

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

A wallpaper group is a topologically discrete group of isometries of the Euclidean plane, i.e. transformations that preserve distance (8). Wallpaper groups differ in the number and kind of these transformations. In mathematical group theory, when the elements of one group is completely contained in another, the inner group is called a subgroup of the outer group (8). 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 (8). 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 (8). The 17 wallpaper groups thus obey a hierarchy of complexity where simpler groups are sub-groups of more complex ones (11). The full set of subgroup relationships is listed in Section 1.4.2 of the Supplementary Material.

The two datasets presented here puts on in the position of being able to assess the extent to which both behavior and brain responses follow that hierarchy. The results show that activity in human visual cortex is remarkably consistent with the hierarchical relationships between the wallpaper groups, with SSVEP amplitudes and psychophysical thresholds preserving 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

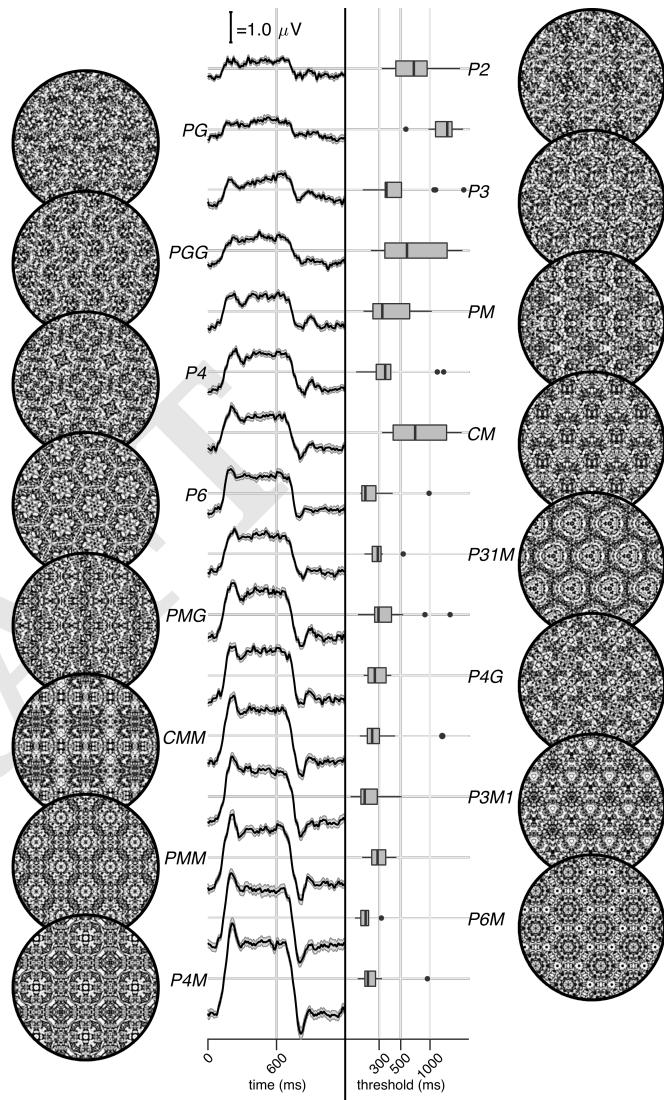


Fig. 1. Examples of each of the 16 wallpaper groups are shown in the left- and right-most column of the figures, next to the corresponding SSVEP (center-left) and psychological (center-right) data from each group. The SSVEP data are odd-harmonic-filtered cycle-average waveforms. In each cycle, a P1 exemplar 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.

62 in the visual environment.

63 Results

64 The stimuli used in our two experiments were multiple exemplar images belonging to each of the wallpaper groups,
65 generated from random-noise textures, as described in detail
66 elsewhere (9). Exemplar images from group P1 was used as
67 control stimuli, and each exemplar from the other 16 groups
68 had a power-spectrum matched P1 exemplar. The matched
69 P1 exemplars were generated by phase-scrambling the exemplar
70 images. Because all wallpapers are periodic due to their
71 lattice tiling structure, the phase-scrambled images all belong
72 to group P1 regardless of group membership of the original
73 exemplar. P1 contains no symmetries other than translation,
74 while all other groups contain translation in combination with
75 one or more of the other three fundamental symmetries (reflec-
76 tion, rotation, glide reflection) (8). In our SSVEP experiment,
77 this stimulus set allowed us to isolate brain activity specific
78 to the symmetry structure in the exemplar images from ac-
79 tivity associated with modulation of low-level features, by
80 alternating exemplar images and control exemplars. In this
81 design, responses to structural features beyond the shared
82 power spectrum, including any symmetries other than transla-
83 tion, are isolated in the odd harmonics of the image update
84 frequency (9, 12, 13). Thus, the combined magnitude of the
85 odd harmonic response components can be used as a measure
86 of the overall strength of the visual cortex response.

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

97 A summary of our brain imaging and psychophysical mea-
98 surements is presented with examples of the wallpaper groups
99 in Figure 1. For our primary SSVEP analysis, we only con-
100 sidered EEG data from a pre-determined region-of-interest
101 (ROI) consisting of six electrodes over occipital cortex (see
102 Supplementary Figure 1.1). SSVEP data from this ROI was
103 filtered so that only the odd harmonics that capture the sym-
104 metry response contribute to the waveforms. While waveform
105 amplitude is quite variable among the 16 groups, all groups
106 have a sustained negative-going response that begins at about
107 the same time for all groups, 180 ms after the transition from
108 the P1 control exemplar to the original exemplar. To reduced
109 the amplitude of the symmetry-specific response to a single
110 number that could be used in further analyses and compared to
111 the psychophysical data, we computed the root-mean-square
112 (RMS) over the odd-harmonic-filtered waveforms. The data
113 in Figure 1 are shown in descending order according to RMS.
114 The psychophysical results, shown in box plots in Figure 1,
115 were also quite variable between groups, and there seems to be
116 a general pattern where wallpaper groups near the top of the
117 figure, that have lower SSVEP amplitudes, also have longer
118 psychophysical display duration thresholds.

119 We now wanted to quantify the degree to which our two
120 measurements were consistent with the subgroup relationships.

We hypothesized that more complex groups would (a) produce symmetric-specific SSVEPs with higher amplitudes and (b) shorter display duration thresholds. [PERHAPS WE NEED TO JUSTIFY THESE ASSUMPTIONS] We tested each of these hypotheses using the same approach. We first fitted a Bayesian model with wallpaper group as a factor and participant as a random effect. We fit the model separately for SSVEP RMS and psychophysical data, and then computed posterior distributions for the difference between supergroup and subgroup. These difference distributions could allow us to compute the conditional probability that the supergroup would produce (a) larger RMS and (b) a shorter threshold durations, when compared to the subgroup. The posterior distributions are shown in Figure 2 for the SSVEP data, and in Figure 3 for the psychophysical data, which distributions color-coded according to conditional probability. For both data sets our hypothesis is confirmed: For the overwhelming majority of the 64 subgroup relationships, supergroups are more likely to produce larger symmetry specific SSVEPs and shorter threshold durations, and in most cases the conditional probability of this happening is extremely high.

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

SSVEP data from four of the wallpaper groups (P2, P3, P4 and P6) was previously published as part of our earlier demonstration of parametric responses to rotation symmetry in wallpaper groups(9). We replicate that result using our Bayesian approach, and find the same parametric effect in the psychophysical data (Supplementary Figure 4.1 - NEEDS TO BE LABELED IN THE SM). We also conducted analyses looking for effects of index and normality in our two datasets, and found that ... Finally, we conducted a correlation analysis comparing SSVEP and behavioral data, and found a small ($R^2 = 0.44$) but above-zero correlation, as indicated by our confidence intervals. There are several factors that might explain the relatively weak correlation, most prominently the fact that the same individuals did not participate in each of the two experiments. Nevertheless, we find the relationship between the two datasets interesting, because it suggests that our psychophysical and SSVEP measurements are tapping into the same underlying mechanisms.

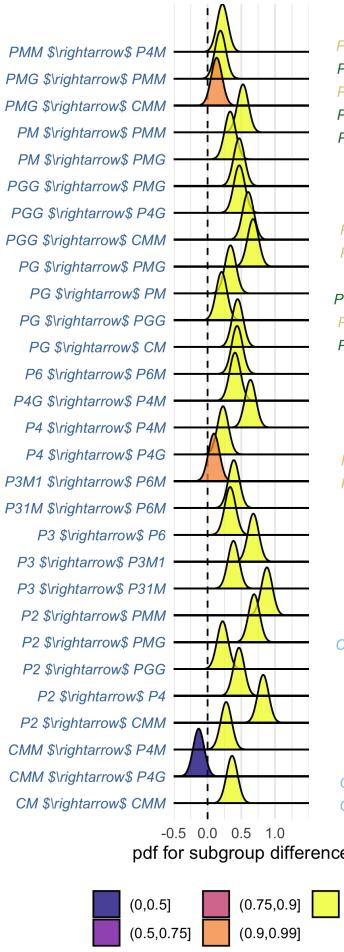


Fig. 2. Posterior distributions for the difference in mean RMS SSVEP response. Colour coding of the text indicates the index of the subgroup, while the colour of the filled distribution relates to the conditional probability that the difference in means is greater than zero. We can see that xx/64 subgroup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

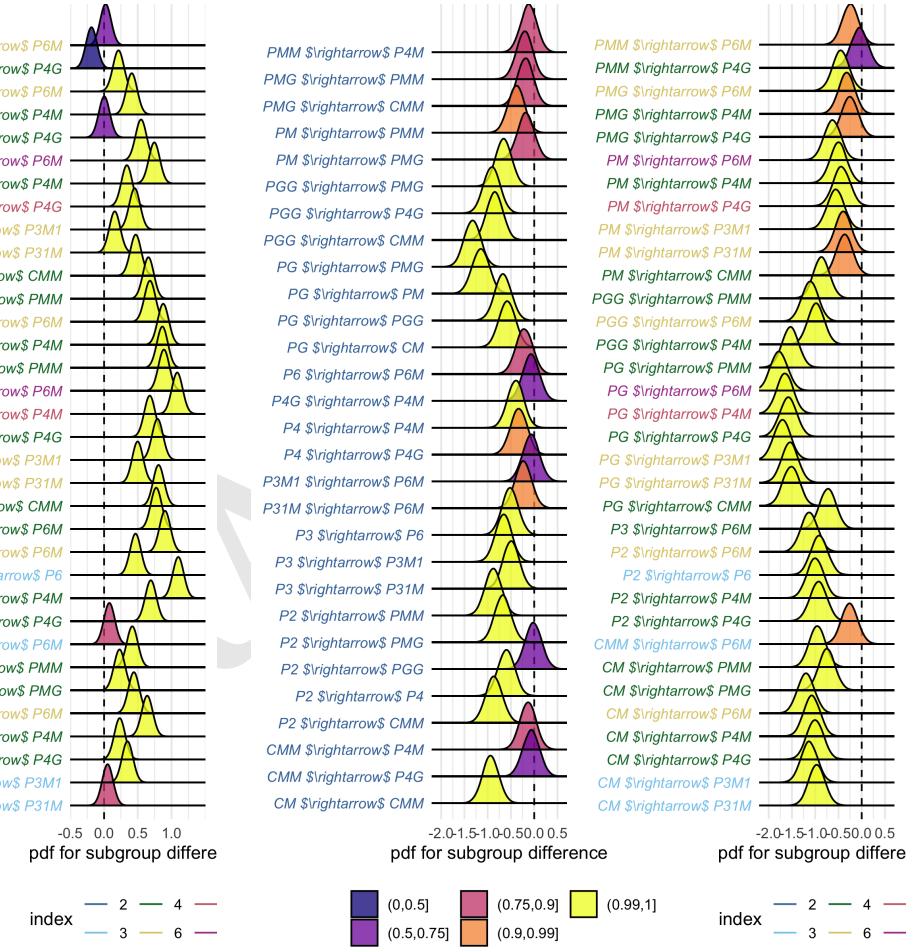


Fig. 3. Posterior distributions for the difference in mean display duration threshold. Colour coding of the text indicates the index of the subgroup, while the colour of the filled distribution relates to the conditional probability that the difference in means is greater than zero. We can see that xx/64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

183 Discussion

184 Here we show that beyond merely responding to the elementary symmetry operations of reflection (14) and rotation (9),
 185 the visual system explicitly represents hierarchical structure
 186 of the 17 wallpaper groups, and thus the compositions of all
 187 four of the fundamental symmetry transformations (rotation,
 188 reflection, translation, glide reflection) which comprise regular
 189 textures. The RMS measure of SSVEP amplitude, preserves
 190 the complex hierarchy of subgroup relationships among the
 191 wallpaper groups (11). This remarkable consistency was spe-
 192 cific to the odd harmonics of the stimulus frequency, that
 193 capture the symmetry-specific response (9) and to electrodes
 194 in an ROI over occipital cortex. When the same analysis was
 195 done using the odd harmonics from a parietal cortex ROI
 196 (Supplementary Figure 3.4) or using the even harmonics of the
 197 occipital cortex ROI (Supplementary Figure 3.4), the data was
 198 much less consistent with the subgroup relationships (yellow
 199 and green lines, Figure 4).

200 The current data provide a complete description of the
 201 visual system's response to symmetries in the 2-D plane. Our
 202 design does not allow us to independently measure the re-
 203 sponse to P1, but because each of the 16 other groups produce
 204 non-zero odd harmonic amplitudes (see Figure 1), we can con-
 205 clude that the relationships between P1 and all other groups,
 206 where P1 is the subgroup, are also preserved by the visual
 207 system. The subgroup relationships are not obvious perceptually,
 208 and most participants had no knowledge of group theory.
 209 Thus, the visual system's ability to preserve the subgroup
 210 hierarchy does not depend on explicit knowledge of the rela-
 211 tionships. Furthermore, behavioral experiments have shown
 212 that although naïve observers can distinguish many of the
 213 wallpaper groups (15), they are generally error-prone when
 214 asked to assign exemplar images to the appropriate group (16).
 215 The correspondence between responses in the visual system
 216 and group theory that we demonstrate here, may reflect a
 217 form of implicit learning that depends on the structure of the
 218 natural world. The environment is itself constrained by physi-
 219 cal forces underlying pattern formation and these forces are
 220 subject to multiple symmetry constraints (17). The ordered
 221 structure of responses to wallpaper groups could be driven by
 222 a central tenet of neural coding, that of efficiency. If coding is
 223 to be efficient, neural resources should be distributed in such
 224 a way that the structure of the environment is captured with
 225 minimum redundancy considering the visual geometric optics,
 226 the capabilities of the subsequent neural coding stages and the
 227 behavioral goals of the organism (18–21). Early work within
 228 the efficient coding framework suggested that natural images
 229 had a $1/f$ spectrum and that the corresponding redundancy
 230 between pixels in natural images could be coded efficiently
 231 with a sparse set of oriented filter responses, such as those
 232 present in the early visual pathway (22, 23). Our results sug-
 233 gest that the principle of efficient coding extends to a much
 234 higher level of structural redundancy – that of symmetries in
 235 visual images. The 17 wallpaper groups are completely regu-
 236 lar, and relatively rare in the visual environment, especially
 237 when considering distortions due to perspective and occlu-
 238 sion. Near-regular textures, however abound in the visual
 239 world, and can be approximated as deformed versions of the
 240 wallpaper groups (24). The correspondence between brain
 241 data and group theory demonstrated here may indicate that
 242 the visual system represents visual textures using a similar

244 scheme, with the wallpaper groups serving as anchor points in
 245 representational space. This framework resembles norm-based
 246 encoding strategies that have been proposed for other stimulus
 247 classes, most notably faces (25), and leads to the prediction
 248 that adaptation to wallpaper patterns should distort percep-
 249 tion of near-regular textures, similar to the aftereffects found
 250 for faces (26). Field biologist have demonstrated that animals
 251 respond more strongly to exaggerated versions of a learned
 252 stimulus, referred to as “supernormal” stimuli (27). In the
 253 norm-based encoding framework, wallpaper groups can be
 254 considered super-textures, exaggerated examples of the near-
 255 regular textures that surround us. Artists may consciously
 256 or unconsciously create supernormal stimuli, to capture the
 257 essence of the subject and evoke strong responses in the audi-
 258 ence (28). Wallpaper groups are visually compelling and have
 259 been widely used in human artistic expression going back to
 260 the Neolithic age (29). If wallpapers are super-textures, their
 261 prevalence may be a direct consequence of the strategy the
 262 human visual system uses for encoding visual textures.

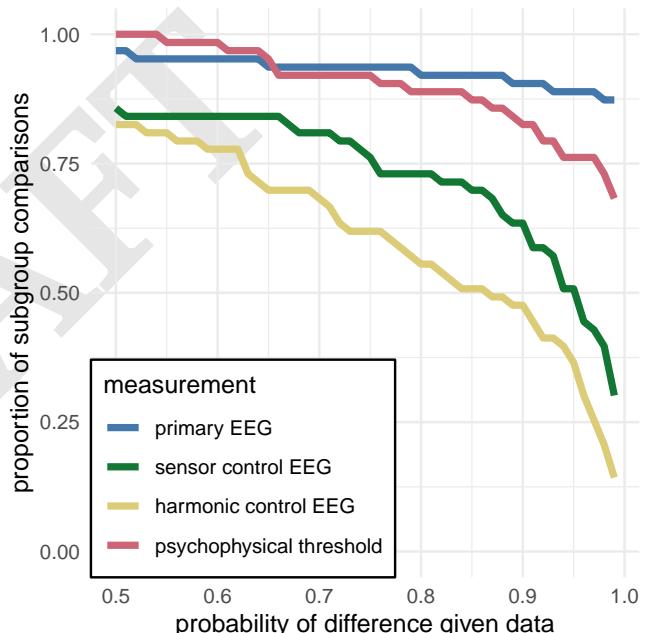


Fig. 4. Here is a caption

263 **Participants.** Twenty-five participants (11 females, mean age
 264 28.7±13.3) took part in the EEG experiment. Their informed
 265 consent was obtained before the experiment under a proto-
 266 col that was approved by the Institutional Review Board of
 267 Stanford University. 11 participants (8 females, mean age
 268 20.73±1.21) took part in the psychophysics experiment. All
 269 participants had normal or corrected-to-normal vision. Their
 270 informed consent was obtained before the experiment under a
 271 protocol that was approved by the University of Essex's Ethics
 272 Committee.

273 **Stimulus Generation.** Exemplars from the different wallpaper
 274 groups were generated using a modified version of the method-
 275 ology developed by Clarke and colleagues(16) that we have
 276 described in detail elsewhere(9). Briefly, exemplar patterns
 277 for each group were generated from random-noise textures,

which were then repeated and transformed to cover the plane, according to the symmetry axes and geometric lattice specific to each group. The use of noise textures as the starting point for stimulus generation allowed the creation of an almost infinite number of distinct exemplars of each wallpaper group. For each exemplar image, phase-randomized control exemplars were generated that had the same power spectrum as the exemplar images for each group. The phase scrambling eliminates rotation, reflection and glide-reflection symmetries within each exemplar, but the phase-scrambled images inherent the spectral periodicity arising from the periodic tiling. This means that all control exemplars, regardless of which wallpaper group they are derived from, degenerate to another symmetry group, namely P1. P1 is the simplest of the wallpaper groups, and contains only translations of a region whose shape derives from the lattice. Because the different wallpaper groups have different lattices, P1 controls matched to different groups have different power spectra. Our experimental design takes these differences into account by comparing the neural responses evoked by each wallpaper group to responses evoked by the matched control exemplars.

Stimulus Presentation. Stimulus Presentation. For the EEG experiment, the stimuli were shown on a 24.5" Sony Trimaster EL PVM-2541 organic light emitting diode (OLED) display at a screen resolution of 1920×1080 pixels, 8-bit color depth and a refresh rate of 60 Hz, viewed at a distance of 70 cm. The mean luminance was 69.93 cd/m² and contrast was 95%. The diameter of the circular aperture in which the wallpaper pattern appeared was 13.8° of visual angle presented against a mean luminance gray background. Stimulus presentation was controlled using in-house software.

For the psychophysics experiment, the stimuli were shown on a 48 × 27cm VIEWPixx/3D LCD Display monitor, model VPX-VPX-2005C, resolution 1920×1080 pixels, with a viewing distance of approximately 40cm and linear gamma. Stimulus presentation was controlled using MatLab and Psychtoolbox-3 (30, 31). The diameter of the circular aperture for the stimuli was 21.5°.

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

the difficulty of the vigilance task was kept constant.

Psychophysics Procedure. The experiment consisted of 16 blocks, one for each of the wallpaper groups (excluding P1). In each trial, participants were presented with two stimuli (one of which was the wallpaper group for the current block of trials, the other being P1), one after the other (inter stimuli interval of 700ms). After each stimuli had been presented, it was masked with white noise for 300ms. After both stimuli had been presented, participants made a response on the keyboard to indicate whether they thought the first or second contained the most symmetry. Each block started with 10 practise trials, (stimulus display duration of 500ms) to allow participants to familiarise themselves with the current block's wallpaper pattern. If they achieved an accuracy of 9/10 in these trials they progressed to the rest of the block, otherwise they carried out another set of 10 practise trials. This process was repeated until the required accuracy of 9/10 was obtained. The rest of the block consisted of four interleaved staircases (using the QUEST algorithm (32), full details given in the SI) of 30 trials each. On average, a block of trials took around 10 minutes to complete.

EEG Acquisition and Preprocessing. Electroencephalogram 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

397 Visual Evoked Potentials (SSVEP) paradigm we used allowed
 398 us to separate symmetry-related responses from non-specific
 399 contrast transient responses. Previous work has demonstrated
 400 that symmetry-related responses are predominantly found in
 401 the odd harmonics of the stimulus frequency, whereas the even
 402 harmonics consist mainly of responses unrelated to symmetry,
 403 that arise from the contrast change associated with the
 404 appearance of the second image[2-4]. This functional distinc-
 405 tion of the harmonics allowed us to generate a single-cycle
 406 waveform containing the response specific to symmetry, by
 407 filtering out the even harmonics in the spectral domain, and
 408 then back-transforming the remaining signal, consisting only of
 409 odd harmonics, into the time-domain. For our main analysis,
 410 we averaged the odd harmonic single-cycle waveforms within
 411 a six-electrode region of interest (ROI) over occipital cortex
 412 (electrodes 70, 74, 75, 81, 82, 83). These waveforms, averaged
 413 over participants, are shown in Figure 2 in the main paper.
 414 The same analysis was done for the even harmonics (see Figure
 415 S1) and for the odd harmonics within a six electrode ROI over
 416 parietal cortex (electrodes 53, 54, 61, 78, 79, 86; see Figure
 417 S2). The root-mean square values of these waveforms, for each
 418 individual participant, were used to determine whether each
 419 of the wallpaper subgroup relationships were preserved in the
 420 brain data.

421 **Bayesian Analysis of EEG and Psychophysical data.** Bayesian
 422 analysis was carried out using R (v3.6.1) (33) with the `brms`
 423 package (v2.9.0) (34) and rStan (v2.19.2 (35)). The data from
 424 each experiment were modelled using a Bayesian generalised
 425 mixed effect model with wallpaper group being treated as a
 426 16 level factor, and random effects for participant. The EEG
 427 data and display thresholds were modelled using log-normal
 428 distributions with weakly informative, $\mathcal{N}(0, 2)$, priors. After
 429 fitting the model to the data, samples were drawn from the pos-
 430 terior distribution for each mean of the EEG response (display
 431 duration) for each wallpaper group. These samples were then
 432 recombined to calculate the distribution of differences for each
 433 pair of subgroup and super-group. These distributions were
 434 then summarised by computing the conditional probability of
 435 obtaining a positive (negative) difference, $p(\Delta|data)$.

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

440 snippets

441 Specifically, the amplitudes of symmetry-specific responses in
 442 individual participants ($n = 25$) preserve these relationships
 443 at an above-chance level in 88.3% (53 out of 60) of cases.

444 we used a steady-state design, in which exemplar images
 445 belonging to 16 of the 17 wallpaper groups alternated with
 446 phase-scrambled images of the same group. Exemplars from
 447 each of the 16 groups alternated at 0.83 Hz with their corre-
 448 sponding set of P1 exemplars, that were matched in terms of
 449 their Fourier power spectrum.

450 Thus, the magnitude of the odd harmonic response compo-
 451 nents can be used as a distance metric for each group, with
 452 distance being measured relative to the simplest group, P1.

453 **ACKNOWLEDGMENTS.** Please include your acknowledgments
 454 here, set in a single paragraph. Please do not include any acknowl-

455 edgments in the Supporting Information, or anywhere else in the
 456 manuscript.

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