1 **Mapping sequences can bias population receptive field estimates**

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Abstract

12 Population receptive field (pRF) modelling is a common technique for estimating the stimulus-
13 selectivity of populations of neurons using neuroimaging. Here, we aimed to address if pRF
14 properties estimated with this method depend on the spatio-temporal structure and the
15 predictability of the mapping stimulus. We mapped the polar angle preference and tuning width of
16 voxels in visual cortex (V1-V4) of healthy, adult volunteers. We compared sequences orderly
17 sweeping through the visual field or jumping from location to location employing stimuli of
18 different width (45° vs 6°) and cycles of variable duration (8s vs 60s). While we did not observe
19 any systematic influence of stimulus predictability, the temporal structure of the sequences
20 significantly affected tuning width estimates. Ordered designs with large wedges and short cycles
21 produced systematically smaller estimates than random sequences. Interestingly, when we used
22 small wedges and long cycles, we obtained larger tuning width estimates for ordered than random
23 sequences. We suggest that, ordered and random mapping protocols show different susceptibility
24 to other design choices such as stimulus type and duration of the mapping cycle and can produce
25 significantly different pRF results.

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Introduction

Topographic organization is a fundamental principle of the human sensory brain and the study of its properties plays a crucial role in understanding how the brain responds adaptively to properties of the environment and current goals. Important progress in brain mapping was encouraged by the introduction of population receptive field (pRF) modelling by Dumoulin & Wandell (2008). This approach aims at estimating the aggregate receptive field of all neurons within a voxel in functional magnetic resonance imaging (fMRI) scans. Essentially, a pRF identifies the location in sensory space that drives a voxel's response, the spread of the responsive region and its shape (Dumoulin & Wandell, 2008; Silson, Reynolds, Kravitz, & Baker, 2018; Wandell & Winawer, 2015; Zeidman, Silson, Schwarzkopf, Baker, & Penny, 2018; Zuiderbaan, Harvey, & Dumoulin, 2012). A flourishing literature in the past ten years has shown that pRF modelling constitutes a powerful and sensitive approach for describing the fundamental properties of human visual cortex. The pRF size increases with increasing eccentricity and along the visual hierarchy (Amano, Wandell, & Dumoulin, 2009; Dumoulin & Wandell, 2008). Heterogeneities in pRF properties have been revealed also between different portions of the visual field (Moutsiana et al., 2016; Silson et al., 2018; Silva et al., 2018), across individuals (Moutsiana et al., 2016) and across populations (Anderson et al., 2016; Schwarzkopf, Anderson, de Haas, White, & Rees, 2014; Smittenaar, Macsweeney, Sereno, & Schwarzkopf, 2016). Moreover, pRF properties have been used to investigate neural plasticity of the visual system during development (Dekker, Schwarzkopf, de Haas, Nardini, & Sereno, 2017, 2019; Gomez, Natu, Jeska, Barnett, & Grill-Spector, 2018) or evaluate adaptive changes in the human brain resulting from diseases or trauma with pRF changes mirroring changes in visual function (Dumoulin & Knapen, 2018).

Interestingly, recent studies have also shown that pRF properties flexibly adapt to how observers engage with the stimulus. Changes in the locus of attention induce shifts in pRFs preferred location in the direction of the attended location across the entire visual field (Kay, Weiner, & Grill-Spector, 2015; Klein, Harvey, & Dumoulin, 2014; Sheremata & Silver, 2015; Vo, Sprague, & Serences, 2017). Such global changes are larger in higher visual areas (Klein et al., 2014) along both the ventral (Kay et al., 2015) and the dorsal stream (Sheremata & Silver, 2015). Moreover, recent studies indicate that pRF size and eccentricity vary in concert when the task requires to move the focus of attention from fixation to the mapping stimulus, suggesting that processing resources are

60 adaptively redistributed to optimize the sampling of the visual stimulus according to task

61 requirements (Kay et al., 2015; van Es, Theeuwes, & Knapen, 2018). Similarly, changes in spatial

62 tuning of population receptive field and in their eccentricity have been observed as a consequence

63 of changes in attentional load at fixation (de Haas, Schwarzkopf, Anderson, & Rees, 2014).

64 One aspect this literature has mostly overlooked is the influence of spatial predictability of visual

65 stimuli in mapping estimates. Phase-encoded retinotopic mapping experiments (Engel et al., 1994;

66 Sereno et al., 1995) and most pRF studies (e.g. Dumoulin & Wandell, 2008; Harvey & Dumoulin,

67 2011; Moutsiana et al., 2016; van Dijk, de Haas, Moutsiana, & Schwarzkopf, 2016; Yildirim,

68 Carvalho, & Cornelissen, 2018 with few exceptions, e.g. Binda, Thomas, Boynton, & Fine, 2013;

69 Kay et al., 2015; Thomas et al., 2015) typically employ ordered stimulus sequences - such as

70 rotating wedges, contracting and expanding rings, or sweeping bars - to map visual areas. In such

71 designs, the orderly presentation of the stimulus carries an inherent spatiotemporal regularity in

72 the mapping sequence. Such regularity has two main consequences: 1) the predictability of the

73 stimulus location, 2) the systematic consecutive stimulation of adjacent spatial locations.

74 Both consequences could result in fMRI responses beyond the directly stimulated voxels.

75 Specifically, the position of a coherently moving stimulus can be anticipated based on its current

76 location and the direction of motion. The predictability of the stimulus location could induce an

77 anticipatory response in such locations (Ekman, Kok, & de Lange, 2017). Moreover, knowledge

78 of the upcoming stimulus location can provide spatial cues to direct attention to the relevant portion

79 of the screen affecting pRF estimates accordingly (Kastner, Pinsk, De Weerd, Desimone, &

80 Ungerleider, 1999). On the other hand, the consecutive stimulation of adjacent locations in space

81 can generate a ''traveling wave'' of activity across the cortical surface that would cause the BOLD

82 signal to spread across neighboring voxels (Engel et al., 1994). The permeability of pRF estimates

83 to spatiotemporal properties of the sequences has important implications also for the reliability of

84 the estimated parameters.

85 In a study aiming to minimize biases when measuring visual cortex reorganization, Binda and

86 colleagues (2013) compared pRF estimates using ordered sequences (i.e. sweeping bars) and m-

87 sequences of multifocal stimuli. The multifocal method consists in the presentation of multiple

88 visual stimuli presented at different locations designed to minimize the spatiotemporal correlation

89 of visual stimulation (Vanni et al., 2005). They fitted a standard 2D-Gaussian model to voxel

90 responses and observed that pRF size estimates (σ) in areas V1-V3 were systematically larger

91   when ordered mapping sequence were employed. The authors suggested that differences in the

92   mapping sequence can lead to different pRF estimates, but they did not directly address the

93   distinctive impact of expectations and spatiotemporal regularities. Moreover, in this study the two

94   mapping protocols differed not only in their spatiotemporal sequence dependencies, but also in

95   stimulus shape and size, field coverage, and scanning protocol.

96   In this study, we aim to characterize to what extent spatiotemporal regularities in the mapping

97   sequence affect the pRF parameter estimates in visual cortex, disentangling the role of spatial

98   expectations and the impact of non-linear summation of the BOLD signal when adjacent locations

99   are stimulated over a short interval. We employed functional MRI and a pRF mapping approach

100   (Dumoulin & Wandell, 2008) to estimate the polar angle preference and the tuning response of

101   voxels in visual cortex. We tested the same participants in three fMRI experiments using mapping

102   sequences that differed in the spatial contingencies of consecutive wedge stimuli and in their

103   predictability: ordered (rotating clockwise or anticlockwise), predictable, and unpredictable. In

104   addition, we compared sequences employing stimuli of different width (wedge angle of 45deg vs

105   6deg) that covered the entire visual field in cycles of variable duration (9s vs 60s). We modelled

106   pRFs of polar angle as a circular Gaussian tuning function with two parameters: the polar angle

107   preferred response and its spread quantified as full-width half-maximum (FWHM). We compared

108   polar angle estimates and tuning functions of pRFs in functionally defined occipital ROIs (V1, V2,

109   V3, V3A, V4) based on the individual maps obtained from an independent mapping experiment

110   using typical methods. Finally, we compared empirical results and simulated data as an aid for

111   understanding the biases and reliabilities of pRF estimates.

112   Results suggest that the spatiotemporal regularities in the mapping protocol significantly affected

113   pRF size (tuning width) estimates in agreement with what was previously observed for pRF size

114   in the visual (Binda et al., 2013) and the auditory domain (Thomas et al., 2015). Moreover, we

115   observed that the direction of the effect depended on the duration of the mapping cycle. Our results,

116   however, do not indicate any reliable influence of stimulus predictability on pRF properties.

117   Finally, we observed that while the ordered sequence led to the highest goodness of fit, the

118   parameters estimated in this condition were not superior to those obtained with random conditions.

Experiment 1

Here we asked whether the spatiotemporal structure of mapping sequences used in retinotopic mapping experiments influences the resulting parameter estimates. In particular, we tested whether pRF parameters depend on the subsequent stimulation of adjacent locations that characterize ordered mapping protocols by contrasting an *ordered rotating condition* with a random one. We further tested the hypothesis that such effects on parameter estimates depend on the predictability of the stimulus location by contrasting a predictable, non-ordered, condition with a random one.

Materials and methods

Participants

Five experienced participants took part in two sessions of the experiment (1 author; age range: [24-35]; 4 females; one left-handed). All participants had normal or corrected-to-normal visual acuity. Participants gave their written informed consent to take part in the study and were financially compensated for their participation. All procedures were approved by the University College London Research Ethics Committee.

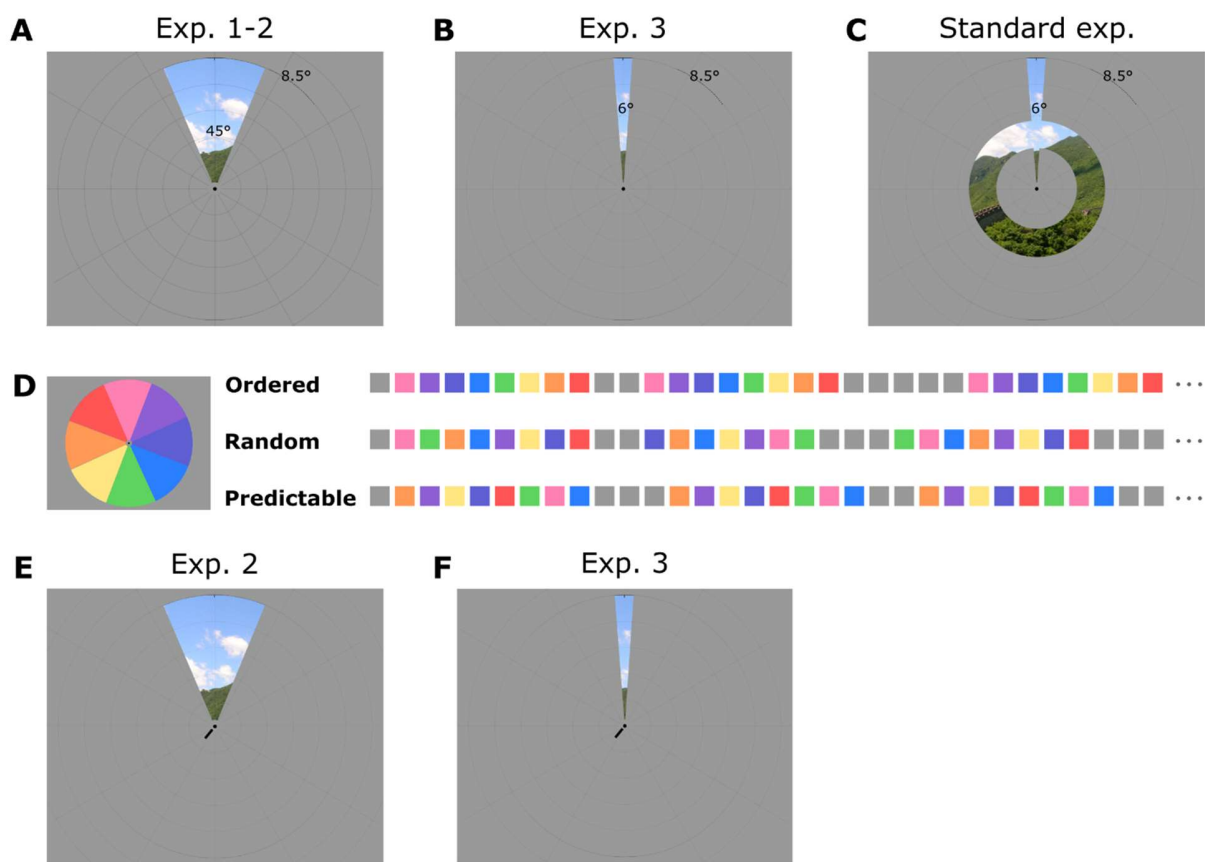### Stimuli and Task

Stimuli were presented using a custom MATLAB script (Mathworks Inc., Massachusetts, USA) and the Psychophysics Toolbox 3.8 (Brainard, 1997; Pelli, 1997). They were projected on a screen (1920 x 1080 pixels; 36.8 x 20.2 cm) at the back of the scanner bore and presented by means of a mirror mounted on the head coil at a total viewing distance of approximately 68 cm.

The mapping stimulus was a discretely moving wedge-shaped aperture that showed coloured natural images (1080 x 1080 pixels) depicting landscapes, textures, animals, faces, or pieces of writing randomly redrawn every 500 ms and presented on a mid-grey background. The wedge aperture extended from 0.38 to 8.5 degrees of visual angle (dva) in eccenticity. Each wedge aperture subtended 45° in terms of polar angle and was centred at one of eight polar angles (0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°) dividing the circle in 8 non-overlapping locations (Figure 1A). The centre of the wedges was shifted by 15° in separate runs in order to increase the spatial granularity of the mapping.

Participants were instructed to continually maintain their gaze on a central fixation dot with a diameter of 0.13° while covertly monitoring the movement of the mapping stimuli in the surround. To ensure that both requirements were met, we used a dual-detection task in which participants

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149   had to report whether the colour of the fixation dot turned red (fixation task) and whether an

150   Anderson tartan pattern was presented on the wedges (image detection task) (Moutsiana et al.,

151   2016; van Dijk et al., 2016). To aid participant's compliance with fixation requirements, a low

152   contrast polar grid (line width of 0.02°; opacity of 10.2%) composed of 10 circles (radii evenly

153   spaced between 0.13° and 15.14°) and 12 evenly spaced radial lines extended from fixation to the

154   edges of the screen was superimposed onto the grey foreground and stimuli at all time. Eye

155   movements were further monitored by means of an MRI-compatible SR Research EyeLink 1000

156   eye tracker.

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158   *Figure 1. Stimuli and mapping sequences for Experiments 1-3 and the standard 2D mapping experiment. A) Large wedge*

159   *mapping stimuli used in Experiments 1-2, B) thin wedge mapping stimulus used in Experiment 3, and C) wedge-and-ring*

160   *mapping stimulus used in the Standard experiment. D) Spatiotemporal structure for ordered, random and predictable sequences*

161   *in Experiment 1, each square represents 1 s and the colour denotes the polar angle (see colour wheel). E-F) Central cue used in*

162   *predictable and random-cue sequences in Experiment 2 and 3.*

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163   Mapping sequences

164   Three mapping conditions were presented to each participant: *ordered*, *predictable* and *random*

165   (i.e. unpredictable*)* (Figure 1D). In the ordered runs, the wedge rotated around fixation either

166   clockwise or anticlockwise starting randomly at one of the 8 locations. The same direction of

167   motion and the same starting location was maintained within each run. In the predictable runs, the

168   wedge was presented at the 8 locations according to a predefined pseudorandomized order such

169   that no adjacent locations were stimulated one after the other. The sequence started at a random

170   location in different runs, but the same starting point and the same order were maintained

171   throughout the run. Six maximally distinctive sequences were selected for each participant, three

172   for each session. In the unpredictable runs, wedges were presented at the 8 locations in

173   pseudorandom order (no adjacent locations could be presented in a row) and from a random

174   starting point. A different, randomly generated, sequence was presented in each cycle (Figure 1D).

175   For all conditions, each step of the wedge was presented for 1 s such that an entire cycle was

176   completed in 8 s. The wedge completed 16 cycles in each run. Cycles were separated by fixation

177   intervals of variable duration pseudo-randomized to range from 1 to 8 s in discrete steps of 1 s.

178   Before entering in the scanner, participants performed a 30-minute task to familiarize themselves

179   with the predictable sequences that they would encounter during the scanning session. Each

180   sequence was presented in a separate block. Each block started with a presentation of the 8-steps

181   sequence, presented for 7 times, after which we introduced a violation of the location order in the

182   sequence. The participant's task was to detect this violation of regularity and report it with a button

183   press. Each sequence was presented in 6 consecutive blocks and was presented 20 times per block

184   (9 correct sequences and 11 sequences with violations). In the scanner, a familiarization block

185   preceded each mapping run in order to familiarize participants with the sequence that they would

186   encounter during the following scanning run. Similar familiarization blocks were repeated before

187   each run of the ordered and random conditions. For both the ordered and the predictable condition,

188   participants performed a sequence violation-detection task in which they reported when a wedge

189   appeared in an unexpected location according to the learned sequence (predictable condition) or

190   the direction of motion (ordered condition). In the random condition, participants performed a 2-

191   back task in which they reported when a stimulus was presented in a location that was occupied 2

192   stimuli before.

193   Reference retinotopic maps were obtained for each participant in an additional experiment using a

194   combined wedge-and-ring aperture (Figure 1C) similar to what has been reported in previous

195   studies (Alvarez, de Haas, Clark, Rees, & Schwarzkopf, 2015; Moutsiana et al., 2016; van Dijk et

196   al., 2016). The wedge aperture extended up to 8.5 degrees of visual angle in eccentricity and

197   subtended 12° rotating either clockwise or counter-clockwise in 60 discrete steps (1 step/s, 6°

198   overlap between consecutive wedges). The ring aperture expanded or contracted in 36 logarithmic

199   steps while keeping the radius of the inner circle 56-58% of that of the outer ring (minimal radius

200   of 0.48 dva, 1 step/s, ~90% overlap between consecutive rings). The mapping stimulus showed

201   coloured natural images or phase-scrambled versions of them that changed every 500 ms and

202   appeared on a mid-grey background. The type of image (intact vs phase-scrambled) alternated

203   every 15 s. The images and the wedge-and-ring aperture were centred on a central black fixation

204   dot (diameter: 0.13 degrees in visual angle) which was superimposed onto central disk (diameter:

205   0.38 degrees in visual angle). Also, a low contrast polar grid was superimposed on the stimulus.

206   As for the previous experiments, participants performed a dual-detection task (fixation task and

207   image detection task) while maintaining fixation on the central fixation dot.

208   The mapping experiment consisted of 3 runs. The wedge-and-ring aperture was presented in four

209   blocks of 90 s (1.5 cycles of wedge rotation; 2.5 cycles of ring expansion/contraction) interleaved

210   with a 30 s blank interval. The order of aperture movement in each run was first clockwise and

211   expanding, then clockwise and contracting, anticlockwise and expanding, or anticlockwise and

212   contracting.

213   Data acquisition

214   We acquired functional and anatomical scans using a Siemens Avanto 1.5 T MRI scanner with a

215   customized 32-channel head coil located at the Birkbeck-UCL Centre for Neuroimaging. The two

216   anterior channels were removed from the front half of the coil to allow unrestricted field of view

217   leaving 30 effective channels.

218   Functional images were acquired using a T2*- weighted 2D echo-planar images multi-band

219   (Breuer et al., 2005) sequence (TR = 1 ms, TE = 55 ms, 36 slices, flip angle = 75°, acceleration =

220   4, FOV = 96 × 96 voxels) at a resolution of 2.3 mm isotropic voxels. Each functional scan consisted

221   of 222 acquisitions. Data were collected in two sessions (performed on consecutive days or one

222 day apart) of 9 runs each taking approximately 90 minutes[1]. Each condition was repeated in 3

223 separate runs in each session. The order of runs was pseudo-randomized, with all conditions

224 repeated every 3 runs. The ring-and-wedge mapping procedure was acquired in a separate session

225 using the same protocol, for a total of 3 runs and 490 volumes per run.

226 A T1-weighted anatomical magnetization-prepared rapid acquisition with gradient echo

227 (MPRAGE) image was acquired in a separate session (TR = 2730 ms, TE = 3.57 ms, 176 sagittal

228 slices, FOV = 256 × 256 voxels) at a resolution of 1 mm isotropic voxels.

229 fMRI pre-processing

230 The data were pre-processed using SPM12 (www.fil.ion.ucl.ac.uk/spm, Wellcome Centre for

231 Human Neuroimaging, London, UK). The first 10 volumes of each run were discarded to allow

232 the signal to reach equilibrium. Functional images were intensity bias-corrected, realigned to the

233 mean image of each run and then co-registered to the structural scan. All further analyses were

234 performed using custom MATLAB code. The time series for each voxel in each run were linearly

235 de-trended and z-score normalized. Finally, all runs belonging to the same condition were

236 concatenated before further analyses whereas in the wedge-and-ring standard mapping experiment,

237 the time series were averaged before the fitting analysis to increase signal to noise ratio. Functional

238 data of each participant were projected on a surface reconstruction of the grey white matter surface

239 estimated with FreeSurfer (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999) by finding

240 the voxel at the medial position between the grey-white matter boundary and the pial surface for

241 each vertex in the mesh (using custom made Matlab scripts and SamSrf toolbox). All the following

242 analyses were performed at the surface level. The same procedures were adopted for Experiment

243 2 and 3.

244 pRF estimates

245 The data from the different protocols were used to obtain independent estimates of the population

246 receptive fields (pRFs) using a custom MATLAB toolbox for pRF analysis (SamSrf v5.84,

247 https://doi.org/10.6084/m9.figshare.1344765.v24). For all mapping sequences, we combined a

248 binary aperture describing the position of the mapping stimuli within each scanning volume with

249 a model of the underlying neuronal population and convolved this with a canonical haemodynamic

250 response function (HRF) to predict the BOLD signal in each experimental condition. For the

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[1] One participant performed 15 runs in one single session in Experiment 1.

251   standard wedge and ring mapping sequence, the binary aperture was a two-dimensional mask

252   (100x100) corresponding to the stimulus location on the screen at each time point. For the main

253   experiment, the binary aperture was a vector mask (1x360) indicating the polar angle coordinates

254   corresponding to the mapping stimulus at each time point.

255   For the standard wedge and ring mapping sequence, we estimated the position and size of pRFs

256   using a two-dimensional Gaussian function (Dumoulin & Wandell, 2008). For the polar mapping

257   experiments, we modelled pRFs using a von Mises distribution, with μ indicating the preferred

258   polar angle of the voxel and k corresponding to the concentration of the response (for clarity k

259   values were transformed into full width half maximum (FWHM) as an indicator of the spread of

260   the response of each voxel). We used a coarse-to-fine approach to determine the pRF parameters

261   to obtain the best possible fit of the predicted time series with the observed data (Alvarez et al.,

262   2015; Dumoulin & Wandell, 2008; Moutsiana et al., 2016; van Dijk et al., 2016). The final fine

263   fitting also included a β parameter for the response amplitude.

264   Analyses

265   We only analysed the fitted parameters of those vertices for which we obtained realistic estimates

266   (k>0) and that had a goodness of fit, R^2, higher than a critical value based on a fixed p-value (p =

267   10^{-8}). This corresponds to $R^2>0.026$ [2] in Experiment 1, and $R^2>0.067$ in the wedge-and-ring

268   experiment depending on the different degrees of freedom in the three experiments[3].

269   The pRF estimated coordinates from the standard wedge and ring mapping experiment were used

270   to compute polar angle and eccentricity. Using the Delineation toolbox in SamSrf, we manually

271   delineated the regions of interest using mirror reversals in the polar angle map, and guided by the

272   eccentricity and field-sign map (Sereno, McDonald, & Allman, 1994). The region of interests

273   included in our analyses were V1, V2, V3, V3A and V4. We performed all the following analyses

274   separately for each visual ROI in each individual participant. Given the small number of

275   participants, we did not report group statistics in the main text, but we summarized the results for

276   single subject statistics instead.

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[2] The R^2 threshold was adjusted to 0.035 for the participant that performed a smaller number of runs in Experiment 1.

[3] Here we are not accounting for the degrees of freedom in the pRF model (the p-value would only be marginally different) but the purpose of this procedure is simply to define an objective threshold for the data rather than accurately estimating p-values.

277   We compared the quality of the fits across the different spatiotemporal sequences. We compared
278   the number of responsive vertices and the median goodness of fit for each individual by means of
279   repeated paired t-tests and Wilcoxon tests. We also used a correlation analyses to evaluate the
280   correspondence between the observed time series for each condition and the predicted response
281   given the stimulus location and the parameter estimates for each vertex obtained with each of the
282   mapping protocols, convolved with an HRF. To further explore the coherence of the maps obtained
283   with different mapping conditions, we computed the vertex-wise circular correlation of polar angle
284   estimates and the Pearson correlation of FWHM and beta estimates between conditions, separately
285   for each visual ROI and participant. Because vertices within a ROI are not statistically
286   independent, we calculated the inter-correlation between the time series of all ROI vertices and
287   used this information to correct the degrees of freedom of the correlation. Specifically, we
288   calculated all unique pair-wise correlations between vertices (note that we treated pairs of vertices
289   that were negatively correlated as independent, i.e. $r = 0$). We then calculated a weight for each
290   vertex by subtracting these correlations from 1 and averaging the values for all pair-wise
291   comparisons of a given vertex. Thus, in theory, if the time series of all vertices were completely
292   independent from one another, each vertex would be weighted as 1. Conversely, if all vertices were
293   identical, they would all be weighted as 0. The sum across these weights plus 1 is therefore a
294   weighted estimate of the sample size which we used to determine the degrees of freedom.

295   Moreover, we correlated the observed time courses for each condition with the predicted time
296   course given the estimated pRF parameters for each vertex in each experimental condition.
297   Finally, we compared the mean FWHM across conditions and ROIs using paired t-tests at the
298   subject level (with degrees of freedom corrected for inter-correlation between time series as
299   described above). In these analyses, we averaged FWHM across vertices encompassing different
300   eccentricities, as our mapping stimulus did not allow differentiating responses at different
301   eccentricities (i.e. each wedge had a fixed radius that covered the entire visual field mapped).

302   Results

303   We obtained reliable polar angle maps with all mapping conditions for our ROIs (Figure 2).
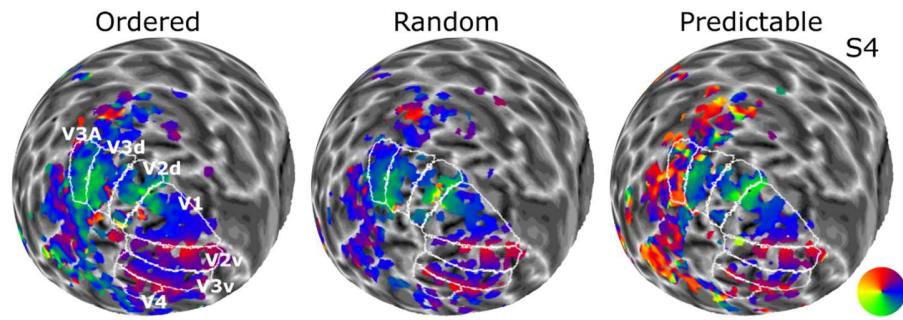
Figure 2. Smoothed polar angle maps for all conditions - ordered, random and predictable - in Experiment 1. In this and the following figures, images display an inflated spherical model of the left hemisphere of participant 4 (S4).

Ordered sequences provided better fits and a larger proportion of responsive vertices than the other mapping sequences in all ROIs (Mean of median R^2 across ROIs: M_{ord} = .10, M_{pred} = .08, M_{rnd} = .08; Mean of responsive vertices across ROIs: M_{ord} = 35%, M_{pred} = 25%, M_{rnd} = 28%). Moreover, we observed better fits for higher visual areas (Figure S 1A, D). The relatively low goodness of fit obtained with this paradigm is not surprising given the high number of degrees of freedom in our paradigm (due to concatenated time series rather than averaging experimental runs) and the simplified model used for fitting. Importantly, all vertices considered for comparisons provided a fitting that met our fixed p-value criterion of 10^{-8} in all the mapping conditions. Interestingly, parameter estimates obtained with different mapping sequences performed similarly well in predicting the observed time series for all mapping protocols, with generally more robust predictions of the ordered sequences regardless of the mapping protocol used for the estimates (Figure S 1A). Consistently, correlation analyses of model fitting results (polar angle, FWHM, beta, and R^2) revealed substantial consistency across different mapping conditions in all experiments and all visual areas tested. We observed high significant vertex-wise correlation between R^2 ($M_{ord\text{-}rand}$ = .79, $M_{ord\text{-}pred}$ = .77, $M_{rand\text{-}pred}$ = .82; Figure 3A) in different conditions for all participants and ROIs (p<.05, Bonferroni corrected for multiple comparisons). The polar angle estimates were highly robust across conditions but showed a decrease in coherence moving up in the visual hierarchy for the predictable condition ($M_{ord\text{-}rand}$= .86, $M_{ord\text{-}pred}$= .56, $M_{rand\text{-}pred}$= .68; Figure 3B).
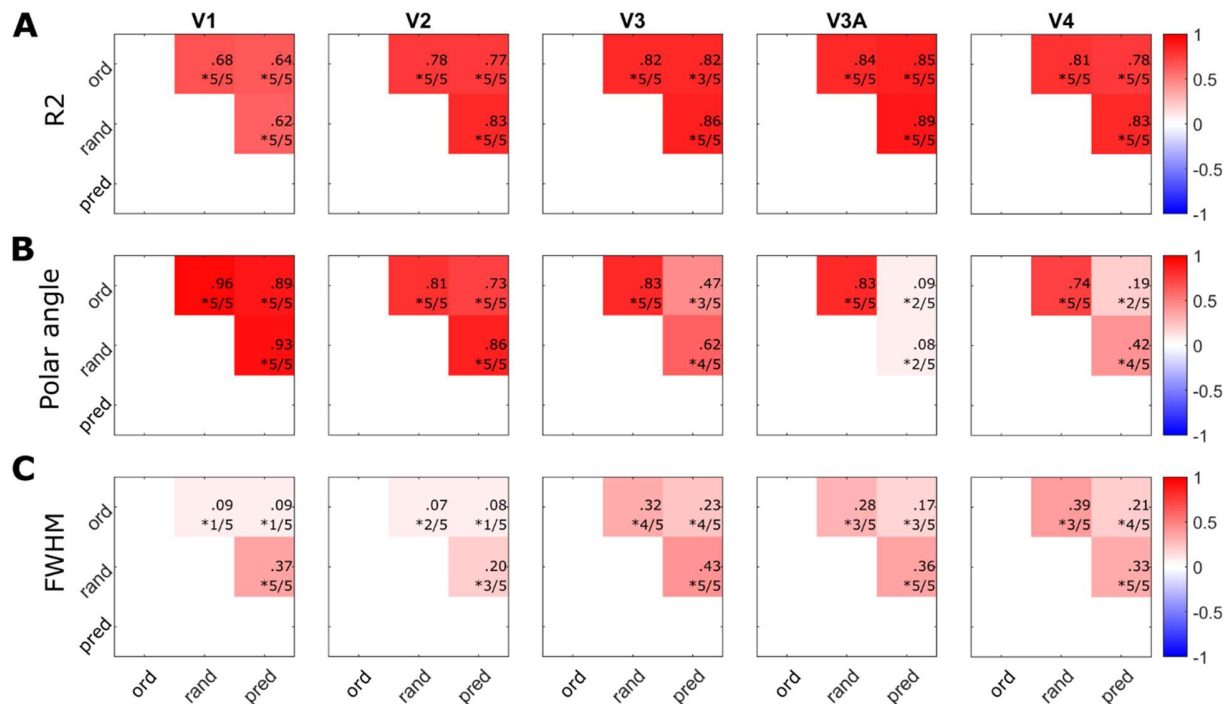
Figure 3. Group mean correlation matrices for A) the model goodness of fit (R^2), B) polar angle estimates), and C) FWHM estimates in Experiment 1. Inset numbers (in this and the following figures) in each cell of the correlation matrix indicate the value of the average correlation and the proportion of participants that showed a significant correlation for each pair of conditions.

We observed positive but substantially weaker correlations for FWHM estimated, particularly in lower visual areas, V1-V2 ($M_{ord-rand}$ = .24, $M_{ord-pred}$ = .17, $M_{rand-pred}$ = .35; Figure 3C).

We further explored potential biases and differences across mapping conditions and ROIs. As expected, FWHM estimates increased in the visual hierarchy. Interestingly, FWHM was also systematically influenced by the mapping sequence and a general pattern emerges for all visual areas (with the exception of V1 that shows noisier results) with results highly consistent across participants (Figure 4; significant results are reported for p<.05, Bonferroni corrected for multiple comparisons). The ordered sequence lead to significantly smaller FWHM estimates than the random sequence for most of the participants and ROIs (Figure 4B). We found similar differences between ordered and predictable sequences, although one participant showed a significant difference in the opposite direction. Interestingly, we measured smaller FWHM for predictable than random sequences (results are clearer for V2, V3 and V4).

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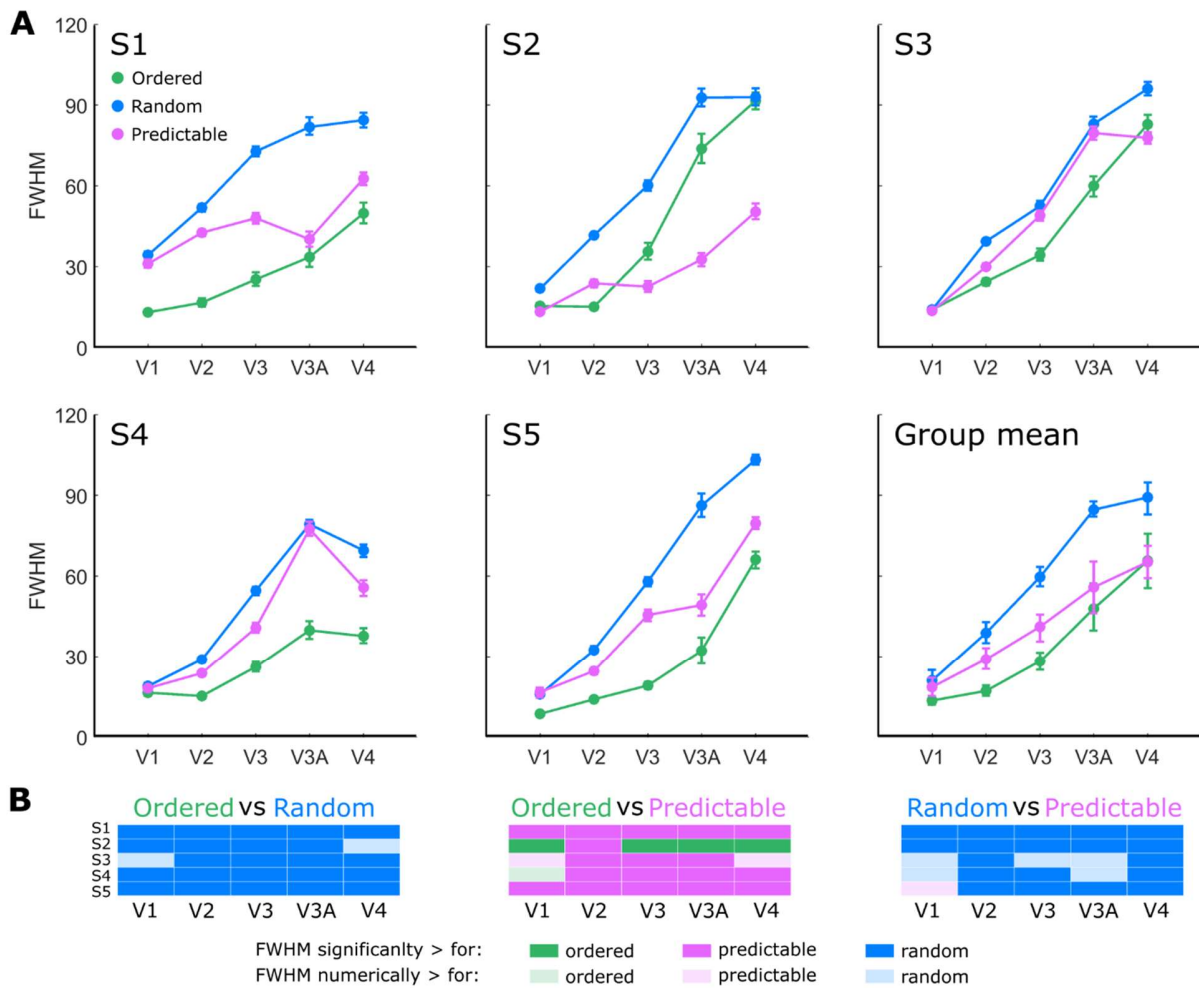
Figure 4. Polar angle tuning width estimates in Experiment 1 (measured as Full-Width Half-Maximum). A) Individual and group mean FWHM estimates for different mapping sequences and visual areas. In this and the following figures, error bars in both the individual and group plots represent bootstrapped 95% confidence intervals. B) Visualisation of single subject statistics (p<.05 corrected for multiple comparisons).

Experiment 2

Experiment 1 revealed systematic differences in polar angle tuning functions estimated with different mapping protocols. This suggests that predictability might influence the tuning response of population of neurons in visual cortex. However, the predictability of our mapping sequences depended on the repetition of fixed spatiotemporal structure throughout each run. Such idiosyncrasies in the predictable sequences could have been responsible for relatively narrow

354   tuning width estimates (Figure 4) and the poorer agreement in polar angle estimates of this

355   sequence with the ordered and the random one (Figure 3B).

356   To address whether the fixed spatiotemporal structure of the predictable sequence was responsible

357   for the observed results, we repeated Experiment 1, but this time creating a predictable sequence

358   that was structurally indistinguishable from the random one. Rather than using a repeated

359   sequence, we rendered the sequence predictable by the use of a small visual cue. We then compared

360   the tuning width response of this sequence with the random, non-predictable one.

361   ## Materials and methods

362   ### Participants

363   Four of the original subjects took part in the two sessions of Experiment 2 (one author; age range:

364   [24-35]; 3 females). All participants had normal or corrected-to-normal visual acuity and gave

365   their written informed consent to participate to the experiment as in Experiment 1.

366   ### Stimuli and Mapping sequences

367   Experiment 2 was set up with the same apparatus and mapping stimuli used in Experiment 1

368   (Figure 1A). We compared four mapping sequences - ordered, predictable and two random ones.

369   Crucially, we changed how we induced the predictability of the wedge location in the predictable

370   condition. The predictable and random sequences were generated using the same algorithm, i.e.

371   wedges were presented at different locations in pseudorandom order with no adjacent locations

372   presented in a row. In contrast to Experiment 1, we generated a different sequence in each cycle

373   thus completely matching the spatiotemporal structure of random and predictable sequences. We

374   maintained the difference in predictability of the wedge locations by means of a centrally presented

375   oriented line that cued the location of the wedges (Figure 1E). The cue (0.33 x 0.07 degrees in

376   visual angle) extended from the centre of the screen. It appeared 200 ms before the onset of each

377   wedge stimulus and remained on the screen for 200 ms (Figure 1C). In the *ordered* and the

378   *predictable* conditions, the cue pointed towards the centre of the upcoming wedge. The two

379   random conditions were both unpredictable but differed for the presence or absence of the central

380   cue. In the random condition with non-predictive cue (*random-cue*), the cue pointed to the location

381   of the previous wedge. In the random condition without cue (*random-no cue*), no cue was

382   presented. Thus, neither of the random conditions contained any information about the location of

383   the upcoming wedge.

384   For all conditions, each step of the wedge was presented for 1 s such that an entire cycle was

385   completed in 8 s. Cycles were separated by fixation intervals of variable duration ranging from 1

386   to 8 s in steps of 1 s. Each functional scan consisted of 303 acquisitions. Data were collected in

387   two sessions (performed on consecutive days or one day apart) of 12 runs each taking

388   approximately 90 minutes. Each condition was repeated in 3 separate runs in each session. All

389   conditions were presented in randomized order every 4 runs.

390   Analyses

391   As in Experiment 1, we only analysed the fitted parameters of those vertices for which we obtained

392   realistic estimates (k>0) and that had a goodness of fit, R^2, higher than a critical value based on a

393   fixed p-value (p = 10^{-8}). This corresponds to $R^2>0.019$ in Experiment 2.

394   Results

395   Experiment 2 mostly replicated the results of Experiment 1 with even clearer polar angle maps

396   (Figure 5) and higher consistencies between parameter estimates (Figure 6), possibly due to the

397   higher number of volumes collected.
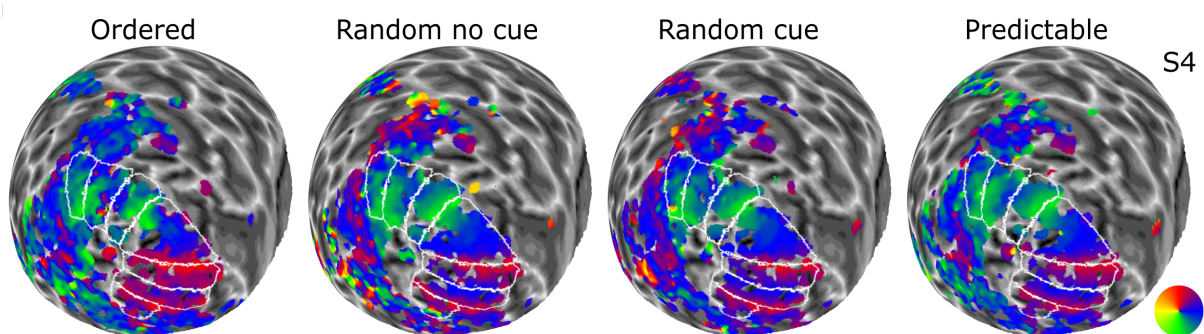
399   *Figure 5. Smoothed polar angle maps for all conditions - ordered, random with or without uninformative cue, and predictable - in*
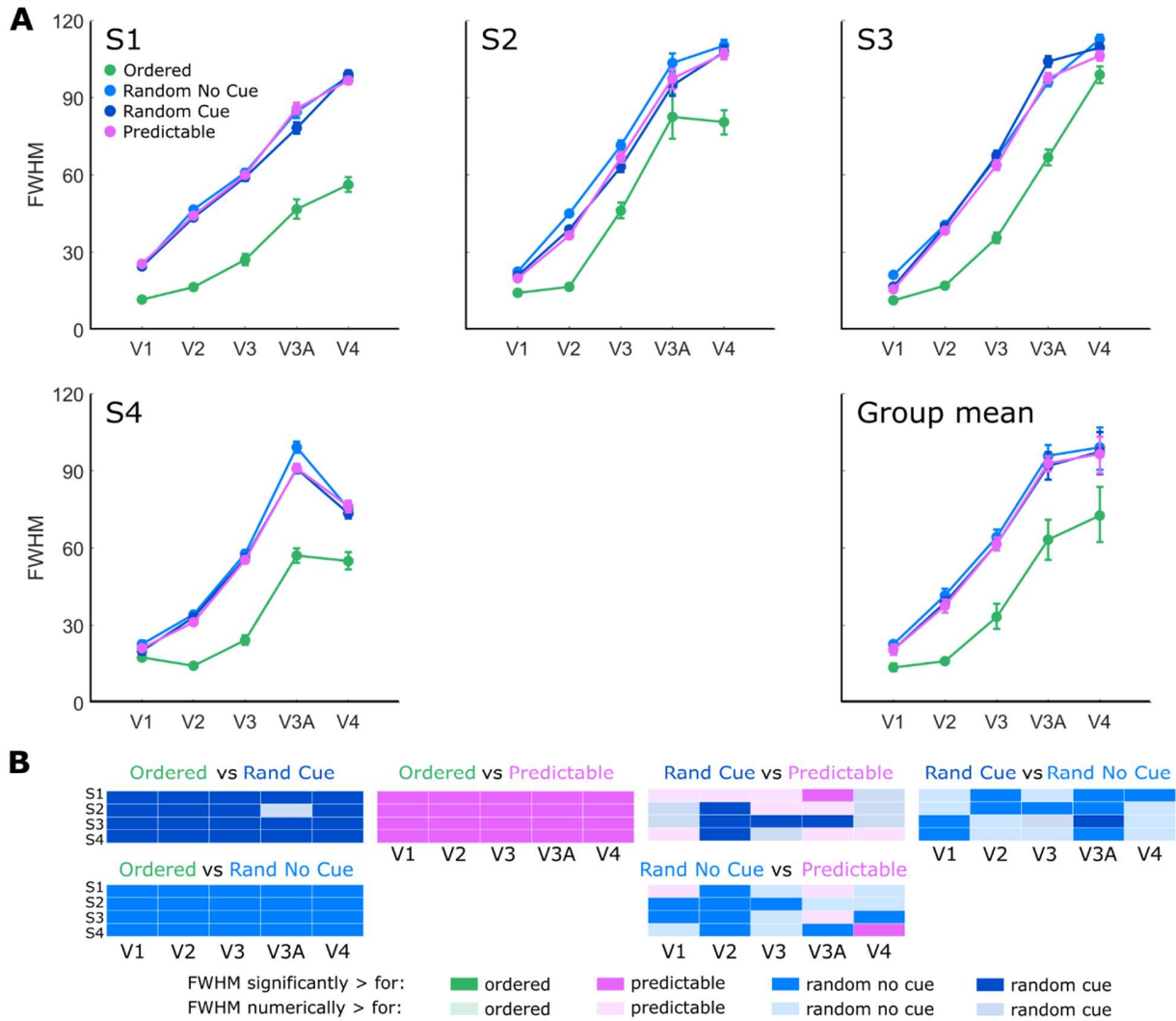
400   *Experiment 2.*

401   Ordered sequences provided better fits to the data than predictable and random sequences (Figure

402   S 1B, E; Mean of median R^2 across ROIs: M_{ord} = .09, M_{pred} = .08, M_{randNC} = .08, M_{randC} = .08; Mean

403   of responsive vertices across ROIs: M_{ord} = 43%, M_{pred} = 41%, M_{randC} = 40%, M_{randNC} = 37%).

404   However, our analyses confirmed that the parameters estimated in the different conditions

405   performed equally well in predicting the time series data (Figure S 2B).

16
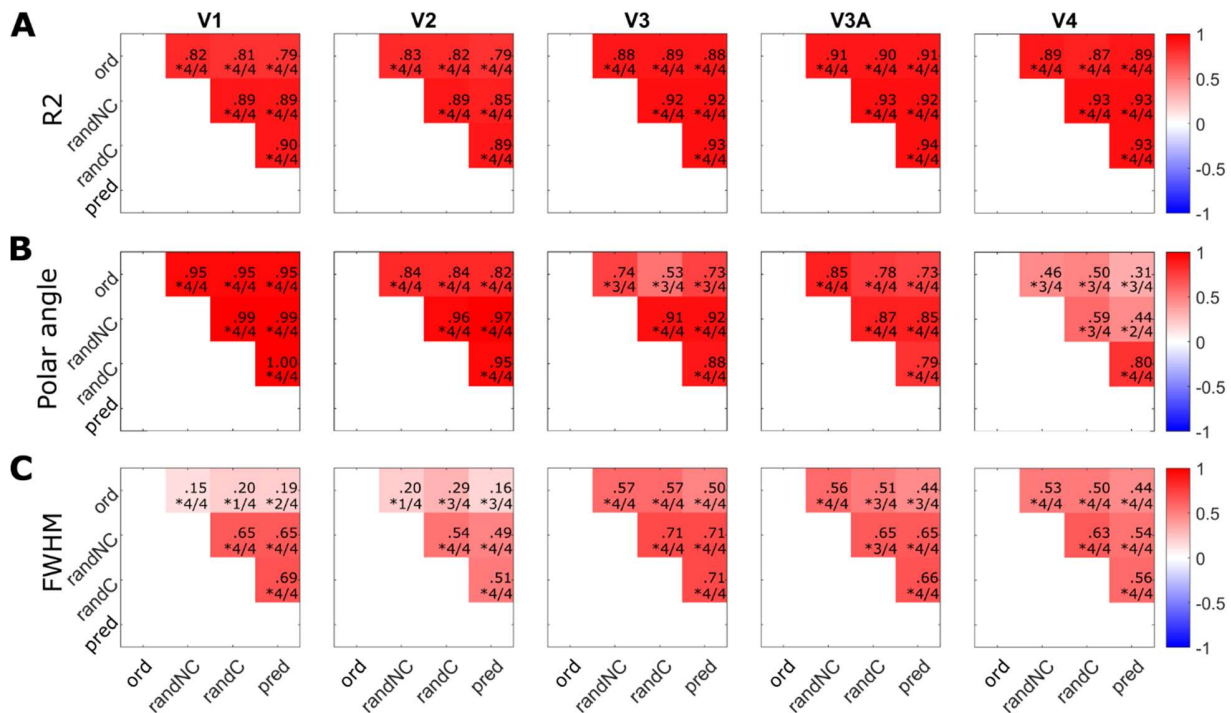
Figure 6. Mean correlation matrices for A) goodness of fit (R^2). B) polar angle, and C) FWHM estimates in Experiment 2.

We also replicated differences in FWHM estimates with different sequence structures with ordered sequences leading to systematically smaller FWHM estimates than random and predictable sequences ($p < .05$ corrected, for all participants and ROIs but one comparison for S2 V3A as illustrated in Figure 7**Error! Reference source not found.**). Importantly, we did not observe any systematic differences between predictable and random sequences with the exception of V2, where FWHM were systematically smaller for predictable than random sequences as also shown in Experiment 1 (significant difference for all participants in the comparison with the random-no cue condition and with all participants but one in the random-cue condition).

17

Figure 7. Polar angle tuning width estimates in Experiment 2. A) Individual and group mean FWHM estimates. B) Visualisation of single subject statistics (p<.05 corrected for multiple comparisons).

Experiment 3

Experiment 2 suggested that the spatiotemporal structure of the mapping sequence, rather than its predictability is responsible for the differences in FWHM estimates. The finding that ordered sequences yielded narrower tuning widths than random sequences in both Experiment 1 and 2 contrasts with previous studies. A comparison of orderly moving bars and multifocal stimuli revealed the opposite pattern of results, with the largest pRF estimates obtained with ordered sequences (Binda et al., 2013). However, it is not clear whether pRF size estimates might have

18

427 been affected by surround suppression of response in the multifocal stimuli (Pihlaja, Henriksson,

428 James, & Vanni, 2008). Moreover, our results might be affected by the short mapping sequences

429 we adopted. To address this hypothesis, we replicated Experiment 2 with the same mapping

430 conditions and the same participants, but we varied the size of the mapping stimulus as well as the

431 duration of the mapping cycle.

Materials and methods

Participants

434 The same four participants (including one author) that took part in Experiment 1 and 2 participated

435 also in both sessions of Experiment 3. All participants gave their written informed consent to

436 participate to the experiment.

Stimuli and Mapping sequences

438 The mapping stimulus in Experiment 3 was a discretely moving wedge aperture subtending 6° and

439 dividing the circle in 60 non-overlapping locations, no shifts were introduced across runs (Figure

440 1B). The mapping sequences used in Experiment 3 were generated in the same way as those in

441 Experiment 2 resulting in four experimental conditions: *ordered*, *predictable*, *random-no cue*, and

442 *random-no cue* (Figure 1F). The distinctive difference between Experiment 2 and 3 is only the

443 aperture size and, consequently, the duration of the mapping cycle. For all conditions, each step of

444 the wedge was presented for 1 s such that an entire cycle was completed in 60 seconds (60 wedges

445 of 6°, 4 cycles). Cycles were separated by fixation intervals of variable duration ranging from 1 to

446 8 s in steps of 1 s. Each functional scan consisted of 295 acquisitions whilst other scanning details

447 remained identical to Experiment 2.

Analyses

449 As in the previous experiments, we only analysed the fitted parameters of those vertices with $k>0$

450 and goodness of fit, $R^2>0.019$ (based on fixed p-value $p = 10^{-8}$).

Results

452 Parameter estimates were consistent across mapping sequences (Figure 8, Figure 9; Figure S 2C).
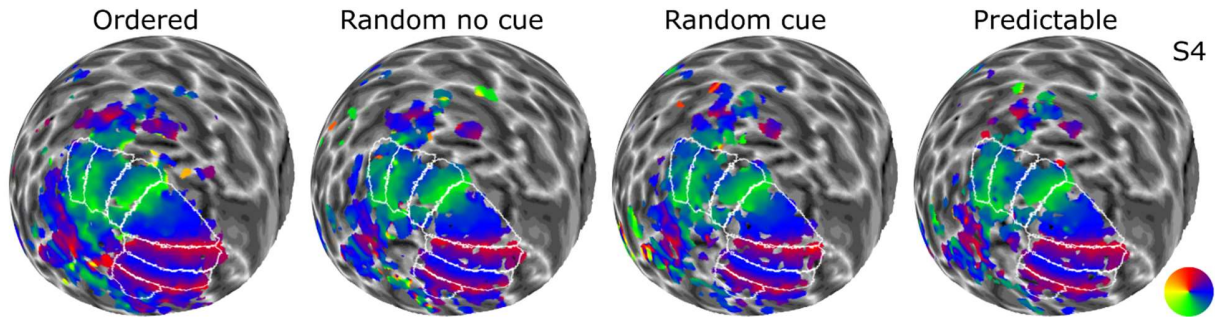
453

454 *Figure 8. Smoothed polar angle maps for all conditions - ordered, random with or without uninformative cue, and predictable - in*
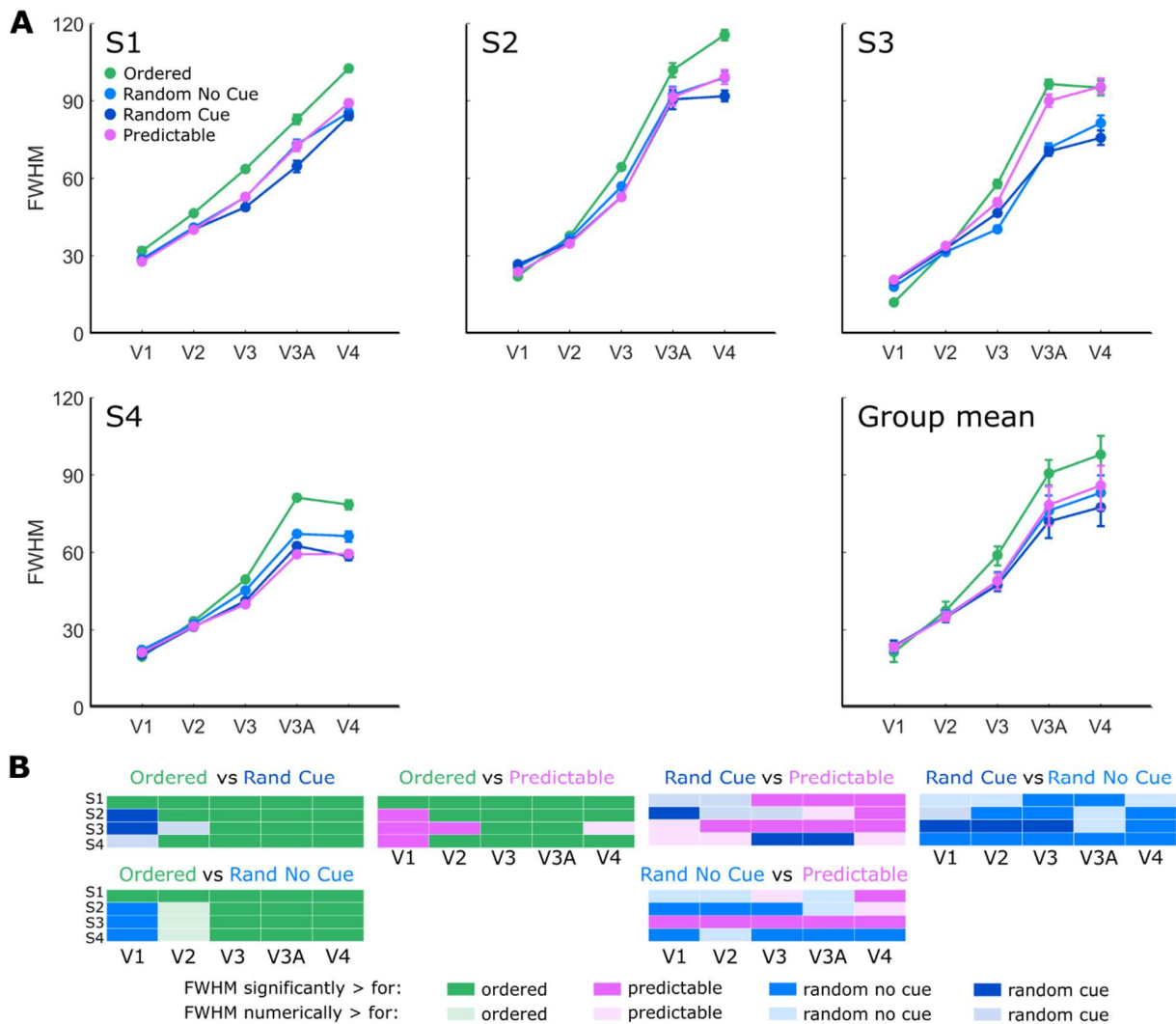
455 *Experiment 3.*

456 Ordered sequences provided much better fits to the data than predictable and random sequences

457 (Mean of of median R^2: M_{ord} = .14, M_{pred} = .06, M_{randNC} = .06, M_{randC} = .06; Mean of responsive

458 vertices across ROIs: M_{ord} = 61%, M_{pred} = 37%, M_{randC} = 38%, M_{randNC} = 38%; Figure S 1C, F).

459 However, the parameters estimated in the different conditions performed equally well in predicting

460 the time series data and they all yielded the best results when predicting the ordered sequence

461 (Figure S 2C).
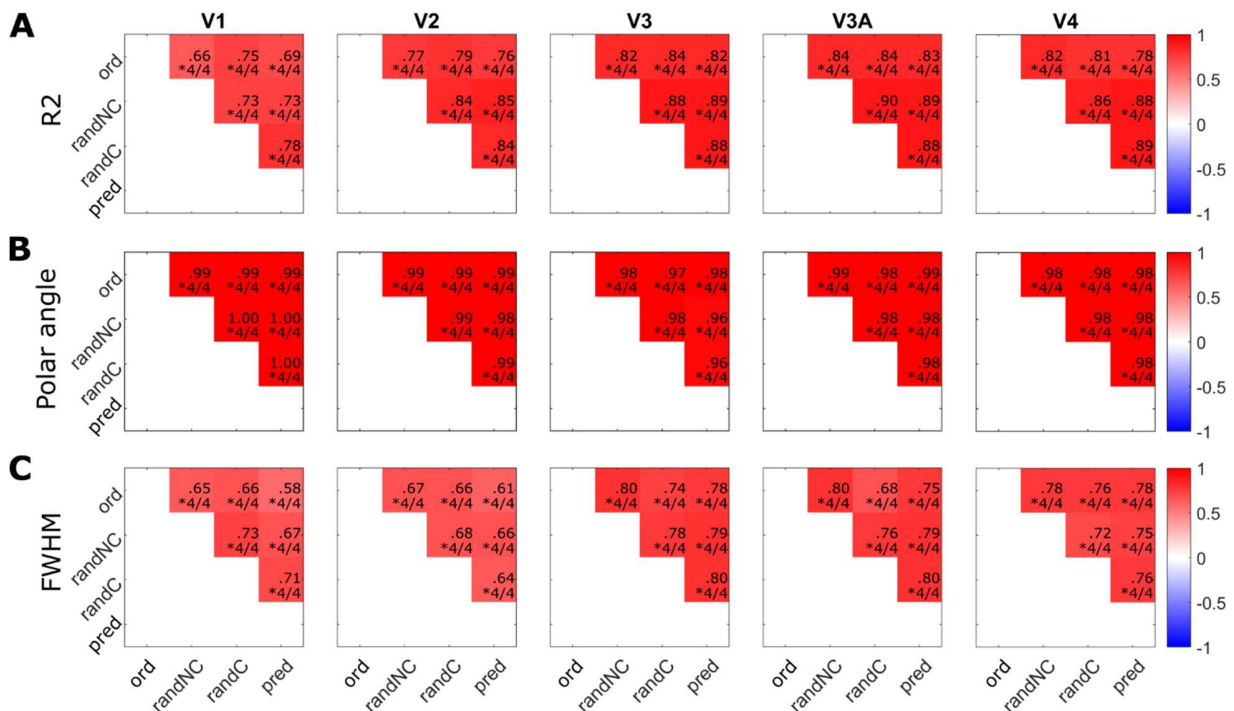
462

463 *Figure 9 Mean correlation matrices for A) goodness of fit (R2). B) polar angle, and C) FWHM estimates in Experiment 3.*

464 Experiment 3 produced an interesting inversion of the pattern of results in terms of FWHM

465 estimates (Figure 10) compared to the previous experiments. Although there was no consistent

20

466   pattern in the contrast between predictable and random sequences, FWHM estimates were

467   systematically larger for ordered than random or predictable sequences for V3, V3A and V4.

468   Similar results were found for V2 but with less consistent results across participants. Results for

469   V1 were less clear but seem to suggest the opposite: FWHM were smaller for estimates obtained

470   with an ordered rather than a random or predictable sequence.

471

472   *Figure 10. Polar angle tuning width estimates in Experiment 3. A) Individual and group mean FWHM estimates. B) Visualisation*

473   *of single subject statistics (p<.05 corrected for multiple comparisons).*

Simulations

475   With the following simulations, we addressed the hypothesis that the discrepancies in tuning width

476   observed for the different mapping sequences in the previous experiments were caused by the

477   spatiotemporal properties of the haemodynamic response (Aquino, Schira, Robinson, Drysdale, &

478   Breakspear, 2012; Kriegeskorte, Cusack, & Bandettini, 2010). To test this possibility, we

479   simulated the BOLD response for Experiments 1 and 3 using the stimBOLD toolbox

480   (https://github.com/KevinAquino/stimBOLD, Aquino, Lacy, Robinson, & Schira, 2015). This

481   toolbox takes a visual input, predicts the cortical neural response that it evokes in early visual

482   cortex (areas V1-V3) and simulates the BOLD response taking into account the poroelastic

483   properties of the brain tissue (Aquino, Robinson, Schira, & Breakspear, 2014; Aquino et al., 2012)

484

485   ## Materials and methods

486   ### Stimuli and mapping

487   We used stimBOLD to simulate the BOLD response in visual areas V1-V3 for the left hemisphere

488   of FreeSurfer average brain (fsaverage) (Benson et al., 2012; Dale et al., 1999; Fischl et al., 1999).

489   We simulated the responses for all the conditions that differed in terms of spatiotemporal structure

490   and stimulus size in the previous experiments. In particular, we selected the ordered, random, and

491   predictable conditions in Experiment 1 – Simulation A – and the ordered and random conditions

492   of Experiment 3 – Simulation B (in both cases we employed the mapping sequences used for

493   participant 4).

494   The mapping stimulus had the same physical properties adopted in our empirical experiments (max

495   eccentricity = 8.5 dva; wedge size of 45° for Experiment 1 and 6° for Experiment 3). Each location

496   of the visual field was stimulated for 1s, before moving to the next location in the sequence. Two

497   images, selected from the original dataset of natural pictures, alternated every 500 ms.

498   Six runs for each condition were simulated separately, then Gaussian noise was added to the signal.

499   Gaussian noise was adjusted in order to produce approximately the same signal-to-noise ratio

500   (SNR) across Simulation A and B (Simulation A, SNR_{ord} = .21; SNR_{pred} = .17; SNR_{ran} = .17.

501   Simulation B: SNR_{ord} = .21; SNR_{ran} = .11. We computed the SNR as the ratio between the standard

502   deviation of the signal and the standard deviation of the residuals). The following analyses were

503   performed for the simulated data with and without Gaussian noise.

504

505   ### Analyses

506   The signal was z-score normalized and the runs concatenated before modelling the pRF profiles

507   following the same approach used for the empirical data. We focused our analyses on the

508 comparison of FWHM in the different conditions for Simulation A and B considering only those
509 vertices with goodness of fit higher than a critical value based on a fixed p-value (p = 10^{-8}, $R^2 >$
510 0.026 for Simulation A and $R^2 > 0.019$ for simulation B). We averaged FWHM across
511 eccentricities and ROIs (V1, V2, and V3) separately for each condition and tested their difference
512 with paired t-tests (degrees of freedom corrected for time series correlation).
513

Results

515 The results qualitatively replicated the difference across conditions observed in the empirical data
516 (Figure 11). In Simulation A, the ordered condition resulted in significantly lower estimates of
517 FWHM than the random condition (V1-V3$_{ord-rand}$: t(196.8) = -7.05, p < .001). The predictable
518 condition lead to intermediate results (V1-V3$_{ord-pred}$: t(205.8) = -2.98, p = .003; V1-V3$_{rand-pred}$:
519 t(200.0) = 2.97, p = .003). Crucially, the pattern of results reversed for Simulation B with the
520 ordered condition leading to the significantly higher FWHM estimates than the random one (V1-
521 V3$_{ord-rand}$: t(263.7) = 5.04, p < .001). The analyses of the predicted BOLD response without
522 addition of Gaussian noise produces an inversion of the pattern of results for the ordered and
523 predictable conditions in Simulation A (V1-V3$_{ord-pred}$: t(618.0) = 10.72, p < .001; V1-V3$_{rand-pred}$:
524 t(593.0) = 10.72, p < .001). However, the crucial difference between ordered and random
525 conditions is replicated in both simulations (Simulation A. V1-V3$_{ord-rand}$: t(569.8) = -5.06, p < .001.
526 Simulation B. V1-V3$_{ord-rand}$: t(1150.7) = 5.51, p < .001) (Figure 11).
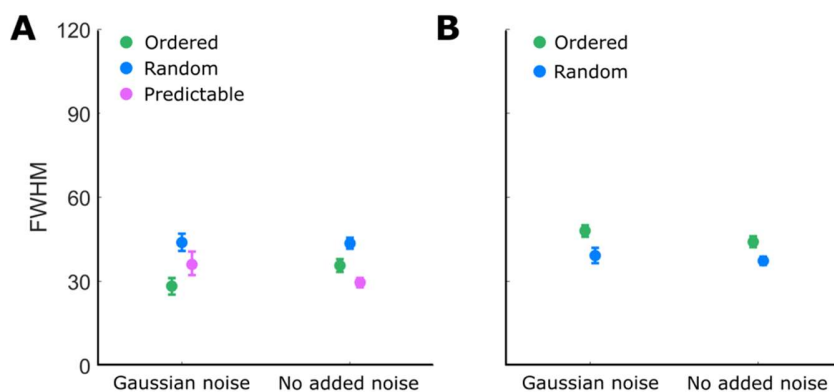
527
528 *Figure 11. Polar angle tuning width estimates for simulated BOLD responses with and without added Gaussian noise. Error bars*
529 *in both the individual and group plots represent bootstrapped 95% confidence interval. A) Simulation A replicating the sequence*
530 *structure and stimulus properties of Experiment 1. B) Simulation B replicating the sequence structure and stimulus properties of*
531 *Experiment 3.*

532

Discussion

534   In this series of experiments, we investigated the reliability and biases of pRF modelling while
535   disambiguating the impact of predictability and spatiotemporal regularities when mapping the
536   visual cortex. We adopted a modified version of the pRF modelling approach (Dumoulin &
537   Wandell, 2008) to estimate the polar angle preference of neural populations in visual cortex and
538   designed mapping sequences characterized by different spatiotemporal structure and different
539   duration.

540   As reported in previous studies, polar angle estimates were robust across mapping sequences while
541   estimates of pRF size were more volatile (van Dijk et al., 2016). Despite their general robustness,
542   the polar angle estimates in visual areas with larger receptive fields (V3, V3A, V4) were more
543   sensitive to the structure of the mapping sequence when short mapping cycles were adopted. This
544   was particularly evident for the predictable condition in Experiment 1 in which the same short
545   sequence was repeated throughout one run introducing systematic deviations in the measured polar
546   angle estimates.

547   In all experiments, we observed striking differences in pRF size for ordered and random sequences
548   across the visual areas tested. Interestingly, in Experiment 1 we observed the narrowest tuning
549   widths for ordered mapping sequences, intermediate results for the regular and predictable
550   sequences and the widest tuning width for random sequences. These results are in contrast with
551   previous reports of larger pRF size estimates for ordered sequences (Binda et al., 2013). To test
552   whether such results were a consequence of the anticipation of the attended stimulus, we ran
553   Experiments 2 and 3 where we used a spatial cue to orient attention and matched the spatiotemporal
554   properties of predictable and random sequences. We replicated the findings for ordered and
555   random sequences only and only when a short mapping cycle was employed while the opposite
556   pattern of results emerged for slower designs. Such results argue against an impact of expectations
557   in pRF estimates and suggest that other factors may contribute to these changes in tuning width.

558   One possibility is that fast-paced designs are more susceptible to nonlinear spatiotemporal
559   interactions of responses. For example, centre-surround suppression mechanisms have been
560   suggested to modulate response amplitude when multiple stimuli are presented during mapping,
561   as happens in multi-focal designs (Pihlaja et al., 2008). Alternatively, the rapid stimulation of

562 adjacent regions might induce hemodynamic stealing (Harel, Lee, Nagaoka, Kim, & Kim, 2002),

563 or induce adaptation phenomena (Krekelberg, Boynton, & van Wezel, 2006) hence reduced BOLD

564 signal. Such phenomena could influence pRF size estimates with greater impact on ordered

565 protocols. While these possibilities are intriguing, they cannot easily explain the inversion of the

566 pattern of results observed in our last experiment. Finally, it is possible that active changes in

567 cortical vasculature might be responsible for spatiotemporal nonlinearities in the BOLD response

568 and significantly affect the pRF estimates, particularly with small voxel sizes (Aquino et al., 2012;

569 Kriegeskorte et al., 2010). Our simulations found general support for the last hypothesis indicating

570 a possible mechanism by which the interplay of stimulus properties and mapping sequence can

571 have a measurable impact of pRF estimates.

572 In our study we did not find any clear evidence that the predictability of stimulus location can

573 significantly bias polar angle or tuning width estimates. This result contradicts previous studies

574 that showed attention can cause both a shift of the preferred location towards the attended location

575 and an increase in pRF size (Kay et al., 2015; Klein et al., 2014; Sheremata & Silver, 2015; van

576 Es et al., 2018; Vo et al., 2017). Such modulation had initially reported only been in the ventral

577 cortex, higher up in the visual cortex (Kay et al., 2015) while more recent evidence suggest that

578 both feature-based and spatial-based spatial attention can induce significant shifts in the response

579 of neurons in areas as early as V1-V3 (van Es et al., 2018). It has been suggested that these changes

580 are functional to increase the precision of the representation of the target at the attended location

581 (Kay et al., 2015). While our design was not tailored to detect systematic changes in polar angle

582 preferences, we hypothesized that the predictability of the mapping sequence would affect the

583 tuning of neuronal responses. The discrepancy between our results and recent observations of

584 attentional effects can be explained by a difference in task requirements among the studies. All

585 former studies manipulated the focus of attention by varying the location at which participants

586 were performing a perceptual task, either at fixation or on the mapping stimulus (Kay et al., 2015;

587 Sheremata & Silver, 2015; van Es et al., 2018). Such demanding tasks required a redistribution of

588 resources at the attended location. On the contrary, in our experiments, our task did not require a

589 fine discrimination and the predictability of stimulus location was not strategically relevant for

590 performing the task. Thus, expectations alone may not dynamically change pRF properties in early

591 visual cortex to a significant extent, as long as there is no computational requirement for that.

25

592   Irrespective of the specific sequence, the fitting results described in the current study produced

593   weaker fits than standard mapping approaches (Dumoulin & Wandell, 2008). Several reasons

594   could contribute to these results. First, R^2 depends considerably on the degrees of freedom. In our

595   experiments, we concatenated the BOLD response in separate runs of the same condition leading

596   to a large number of time points per condition (up to 1818 in Experiment 2) massively increasing

597   the degrees of freedom and generally reducing R^2 for at statistical significance levels equivalent to

598   other studies. Second, in order to facilitate learning of the predictable sequences, we designed

599   protocols with unusually short cycles in Experiment 1 while long cycles but thin mapping stimuli

600   were employed in the last study. Despite these limitations, we obtained reliable maps in all

601   conditions (Figure 2, Figure 5, Figure 8).

602   Our study shows that pRF estimates are susceptible to the spatiotemporal properties of the mapping

603   sequence. In particular, ordered and random mapping protocols show different susceptibility to

604   other design choices such as stimulus type and duration of the mapping cycle and can produce

605   significantly different pRF results. Finally, it is worth noting that while ordered sequences are

606   typically preferred for their higher goodness of fit, this is not a guarantee of their robustness. More

607   specifically, the pRF estimates obtained with different sequences, both ordered and random,

608   performed comparably well in predicting the response to different mapping stimuli. To conclude,

609   depending on other design constraints, one should consider which protocol is more suitable for the

610   experimental purposes.

611

Acknowledgments

615

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Supplementary Materials

Control analyses and results

In all three experiments, to ensure consistency in fixation stability and task engagement across conditions, we measured target detection accuracy in the dual-task across conditions. Moreover, we measured the mean absolute deviation of eye position from fixation along the x and y axes in degrees of visual angle (dva).

In Experiment 1, we did not observe noticeable differences in participants' accuracy in performing the dual-task (p(Hit): $M_{ord}(SD)$ = .77 (.11), $M_{pred}(SD)$ =.74(.14), $M_{rand}(SD)$ = .81(.05)) nor in stability of fixation (Absolute deviation from fixation along in dva. Deviation along x axis: $M_{ord}(SD)$ = .28(.15); $M_{pred}(SD)$ =.24(.11); $M_{rand}(SD)$ =.25(.10). Deviation along y axis: $M_{ord}(SD)$ = .46(.42), $M_{pred}(SD)$ = .41(.33), $M_{rand}(SD)$ = .36(.26)) across conditions.

Similarly, in Experiment 2, we did not observe significant differences in participants' accuracy in the dual-task (p(Hit): $M_{ord}(SD)$ = .72 (.16), $M_{pred}(SD)$ =.74(.17) , $M_{randNC}(SD)$ = .68(.08), $M_{randC}(SD)$ = .69(.14)) nor in stability of fixation (Absolute deviation from fixation along in dva. Deviation along x axis: $M_{ord}(SD)$ = .21(.08), $M_{pred}(SD)$ =.19(.06), $M_{randNC}(SD)$ =.23(.09) , $M_{randC}(SD)$ =.21(.09). Deviation along y axis: $M_{ord}(SD)$ = .31(.23), $M_{pred}(SD)$ = .30(.20), $M_{randNC}(SD)$ = .32(.20) , $M_{randC}(SD)$ =.34(.24) across conditions.

Consistent with the previous experiments, also in Experiment 3, we did not observe significant differences in participants' accuracy in the dual-task (p(Hit): $M_{ord}(SD)$ = .89 (.07), $M_{pred}(SD)$ =.86(.15) , $M_{randNC}(SD)$ = .89(.12), $M_{randC}(SD)$ = .93(.06)) nor in stability of fixation (Absolute deviation from fixation along in dva. Deviation along x axis: $M_{ord}(SD)$ = .23(.12), $M_{pred}(SD)$ =.24(.10), $M_{randNC}(SD)$ =.32(.21) , $M_{randC}(SD)$ =.27(.13). Deviation along y axis: $M_{ord}(SD)$ = .31(.22), $M_{pred}(SD)$ = .42(.38), $M_{randNC}(SD)$ = .54(.61) , $M_{randC}(SD)$ =.37(.58) across conditions.

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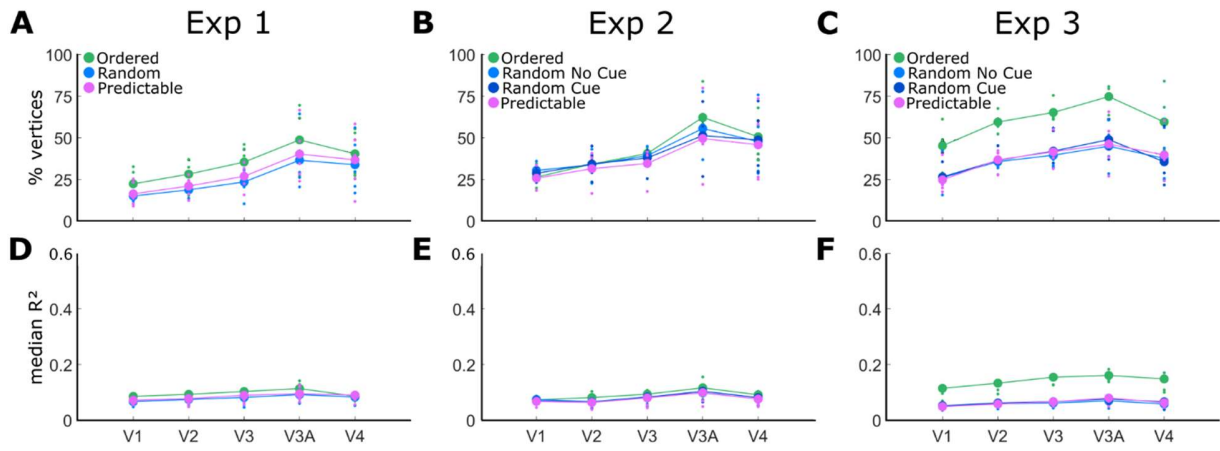
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788 *Figure S 1 Data quality in Experiments 1-3. (A-C) Percentage of responsive vertices in each visual area and condition tested. (D-F)*

789 *Median goodness of fit (R^2). Large dots indicate mean group results and small dots indicate individual participants' data. Ordered*

790 *(green), random (blue) and predictable (fuchsia) sequences are displayed for all experiments. In Experiments 2 and 3, the light*
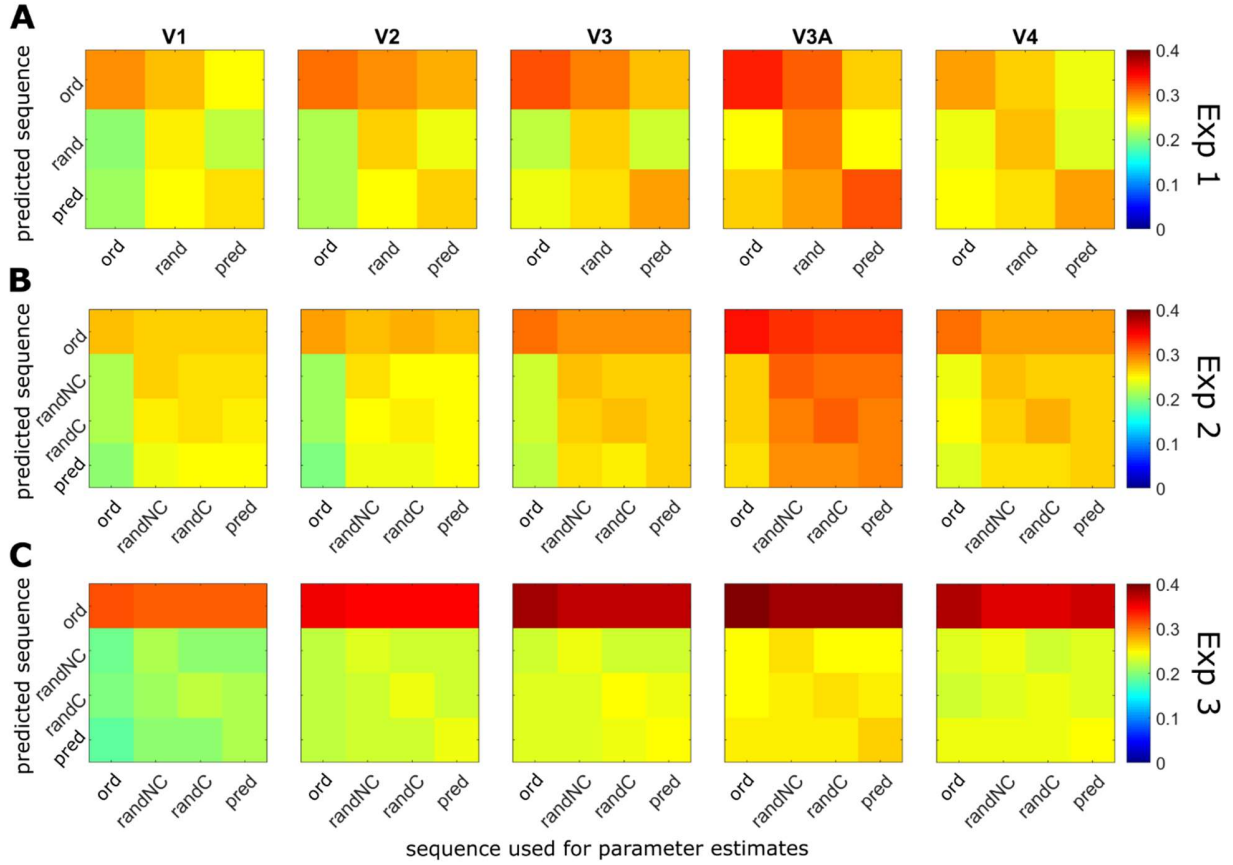
791 *blue dots and the dark blue dots depict results for the random no-cue and random cue conditions respectively.*

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