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A century of vision research has demonstrated that symmetry contributes to numerous domains of visual perception (? ? ? ?). In a 2-D image, the four fundamental symmetries, reflection, rotation, translation and glide reflection, can be combined in 17 distinct ways. These 17 "wallpaper" groups (? ? ?) obey a hierarchy, determined by mathematical group theory, where simpler groups are subgroups of more complex ones(?). Here we probe representations of symmetries in wallpaper groups using two methods: Steady-State Visual Evoked Potentials (SSVEPs) recorded using EEG and psychophysical detection thresholds. We find that the hierarchical relationships between the wallpaper groups are almost perfectly preserved in both behavior and response amplitudes in visual cortex. This remarkable consistency between the structure of symmetry representations and mathematical group theory, is likely generated over visual development, through implicit learning of regularities in the environment.

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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 (? ?), scenes (?) and surface properties (?), as well as the social process of mate selection (?). Most of this work has focused on mirror symmetry,

In the two spatial dimensions relevant for images, the four fundamental symmetries, reflection, rotation, translation and glide reflection, can be combined in 17 distinct ways, the "wallpaper" groups (? ? ?). The 17 wallpaper groups obey a hierarchy of complexity, determined by mathematical group theory, where simpler groups are sub-groups of more complex ones (?). Here we use Steady-State Visual Evoked Potentials (SSVEPs) to measure responses to 16 out of 17 wallpaper groups and show that activity in human visual cortex is remarkably consistent with the hierarchical relationships between the wallpaper groups. Specifically, the amplitudes of symmetry-specific responses in individual participants ($n = 25$) preserve these relationships at an above-chance level in 88.3% (53 out of 60) of cases. Visual cortex thus encodes all 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 visual stimuli for our experiment were multiple exemplar images belonging to each of the 17 wallpaper groups, generated from random-noise textures, as described in detail elsewhere (?). To isolate brain activity specific to the symmetry structure in the images from activity associated with modulation of low-level features, we used a steady-state design, in which exemplar images belonging to 16 of the 17 wallpaper groups alternated with phase-scrambled images of the same group. Because all wallpapers are periodic images due to their lattice tiling structure, the phase-scrambled images are also a wallpaper group (P1). 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) (?). Exemplars from each of the 16 groups alternated at 0.83 Hz with their corresponding set of P1 exemplars, that were matched in terms of their Fourier power spectrum. Because the P1 group serves a control stimulus in this approach, the experiment was restricted to the remaining 16 groups. This design allows us to isolate responses to structural features beyond the shared power spectrum, including any symmetries other than translation, in the odd harmonics of the image update frequency (? ?) [NORCIA 2002 MISSING]. Thus, the magnitude of the odd harmonic response components can be used as a distance metric for each group, with distance being measured relative to the simplest group, P1. A wallpaper group is a topologically discrete group of isometries of the Euclidean plane, i.e. transformations that preserve distance (?). 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 (?). 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

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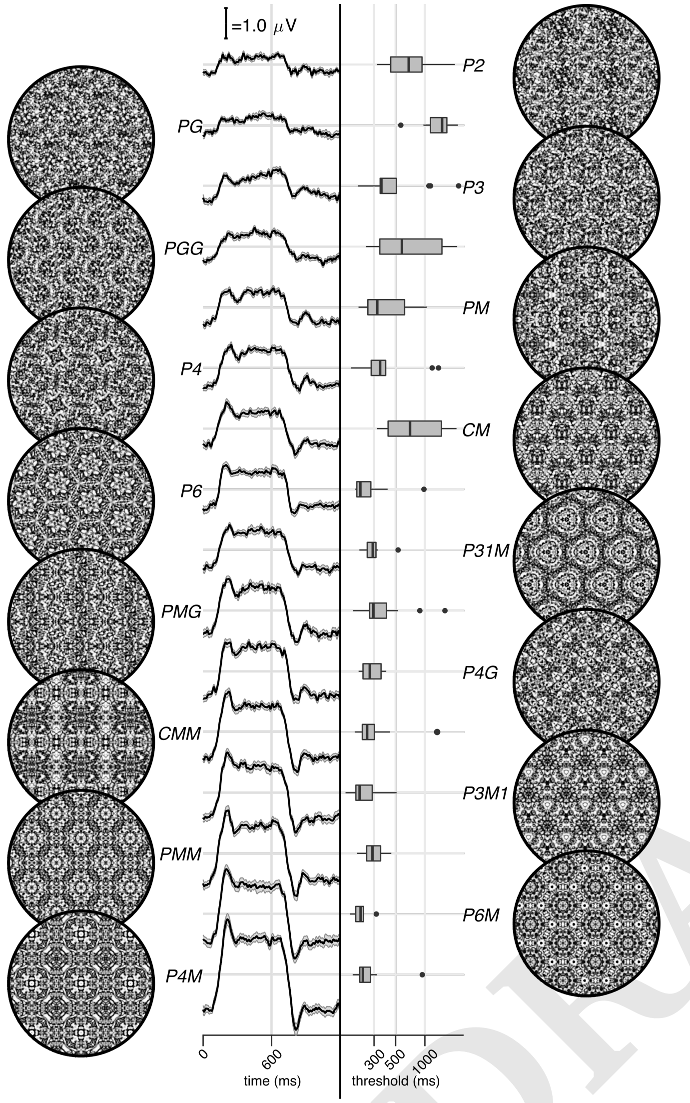

Fig. 1. Posterior distributions for the difference in mean RMS EEG response. Colour coding of the text indicates the index of the subgroup, while the colour of the filled distribution relates to the conditional probability that the difference in means is greater than zero. We can see that 55/64 subgroup relationships have $p(\Delta|data) > 0.9$.

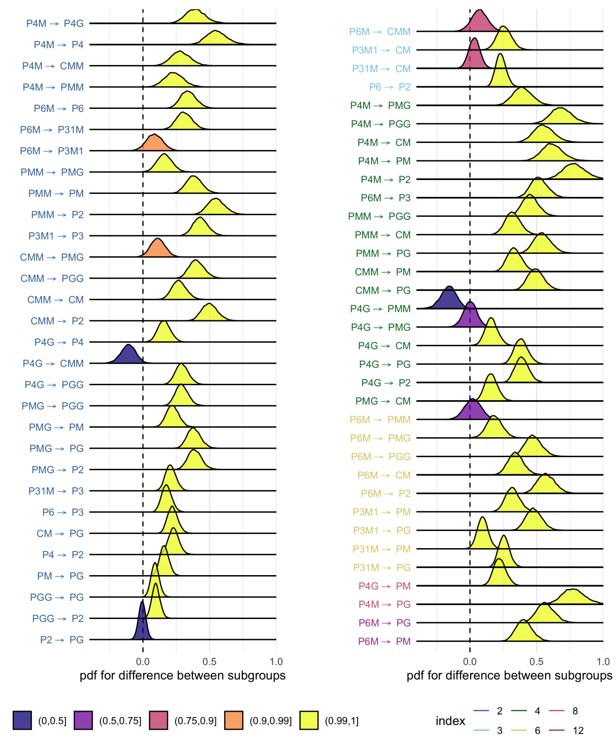

Fig. 2. Posterior distributions for the difference in mean RMS EEG response. Colour coding of the text indicates the index of the subgroup, while the colour of the filled distribution relates to the conditional probability that the difference in means is greater than zero. We can see that 55/64 subgroup relationships have $p(\Delta|data) > 0.9$.

the subgroup is found in the outer group (**?**). 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°, 60°, 120°, 180°, 240°, 300°, in which P2 0°, 180° 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°, 120°, 240°. Because P2 is repeated three times in P6, P2 is a subgroup of P6 with index 3 (**?**).

Discussion

Here we show that beyond merely responding to the elementary symmetry operations of reflection (**?**) and rotation (**?**), the visual system explicitly represents hierarchical structure of the 17 wallpaper groups, and thus the compositions of all four of the fundamental symmetry transformations (rotation, reflection, translation, glide reflection) which comprise regular textures. The RMS measure of SSVEP amplitude, preserves the complex hierarchy of subgroup relationships among the wallpaper groups (?). Out of a total of 60 relationships, 53 were preserved in a significant number of participants, and 49 were significant even at a stricter threshold ($p < 0.002$). The ordering was highly stable in individual participants, with an average preservation rate of 21 of 25 participants across all 60 relationships (see Figure 3). This remarkable consistency was specific to the odd harmonics of the stimulus frequency, that capture the symmetry-specific response (?) and to electrodes in an ROI over occipital cortex. When the same analysis was done on the even harmonics of the occipital cortex ROI, the ordering of responses was much less apparent (see Figure S2) and preservation rates much lower (see Figure S4). The odd harmonics from electrodes in an ROI over parietal cortex, showed even weaker evidence of preserving the hierarchy among subgroups (see Figure S5). Importantly, no relationships were preserved in either of these control analyses that were not also preserved in the main analysis of the odd harmonics in the occipital cortex ROI. The current data provide a complete description of the visual system's response to symmetries in the 2-D plane. Our design does not allow us to independently measure the response to P1, but because each of the 16 other groups produce non-zero odd harmonic amplitudes (see Figure 2), 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 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, behavioral experiments have shown that although naïve observers can distinguish many of the wallpaper groups (?), they are generally error-prone when asked to assign exemplar images to the appropriate group (?). 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 (?). 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 (? ? ? ?). 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 (? ?). 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 (?). The correspondence between brain data 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 (?), and leads to the prediction that adaptation to wallpaper patterns should distort perception of near-regular textures, similar to the aftereffects found for faces (?). Field biologist have demonstrated that animals respond more strongly to exaggerated versions of a learned stimulus, referred to as "supernormal" stimuli (?). 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 (?). Wallpaper groups are visually compelling and have been widely used in human artistic expression going back to the Neolithic age (?). If wallpapers are super-textures, their prevalence may be a direct consequence of the strategy the human visual system uses for encoding visual 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 informed consent was obtained before the experiment under a protocol that was approved by the University of Essex's Ethics Committee.

Stimulus Generation. Exemplars from the different wallpaper groups were generated using a modified version of the methodology developed by Clarke and colleagues(?) that we have described in detail elsewhere(?). Briefly, exemplar patterns 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 (? ?). 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 (?), 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 μV) 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, δf = 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.

EEG 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 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.

Bayesian Analysis of EEG and Psychophysical data. Bayesian analysis was carried out using R (v3.6.1) (?) with the `brms` package (v2.9.0 (?) and rStan (v2.19.2 (?)). 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 ($N(0, 2)$) 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 that of obtaining a positive (negative) difference, $p(\Delta|data)$.

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

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