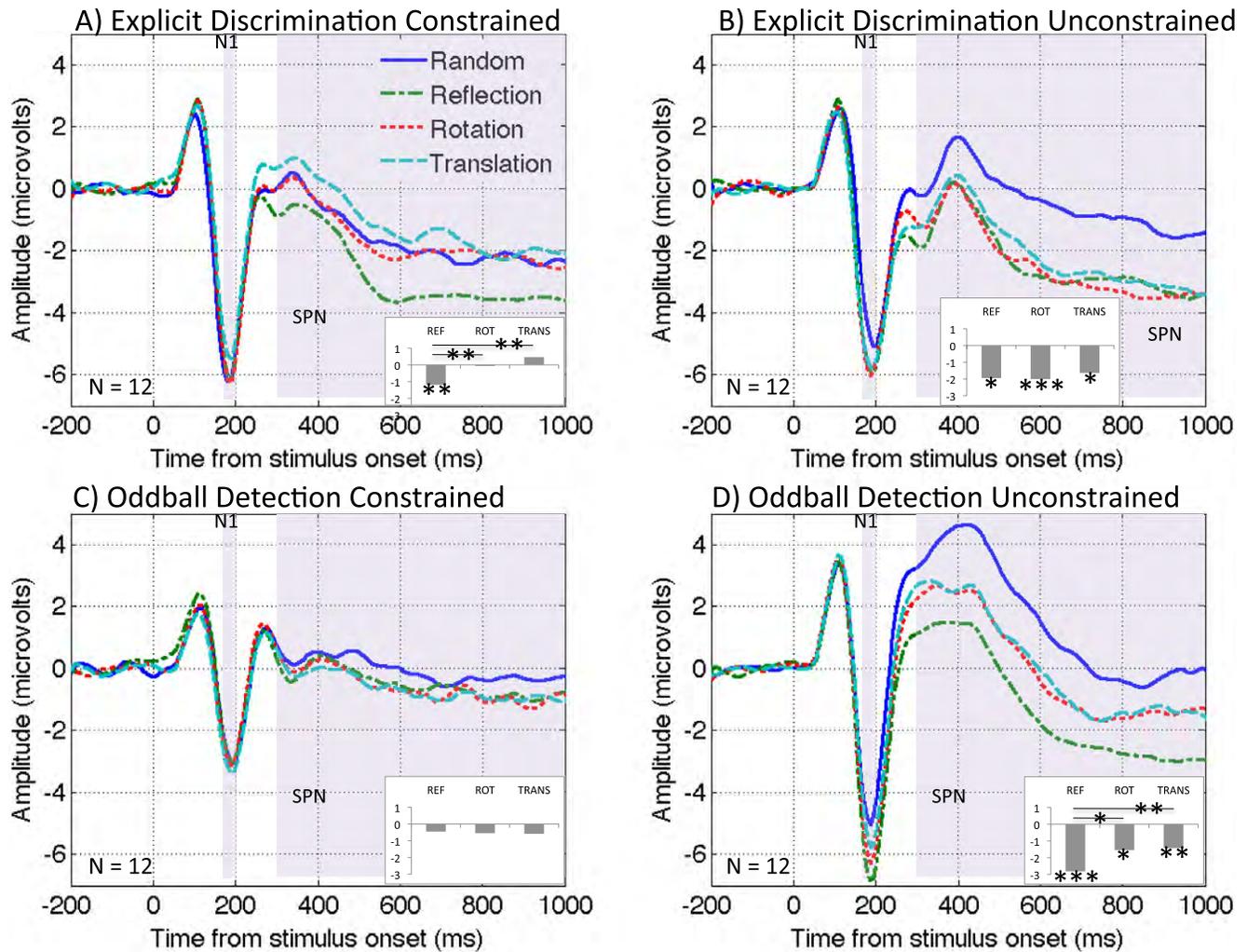


Figure 5. Grand average ERPs in each subcondition ($N = 12$). A: Explicit discrimination task with constrained random patterns. B: Explicit discrimination task with unconstrained random patterns. C: Oddball detection task with constrained random patterns. D: Oddball detection task with unconstrained random patterns. Insets are based on the same conventions as Figure 4. (See online version for color figure.)

N1

Figure 3A suggests that the regularity-related amplitude differences are present as early as the N1 wave, with N1 less pronounced for random patterns (see left topographic plot in Figure 3B). N1 amplitude was calculated as mean amplitude between 170 and 200 ms in the PO8/PO8 electrodes. These data were analyzed using the same factors as the SPN.

There was a main effect of regularity, $F(3,132) = 6.033, p = .002$, partial $\eta^2 = .121, \epsilon = .841$. Paired-sample t tests revealed significant differences between reflection and random, $t(47) = 2.925, p = .005, d = 0.186$; rotation and random, $t(47) = 3.195, p = .002, d = 0.173$; reflection and translation, $t(47) = 2.752, p = .008, d = 0.117$; and rotation and translation, $t(47) = 2.146, p = .037, d = 0.102$; but not between reflection and rotation, $t(47) < 1, ns$, or translation and random, $t(47) = 1.236, p = .223$.

There was also a Regularity \times Constraints interaction, $F(1,132) = 3.091, p = .038$, partial $\eta^2 = .066, \epsilon = .841$, which can be seen by comparing N1 in Figures 4C and 4D. In the constrained condition, there was no effect of regularity on N1 amplitude, $F(3.69) = 1.106, p = .353$ (Figure 4C). Conversely, there was a

strong effect of regularity on N1 amplitude in the unconstrained condition, $F(3.69) = 5.927, p = .001$, partial $\eta^2 = .205$ (Figure 4D). There were no other main effects or interactions, $F(1,44) < 2.892, p > .097$.

P300

It is well known that rare oddballs produce a positive wave in parietal electrodes compared to higher frequency nonoddball trials from 300 ms onwards (the parietal P300, e.g., Luck, 2005). We thus compared ERP waveforms on the oddball trials (with squares) to the normal trials (without squares) in our oddball detection task. As can be seen in Figures 3C and D, the oddball trials produced the expected P300 response, that is, greater amplitude in the oddball trials from 300–800 ms poststimuli at the P1, PZ, and P2. ERP data at this interval were analyzed with mixed ANOVA with a single within-subjects factor, trial type (oddball, normal) and a single between-subjects factor, random constraints (constrained, unconstrained). The difference between normal and oddball trials was significant, $F(1,22) = 44.630, p < .001$, partial $\eta^2 = .670$. There was no difference between constrained and unconstrained conditions,

$F(1,22) = 2.360$, $p = .139$, and no interaction, $F(1,22) < 1$, *ns*. There was no correlation between the size of the P300 response and sensitivity (d') in the oddball detection task ($r = -.325$, $p = .121$).

Discussion

This experiment was designed to measure electrophysiological responses to different kinds of spatial regularity. Previous studies have demonstrated that reflectional symmetry is more salient and more rapidly detected than rotational symmetry or translation, even though all these patterns are equally regular in terms of isometric transformations (Mach, 1886/1959; Makin, Wilton et al., 2012; Makin, Pecchinenda et al., 2012; Royer, 1981). Before EEG recording began, we presented our participants with a discrimination task, in which they had to classify patterns as regular or random. In a replication of previous work, they were quickest to detect reflection, then translation, then 180° rotation. We explored the electrophysiological correlates of the saliency difference between regularities.

Sustained Posterior Negativity (SPN)

Previous ERP research has found an SPN, which differs between symmetrical and asymmetrical patterns (Höfel & Jacobsen, 2007a, 2007b; Jacobsen & Höfel, 2003; Makin, Wilton et al., 2012); however, no previous work has explored the neural correlates of the saliency differences between the different regularities.

We considered three possibilities. First, The SPN could be uniquely associated with reflectional symmetry. In this case, the waveforms for random, rotation, and translation patterns should be similar to each other, and all different from reflection. Secondly, the neural generators of the SPN could be equally sensitive to all regularity types, and therefore the waveforms for reflection, rotation, and translation should be the same, but different from random. Third, the SPN could follow the ordinal sequence of visual saliency, that is, largest for reflection, translation, then rotation (as suggested by our RT data). This result would suggest that the neural generators that produce the SPN are also responsible for the RT differences.

Considering the combined results of all experiments shown in Figure 3A, it seems that our results are not compatible with the first hypothesis (that neural populations uniquely sensitive to reflectional symmetry generate the SPN). We found that reflection, rotation, and translation patterns all produced a posterior ERP component that was significantly lower amplitude than the random waveform. Instead, our combined data were consistent with the third hypothesis: we found that the SPN was larger for reflection than rotation or translation. This result suggests that the visual system does not have unique reflection detectors, but rather that reflectional symmetry is the preferred stimulus for more general regularity sensitive networks.

The SPN was similar in the explicit discrimination task, where participants were overtly classifying the patterns as reflection, rotation, random, or translation on every trial, and in the oddball detection task, where the participants were not actively classifying the patterns in terms of their regularity (instead they were looking for rare oddball trials, defined by the presence of a square, i.e., an orthogonal visual dimension). This result alone suggests that relatively automatic, bottom-up visual processes generated SPN (although there are other reasons to doubt this conclusion, discussed below). However, before considering these caveats, we first

acknowledge that pretraining on the manipulation check experiment may have enhanced our regularity-related ERPs. We leave this topic for future work, although we note that Höfel and Jacobsen (2007a) recorded an SPN in an oddball detection task, so we do not think the SPN in our oddball detection task was purely an aftereffect of training in the manipulation check experiment.

In the explicit discrimination task, participants could accurately discriminate all the patterns from each other. Given this, one might expect an ERP that also distinguishes between these patterns, but we found no difference between rotation and translation waves. We think these differences become apparent later in the epoch; however, the data become noisier the further from the baseline period, so we did not explore this in detail. There are other interesting questions about the SPN latency. In our experiments, the SPN began at around 300 ms, if not earlier, while Höfel and Jacobsen (2007a) defined the SPN as lower amplitude from 600 to 1,100 ms (although the component does appear to begin earlier than 600 ms judging by their Figure 2). We note that in Höfel and Jacobsen's experiment, a high contrast black and white background appeared simultaneously with the regular and random elements, and this may have masked differences at earlier latencies.

Random Constraints

The SPN was altered by the characteristics of the random patterns in different ways depending on whether people were engaged in explicit discrimination or oddball detection (Figure 5). These interactions were not anticipated but are instructive nevertheless. In the oddball detection task, the SPN was more pronounced when the random patterns were unconstrained. This is perhaps not surprising, because the difference between unconstrained random patterns and the regular patterns is more visually salient.¹

In the explicit discrimination task, when the random patterns were constrained (and less obviously different from the regular ones), the SPN was unique to reflectional symmetry, and the waveforms for rotation, random, and translation were similar (Figure 5A). Conversely, when the random patterns were unconstrained, SPN was similar for all kinds of regularity (Figure 5B). This interaction suggests that the SPN is sensitive not only to stimulus characteristics, but also to the different classification strategies employed under different conditions. It cannot, therefore, be concluded that the SPN is generated by purely bottom-up, automatic visual regularity detection.

Any explanation for the interactions involving random constraints in the explicit discrimination task are admittedly speculative. However, we venture the following: Neurocognitive processes that respond to deviation from expected regularity contribute to the SPN. We note that reflection patterns appeared uniquely regular compared to random, rotation, and translation when the random patterns were constrained. Conversely, when random patterns were unconstrained, they appeared uniquely irregular compared to the other three. The SPN was clearly influenced by these contingencies, so they must result from expectations developed over the

1. However, ERP power was reduced throughout the epoch for this group (i.e., the visual evoked potential was smaller), so we interpret this difference with some caution. Normalizing according to the overall amplitude variations of ERPs eliminates this difference. In an earlier analysis of the oddball detection task data, amplitude at each time point (t) was recalculated as a proportion of the difference between maximum and minimum amplitude for that condition: $[Amplitude(t) = Amplitude(t) / (\max - \min)]$, and there was no significant difference between constrained and unconstrained random conditions.

course of the experiment. Moreover, this account is consistent with the known architecture of visual systems, where prediction error signals are involved at a very early stage in the ascending visual hierarchy (Summerfield & Koechlin, 2008; Van de Cruys & Wagemans, 2011). This is a topic for future work.

Visual Evoked Potentials

P1 was not reliably affected by regularity in our experiment, suggesting that the SPN was probably produced by extrastriate visual activity and not by neurons in the primary visual cortex.² This is in line with the fMRI studies of Tyler et al. (2005), Sasaki et al. (2005), and Chen et al. (2007), where V1 was equally activated by reflection and random images, and by the TMS study of Cattaneo et al. (2011), who found no effect of V1 disruption on symmetry processing. Despite this converging evidence against V1 involvement, it is worth remembering that van der Zwan, Leo, Joung, Latimer, and Wenderoth (1998) found that axis of symmetry information could be coded by orientation-sensitive cells in V1.

Makin, Wilton et al. (2012) also found no difference in P1 amplitude produced by reflectional or random patterns in an explicit discrimination task—a finding consistent with the current results. However, in Experiment 3 of that paper rotational symmetry produced a larger P1 than random patterns. The current work found no special P1 for rotation, so the reliability of the previous result must be questioned.

Unlike some previous ERP symmetry experiments, (Jacobsen & Höfel, 2003; Norcia, Candy, Pettet, Vildavski, & Tyler, 2002; Oka, Victor, Conte, & Yanagida, 2007), we found that regularity altered N1 amplitude, with greater N1 for reflection and rotation patterns than random or translation patterns. N1 effects were unique to the group of participants where random patterns were unconstrained. However, Makin, Wilton et al. (2012) reported an effect of N1 when reflection and random patterns were well controlled for low-level visual variables, and other kinds of perceptual grouping also alter N1 (Shpaner, Murray, & Foxe, 2009), so it can be concluded regularity detection often begins at this latency.

2. There were some P1 differences centered on the PO3, POZ, and PO4 electrodes; however, it was unclear whether this reflected differences in the amplitude of the P1 peak or differences during the baseline period, so we do not overinterpret this.

Summary

This study investigated the neural substrates of visual regularity perception. We found that a previously reported ERP component, the SPN, was not uniquely generated by reflectional symmetry, but is produced by rotational symmetry and translation as well. Moreover, the amplitude of the SPN indexed the relative perceptual salience of these regularities. In light of this result, we suggest that the same or overlapping extrastriate mechanisms are sensitive to all visual regularities, rather than being specific to reflection. Although reflectional symmetry seems to be the preferred stimulus for this network under most conditions, expectation about the range of regularities presented and task demands also affected the SPN. We conclude that SPN is sensitive to top-down influences as well as bottom-up stimulus characteristics.

This work goes some way to characterizing electrophysiological responses to different forms of visual regularity. Given that the SPN component seems robust and sensitive to experimental manipulations, we finish by considering how it could be used in future studies of visual symmetry perception. For example, it is possible that the SPN is produced by interhemispheric connections between receptive fields on either side of the midline. According to this hypothesis, the SPN would be absent if the symmetrical patterns were presented to one hemisphere only. However, psychophysical studies have shown that peripheral and foveal symmetry detection are comparable once the images are size-scaled for acuity differences, so interhemispheric connections may not be so important (e.g., Barrett, Whitaker, McGraw, & Herbert, 1999). Second, it is worth considering that our symmetrical patterns produced symmetrical 2D retinal images, but symmetry can still be recognized in 3D objects when they are tilted so that the 2D retinal image is no longer symmetrical (Koning & Wagemans, 2009; Wagemans, 1993). It is not known whether this kind of tilted 3D symmetry recruits the same symmetry detectors in the visual system. If it does, then tilted 3D objects would produce an SPN, perhaps with a later onset due to time required for mental object rotation. Thirdly, we note that the SPN is spread over both hemispheres, and is thus different from the sustained posterior contralateral negativity (SPCN), which is a lateralized negative potential generated by the focus of spatial attention to the left or right hemifield (e.g., Lefebvre, Dell'acqua, Roelfsema, & Jolicoeur, 2011). However, it is possible that the SPN is produced by rapidly shifting attention from left to right as part of a point-to-point matching strategy, so these potentials may have a common origin.

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