

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

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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 Symmetries 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 has focused on four of the wall-
15 paper groups, and used functional MRI to show that rotation
16 symmetries within wallpapers are represented parametrically
17 in several areas in occipital cortex, beginning with visual
18 area V3 (10). This effect is also robust in electroencephalog-
19 graphy (EEG), whether measured using Steady-State Visual
20 Evoked Potentials (SSVEPs)(10) or event-related paradigms
21 (11). Here we extend on this work by collecting SSVEPs
22 and psychophysical data from human participants viewing the
23 complete set of wallpaper groups. We measure responses in
24 visual cortex to 16 out of the 17 wallpaper groups, with the
25 17th serving as a control stimulus, with the goal of providing
26 a more complete picture of how wallpaper groups are repre-
27 sented in the human visual system. The 17 wallpaper groups
28 obey a hierarchy of complexity, determined by mathematical
29 group theory, where simpler groups are sub-groups of more
30 complex ones (8). The two datasets presented here puts on
31 the position of being able to assess the extent to which
32 both behavior and brain responses follow that hierarchy. The

33 results show that activity in human visual cortex is remark-
34 ably consistent with the hierarchical relationships between the
35 wallpaper groups, with SSVEP amplitudes and psychophysical
36 thresholds preserving these relationships at a level that is far
37 beyond chance. Visual cortex thus appears to encode all of the
38 fundamental symmetries using a representational structure
39 that closely approximates the subgroup relationships from
40 group theory. Given that most participants had no knowledge
41 of group theory, the ordered structure of visual responses to
42 wallpaper groups is likely learned implicitly from regularities
43 in the visual environment.

Results

44 The visual stimuli for our experiment were multiple exem-
45 plar images belonging to each of the 17 wallpaper groups,
46 generated from random-noise textures, as described in detail
47 elsewhere (10). To isolate brain activity specific to the sym-
48 metry structure in the images from activity associated with
49 modulation of low-level features, we used a steady-state design,
50 in which exemplar images belonging to 16 of the 17 wallpaper
51 groups alternated with phase-scrambled images of the same
52 group. Because all wallpapers are periodic images due to their
53 lattice tiling structure, the phase-scrambled images are also
54 a wallpaper group (P1). P1 contains no symmetries other
55 than translation, while all other groups contain translation in
56 combination with one or more of the other three fundamental
57 symmetries (reflection, rotation, glide reflection) (7). Exem-
58 plars from each of the 16 groups alternated at 0.83 Hz with
59 their corresponding set of P1 exemplars, that were matched in
60

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.

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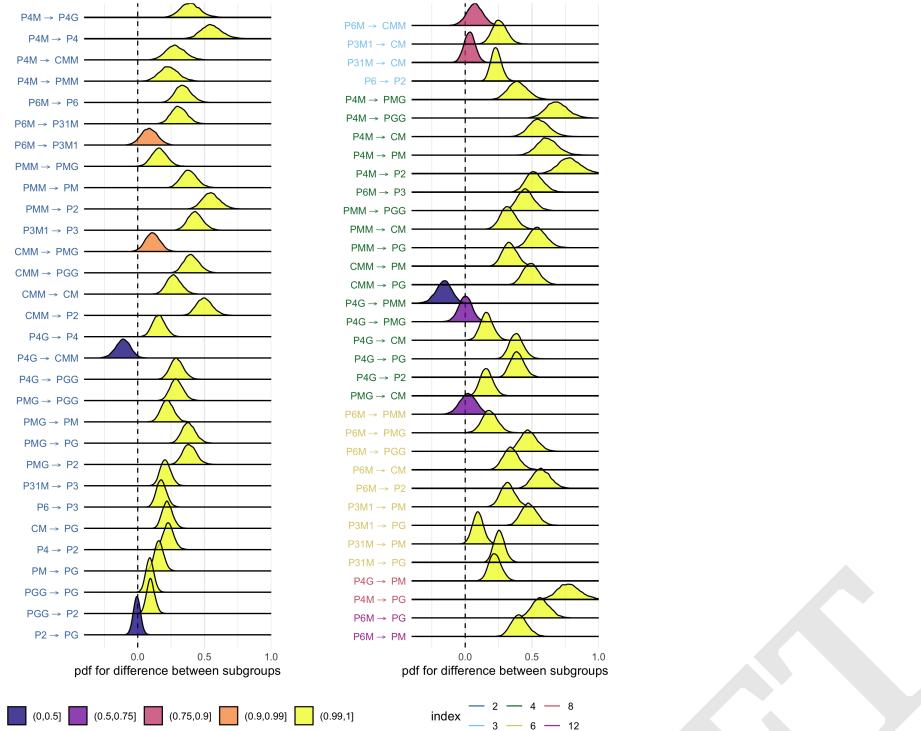


Fig. 2. Posterior distributions for the difference in mean RMS EEG response. Colour coding of the text indicates the index of the subgroup, while the colour of the filled distribution relates to the conditional probability that the difference in means is greater than zero. We can see that 55/64 subgroup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

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 (10, 12, 13). 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 (7). 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 (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).

Discussion

Here we show that beyond merely responding to the elementary symmetry operations of reflection (14) and rotation (10), 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 (8). 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 (10) 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

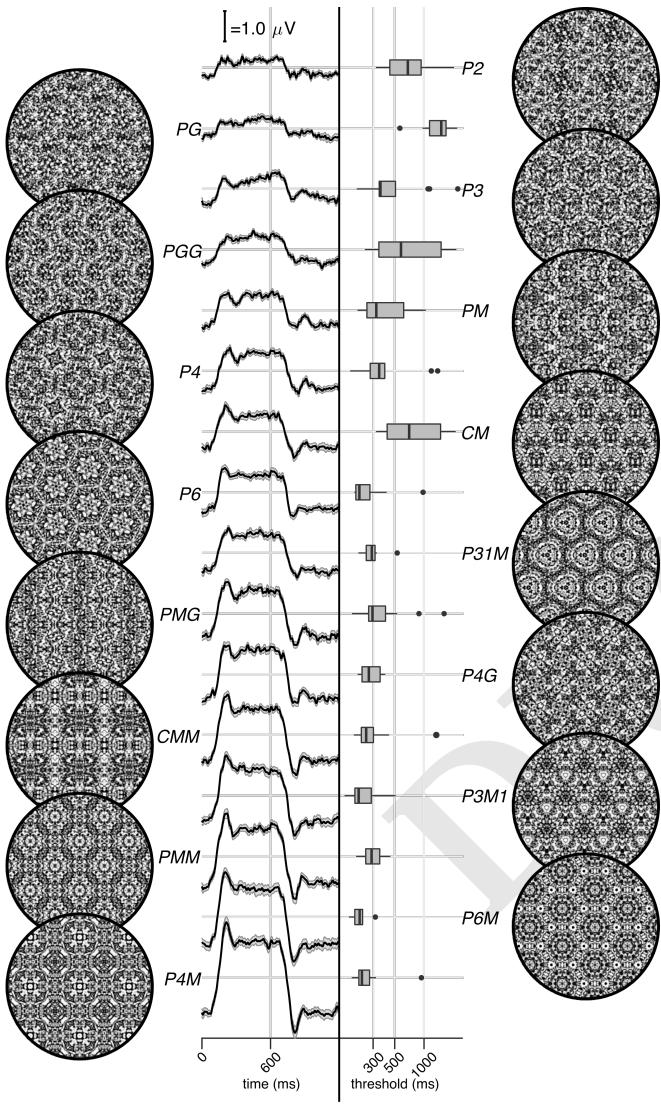


Fig. 1. Posterior distributions for the difference in mean RMS EEG response. Colour coding of the text indicates the index of the subgroup, while the colour of the filled distribution relates to the conditional probability that the difference in means is greater than zero. We can see that 55/64 subgroup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

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 (15), they are generally error-prone when asked to assign exemplar images to the appropriate group (16). 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 (17). 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 (18–21). 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 (22, 23). 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 (24). 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 (25), and leads to the prediction that adaptation to wallpaper patterns should distort perception of near-regular textures, similar to the aftereffects found for faces (26). Field biologist have demonstrated that animals respond more strongly to exaggerated versions of a learned stimulus, referred to as “supernormal” stimuli (27). 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 (28). Wallpaper groups are visually compelling and have been widely used in human artistic expression going back to the Neolithic age (29). If wallpapers are super-textures, their prevalence may be a direct consequence of the strategy the human visual system uses for encoding visual textures.

175 **snippets**

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

179 **Participants.** Twenty-five participants (11 females, mean age
180 28.7 ± 13.3) took part in the EEG experiment. Their informed
181 consent was obtained before the experiment under a protocol
182 that was approved by the Institutional Review Board of
183 Stanford University. 11 participants (8 females mean age
184 20.73 ± 1.21) took part in the psychophysics experiment. All
185 participants had normal or corrected-to-normal vision. Their
186 informed consent was obtained before the experiment under a
187 protocol that was approved by the University of Essex's Ethics
188 Committee.

189 **Stimulus Generation.** Exemplars from the different wallpaper
190 groups were generated using a modified version of the methodology
191 developed by Clarke and colleagues(16) that we have
192 described in detail elsewhere(10). Briefly, exemplar patterns
193 for each group were generated from random-noise textures,
194 which were then repeated and transformed to cover the plane,
195 according to the symmetry axes and geometric lattice specific
196 to each group. The use of noise textures as the starting
197 point for stimulus generation allowed the creation of an almost
198 infinite number of distinct exemplars of each wallpaper
199 group. For each exemplar image, phase-randomized control
200 exemplars were generated that had the same power spectrum
201 as the exemplar images for each group. The phase scrambling
202 eliminates rotation, reflection and glide-reflection symmetries
203 within each exemplar, but the phase-scrambled images inherit
204 the spectral periodicity arising from the periodic tiling.
205 This means that all control exemplars, regardless of which
206 wallpaper group they are derived from, degenerate to another
207 symmetry group, namely P1. P1 is the simplest of the wallpaper
208 groups, and contains only translations of a region whose
209 shape derives from the lattice. Because the different wallpaper
210 groups have different lattices, P1 controls matched to different
211 groups have different power spectra. Our experimental design
212 takes these differences into account by comparing the neural
213 responses evoked by each wallpaper group to responses evoked
214 by the matched control exemplars.

215 **Stimulus Presentation.** Stimulus Presentation. For the EEG
216 experiment, the stimuli were shown on a 24.5" Sony Trimaster
217 EL PVM-2541 organic light emitting diode (OLED) display
218 at a screen resolution of 1920×1080 pixels, 8-bit color depth
219 and a refresh rate of 60 Hz, viewed at a distance of 70 cm.
220 The mean luminance was 69.93 cd/m^2 and contrast was 95%.
221 The diameter of the circular aperture in which the wallpaper
222 pattern appeared was 13.8° of visual angle presented against
223 a mean luminance gray background. Stimulus presentation
224 was controlled using in-house software.

225 For the psychophysics experiment, the stimuli were shown
226 on a $48 \times 27\text{cm}$ VIEWPixx/3D LCD Display monitor, model
227 VPX-VPX-2005C, resolution 1920×1080 pixels, with a viewing
228 distance of approximately 40cm and linear gamma. Stimulus
229 presentation was controlled using MatLab and Psychtoolbox-3
230 (30, 31). The diameter of the circular aperture for the stimuli
231 was 21.5° .

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

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

275 **EEG Acquisition and Preprocessing.** Electroencephalogram
276 Acquisition and Preprocessing. The time-locked Steady-State
277 Visual Evoked Potentials were collected with 128-sensor HydroCell
278 Sensor Nets (Electrical Geodesics, Eugene, OR) and were
279 band-pass filtered from 0.3 to 50 Hz. Raw data were evaluated
280 off line according to a sample-by-sample thresholding
281 procedure to remove noisy sensors that were replaced by the
282 average of the six nearest spatial neighbors. On average, less
283 than 5% of the electrodes were substituted; these electrodes
284 were mainly located near the forehead or the ears. The substitutions
285 can be expected to have a negligible impact on our
286 results, as the majority of our signal can be expected to come
287 from electrodes over occipital, temporal and parietal cortices.
288 After this operation, the waveforms were re-referenced to the
289 common average of all the sensors. The data from each 12s
290 trial were segmented into five 2.4 s long epochs (i.e., each
291 of these epochs was exactly 2 cycles of image modulation).

292 Epochs for which a large percentage of data samples exceeding
 293 a noise threshold (depending on the participant and ranging
 294 between 25 and 50 μ V) were excluded from the analysis on a
 295 sensor-by-sensor basis. This was typically the case for epochs
 296 containing artifacts, such as blinks or eye movements. The use
 297 of steady-state stimulation drives cortical responses at specific
 298 frequencies directly tied to the stimulus frequency. It is thus
 299 appropriate to quantify these responses in terms of both phase
 300 and amplitude. Therefore, a Fourier analysis was applied on
 301 every remaining epoch using a discrete Fourier transform with
 302 a rectangular window. The use of epochs two-cycles (i.e., 2.4
 303 s) long, was motivated by the need to have a relatively high
 304 resolution in the frequency domain, $\delta f = 0.42$ Hz. For each
 305 frequency bin, the complex-valued Fourier coefficients were
 306 then averaged across all epochs within each trial. Each participant
 307 did two sessions of 8 trials per condition, which resulted
 308 in a total of 16 trials per condition.

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

337 **Bayesian Analysis of EEG and Psychophysical data.** Bayesian
 338 analysis was carried out using R (v3.6.1) (33) with the `brms`
 339 package (v2.9.0 (34)) and rStan (v2.19.2 (35)). The data from
 340 each experiment were modelled using a Bayesian generalised
 341 mixed effect model with wallpaper group being treated as a
 342 16 level factor, and random effects for participant. The EEG
 343 data and display thresholds were modelled using log-normal
 344 distributions with weakly informative ($N(0, 2)$) priors. After
 345 fitting the model to the data, samples were drawn from the pos-
 346 terior distribution for each mean of the EEG response (display
 347 duration) for each wallpaper group. These samples were then
 348 recombined to calculate the distribution of differences for each
 349 pair of subgroup and super-group. These distributions were
 350 then summarised by computing the conditional probability
 351 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. 352
 353
 354

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 manuscript. 355
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