

The human visual system preserves the hierarchy of 2-dimensional pattern regularity

Peter J. Kohler^{a, b, 1} and Alasdair D. F. Clarke^c

^aYork University, Department of Psychology, Toronto, ON M3J 1P3, Canada; ^bCentre for Vision Research, York University, Toronto, ON, M3J 1P3, Canada; ^cStanford University, Department of Psychology, Stanford, CA 94305, United States; ^dUniversity of Essex, Department of Psychology, Colchester, UK, CO4 3SQ

This manuscript was compiled on September 11, 2020

1 A century of vision research has demonstrated that symmetry contributes to numerous domains of visual perception (1–4). In a 2-D
2 image, the four fundamental symmetries, reflection, rotation, translation and glide reflection, can be combined in 17 distinct ways. These
3 17 “wallpaper” groups (5–7) obey a hierarchy, determined by mathematical group theory, in which simpler groups are subgroups of more
4 complex ones(8). Here we probe representations of symmetries in
5 wallpaper groups using two methods: (1) Steady-State Visual Evoked
6 Potentials (SSVEPs) recorded using EEG and (2) symmetry detection
7 thresholds measured psychophysically. We find that hierarchical re-
8 lationships between the wallpaper groups are almost perfectly pre-
9 served in both behavior and response amplitudes in visual cortex.
10 This remarkable consistency between the structure of symmetry rep-
11 resentations and mathematical group theory, is likely generated over
12 visual development, through implicit learning of regularities in the
13 environment.

Keyword 1 | Keyword 2 | Keyword 3 | ...

1 **S**ymmetries are present at many scales in images of natu-
2 ral scenes, due to a complex interplay of physical forces
3 that govern pattern formation in nature. The importance of
4 symmetry for visual perception has been known at least since
5 the gestalt movement of the early 20th century. Since then,
6 symmetry has been shown to contribute to the perception of
7 shapes (1, 3), scenes (4) and surface properties (2), as well
8 as the social process of mate selection (9). Most of this work
9 has focused on mirror symmetry or *reflection*, with much less
10 attention being paid to the other fundamental symmetries:
11 *rotation*, *translation* and *glide reflection*. In the two spatial
12 dimensions relevant for images, these four fundamental sym-
13 metries can be combined in 17 distinct ways, the “wallpaper”
14 groups (5–7). Previous work on a subset of four wallpaper
15 groups used functional MRI to demonstrate that rotation sym-
16 metries in wallpapers elicit parametric responses in several
17 areas in occipital cortex, beginning with visual area V3 (10).
18 This effect is also robust with electroencephalography (EEG),
19 whether measured using Steady-State Visual Evoked Poten-
20 tials (SSVEPs)(10) or event-related paradigms (11). Here we
21 extend this work by collecting SSVEPs and psychophysical data
22 from human participants viewing the full set of wallpaper
23 groups. We measure responses in visual cortex to 16 out of
24 the 17 wallpaper groups, with the 17th serving as a control
25 stimulus. Our goal is to provide a more complete picture of
26 how wallpaper groups are represented in the human visual
27 system.

28 A wallpaper group is a topologically discrete group of isome-
29 tries of the Euclidean plane, i.e. transformations that preserve
30 distance (7). Wallpaper groups differ in the number and
31 kind of these transformations. In mathematical group theory,
32 when the elements of one group is completely contained in

another, the inner group is called a subgroup of the outer group (7). Subgroup relationships between wallpaper groups can be distinguished by their indices. The index of a subgroup relationship is the number of cosets, i.e. the number of times the subgroup is found in the outer group (7). As an example, let us consider groups P6 and P2. If we ignore the translations in two directions that both groups share, group P6 consists of the set of rotations $0^\circ, 60^\circ, 120^\circ, 180^\circ, 240^\circ, 300^\circ$, in which P2 $0^\circ, 180^\circ$ is contained. P2 is thus a subgroup of P6, and the full P6 set can be generated by every combination of P2 and rotations $0^\circ, 120^\circ, 240^\circ$. Because P2 is repeated three times in P6, P2 is a subgroup of P6 with index 3 (7). The 17 wallpaper groups thus obey a hierarchy of complexity where simpler groups are sub-groups of more complex ones (8). The full set of subgroup relationships is listed in Section 1.4.2 of the Supplementary Material.

49 The two datasets presented here puts on in the position of
50 being able to assess the extent to which both behavior and
51 brain responses follow that subgroup hierarchy. Based on pre-
52 vious imaging work showing that patterns with more axes of
53 symmetry produce greater activity in visual cortex (10–13), we
54 hypothesized that more complex groups would produce larger
55 SSVEPs. For the psychophysical data, we hypothesized that
56 more complex groups would lead to shorter symmetry detec-
57 tion thresholds, based on previous data showing that under a
58 fixation presentation time, discriminability increases with the
59 number of symmetry axes in the pattern (14). Our results con-
60 firm both hypotheses, and show that activity in human visual
61 cortex is remarkably consistent with the hierarchical relation-
62 ships between the wallpaper groups, with SSVEP amplitudes

Significance Statement

Wallpaper groups were discovered in the mid-19th century, and the 17 groups constitute the complete set of possible ways of regularly tiling the 2D-plane. In recent years wallpaper groups have found use in the vision science community, as an ideal stimulus set for studying the perception of symmetries in textures. Here we present brain imaging and psychophysical data on the complete set of wallpaper groups and show the hierarchical organization among wallpaper groups in reflected in both representations in visual cortex and performance on a symmetry detection task. This shows that the visual system is highly sensitive to regularities in textures, and suggest that symmetries may play an important role in texture perception.

PJK and ADFC designed the study, PJK collected EEG data, ADFC collected psychophysical data, PJK and ADFC wrote the paper.

The authors have no conflicts of interests to declare

¹To whom correspondence should be addressed. E-mail: pj.kohler@yorku.ca

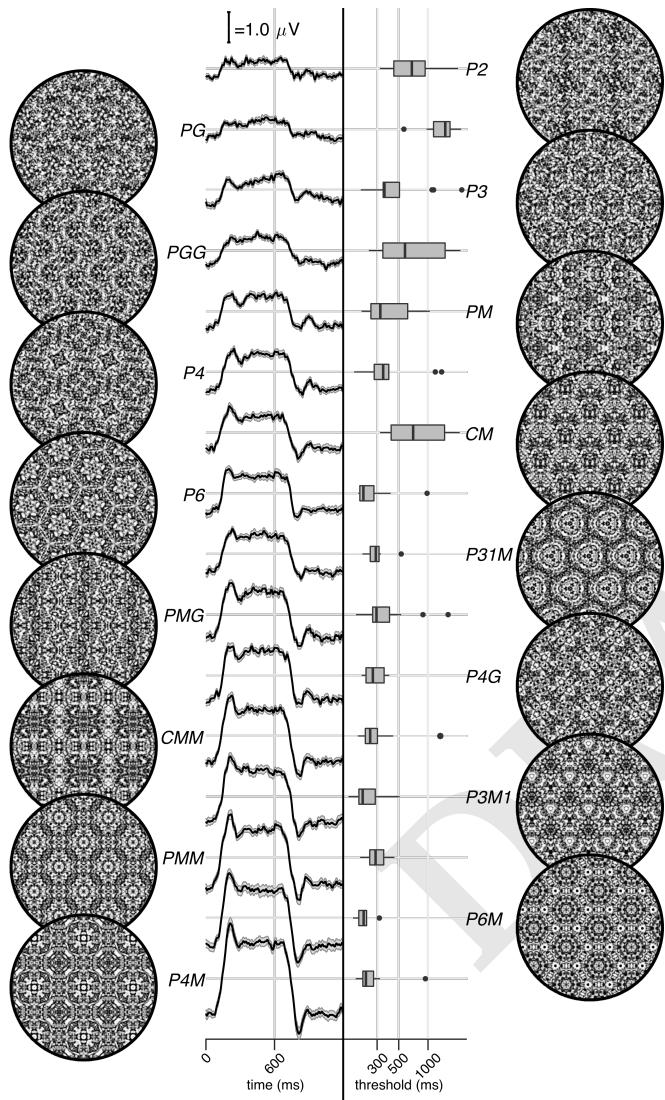
63
64
65
66
67
68
69
70

Fig. 1. Examples of each of the 16 wallpaper groups are shown in the left- and right-most column of the figures, next to the corresponding SSVEP (center-left) and psychological (center-right) data from each group. The SSVEP data are odd-harmonic-filtered cycle-average waveforms. In each cycle, a P1 exemplar was shown for the first 600 ms, followed by the original exemplar for the last 600 ms. Errorbars are standard error of the mean. Psychophysical data are presented as boxplots reflecting the distribution of display duration thresholds. The 16 groups are ordered by the strength of the SSVEP response, to highlight the range of response amplitudes.

and psychophysical thresholds following these relationships at a level that is far beyond chance. Visual cortex thus appears to encode all of the fundamental symmetries using a representational structure that closely approximates the subgroup relationships from group theory. Given that most participants had no knowledge of group theory, the ordered structure of visual responses to wallpaper groups is likely learned implicitly from regularities in the visual environment.

Results

The stimuli used in our two experiments were multiple exemplar images belonging to each of the wallpaper groups, generated from random-noise textures, as described in detail elsewhere (10). Exemplar images from group P1 was used as control stimuli, and each exemplar from the other 16 groups had a power-spectrum matched P1 exemplar. The matched P1 exemplars were generated by phase-scrambling the exemplar images. Because all wallpapers are periodic due to their lattice tiling structure, the phase-scrambled images all belong to group P1 regardless of group membership of the original exemplar. P1 contains no symmetries other than translation, while all other groups contain translation in combination with one or more of the other three fundamental symmetries (reflection, rotation, glide reflection) (7). In our SSVEP experiment, this stimulus set allowed us to isolate brain activity specific to the symmetry structure in the exemplar images from activity associated with modulation of low-level features, by alternating exemplar images and control exemplars. In this design, responses to structural features beyond the shared power spectrum, including any symmetries other than translation, are isolated in the odd harmonics of the image update frequency (10, 15, 16). Thus, the combined magnitude of the odd harmonic response components can be used as a measure of the overall strength of the visual cortex response.

The psychophysical experiment took a distinct but related approach. In each trial an exemplar image was shown with its matched control, one image after the other, and the order varied pseudo-randomly such that in half the trials the original exemplar was shown first, and in the other half the control image was shown first. After each trial, participants were told to indicate whether the first or second image contained more structure, and the duration of both images was controlled by a staircase procedure so that a display duration threshold could be computed for each wallpaper group.

A summary of our brain imaging and psychophysical measurements is presented with examples of the wallpaper groups in Figure 1. For our primary SSVEP analysis, we only considered EEG data from a pre-determined region-of-interest (ROI) consisting of six electrodes over occipital cortex (see Supplementary Figure 1.1). SSVEP data from this ROI was filtered so that only the odd harmonics that capture the symmetry response contribute to the waveforms. While waveform amplitude is quite variable among the 16 groups, all groups have a sustained negative-going response that begins at about the same time for all groups, 180 ms after the transition from the P1 control exemplar to the original exemplar. To reduced the amplitude of the symmetry-specific response to a single number that could be used in further analyses and compared to the psychophysical data, we computed the root-mean-square (RMS) over the odd-harmonic-filtered waveforms. The data in Figure 1 are shown in descending order according to RMS.

123 The psychophysical results, shown in box plots in Figure 1,
 124 were also quite variable between groups, and there seems to be
 125 a general pattern where wallpaper groups near the top of the
 126 figure, that have lower SSVEP amplitudes, also have longer
 127 psychophysical display duration thresholds.

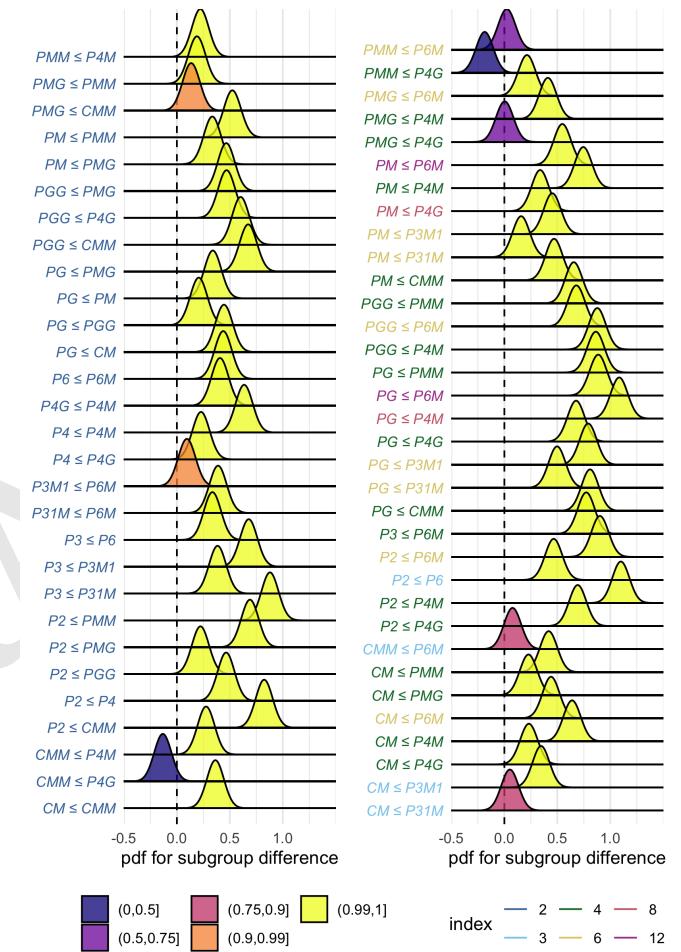
128 We now wanted to test our two assumptions about how
 129 SSVEP amplitudes and duration thresholds would follow sub-
 130 group relationships, and thereby quantify the degree to which
 131 our two measurements were consistent with group theory. We
 132 tested each of the two hypotheses using the same approach.
 133 We first fitted a Bayesian model with wallpaper group as a
 134 factor and participant as a random effect. We fit the model
 135 separately for SSVEP RMS and psychophysical data, and then
 136 computed posterior distributions for the difference between
 137 supergroup and subgroup. These difference distributions could
 138 allow us to compute the conditional probability that the
 139 supergroup would produce (a) larger RMS and (b) a shorter
 140 threshold durations, when compared to the subgroup. The
 141 posterior distributions are shown in Figure 2 for the SSVEP
 142 data, and in Figure 3 for the psychophysical data, which distri-
 143 butions color-coded according to conditional probability. For
 144 both data sets our hypothesis is confirmed: For the overwhelm-
 145 ing majority of the 64 subgroup relationships, supergroups are
 146 more likely to produce larger symmetry specific SSVEPs and
 147 shorter threshold durations, and in most cases the conditional
 148 probability of this happening is extremely high.

149 We also ran a control analysis using (1) odd-harmonic
 150 SSVEP data from a six-electrode ROI over parietal cortex (see
 151 Supplementary Figure 1.1) and (2) even-harmonic SSVEP data
 152 from the same occipital ROI that was used in our primary
 153 analysis. By comparing these two control analysis to our
 154 primary SSVEP analysis, we can address the specify of our
 155 effects in terms of location (occipital cortex vs parietal cortex)
 156 and harmonic (odd vs even). For both control analyses (plotted
 157 in Supplementary Figures 3.3 and 3.4), the correspondence
 158 between data and subgroup relationships was weaker than in
 159 the primary analysis. We can quantify the strength of the
 160 association between the data and the subgroup relationships,
 161 by asking what proportion of subgroup relationships that
 162 reach or exceed a range of probability thresholds. This is
 163 plotted in Figure 4, for our psychophysical data, our primary
 164 SSVEP analysis and our two control SSVEP analyses. It it
 165 that odd-harmonic SSVEP data from an occipital ROI and
 166 display duration thresholds both have a strong association
 167 with the subgroup relations, that for a clear majority of the
 168 subgroups survive even at the highest threshold we consider
 169 ($p(\Delta > 0 | \text{data}) > 0.99$), and that the association is far weaker
 170 for the two control analyses.

171 SSVEP data from four of the wallpaper groups (P2, P3,
 172 P4 and P6) was previously published as part of our earlier
 173 demonstration of parametric responses to rotation symmetry
 174 in wallpaper groups(10). We replicate that result using our
 175 Bayesian approach, and find the same parametric effect in
 176 the psychophysical data (Supplementary Figure 4.1). We also
 177 conducted an analysis **DOES THIS NEED TO BE SPELLED**
OUT MORE looking for effects of index and normality in
 178 our two datasets, and found that subgroup relationships with
 179 higher indices tended to produce stronger effects for both
 180 SSVEP RMS and symmetry detection thresholds, as shown
 181 by the fact that a leave-one-out test ... **MORE DETAILS**
NEEDED HERE. The effect of index did not (???) reach

significance.

184 Finally, we conducted a correlation analysis comparing
 185 SSVEP and psychophysical data, and found a small ($R^2 =$
 186 0.44) but above-zero correlation, as indicated by our confidence
 187 intervals. There are several factors that might explain the
 188 relatively weak correlation, most prominently the fact that
 189 the same individuals did not participate in each of the two
 190 experiments. Nevertheless, we find the relationship between
 191 the two datasets interesting, because it suggests that our
 192 psychophysical and SSVEP measurements are tapping into
 193 the same underlying mechanisms.



194 **Fig. 2.** Posterior distributions for the difference in mean RMS SSVEP response. Colour coding of the text indicates the index of the subgroup, while the colour of the filled distribution relates to the conditional probability that the difference in means is greater than zero. We can see that $xx/64$ subgroup relationships have $p(\Delta | \text{data}) > 0.9$.

Discussion

195 Here we show that beyond merely responding to the elementary
 196 symmetries operations of reflection (12) and rotation (10), the
 197 visual system explicitly represents hierarchical structure of
 198 the 17 wallpaper groups, and thus the compositions of all
 199 four of the fundamental symmetry transformations (rotation,
 200 reflection, translation, glide reflection) which comprise regular
 201 textures. The SSVEP amplitude and the symmetry detection
 202 threshold both preserve the complex hierarchy of subgroup
 203

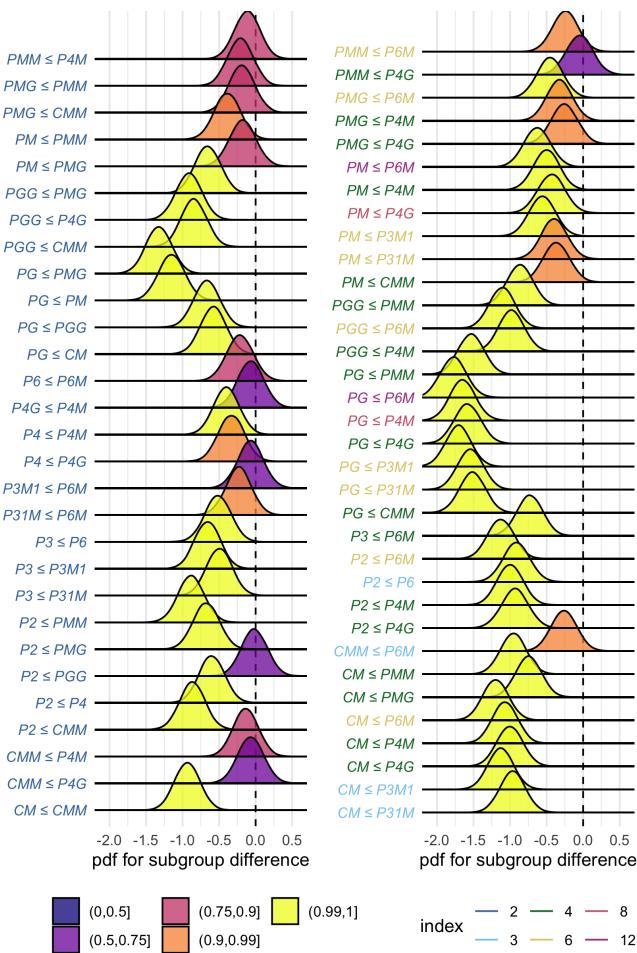


Fig. 3. Posterior distributions for the difference in mean display duration threshold. Colour coding of the text indicates the index of the subgroup, while the colour of the filled distribution relates to the conditional probability that the difference in means is greater than zero. We can see that $xx/64$ subgroup relationships have $p(\Delta|data) > 0.9$.

relationships among the wallpaper groups (8). For the SSVEP, this remarkable consistency was specific to the odd harmonics of the stimulus frequency, that capture the symmetry-specific response (10) and to electrodes in an ROI over occipital cortex. When the same analysis was done using the odd harmonics from electrodes over parietal cortex (Supplementary Figure 3.3) or even harmonics from electrodes over occipital cortex (Supplementary Figure 3.4), the data was much less consistent with the subgroup relationships (yellow and green lines, Figure 4).

The current data provide a complete description of the visual system's response to symmetries in the 2-D plane. Our design precludes us from independently measure the response to P1, but because each of the 16 other groups produce non-zero odd harmonic amplitudes (see Figure 1), we can conclude that the relationships between P1 and all other groups, where P1 is the subgroup, are also preserved by the visual system. The subgroup relationships are in many cases not obvious perceptually, and most participants had no knowledge of group theory. Thus, the visual system's ability to preserve the subgroup hierarchy does not depend on explicit knowledge of the relationships. Furthermore, previous behavioral experiments

have shown that although naïve observers can distinguish many of the wallpaper groups (17), they are generally error-prone when asked to assign exemplar images to the appropriate group (18) **ALASDAIR PERHAPS YOU WANT TO SAY MORE OR DIFFERENT HERE.**

The correspondence between responses in the visual system and group theory that we demonstrate here, may reflect a form of implicit learning that depends on the structure of the natural world. The environment is itself constrained by physical forces underlying pattern formation and these forces are subject to multiple symmetry constraints (19). The ordered structure of responses to wallpaper groups could be driven by a central tenet of neural coding, that of efficiency. If coding is to be efficient, neural resources should be distributed in such a way that the structure of the environment is captured with minimum redundancy considering the visual geometric optics, the capabilities of the subsequent neural coding stages and the behavioral goals of the organism (20–23). Early work within the efficient coding framework suggested that natural images had a $1/f$ spectrum and that the corresponding redundancy between pixels in natural images could be coded efficiently with a sparse set of oriented filter responses, such as those present in the early visual pathway (24, 25). Our results suggest that the principle of efficient coding extends to a much higher level of structural redundancy – that of symmetries in visual images.

The 17 wallpaper groups are completely regular, and relatively rare in the visual environment, especially when considering distortions due to perspective and occlusion. Near-regular textures, however abound in the visual world, and can be approximated as deformed versions of the wallpaper groups (26). The correspondence between visual cortex responses and group theory demonstrated here may indicate that the visual system represents visual textures using a similar scheme, with the wallpaper groups serving as anchor points in representational space. This framework resembles norm-based encoding strategies that have been proposed for other stimulus classes, most notably faces (27), and leads to the prediction that adaptation to wallpaper patterns should distort perception of near-regular textures, similar to the aftereffects found for faces (28). Field biologists have demonstrated that animals respond more strongly to exaggerated versions of a learned stimulus, referred to as “supernormal” stimuli (29). In the norm-based encoding framework, wallpaper groups can be considered super-textures, exaggerated examples of the near-regular textures that surround us. Artists may consciously or unconsciously create supernormal stimuli, to capture the essence of the subject and evoke strong responses in the audience (30). Wallpaper groups are visually compelling and have been widely used in human artistic expression going back to the Neolithic age (31). If wallpapers are in fact super-textures, it would imply that this prevalence may be a direct consequence of the strategy the human visual system uses for encoding textures.

Participants. Twenty-five participants (11 females, mean age 28.7 ± 13.3) took part in the EEG experiment. Their informed consent was obtained before the experiment under a protocol that was approved by the Institutional Review Board of Stanford University. 11 participants (8 females, mean age 20.73 ± 1.21) took part in the psychophysics experiment. All participants had normal or corrected-to-normal vision. Their

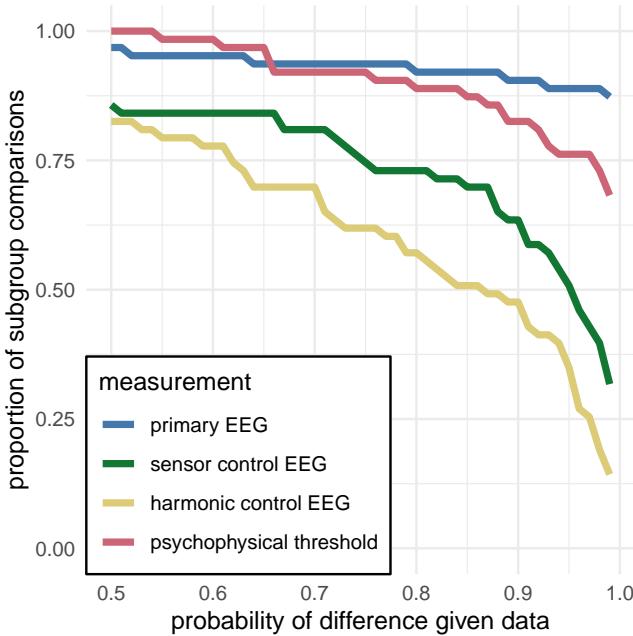


Fig. 4. This plot shows the proportion of subgroup relations that satisfy $p(\Delta > 0 | \text{data}) > x$. We can see that if we take $x = 0.95$ as our threshold, the subgroup relations are preserved in $56/63 = 89\%$ and $49/64 = 78\%$ of the comparisons for the primary EEG and display durations respectively. This compares to the $32/64 = 50\%$ and $22/64 = 35\%$ for the control EEG conditions.

287 informed consent was obtained before the experiment under a
288 protocol that was approved by the University of Essex's Ethics
289 Committee.

290 **Stimulus Generation.** Exemplars from the different wallpaper
291 groups were generated using a modified version of the method-
292 ology developed by Clarke and colleagues (18) that we have
293 described in detail elsewhere (10). Briefly, exemplar patterns
294 for each group were generated from random-noise textures,
295 which were then repeated and transformed to cover the plane,
296 according to the symmetry axes and geometric lattice spec-
297 ific to each group. The use of noise textures as the starting
298 point for stimulus generation allowed the creation of an al-
299 most infinite number of distinct exemplars of each wallpaper
300 group. For each exemplar image, phase-randomized control
301 exemplars were generated that had the same power spectrum
302 as the exemplar images for each group. The phase scrambling
303 eliminates rotation, reflection and glide-reflection symmetries
304 within each exemplar, but the phase-scrambled images inher-
305 ent the spectral periodicity arising from the periodic tiling.
306 This means that all control exemplars, regardless of which
307 wallpaper group they are derived from, degenerate to another
308 symmetry group, namely P1. P1 is the simplest of the wallpa-
309 per groups, and contains only translations of a region whose
310 shape derives from the lattice. Because the different wallpaper
311 groups have different lattices, P1 controls matched to different
312 groups have different power spectra. Our experimental design
313 takes these differences into account by comparing the neural
314 responses evoked by each wallpaper group to responses evoked
315 by the matched control exemplars.

316 **Stimulus Presentation.** Stimulus Presentation. For the EEG
317 experiment, the stimuli were shown on a 24.5" Sony Trimaster

318 EL PVM-2541 organic light emitting diode (OLED) display
319 at a screen resolution of 1920×1080 pixels, 8-bit color depth
320 and a refresh rate of 60 Hz, viewed at a distance of 70 cm.
321 The mean luminance was 69.93 cd/m^2 and contrast was 95%.
322 The diameter of the circular aperture in which the wallpaper
323 pattern appeared was 13.8° of visual angle presented against
324 a mean luminance gray background. Stimulus presentation
325 was controlled using in-house software.

326 For the psychophysics experiment, the stimuli were shown
327 on a $48 \times 27\text{cm}$ VIEWPixx/3D LCD Display monitor, model
328 VPX-VPX-2005C, resolution 1920×1080 pixels, with a viewing
329 distance of approximately 40cm and linear gamma. Stimulus
330 presentation was controlled using MatLab and Psychtoolbox-3
331 (32, 33). The diameter of the circular aperture for the stimuli
332 was 21.5° .

333 **EEG Procedure.** Visual Evoked Potentials were measured using
334 a steady-state design, in which P1 control images alternated
335 with test images from each of the 16 other wallpaper groups [2].
336 Exemplar images were always preceded by their matched P1
337 control image. A single 0.83 Hz stimulus cycle consisted of a
338 control P1 image followed by an exemplar image, each shown
339 for 600 ms. A trial consisted of 10 such cycles (12 sec) over
340 which 10 different exemplar images and matched controls from
341 the same rotation group were presented. For each group type,
342 the individual exemplar images were always shown in the same
343 order within the trials. Participants initiated each trial with
344 a button-press, which allowed them to take breaks between
345 trials. Trials from a single wallpaper group were presented
346 in blocks of four repetitions, which were themselves repeated
347 twice per session, and shown in random order within each
348 session. To control fixation, the participants were instructed
349 to fixate a small white cross in the center of display. To control
350 vigilance, a contrast dimming task was employed. Two times
351 per trial, an image pair was shown at reduced contrast, and the
352 participants were instructed to press a button on a response
353 pad. We adjusted the contrast reduction such that average
354 accuracy for each participant was kept at 85% correct, so that
355 the difficulty of the vigilance task was kept constant.

356 **Psychophysics Procedure.** The experiment consisted of 16
357 blocks, one for each of the wallpaper groups (excluding P1).
358 In each trial, participants were presented with two stimuli
359 (one of which was the wallpaper group for the current block of
360 trials, the other being P1), one after the other (inter stimulus
361 interval of 700ms). After each stimuli had been presented, it
362 was masked with white noise for 300ms. After both stimuli had
363 been presented, participants made a response on the keyboard
364 to indicate whether they thought the first or second contained
365 the most symmetry. Each block started with 10 practise trials,
366 (stimulus display duration of 500ms) to allow participants
367 to familiarise themselves with the current block's wallpaper
368 pattern. If they achieved an accuracy of 9/10 in these trials
369 they progressed to the rest of the block, otherwise they carried
370 out another set of 10 practise trials. This process was repeated
371 until the required accuracy of 9/10 was obtained. The rest of
372 the block consisted of four interleaved staircases (using the
373 QUEST algorithm (34), full details given in the SI) of 30 trials
374 each. On average, a block of trials took around 10 minutes to
375 complete.

EEG Acquisition and Preprocessing.

Electroencephalogram (EEG) Acquisition and Preprocessing. The time-locked Steady-State Visual Evoked Potentials were collected with 128-sensor HydroCell Sensor Nets (Electrical Geodesics, Eugene, OR) and were band-pass filtered from 0.3 to 50 Hz. Raw data were evaluated off line according to a sample-by-sample thresholding procedure to remove noisy sensors that were replaced by the average of the six nearest spatial neighbors. On average, less than 5% of the electrodes were substituted; these electrodes were mainly located near the forehead or the ears. The substitutions can be expected to have a negligible impact on our results, as the majority of our signal can be expected to come from electrodes over occipital, temporal and parietal cortices. After this operation, the waveforms were re-referenced to the common average of all the sensors. The data from each 12s trial were segmented into five 2.4 s long epochs (i.e., each of these epochs was exactly 2 cycles of image modulation). Epochs for which a large percentage of data samples exceeding a noise threshold (depending on the participant and ranging between 25 and 50 μ V) were excluded from the analysis on a sensor-by-sensor basis. This was typically the case for epochs containing artifacts, such as blinks or eye movements. The use of steady-state stimulation drives cortical responses at specific frequencies directly tied to the stimulus frequency. It is thus appropriate to quantify these responses in terms of both phase and amplitude. Therefore, a Fourier analysis was applied on every remaining epoch using a discrete Fourier transform with a rectangular window. The use of epochs two-cycles (i.e., 2.4 s) long, was motivated by the need to have a relatively high resolution in the frequency domain, $\delta f = 0.42$ Hz. For each frequency bin, the complex-valued Fourier coefficients were then averaged across all epochs within each trial. Each participant did two sessions of 8 trials per condition, which resulted in a total of 16 trials per condition.

SSVEP Analysis. Response waveforms were generated for each group by selective filtering in the frequency domain. For each participant, the average Fourier coefficients from the two sessions were averaged over trials and sessions. The Steady-State Visual Evoked Potentials (SSVEP) paradigm we used allowed us to separate symmetry-related responses from non-specific contrast transient responses. Previous work has demonstrated that symmetry-related responses are predominantly found in the odd harmonics of the stimulus frequency, whereas the even harmonics consist mainly of responses unrelated to symmetry, that arise from the contrast change associated with the appearance of the second image[2-4]. This functional distinction of the harmonics allowed us to generate a single-cycle waveform containing the response specific to symmetry, by filtering out the even harmonics in the spectral domain, and then back-transforming the remaining signal, consisting only of odd harmonics, into the time-domain. For our main analysis, we averaged the odd harmonic single-cycle waveforms within a six-electrode region of interest (ROI) over occipital cortex (electrodes 70, 74, 75, 81, 82, 83). These waveforms, averaged over participants, are shown in Figure 2 in the main paper. The same analysis was done for the even harmonics (see Figure S1) and for the odd harmonics within a six electrode ROI over parietal cortex (electrodes 53, 54, 61, 78, 79, 86; see Figure S2). The root-mean square values of these waveforms, for each individual participant, were used to determine whether each of the wallpaper subgroup relationships were preserved in the

brain data.

377

Bayesian Analysis of EEG and Psychophysical data. Bayesian analysis was carried out using R (v3.6.1) (35) with the `brms` package (v2.9.0) (36) and rStan (v2.19.2 (37)). The data from each experiment were modelled using a Bayesian generalised mixed effect model with wallpaper group being treated as a 16 level factor, and random effects for participant. The EEG data and display thresholds were modelled using log-normal distributions with weakly informative, $\mathcal{N}(0, 2)$, priors. After fitting the model to the data, samples were drawn from the posterior distribution for each mean of the EEG response (display duration) for each wallpaper group. These samples were then recombined to calculate the distribution of differences for each pair of subgroup and super-group. These distributions were then summarised by computing the conditional probability of obtaining a positive (negative) difference, $p(\Delta|data)$.

For further technical details, please see the supplementary materials where the full R code, model specification, prior and posterior predictive checks, and model diagnostics, can be found.

ACKNOWLEDGMENTS. Please include your acknowledgments here, set in a single paragraph. Please do not include any acknowledgments in the Supporting Information, or anywhere else in the manuscript.

- Palmer SE (1985) The role of symmetry in shape perception. *Acta Psychologica* 59(1):67–90.
- Cohen EH, Zaidi Q (2013) Symmetry in context: Salience of mirror symmetry in natural patterns. *Journal of vision* 13(6).
- Li Y, Sawada T, Shi Y, Steinman R, Pizlo Z (2013) *Symmetry Is the sine qua non of Shape*, Advances in Computer Vision and Pattern Recognition, eds. Dickinson SJ, Pizlo Z. (Springer London), pp. 21–40.
- Apthorpe D, Bell J (2015) Symmetry is less than meets the eye. *Current Biology* 25(7):R267–R268.
- Fedorov E (1891) Symmetry in the plane in *Zapiski Imperatorskogo S. Peterburgskogo Mineralogicheskogo Obshchestva* [Proc. S. Peterb. Mineral. Soc.], Vol. 2, pp. 345–390.
- Polya G (1924) XII. Über die analogie der kristallsymmetrie in der ebene. *Zeitschrift für Kristallographie-Crystalline Materials* 60(1):278–282.
- Liu Y, Hel-Or H, Kaplan CS, Van Gool L (2010) Computational symmetry in computer vision and computer graphics. *Foundations and Trends® in Computer Graphics and Vision* 5(1–2):1–195.
- Coxeter HSM, Moser WOJ (1972) *Generators and relations for discrete groups*, Ergebnisse der Mathematik und ihrer Grenzgebiete ; Bd. 14. (Springer-Verlag, Berlin, New York).
- Möller AP (1992) Female swallow preference for symmetrical male sexual ornaments. *Nature* 357(6375):238–240.
- Kohler PJ, Clarke A, Yakovleva A, Liu Y, Norcia AM (2016) Representation of maximally regular textures in human visual cortex. *The Journal of Neuroscience* 36(3):714–729.
- Kohler PJ, Cottereau BR, Norcia AM (2018) Dynamics of perceptual decisions about symmetry in visual cortex. *NeuroImage* 167(Supplement C):316–330.
- Sasaki Y, Vanduffel W, Knutson T, Tyler C, Tootell R (2005) Symmetry activates extrastriate visual cortex in human and nonhuman primates. *Proceedings of the National Academy of Sciences of the United States of America* 102(8):3159–3163.
- Keefe BD, et al. (2018) Emergence of symmetry selectivity in the visual areas of the human brain: fMRI responses to symmetry presented in both frontoparallel and slanted planes. *Human Brain Mapping* 39(10):3813–3826.
- Wagemans J, Van Gool L, d'Ydewalle G (1991) Detection of symmetry in tachistoscopically presented dot patterns: effects of multiple axes and skewing. *Perception & Psychophysics* 50(5):413–27.
- Norcia AM, Appelbaum LG, Ales JM, Cottereau BR, Rossion B (2015) The steady-state visual evoked potential in vision research: A review. *Journal of Vision* 15(6):4–4.
- Norcia AM, Candy TR, Pettet MW, Vildavski VY, Tyler CW (2002) Temporal dynamics of the human response to symmetry. *Journal of Vision* 2(2):132–139.
- Landwehr K (2009) Camouflaged symmetry. *Perception* 38:1712–1720.
- Clarke ADF, Green PR, Halley F, Chantler MJ (2011) Similar symmetries: The role of wallpaper groups in perceptual texture similarity. *Symmetry* 3(4):246–264.
- Hoyle RB (2006) *Pattern formation: an introduction to methods*. (Cambridge University Press).
- Attnave F (1954) Some informational aspects of visual perception. *Psychol Rev* 61(3):183–93.
- Barlow HB (1961) *Possible principles underlying the transformations of sensory messages*, ed. Rosenblith WA. (MIT Press), pp. 217–234.
- Laughlin S (1981) A simple coding procedure enhances a neuron's information capacity. *Z Naturforsch C* 36(9–10):910–2.
- Geisler WS, Najemnik J, Ing AD (2009) Optimal stimulus encoders for natural tasks. *Journal of Vision* 9(13):17–17.

24. Field DJ (1987) Relations between the statistics of natural images and the response properties of cortical cells. *J Opt Soc Am A* 4(12):2379–94.
- 510
511
- 512 25. Olshausen BA, Field DJ (1997) Sparse coding with an overcomplete basis set: a strategy employed by v1? *Vision Res* 37(23):3311–25.
- 513
514 26. Liu Y, Lin WC, Hays J (year?) Near-regular texture analysis and manipulation in *ACM Transactions on Graphics (TOG)*. (ACM), Vol. 23, pp. 368–376.
- 515
516 27. Leopold DA, Bondar IV, Giese MA (2006) Norm-based face encoding by single neurons in the monkey inferotemporal cortex. *Nature* 442(7102):572–5.
- 517
518 28. Webster MA, MacLin OH (1999) Figural aftereffects in the perception of faces. *Psychon Bull Rev* 6(4):647–53.
- 519
520 29. Tinbergen N (1953) *The herring gull's world: a study of the social behaviour of birds*. (Frederick A. Praeger, Inc., Oxford, England), pp. xvi, 255.
- 521
522 30. Ramachandran VS, Hirstein W (1999) The science of art: A neurological theory of aesthetic experience. *Journal of Consciousness Studies* 6(6–7):15–41.
- 523
524 31. Jablan SV (2014) *Symmetry, Ornament and Modularity*. (World Scientific Publishing Co Pte Ltd, Singapore, SINGAPORE).
- 525
526 32. Kleiner M, et al. (2007) What's new in psychtoolbox-3. *Perception* 36:1–16.
- 527
528 33. Brainard DH (1997) Spatial vision. *The psychophysics toolbox* 10:433–436.
- 529
530 34. Watson AB, Pelli DG (1983) Quest: A bayesian adaptive psychometric method. *Perception & Psychophysics* 33(2):113–120.
- 531
532 35. R Core Team (2019) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria).
- 533
534 36. Bürkner PC (2017) Advanced bayesian multilevel modeling with the r package brms. *arXiv preprint arXiv:1705.11123*.
37. Stan Development Team (2019) RStan: the R interface to Stan. R package version 2.19.2.

DRAFT