

# Human Primary Visual Cortex Shows Larger Population Receptive Fields for Binocular Disparity-Defined Stimuli

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## Research Article

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1 Human primary visual cortex shows larger population receptive fields  
2 for binocular disparity-defined stimuli

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20

## 21 **1 Abstract**

22 The visual perception of 3D depth is underpinned by the brain's ability to combine signals from  
23 the left and right eyes to produce a neural representation of binocular disparity for perception  
24 and behavior. Electrophysiological studies of binocular disparity over the past two decades  
25 have investigated the computational role of neurons in area V1 for binocular combination,  
26 while more recent neuroimaging investigations have focused on identifying specific roles for  
27 different extrastriate visual areas in depth perception. Here we investigate the population  
28 receptive field properties of neural responses to binocular information in striate and  
29 extrastriate cortical visual areas using ultra-high field fMRI. We measured BOLD fMRI  
30 responses while participants viewed retinotopic-mapping stimuli defined by different visual  
31 properties: contrast, luminance, motion, correlated and anti-correlated stereoscopic disparity.  
32 By fitting each condition with a population receptive field model, we compared quantitatively  
33 the size of the population receptive field for disparity-specific stimulation. We found larger  
34 population receptive fields for disparity compared with contrast and luminance in area V1, the  
35 first stage of binocular combination, which likely reflects the binocular integration zone, an  
36 interpretation supported by modelling of the binocular energy model. A similar pattern was  
37 found in region LOC, where it may reflect the role of disparity as a cue for 3D shape. These  
38 findings provide insight into the binocular receptive field properties underlying processing for  
39 human stereoscopic vision.

## 40 **2 Keywords**

41 Stereopsis, disparity, V1, visual cortex, fMRI, population receptive field

### 42 **3 Introduction**

43 Binocular stereopsis underlies our perceptual experience of stereoscopic depth and visual  
44 three-dimensional structure. Stereopsis is supported by a set of neural mechanisms for  
45 disparity selectivity and binocular integration that are distributed across multiple cortical  
46 regions in the human visual cortex (Backus et al. 2001; Bridge and Parker 2007; Preston et al.  
47 2008; Ip et al. 2014; Goncalves et al. 2015; Li et al. 2019) and characterized by selective  
48 responses to specific stimulus features, such as absolute and relative disparity, surface  
49 curvature, slant, or separation in depth (Parker 2007).

50

51 To fully understand stereopsis, it is necessary to establish the relevant region of visual space  
52 over which binocular disparity is computed. We define this as the binocular integration zone,  
53 comprising the coincident retinal spaces of left and right eyes over which the two monocular  
54 inputs are pooled to form a unified binocular representation of disparity in cortical processing  
55 (Parker et al. 2016). The site of binocular combination can be localized to the primary visual  
56 cortex (V1) in the macaque monkey (Cumming and Parker 1999, 2000; Parker and Cumming  
57 2001), with extrastriate areas performing computations relevant to binocular perception on an  
58 integrated representation of the binocular signal. Properties of the binocular integration zone  
59 could potentially be similar to the receptive field properties of responses driven by luminance  
60 contrast. Alternatively the binocular integration zone could differ in its spatial or temporal  
61 properties, revealing limits specific to disparity processing (Prince et al. 2002a; Nienborg et al.  
62 2004, 2005; Anzai et al. 2011).

63

64 Neighboring binocular neurons display similar disparity selectivity, leading to clusters of cells  
65 encoding near or far disparities (Chen et al. 2008, 2017). This is compounded by the retinotopic  
66 organization of visual cortex, leading to regions preferentially responding to a particular

67 binocular disparity, at a particular retinal location. This population-level organization makes  
68 disparity selectivity amenable to study with fMRI, a technique that samples cortical responses  
69 with a spatial resolution in the range of 1-2 millimeters. Neuroimaging studies of binocular  
70 disparity have characterized the spatial selectivity for binocular information across human  
71 visual cortex (Backus et al. 2001; Neri et al. 2004; Preston et al. 2008; Minini et al. 2010;  
72 Cottureau et al. 2011; Ip et al. 2014; Ban and Welchman 2015), within cortical areas (Nasr et al.  
73 2016; Tootell and Nasr 2017), as well as the role they play in perceptual judgements of disparity  
74 (Backus et al. 2001; Goncalves et al. 2015; Bridge 2016). A previous study by Barendregt et al.  
75 (2015) found that a dichoptic bar stimulus presented in spatially offset positions in the two  
76 eyes led to larger population receptive fields in V1 compared to extrastriate regions. What  
77 remains unclear is how the characteristics of the binocular integration zone in V1 and  
78 extrastriate regions perform spatial integration when stimulated with pure binocular disparity,  
79 without any monocular cues compared to receptive fields driven by luminance and contrast.

80

81 We analyzed quantitatively the receptive field properties of binocularly driven receptive fields  
82 with population receptive field (pRF) methods. Using dynamic random dot stereograms in  
83 which sequential retinotopic positions are stimulated by changes in binocular disparity, we  
84 derived a pRF spatial model of fMRI signals that are specific to processing of a particular  
85 binocular disparity. The output of the pRF model summarizes the spatial extent of retinal  
86 locations over which a disparity signal increases cortical responses. This, in turn, is dictated by  
87 the properties of the neurons falling within the stimulated population, specifically the disparity  
88 selectivity and spatial selectivity of the receptive fields. As the maximum extent of the disparity-  
89 defined pRF is limited by the population-level binocular integration zone of binocular neurons  
90 in the sampled cortical space, we take the estimated pRF size as a valid estimate of the binocular  
91 integration zone. Sampling across multiple cortical visual areas, we show a pattern of larger  
92 pRFs for disparity-defined compared to checkerboard and luminance-defined stimuli in the

93 primary visual area V1 and also in the lateral occipital complex (LOC), supporting a distinct role  
94 for this extrastriate region in disparity processing. Model simulations reveal that the increase  
95 in estimated pRF size to disparity-defined stimuli in primary visual cortex is predicted by a  
96 standard binocular energy model (Ohzawa et al. 1990; Cumming and Parker 1997; Anzai et al.  
97 1999).

98

## 99 **4 Materials and methods**

### 100 **4.1 Participants**

101 Eight healthy participants with normal or corrected-to-normal vision took part in the study  
102 (mean age 27.6 yr, age range 19-42, 6 female). They were screened for normal visual acuity  
103 (Snellen chart at 6 meters, <20/20 corrected) and stereoscopic vision (TNO test, <60 arcsec  
104 correct detection). This study received ethical approval from the University of Oxford Central  
105 University Research Ethics Committee (MS-IDREC-C1-2015-040) and was conducted in  
106 accordance with the Declaration of Helsinki (2013 revision). One participant was unable to  
107 successfully fuse the stereoscopic images, so they were not included in any of the analyses,  
108 leaving 7 participants included in the results.

109

### 110 **4.2 Stimulus presentation**

111 Visual stimuli were generated in MATLAB (v8.0, Mathworks Inc., Natick, MA, USA) using  
112 Psychtoolbox (v3.0, <http://psychtoolbox.org>) and displayed through a LCD projector (LC-XL  
113 100, Eiki Industrial Company, Japan) via a back-projection screen situated inside the bore of  
114 the MRI scanner (peak luminance = 552 cd/m<sup>2</sup>). All stimuli were viewed through red and green  
115 anaglyph filters (Wratten 2 Optical Filters #29 and #61, Eastman Kodak, Rochester, NY, USA),  
116 both to provide stereoscopic display in the case of disparity-containing stimuli, and to ensure

117 equal luminance attenuation across conditions. Luminance crosstalk, defined as the percentage  
118 of unintended signal to intended signal, was measured for the red and green filters at 0.16%  
119 and 0.82%, respectively. The red filter was always placed over the left eye.

120 Stimuli were arranged across five conditions (Figure 1): checkerboard, correlated disparity,  
121 motion, luminance, and anti-correlated disparity conditions. All stimuli were presented within  
122 the confines of a 'wedge' or 'ring' aperture, similar to that used in a standard retinotopic  
123 mapping design (Engel et al. 1994; Sereno et al. 1995). Four configurations were used: two  
124 types of wedge, rotating either clockwise or counter-clockwise, and two types of ring, either  
125 expanding or contracting. In the following section, we refer to the stimulus content within the  
126 aperture as the foreground and stimulus content outside the aperture as the background.

127 The checkerboard condition (Figure 1A) consisted of a foreground of radial contrast-reversing  
128 (2Hz) checkerboard (contrast = 100%), while the background was set to 50% luminance,  
129 matched to the mean of the foreground stimulus. Stimuli were viewed binocularly through the  
130 red-green anaglyph filters.

131 The correlated disparity stimulus (Figure 1B), consisted of a dynamically changing array of  
132 randomly placed dots, half of them white and half black on a grey background. Foreground dots  
133 were fully correlated in position between left and right eyes and modulated in binocular  
134 disparity. Foreground dots were presented at either  $+0.2^\circ$  or  $-0.2^\circ$  disparity, corresponding to  
135 near and far positions relative to the fixation plane, and swapping every 1.45s. Background dots  
136 were randomly placed in left and right eyes and were therefore uncorrelated binocularly. Both  
137 foreground and background contained black and white dots (50% each), and dots refreshed at  
138 a frequency of 60 Hz.

139 The motion stimulus (Figure 1C) consisted of a dynamic random dot array, with dot positions  
140 fully correlated binocularly. Background dots were static, while foreground dots moved in  
141 either clockwise or counterclockwise motion (50% of dots in each direction) at  $7^\circ/s$ . To ensure  
142 dot motion was visible, dots were refreshed at a rate of 0.33 Hz, slower than the 60 Hz refresh

143 rate for the correlated disparity stimulus. Both foreground and background contained black  
144 and white dots (50% each).

145

146 The luminance stimulus (Figure 1D) consisted of a dynamic random dot array, with dot  
147 positions fully correlated binocularly, refreshing at a rate of 60 Hz, and containing both black  
148 and white dots (50% each). Foreground dots were either 100% black or 100% white, with the  
149 luminance of foreground dots reversing at a rate of 0.69 Hz.

150

151 The anti-correlated disparity stimulus (Figure 1E) consisted of a dynamic random dot array,  
152 which was identical in layout to the correlated disparity stimulus (Figure 1B), except for the  
153 arrangement of foreground dot colors. Dots falling inside the aperture always had opposite  
154 contrasts in left and right eyes, so that they were presented in matching positions but displayed  
155 as either white in the left eye and black in the right eye, or the opposite. This manipulation  
156 negates the sensory percept of depth, while retaining binocular disparity information that is  
157 registered by V1 neurons (Cumming and Parker 1997). All stimuli were viewed binocularly  
158 through the red-green filters, with dynamic random dot arrays presented at a dot density of  
159 40%, and a dot radius of  $0.12^\circ$  for 6 participants and  $0.15^\circ$  for 2 participants.

160

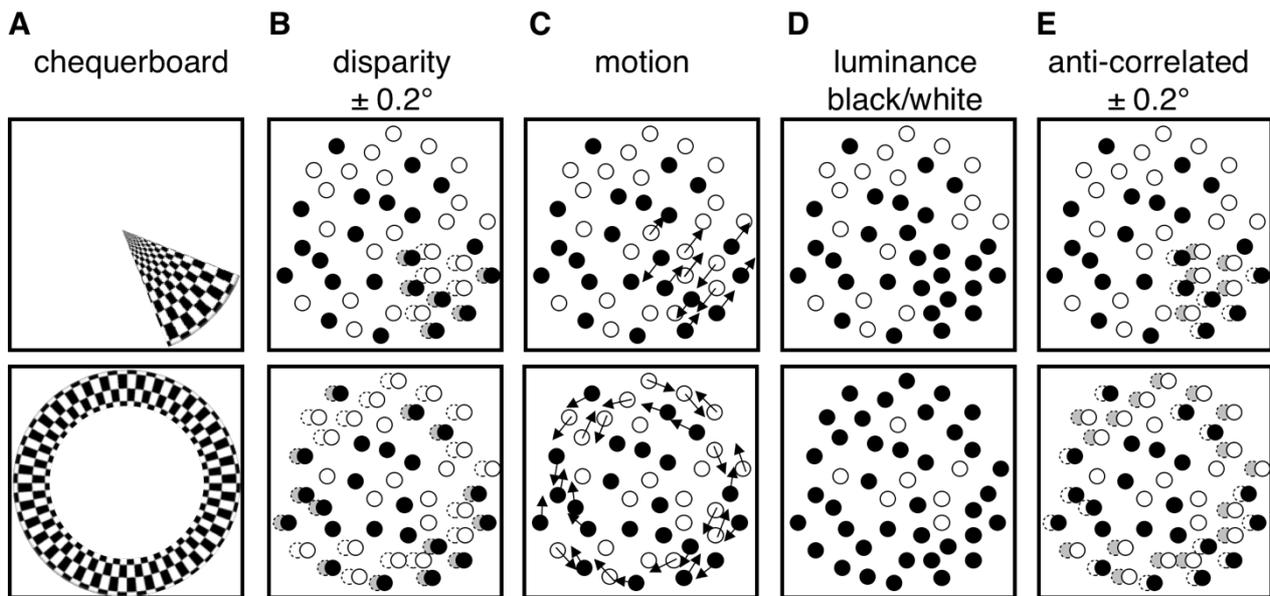
161 In addition to the main experimental stimuli, a single full-field radial checkerboard stimulus  
162 alternating with a grey background (2.5 s ON, 30 s OFF) was used to estimate the hemodynamic  
163 response functions (HRF) of visual cortex individually for each participant.

164

165 In order to control participants' attention, a fixation cross was present throughout stimulation,  
166 and participants were required to detect a change of color of this cross from black to red. The  
167 fixation cross was presented in a radial  $0.5^\circ$  cut-out for all stimuli, and therefore any  
168 reconstructed pRFs with eccentricities  $<0.5^\circ$  were discarded, due to overlap with the fixation

169 cross. The color change was brief (200 ms) and occurred pseudo-randomly 80-100 times  
170 during a single run. Participants responded to this vigilance task via an MRI-compatible button  
171 box, and responses were monitored to ensure participant alertness. The average percentage of  
172 events detected was  $88\% \pm 5\%$  SEM.

173



174

175 **Figure 1.** Experimental stimulus cartoon. Stimuli consisted of a contrast-  
176 reversing checkerboard (A) or dynamic random dot field (B-E) presented in a  
177 dynamically varied aperture of a wedge (upper row) or a ring (lower row). (A)  
178 Radial checkerboard reversing in contrast at 2Hz; (B) Disparity with random  
179 dot stimuli, dots inside aperture were binocularly correlated and changed in  
180 disparity ( $\pm 0.2^\circ$  from fixation); (C) Motion with clockwise and counter-  
181 clockwise components (dot speed =  $7^\circ/s$ ); (D) Luminance reversal between  
182 fully black and fully white; (E) Anti-correlated binocular disparity ( $\pm 0.2^\circ$  from  
183 fixation).

184 In all cases, modulation was displayed first within a wedge-aperture rotating clockwise or  
185 counterclockwise around the apex of the wedge, and subsequently within a ring-aperture

186 expanding from or contracting into the centre. Dot positions were randomly generated for  
187 every frame, with 50% black and 50% white, except for the luminance modulation stimulus  
188 (for which dots are illustrated in black for clarity). Periods of no modulation (24/168 volumes  
189 per run) with a blank grey screen were used to estimate baseline response.

### 190 **4.3 MRI acquisition**

191 MR images were acquired with an ultra-high field 7T MRI system (Siemens Healthcare,  
192 Germany) using a 32-channel head coil (Nova Medical, USA). Functional imaging during visual  
193 stimulation was conducted with a gradient echo echo-planar imaging sequence (TR = 2488 ms,  
194 TE = 27.8 ms, 64 slices, resolution = 1.2 mm isotropic) with in-plane acceleration using parallel  
195 imaging (GRAPPA factor = 2) (Griswold et al. 2002) and through-slice acceleration using  
196 multiband imaging (MB factor = 2) (Moeller et al. 2010). Four runs were acquired for each  
197 stimulus condition, totaling 672 volumes per condition. The order of conditions and aperture  
198 order was randomized within and across sessions. For HRF estimation, three runs were  
199 acquired per participant, total 234 volumes. B<sub>0</sub> field maps were acquired in-plane in each run  
200 to correct distortions due to field inhomogeneity. (TR = 620 ms, TE<sub>1/2</sub> = 4.08 / 5.1 ms, resolution  
201 = 2 mm isotropic). A T1-weighted (T1w) whole-brain anatomical image was acquired to  
202 reconstruct the cortical surface and anatomically localize functional data (MP-RAGE, TR = 2200  
203 ms, TE = 2.82 ms, TI = 1050 ms, flip angle = 7°, slices = 176, resolution = 1 mm isotropic).

### 204 **4.4 MRI pre-processing**

205 Functional images for each participant were pre-processed with FSL (FMRIB Software Library  
206 v5.0.8; <http://www.fmrib.ox.ac.uk/fsl>). EPI images were corrected for distortions caused by  
207 magnetic field inhomogeneities using FUGUE (Jenkinson et al. 2012), image portions showing  
208 brain tissue were isolated, and corrected for participant motion by linear realignment to the  
209 middle time point of each run. Low-frequency fluctuations were removed using a high-pass

210 filter with cut-off at 0.02 Hz. Each run was then registered to the subject-specific T1w structural  
211 image using boundary-based registration (Greve and Fischl 2009).

212

213 Cortical surfaces were reconstructed from T1w structural images with FreeSurfer (v5.3.0,  
214 <http://www.freesurfer.net>). Volumes underwent automated segmentation to generate grey  
215 and white matter boundaries, and the grey matter surface reconstructed to create a two-  
216 dimensional representation of the cortical surface.

#### 217 **4.5 pRF analysis**

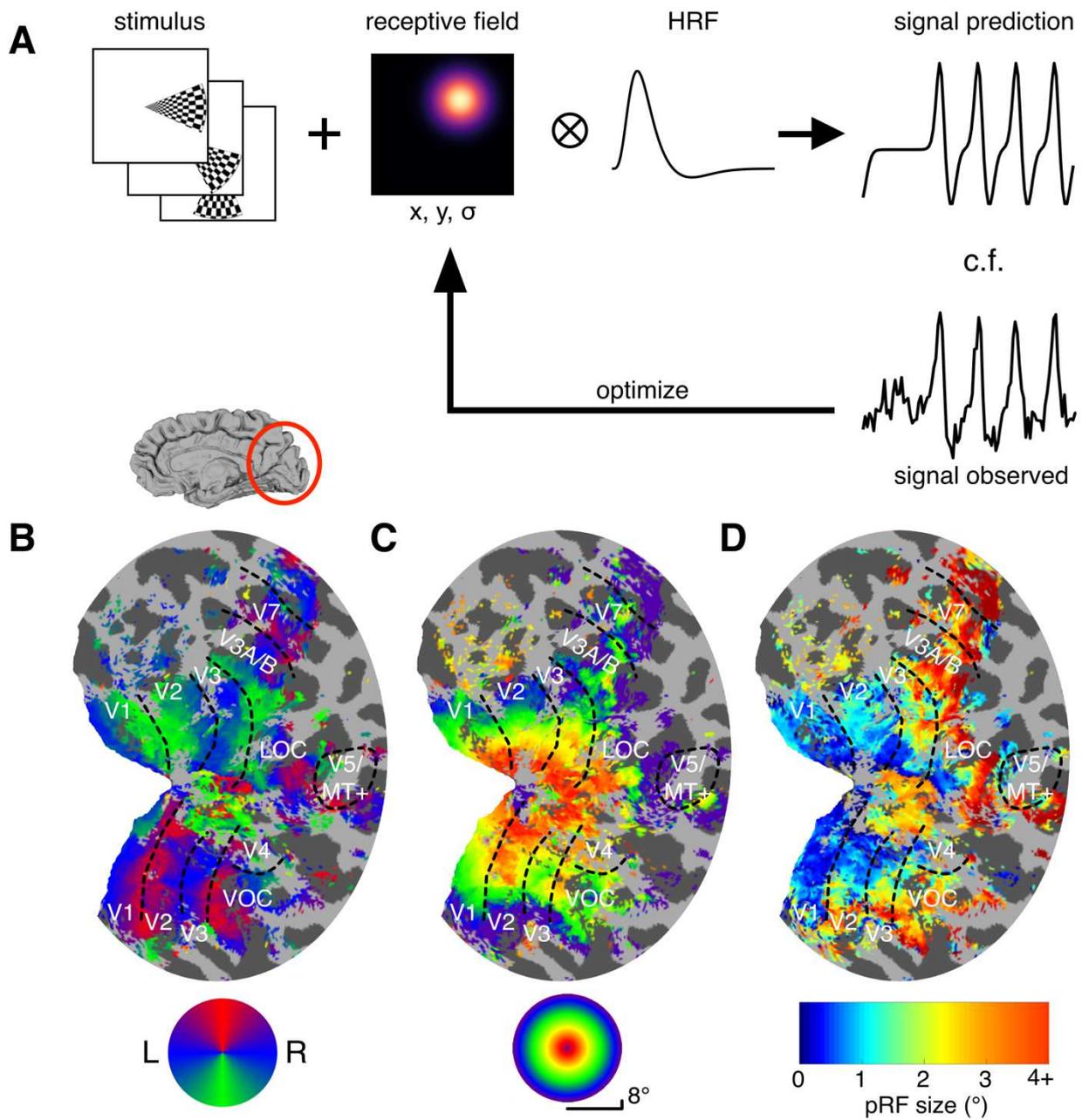
218 fMRI data were analyzed using a Gaussian population receptive field (pRF) model (Dumoulin  
219 and Wandell 2008; Wandell and Winawer 2015). The analysis software was implemented in  
220 MATLAB and is described detail in (Alvarez et al. 2015). In brief, the participant-specific  
221 hemodynamic response function (HRF) was estimated by averaging 18 trials over the occipital  
222 lobes during full field checkerboard stimulation and fitting a double gamma function (Friston  
223 et al. 1995). Model predictions were constructed by combining the *a priori* position of the  
224 stimulus aperture at each MRI volume acquired and a radially symmetric two-dimensional  
225 Gaussian pRF. Predictions were then convolved with the participant-specific HRF and  
226 compared to the observed signal in a two-stage procedure. First, the spatially smoothed (full  
227 width half maximum = 5 mm, on spherical mesh) BOLD time courses were correlated with  
228 signal predictions generated by an exhaustive grid of combinations of the three pRF parameters  
229 (X coordinate, Y coordinate,  $\sigma$  size of pRF). The parameters resulting in the highest correlation  
230 at each vertex formed the starting point for the second stage, in which the original unsmoothed  
231 BOLD time courses were fitted using the Nelder-Mead algorithm for unconstrained nonlinear  
232 minimization (Lagarias et al. 1998) to identify parameter combinations for each vertex that  
233 maximize the variance explained by the model. Best-fitting model predictions yielded estimates  
234 of retinotopic location (X and Y coordinates) and pRF size ( $\sigma$ ) for each vertex. Each condition

235 (checkerboard, luminance, motion, correlated disparity, anti-correlated disparity) was fitted  
236 independently. Regions of interest were delineated for each participant based on polar angle  
237 and eccentricity estimates obtained in the checkerboard condition (see Figure 2).  
238 Model performance was assessed with the normalized correlation coefficient metric (CCnorm)  
239 (Schoppe et al. 2016). Each stimulus run was divided into two, with each half split considered  
240 an independent stimulus presentation. Signal reliability was used to normalize the correlation  
241 between pRF model prediction and empirically observed BOLD signals. Vertices were  
242 thresholded at  $CCnorm > 0.5$ , approximately equivalent to 50% of explainable variance  
243 explained by the pRF model.

#### 244 **4.6 Regions of interest**

245 Regions of interest V1, V2, V3, V3A/B, V5/MT+, V7, V4, LOC and VOC were identified for each  
246 participant in each hemisphere tested. Since precise retinotopic boundaries could not be  
247 observed for all participants in some portions of visual cortex, a merged-region definition was  
248 adopted for areas LOC, VOC and V5/MT+. Specifically, the lateral occipital complex (LOC)  
249 encompassed retinotopic definitions of areas LO-1 and LO-2, the ventral occipital complex  
250 (VOC) encompassed areas VO-1 and VO-2 (Larsson and Heeger 2006; Wandell et al. 2007;  
251 Winawer and Witthoft 2015), and the region V5/MT+ encompassed the temporal-occipital  
252 areas TO-1 and TO-2 (Amano et al. 2009). Further, the region V5/MT+ was compared with an  
253 atlas definition of human occipital area 5 (hOc5), a cytoarchitectonic correlate of area V5/MT+,  
254 for anatomical agreement (Malikovic et al. 2006). This comparison showed a minimum of 50%  
255 overlap between vertices in retinotopically-defined V5/MT+ and the atlas-based  
256 cytoarchitectonic definition of hOc5 in all hemispheres tested (Mean overlap = 74%,  $SD = 12\%$ ,  
257  $N = 14$  hemispheres). The variability in alignment between structural and functional markers  
258 of V5/MT+ in human cortex has been noted before (Large et al. 2016).

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**Figure 2.** Cortical signals obtained under contrast-reversing checkerboard stimulation fitted with pRF model. (A) Model based on response to spatial and temporal sequence of visual stimulation of a Gaussian RF centered at location  $(X, Y)$  with spread  $(\sigma)$ . Convolution with the participant-specific hemodynamic response function (HRF) gives a time-course prediction of the BOLD signal, which was in turn compared with the observed signal. Receptive field parameters  $(X, Y, \sigma)$  were then optimized iteratively to find the best-fitting pRF model for the data observed. (B) Polar angle delineation of visual areas;

269 inflated right hemisphere for one participant (S1). Best-fitting model  
270 prediction shown. (C) visual field eccentricity of estimated pRFs. (D) pRF size  
271 across the visual cortex.

#### 272 **4.7 Experimental design and statistical analysis**

273 Differences in model performance between stimulation conditions were assessed in two ways.  
274 First, the distributions of CCnorm values were pairwise-compared between conditions with  
275 independent Kolmogorov-Smirnov tests. Note that p-values are unsuitable as measures of  
276 distribution similarity in the case of KS statistics (Vermeesch 2013), so only effect sizes are  
277 presented. Second, differences in mean CCnorm between conditions were assessed with a  
278 repeated measures ANOVA, introducing stimulation condition and region of interest as within-  
279 subject variables and participant identity as between-subject variable. Estimates of pRF size  
280 were also assessed for each visual area using a mixed effects model implemented in Prism  
281 (GraphPad Software, San Diego, California) with stimulus condition and eccentricity bin as  
282 within-subject variables and participant identity as between-subject variable. The anti-  
283 correlated disparity condition was not included in this analysis as there were too few vertices  
284 for which the pRF model could be successfully fit. This mixed-effects model was used rather  
285 than a repeated-measures ANOVA to account for vertices where no pRF model could be fit,  
286 hereafter labeled as missing values. Across all stimulus conditions (excepting anti-correlated  
287 disparity), visual areas, participants and eccentricities, 2.1% of values were missing. The  
288 disparity condition had the greatest number of missing values at 4.9%, but no individual visual  
289 area was missing more than 10% of values. Geisser-Greenhouse correction was applied where  
290 necessary and where random effects were zero, the term was removed and a simpler model fit  
291 used. Where there was a significant effect of condition in the main analysis, post-hoc mixed-  
292 effect models were conducted to assess the effect of specific condition pairs at each region of

293 interest, with eccentricity bin introduced as a nuisance variable. All other statistical tests were  
294 implemented in MATLAB or SPSS (v24, IBM Corp., Armonk, NY, USA).

#### 295 **4.8 Binocular energy model**

296 The response of binocular neurons in V1 to disparity information has been previously  
297 characterized as a set of canonical computations, formalized in the binocular energy model  
298 (Ohzawa et al. 1990; Cumming and Parker 1997; Anzai et al. 1999). In brief, the monocular  
299 inputs from left and right eyes arriving at a binocular simple V1 cell are each passed through a  
300 an eye-specific, weighting function approximated by a two-dimensional Gabor filter. Such  
301 filters are used in paired combination to capture the response to inputs to the left and right  
302 eyes, with horizontal displacement between the eye-specific filters conferring sensitivity to  
303 binocular disparity. A group of such filter pairs is set in quadrature, that is, with the spatial  
304 phase of the sinusoidal element of the Gabor functions offset by  $\pi/2$  radians. Paired responses  
305 are summed, followed by a half-wave rectification and squaring nonlinearity. The summed  
306 output reflects the model binocular complex cell response (Ohzawa et al. 1990).

307

308 A population of 1,000 binocular complex neurons was simulated, with receptive fields  
309 positioned in the center of the visual field. A small normally distributed position offset (SD =  
310  $0.1^\circ$ ) was introduced to eliminate, by averaging, the spatial response of the population to  
311 detailed positions of the dots forming the randomly generated RDS patterns. The horizontal  
312 size of the Gabor profile, orthogonal to grating orientation, was manipulated to simulate  
313 receptive field size increase with eccentricity. Spatial frequency and disparity tuning were  
314 similarly manipulated to simulate the experimentally determined range of V1 receptive field  
315 properties found in recordings from macaque visual cortex (see below). The vertical size of the  
316 filter, parallel to grating orientation, was set to 1.5 times the horizontal size across eccentricity,

317 also based on V1 recordings in the macaque monkey (Ringach et al. 2003). All filters were  
318 vertically oriented.

319

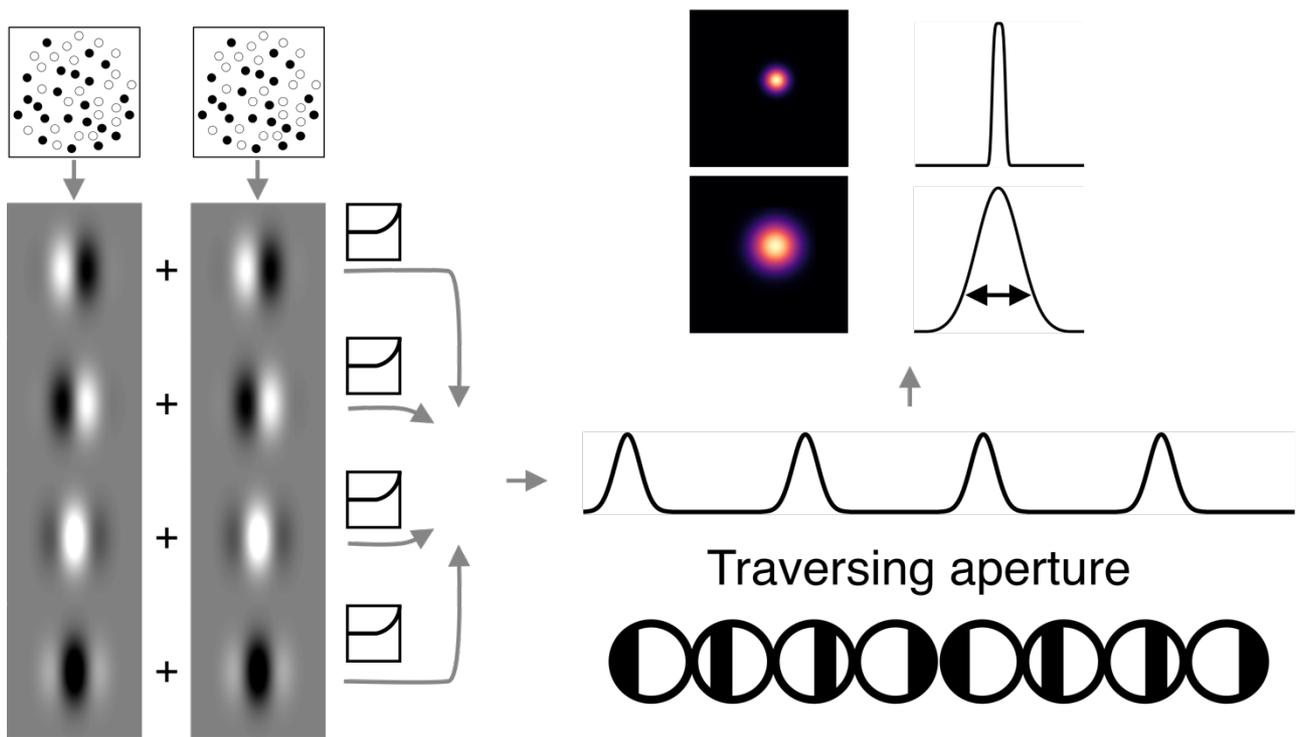
320 The stimuli delivered to the model receptive field consisted of (1) binocularly presented,  
321 contrast-reversing checkerboards (2) binocularly correlated dots in the aperture with  
322 binocularly uncorrelated dots in the background and (3) opposite polarity zero-disparity dots  
323 in the aperture and same polarity, zero-disparity dots in the background, just like the  
324 checkerboard, correlated disparity and luminance stimuli respectively viewed by participants.  
325 Stimuli were presented through a sweeping bar aperture in 100 steps, to create a timeseries of  
326 responses to the transient presence of contrast or disparity information. Random dots were  
327 binocularly correlated within the aperture at the programmed binocular disparity, but were  
328 uncorrelated in the background, while in the luminance condition dots were opposite polarity  
329 within the aperture and matched polarity in the background. For these random dot stimuli,  
330 1,000 unique RDS frames were generated at each aperture step, and responses averaged  
331 together. Resulting responses were fitted with the Gaussian pRF model described in section 4.5.  
332 As estimation of the receptive field location is not of concern here, the location parameters were  
333 fixed *a priori* and only the receptive field size was estimated (Figure 3).

334

335 Three manipulations of model receptive field properties were conducted, in order to observe  
336 the effects on pRF model fits. First, the horizontal filter size was set to 15 different values  
337 between  $SD = 0.2^\circ$  and  $SD = 3^\circ$  to simulate RF size increase with eccentricity. The spatial  
338 frequency of the sinusoidal component of the Gabor was fixed to  $\times 0.5$  the horizontal size, and  
339 all cells were set to be tuned to the stimulus disparity (checkerboard and luminance =  $0^\circ$ ,  
340 disparity stimulus =  $0.2^\circ$ ). Second, the same filter size points were sampled, while allowing  
341 spatial frequency of the Gabor filter to vary between  $\times 0.5$  and  $\times 3.5$  horizontal size, reflecting  
342 the variability in spatial tuning of V1 cells, while constrained by the size-disparity correlations

343 observed in macaque V1 (Prince et al. 2002b). Third, both spatial frequency and disparity  
 344 tuning were allowed to vary, with the latter allowing horizontal position of filters for left and  
 345 right eyes to vary by  $SD \pm 0.25^\circ$ . This final manipulation most closely resembles the distribution  
 346 of receptive field properties reported for V1 cells in electrophysiological studies in macaque  
 347 visual cortex. These simulations were designed to directly compare model responses generated  
 348 by disparity-defined stimuli with checkerboard and luminance for the specific case when all  
 349 model units are tuned to the stimulus disparity. A more comprehensive model would include  
 350 units tuned to many different disparities, but this is beyond the scope of the current  
 351 implementation.

352



353

354 **Figure 3.** Binocular energy model implementation. Stimulus frames for the left  
 355 and right eye were passed through a disparity-tuned Gabor filter bank, from  
 356 which the monocular responses of each eye were linearly added, passed  
 357 through a half-squaring non-linearity, and then pooled again by linear addition  
 358 to produce the model complex cell response. The model cell responds

359 periodically as the aperture defined by binocular correlation passes across its  
360 receptive field. The response timeseries of the population of RFs was fitted  
361 with the pRF model described. In the presence of a disparity-defined aperture,  
362 the width of the response is directly related to the area over which binocular  
363 information is integrated.

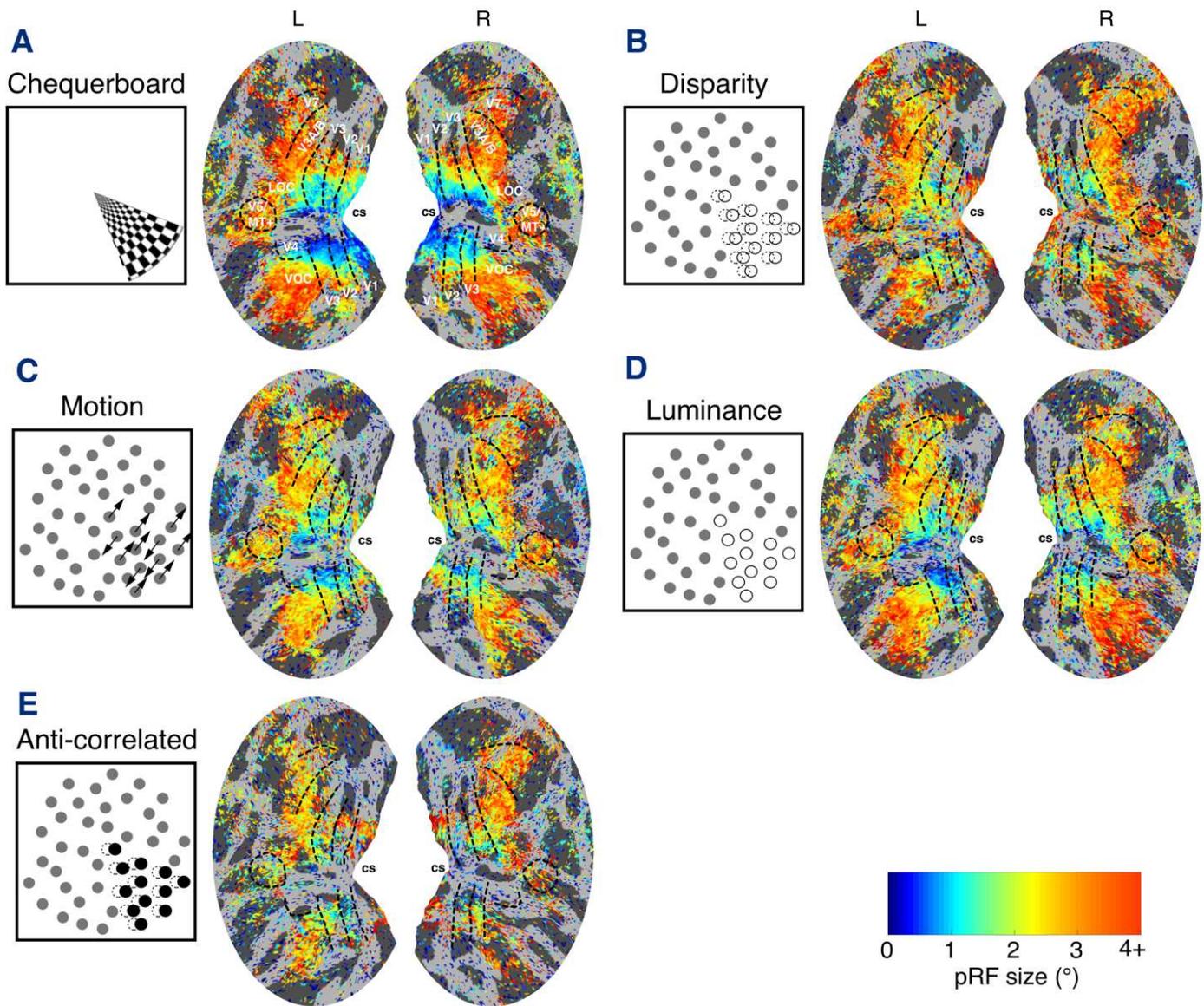
## 364 **5 Results**

### 365 **5.1 Disparity responses are widespread across visual cortex**

366 All visual cortical areas and regions of interest gave significant responses to binocular disparity  
367 stimulation as well as contrast stimulation. When considering the distributions of CCnorm,  
368 negligible effect sizes were detected when comparing the correlated disparity condition with  
369 the checkerboard (Kolmogorov-Smirnov distance,  $KS = 0.12$ ,  $D = 10^{-4}$ ), motion ( $KS = 0.07$ ,  $D =$   
370  $10^{-4}$ ), luminance ( $KS = 0.07$ ,  $D = 10^{-4}$ ) or anti-correlated conditions ( $KS = 0.15$ ,  $D = 10^{-4}$ ).  
371 Variability in mean CCnorm was assessed with a repeated measure ANOVA, revealing a  
372 significant effect of condition ( $F(5,1) = 64.56$ ,  $p = 10^{-3}$ ) and visual area ( $F(5,1) = 57.05$ ,  $p = 10^{-3}$ ).  
373 Post-hoc *t*-tests showed all conditions outperformed the anti-correlated disparity condition  
374 (all comparisons  $p < 0.05$ ), with no significant differences between the remaining conditions.

375  
376 Figure 4 shows the pRF size averaged across all participants for each type of visual stimulation.  
377 The spatial distribution of pRF size estimates follows the expected pattern of small pRFs in  
378 areas representing the central visual field and larger in the periphery.

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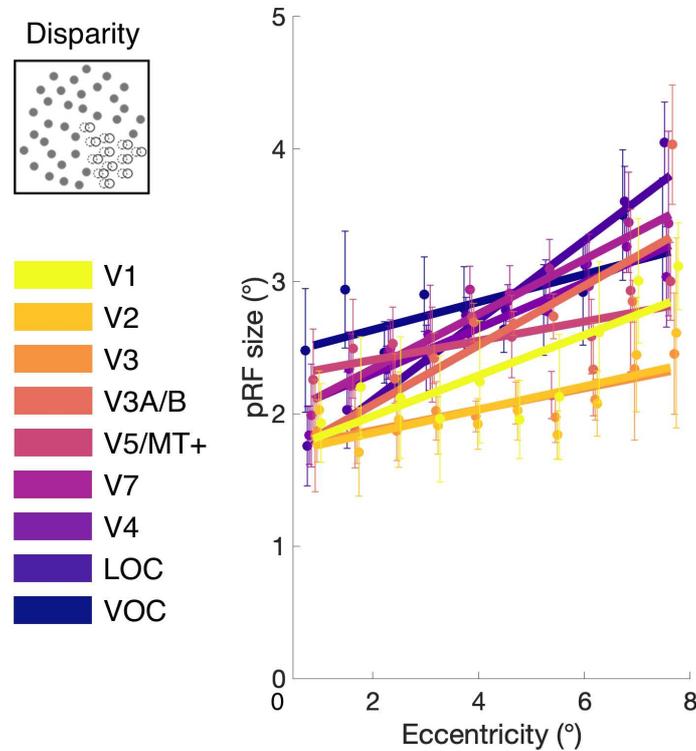
**Figure 4.** Group average estimates ( $N=7$ ) of pRF size obtained under (A) checkerboard, (B) correlated disparity, (C) motion, (D) luminance and (E) anti-correlated disparity stimulation. pRF size estimates displayed on the normalized and flattened cortical surface, with cortical visual areas demarcated and calcarine sulcus (cs) labelled for reference. Vertices thresholded at  $CC_{norm} > 0.5$ .

387

## 5.2 pRF size for disparity varies systematically across the visual hierarchy

388 Estimates of pRF size obtained under the disparity condition may capture the binocular  
 389 integration zone (Parker et al. 2016) over which monocular signals are combined, and  
 390 consequently reflect the role that cortical areas play in the integration mechanism of binocular  
 391 stereopsis. Examining the spatial distribution of pRF size estimates across the visual cortex  
 392 reveals systematic variation: in particular, there are locations where pRF size estimates differ  
 393 between the disparity and other conditions. We observed larger pRFs for correlated disparity  
 394 in the calcarine sulcus, close to representation of the horizontal meridian, when compared to  
 395 all other control conditions (Figure 4).

396



397

398 **Figure 5.** pRF size at different visual field eccentricities under disparity  
 399 stimulation in the visual areas of interest. Estimates of stereoscopic pRF size  
 400 were binned in 0.75° steps, with error bars indicating group SEM (N=7). pRF  
 401 size increases both with eccentricity, and through the visual hierarchy.  
 402 Vertices thresholded at CCnorm > 0.5. Small shift in eccentricity bin positions  
 403 added to display differences between visual areas.

404 Binned estimates of pRF size for disparity across eccentricity are shown in Figure 5. Differences  
405 in binned values of pRF size between the correlated disparity condition and other conditions  
406 were assessed with a full factorial ANOVA model, introducing eccentricity and region of interest  
407 as independent variables. Anti-correlated responses were omitted from this comparison, owing  
408 to the low number of vertices successfully fitted by the pRF model under that condition. There  
409 was a significant interaction between condition and region of interest ( $F = 43.45$ ,  $df = 14, 98$ ,  $p$   
410  $= 0.001$ ). In order to assess the effect of stimulus condition on a region-by-region basis, we  
411 conducted a series of linear mixed models, which are presented in the following section.

### 412 **5.3 pRF size for disparity differs from non-disparity pRFs in V1**

#### 413 *5.3.1 Early visual regions: V1, V2 and V3*

414 Figure 6 shows a summary of the pRF sizes at each eccentricity and for the different stimulus  
415 conditions across the early visual areas. In V1, a mixed effects model showed a significant effect  
416 of condition ( $F(2.1, 119.3) = 5$ ;  $p = 0.007$ ), although there was no effect of eccentricity ( $F(9, 60)$   
417  $= 1.9$ ;  $p = 0.06$ ) nor a significant interaction ( $F(27, 174) = 0.9$ ;  $p = 0.62$ ). Post-hoc paired  
418 comparisons showed that mean pRF size across all eccentricities for disparity ( $2.4^\circ$ ) were  
419 significantly greater than checkerboard ( $1.8^\circ$ ;  $F(1, 116) = 15$ ;  $p = 0.0002$ ) and luminance ( $2.0^\circ$ ;  
420  $F(1,56) = 5.3$ ;  $p = 0.02$ ). Disparity pRFs did not differ in size from those defined by motion ( $2.1^\circ$ ;  
421  $F(1,114) = 1.3$ ;  $p = 0.26$ ).

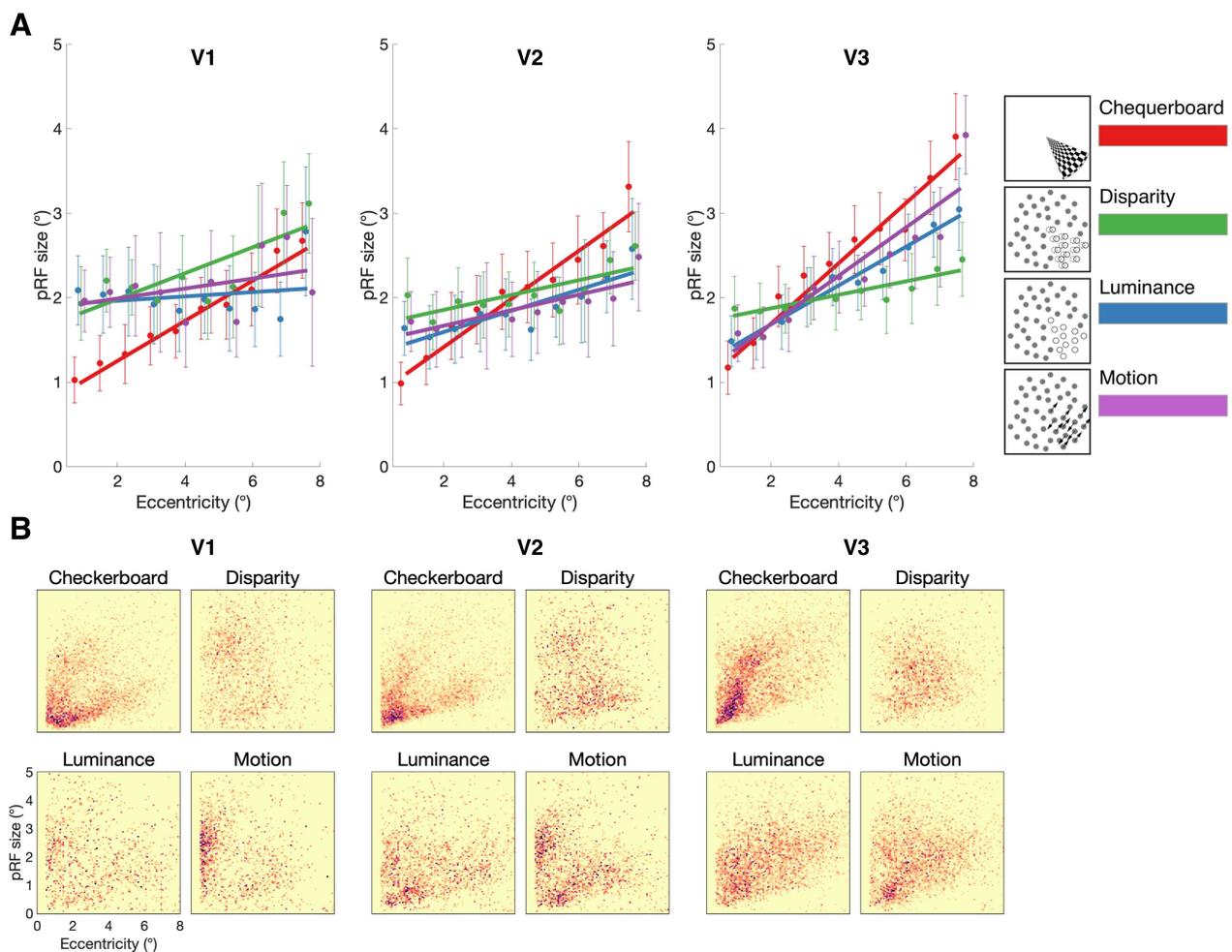
422

423 In comparison, in V2, there was a significant effect of eccentricity on pRF size ( $F(9,60) = 3.8$ ;  $p$   
424  $= 0.0008$ ), but no difference according to stimulus condition ( $F(2.6,147.9) = 2.2$ ;  $p = 0.11$ ) or  
425 interaction ( $F(27,174) = 0.75$ ;  $p = 0.81$ ). Finally, in V3 there was a significant effect of  
426 eccentricity on pRF size ( $F(9,60) = 26.9$ ;  $p < 0.0001$ ), and stimulus condition ( $F(2.3, 136.6) =$   
427  $5.5$ ;  $p = 0.003$ ) but no significant interaction ( $F(27,177) = 1.5$ ;  $p = 0.06$ ). However, while pRFs  
428 with the disparity stimulus ( $2.1^\circ$ ) were significantly smaller than with the checkerboard ( $2.5^\circ$ ;

429  $F(1, 117) = 16.2$ ;  $p = 0.0001$ ), they did not differ from either luminance ( $2.2^\circ$ ;  $F(1, 117) = 0.8$ ;  $p$   
 430  $= 0.37$ ) or motion ( $2.3^\circ$ ;  $F(1, 57) = 3.1$ ;  $p = 0.08$ ).

431

432 Thus, it appears that only in V1 are pRF sizes greater for disparity than both checkerboard and  
 433 luminance-defined stimuli. It is also the case in V1, and to a lesser extent in V2 that the  
 434 checkerboard stimulus resulted in smaller pRF sizes at low eccentricities compared to the  
 435 stimuli defined by dots. This effect may have been driven by spatial integration effects since the  
 436 aperture boundaries formed by dot-defined stimuli require spatial integration over a larger  
 437 region of the visual field compared to the stimuli with clear contrast-defined borders, such as  
 438 the checkerboard stimulus.



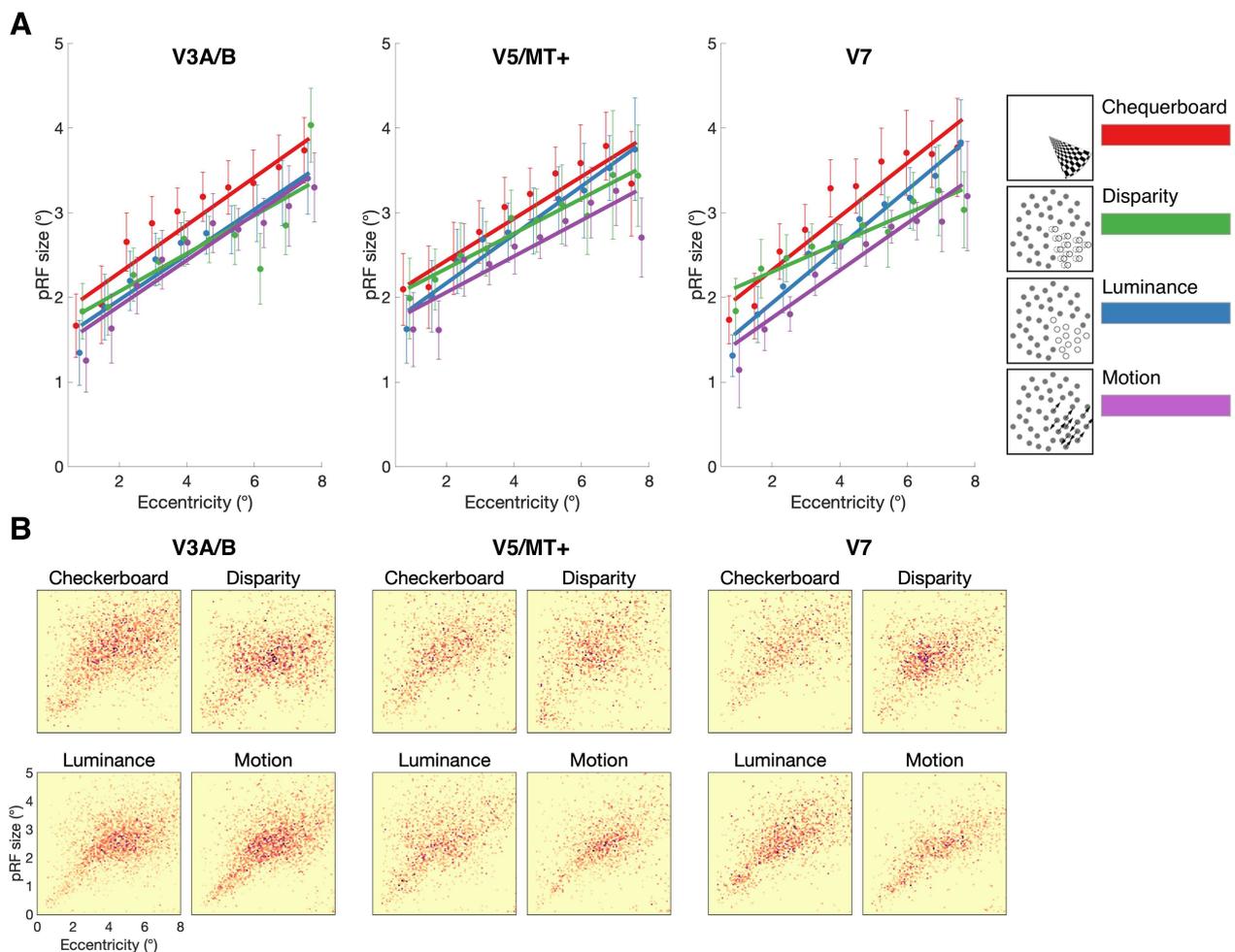
439

440 **Figure 6.** (A) pRF size estimates across visual field eccentricity for checkerboard,  
 441 disparity, luminance, and motion stimuli, across visual areas V1, V2 and V3.

442 pRF size values were binned in  $0.75^\circ$  steps and fitted with a linear regression  
443 model. Error bars indicate mean standard errors across participants. (B)  
444 Distribution of pRF size against visual field eccentricity across cortical surface  
445 points in all (N=7) participants tested. 2D binned histogram with 100x100  
446 equal size bins. Darker colors indicate higher density of significant vertices.

### 447 5.3.2 Dorsal visual regions: V3A/B, V5/MT+ and V7

448 The pRFs measured with the checkerboard stimuli were larger than those with the dot-defined  
449 stimuli across all dorsal visual areas (Figure 7). As evident from the graphs, there was a highly  
450 significant effect of eccentricity in all dorsal areas (V3A/B:  $F(9, 60) = 32.3$ ;  $p < 0.0001$ ;  
451 V5/hMT+:  $F(9,235) = 19.6$ ;  $p < 0.0001$ ; V7:  $F(9,236) = 38.6$ ;  $p < 0.0001$ ). Similarly, all areas  
452 showed a significant effect of stimulus type (V3A/B:  $F(2.3,136.3) = 11.1$ ;  $p < 0.0001$ ; V5/hMT+:  
453  $F(2.0,158.0) = 4.4$ ;  $p = 0.01$ ; V7:  $F(2.7,214.5) = 16.3$ ;  $p < 0.0001$ ). However, the disparity-defined  
454 pRF size only differed from the pRF sizes defined using the checkerboard in V3A/B ( $F(1, 119)$   
455  $= 12.6$ ;  $p = 0.0006$ ) and V7 ( $F(1, 117) = 13.9$ ;  $p = 0.0003$ ). This suggests that any difference in  
456 these areas was more likely related to the use of dot-defined stimuli rather than disparity *per*  
457 *se*.



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**Figure 7.** (A) pRF size estimates across visual field eccentricity for checkerboard, disparity, luminance, and motion stimuli, across visual areas V3A/B, V5/MT+, V7. pRF size values were binned in 0.75° steps and fitted with a linear regression model. Error bars indicate mean standard errors across participants. (B) Distribution of pRF size against visual field eccentricity across cortical surface points in all (N=7) participants tested. 2D binned histogram with 100x100 equal size bins. Darker colors indicate higher density of significant vertices.

467

### 5.3.3 Ventral visual regions: V4, LOC and VOC

468

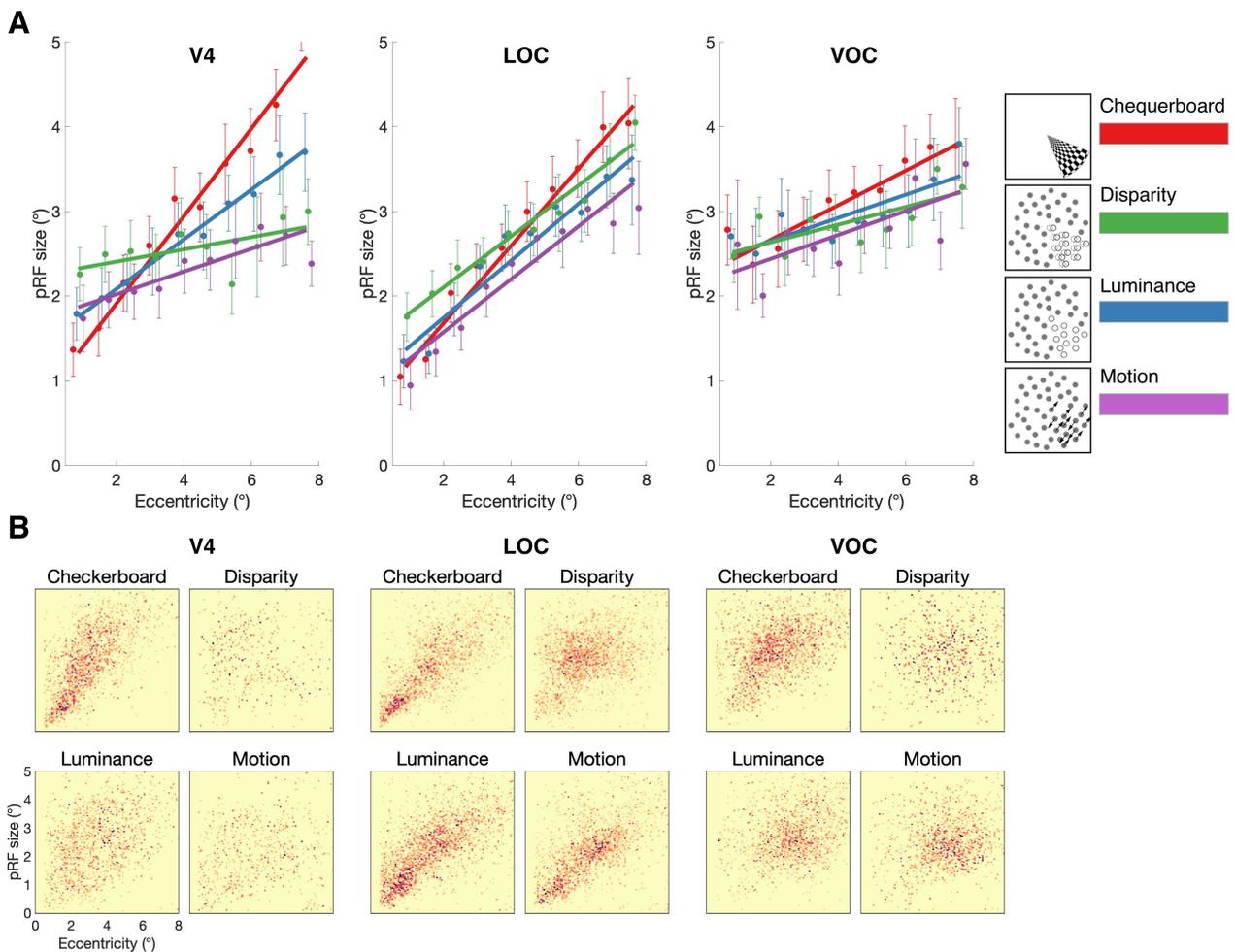
Figure 8 shows that in the ventral visual areas, like the dorsal regions, pRF size increased with

469

eccentricity (V4:  $F(9, 230) = 16.6$ ;  $p < 0.0001$ ; VOC:  $F(9,60) = 5$ ;  $p < 0.0001$ ; LOC:  $F(9,60) = 50.3$ ;

470  $p < 0.0001$ ). There was a significant effect of stimulus type in both V4 ( $F(2.5, 193.0) = 10.8$ ;  $p <$   
 471  $0.0001$ ) and LOC ( $F(2.4, 137.4) = 5.4$ ;  $p < 0.003$ ) and V4 also showed a significant interaction  
 472 between eccentricity and stimulus type ( $F(27, 230) = 2.4$ ;  $p < 0.0002$ ).

473 In V4, while there was a significant difference in pRF size when defined by disparity ( $2.6^\circ$ ) and  
 474 checkerboard ( $3.1^\circ$ ;  $F(1, 112) = 12.5$ ;  $p = 0.0006$ ), disparity did not differ from either luminance  
 475 ( $2.7^\circ$ ;  $F(1, 113) = 1.9$ ) or motion ( $2.4^\circ$ ;  $F(1, 111) = 1.8$ ). In contrast, pRF size in LOC was greater  
 476 when defined by disparity ( $2.8^\circ$ ) compared to both luminance ( $2.5^\circ$ ;  $F(1, 44) = 10.3$ ;  $p = 0.002$ )  
 477 and motion ( $2.5^\circ$ ;  $F(1, 54) = 9.7$ ;  $p = 0.003$ ). When compared to checkerboard ( $2.7^\circ$ ), there was  
 478 no difference in mean pRF size ( $F(1, 115) = 0.7$ ), but there was a significant interaction ( $F(9,$   
 479  $115) = 2.4$ ;  $p = 0.01$ ) reflecting the larger pRF sizes for disparity at lower eccentricities, and  
 480 smaller at the highest eccentricities.



481

482 **Figure 8.** (A) pRF size estimates across visual field eccentricity for checkerboard,  
483 disparity, luminance, and motion stimuli, across visual areas V4, LOC and VOC.  
484 pRF size values were binned in 0.75° steps and fitted with a linear regression  
485 model. Error bars indicate SEM. (B) Distribution of pRF size against visual field  
486 eccentricity across cortical surface points in all (N=7) participants tested. 2D  
487 binned histogram with 100x100 equal size bins. Darker colors indicate higher  
488 density of significant vertices.

#### 489 **5.4 Binocular energy model predictions of V1 integration zone**

490 The disparity-defined stimulus used in the fMRI experiment contained a single magnitude of  
491 disparity (modulating from +0.2° to -0.2°), operating under the assumption that the estimated  
492 binocular integration zone would reflect the sub-population of binocular neurons that are  
493 tuned to these disparities, irrespective of the cortical territory being examined. However,  
494 electrophysiological studies have shown that disparity tuning co-varies with receptive field  
495 size, and by extension, with eccentricity (Prince et al. 2002a). This size-disparity correlation  
496 means the size of the binocular integration zone is dependent on eccentricity, as well as  
497 sensitivity to disparity-defined stimuli.

498  
499 The binocular energy model provides a parsimonious account of the responses of binocular  
500 cells in area V1 in the presence of binocular disparity information, building disparity sensitivity  
501 from the linear combination of monocular receptive fields (Ohzawa et al. 1990; Cumming and  
502 Parker 1997; Anzai et al. 1999). In this model, the monocular receptive field is defined as a  
503 Gabor filter, that is, the product of a sinusoidal grating and a Gaussian envelope given by

504 
$$M_{(x,y)} = \sin[2\pi fx + \theta] * \frac{1}{2\pi\sigma^2} e^{-\frac{x^2+y^2}{2\sigma^2}}$$

505 where  $x$  and  $y$  are point locations in 2D space,  $f$  is the spatial frequency of the sinusoidal grating,  
 506  $\theta$  is the grating phase, and  $\sigma$  is the standard deviation of the Gaussian envelope. In the presence  
 507 of stimulus image  $I$ , the simple cell response is

$$508 \quad Sx = \iint M_{(x,y)} I_{(x,y)} dx dy$$

509 As the monocular receptive fields for the left and right eyes are independent, a position offset  
 510 is introduced to generate sensitivity to binocular disparity. Summing and squaring the products  
 511 of the monocular cells, create a linear-nonlinear 'LN' element

$$512 \quad LN = (Sx_L + Sx_R)^2$$

513 encoding disparity information at a particular phase and spatial frequency. A binocular  
 514 complex cell is constructed by simply summing the LN elements of four pairs of monocular cells,  
 515 set in phase-offset in quadrature

$$516 \quad Cx = \sum LN_0 + LN_{0.5\pi} + LN_{\pi} + LN_{1.5\pi}$$

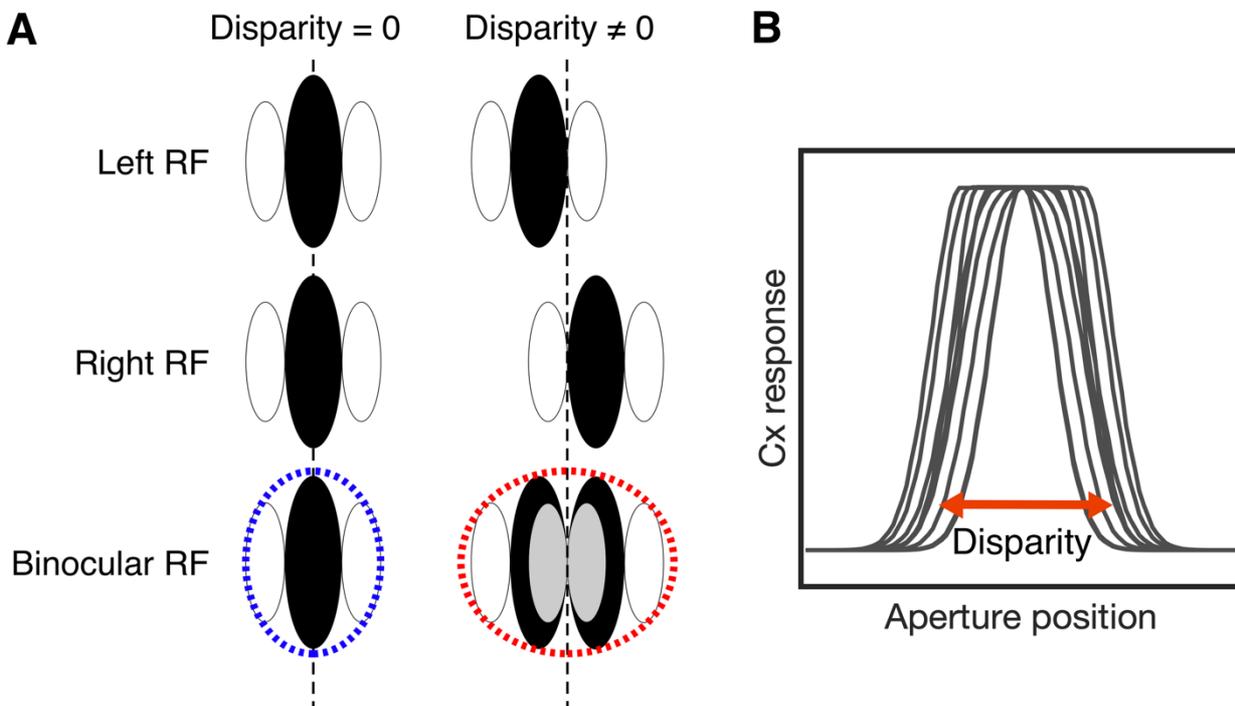
517 where two pairs of LN elements ( $\theta = 0, \pi$  and  $\theta = 0.5\pi, 1.5\pi$ ) are anti-phase with each other.  
 518 The response of the complex binocular cell can then be examined for the transient effect of  
 519 stimulation; as matching retinal images overlap (or not) with the receptive fields, the response  
 520 of the complex cell is modulated. In analogy with the fMRI task described above, this is  
 521 equivalent to the stimulus aperture transiting across the model receptive field. Let us designate  
 522 the aperture position  $A$ , for an arbitrary number of positions. In the case of a luminance-defined  
 523 stimulus, the complex cell response is given by

$$524 \quad Sx_L = \iint M_{L(x,y)} I_{(x,y)}^A dx dy$$

$$525 \quad Sx_R = \iint M_{R(x,y)} I_{(x,y)}^A dx dy$$

$$526 \quad Cx_A = \sum_{\theta=1}^4 (Sx_{L(\theta)} + Sx_{R(\theta)})^2$$

527 where the output of the complex cell is dependent on the overlap of the stimulus aperture  $I^A$   
 528 and the monocular receptive fields,  $M_L$  and  $M_R$ . In the case of a non-disparity defined stimulus,  
 529 the binocular receptive field reflects the simple sum of the monocular overlaps between the  
 530 receptive fields. However, in the presence of stimulus disparity, a disparity-tuned complex cell  
 531 pools information over an extended region of space, creating an expanded receptive field  
 532 (Figure 9). In the presence of a transient aperture, this is translated into a wider window of  
 533 response to disparity-defined stimuli. Thus, the relationship between the monocular receptive  
 534 field width and the complex cell response to a transient stimulus is a function of disparity  
 535 tuning.

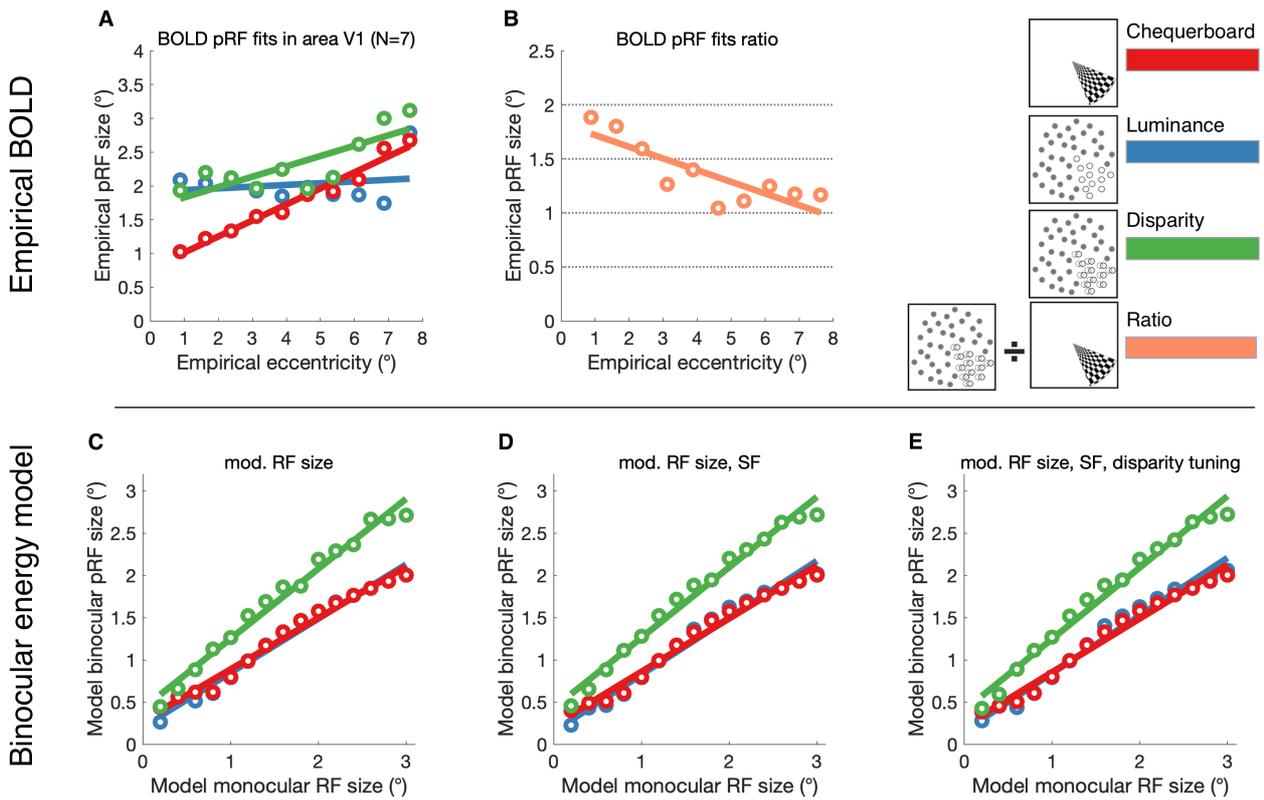


536  
 537 **Figure 9.** Binocular energy model construction in the presence of a transient  
 538 disparity aperture. (A) The monocular receptive fields for the left and right eye  
 539 are combined to form a binocular receptive field. Tuning to non-zero disparity  
 540 increases the size of the binocular receptive field, proportional to the  
 541 horizontal displacement between the monocular receptive fields. (B) In the  
 542 presence of a disparity-defined transient aperture, the window of response

543 from a complex binocular cell is determined by the magnitude of the stimulus  
544 disparity, the cell's receptive field size and disparity tuning, i.e. the horizontal  
545 displacement between left and right monocular receptive fields. In the  
546 implementation presented here, both stimulus and model disparity are fixed  
547 at  $0.2^\circ$

548  
549 Implementing the binocular energy model described above, we examined the effect of  
550 modulating monocular receptive field sizes of a population of synthetic V1 neurons, and fitted  
551 the model responses with the pRF procedure, with results shown in Figure 10. A linear  
552 relationship between the model-defined receptive field size and the fitted binocular pRF size  
553 was observed, with responses to disparity-defined stimuli exhibiting larger pRFs compared to  
554 contrast-defined checkerboard and luminance-defined random dot stimuli. Using populations  
555 of model neurons with differing (i) receptive field size, (ii) spatial frequency, and (iii) disparity  
556 tuning produced a similar pattern of results similar discrepancies between stimulus content.  
557 These discrepancies qualitatively matched the pattern observed in the empirically estimated  
558 pRF sizes from BOLD data in area V1, which also displayed larger pRF sizes for disparity-  
559 defined stimuli when compared with contrast- and luminance-defined stimuli. Therefore, while  
560 size-disparity correlation limits the size of the binocular integration zone, these results support  
561 the view that the receptive field size, constrained by eccentricity, is the principal limiting factor  
562 on the size of the binocular integration zone.

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**Figure 10.** BOLD pRF fits compared to binocular energy model predictions. (A) Empirical BOLD pRF size increases with pRF eccentricity in area V1. pRFs measured under stimulation by disparity-defined RDS are larger than those measured contrast-defined checkerboard stimuli. Error bars omitted for clarity. (B) The ratio of pRF size for disparity over contrast is shown across eccentricities. (C-E) Binocular energy model predictions of simulated V1 cell populations show a similar pattern of pRF sizes, estimated by obtaining the model cell responses under disparity-, luminance- and contrast-defined stimulation and fitting the population-level responses with a pRF model. Varying model cell parameters across the model population in (C) receptive field (RF) size, (D) RF size and spatial frequency (SF) or (E) RF size, SF and disparity tuning, did not affect pRF size significantly under any type of stimulation.

578 **6 Discussion**

579 This study provides estimates of pRFs for binocular disparity across human cortical visual  
580 areas and compares them to estimates of pRF size for non-disparity defined stimuli. In  
581 particular, the derived pRFs obtained under correlated disparity stimulation are proposed to  
582 reflect the binocular integration zones of a given cortical site at the population level. Stimuli not  
583 defined by disparity, such as the luminance edges of the checkerboard, elicit responses across  
584 a wide variety of classical receptive fields, including both monocular and binocular RFs. By  
585 comparison, the stereoscopic RDS stimuli that define the wedge or ring aperture used to map  
586 the pRFs here only deliver aperture-related information encoded in binocular disparity.  
587 Therefore, where pRF estimates diverge between the disparity condition and pRFs estimated  
588 under luminance or contrast edges, differences should reflect the role of disparity-specific  
589 processing.

590

591 Our findings are consistent with previous fMRI evidence, which report widespread binocular  
592 disparity processing across visual cortex (Backus et al. 2001; Bridge and Parker 2007; Preston  
593 et al. 2008; Minini et al. 2010; Ip et al. 2014; Goncalves et al. 2015; Ban and Welchman 2015),  
594 and a specific role for area V1, as the site of binocular integration (Barendregt et al. 2015). An  
595 important point of interpretation for our study is that, unlike studies such as Barendregt et al.,  
596 (2015), who compared binocular with monocular stimulation, the current study used binocular  
597 viewing in all tested conditions. Therefore, the stereoscopic stimuli used here probe the  
598 neuronal mechanisms that are responsible for the extraction of depth from binocular disparity.  
599 Second, our study makes direct comparisons of pRF size estimated in stereoscopic viewing-  
600 conditions for both disparity- and non disparity-defined stimuli, whereas the paper by  
601 Barendregt et al. (2015) compared overall quality of fits of the pRF model to the monocular and  
602 binocular stimulation conditions.

603

## 604           **6.1 Estimates of the binocular integration zone in area V1**

605   Our results demonstrate a discrepancy between pRFs estimated from disparity and non-  
606   disparity information in area V1, with larger receptive fields for disparity in agreement with  
607   the electrophysiological literature (Nienborg et al. 2004). This is consistent with the proposal  
608   that the binocular combination in disparity-specific neurons of V1 is a fundamental limiting  
609   stage in determining the size of the pRF (Cumming and Parker 1999, 2000; Parker and  
610   Cumming 2001). The lack of discrepancy of pRF size in areas V2 and V3 suggests little further  
611   combination of the retinal inputs in early extrastriate cortex, at least at levels detectable by  
612   population-level methods. In this regard, our findings are similar to those of Barendregt et al.  
613   (2015).

614

615   The relationship between the sizes of the non-disparity receptive field and the binocular  
616   integration zone in V1 is described by the general form of the binocular energy model (Banks  
617   et al. 2004; Nienborg et al. 2004). In this model, the ability of disparity-tuned V1 cells to detect  
618   changes in binocular disparity is limited by the width of the correlation window over which  
619   monocular signals are compared. If the window is too large, binocular matches become  
620   ambiguous; if the window is too small, the binocular image will not contain enough information  
621   to compute disparity (Banks et al. 2004; Nienborg et al. 2004). Notably, this constraint is  
622   independent of depth variation within the window, or limits imposed by optical effects, retinal  
623   sampling or stimulus construction (Tyler 1974; Schlesinger and Yeshurun 1998; Banks et al.  
624   2004). As the correlation window is defined by the size and location of the paired monocular  
625   receptive fields, the latter impose the minimum area over which disparity information may be  
626   integrated. Indeed, the disparity energy model predicts a binocular integration zone whose  
627   effective receptive field is the half-squared product of the monocular receptive fields over  
628   which binocular cross-correlation takes place (Banks et al. 2004; Nienborg et al. 2004, 2005).  
629   This prediction is borne out in electrophysiological studies; for example, (Nienborg et al. 2004)

630 showed that for disparity-tuned V1 neurons, the relationship between monocular receptive  
631 field size and the width of the correlation window corresponds to a half-squaring output  
632 nonlinearity and is approximately linear across eccentricities. Extrapolating this idea to  
633 neuronal population level, the binocular integration zone is predicted to display a half-square  
634 non-linearity in relation to other conditions, equivalent to a positive slope in the pRF size ratios  
635 between disparity and control conditions in Figure 6B.

636

## 637 **6.2 Comparison of binocular energy model prediction and the empirical** 638 **binocular integration zone**

639 An explicit, but restricted implementation of the binocular energy model allowed us to assess  
640 the effects of monocular receptive field parameters on the conjugate signal of a model V1 cell  
641 population. By manipulating the model monocular receptive field size and fitting the mean  
642 population signal with a pRF model, we confirmed that pRF size for disparity is a linear function  
643 of monocular receptive field size. We also confirmed that disparity-defined stimuli resulted in  
644 larger pRFs compared to both contrast- and luminance-defined stimuli, reflecting the wider  
645 binocular integration zone necessary for integrating horizontal discrepancies in the monocular  
646 inputs, absent in the case of contrast information. Deriving the pRF from a population of model  
647 cells with different receptive field sizes, SF and disparity tuning produced a relationship  
648 between responses to disparity-defined and contrast-defined stimuli that was comparable to  
649 the empirically-estimated pRF sizes from BOLD data in area V1.

650 Nonetheless, there were several discrepancies between the empirical data and modeling  
651 results. Firstly, when comparing the pRF size for disparity with the checkerboard, in the model  
652 the difference between the two conditions appears to include with receptive field size, whereas  
653 the empirical data appears to converge. However, the model data indicate that at the largest  
654 sizes the curves being to converge. Secondly, the model pRF sizes for contrast and luminance

655 stimuli show almost exactly the same pattern. In contrast, the empirical data for these two  
656 conditions varied considerably, with smaller pRFs at low eccentricities and larger pRFs at high  
657 eccentricities for the checkerboard. Why such a discrepancy exists is not clear, but may reflect  
658 salience of the stimulus, which is lower in the luminance condition.

659 Finally, as stated earlier, the current implementation of the energy model uses populations of  
660 units, but all have the same disparity tuning, which imposes limits the size of the pRF for the  
661 disparity-defined stimulus. As more units are incorporated that are tuned to different  
662 disparities, it is likely that the pRF size will increase, but this requires considerably more  
663 modeling that is beyond the scope of the current study.

664

### 665 **6.3 pRF size is comparable for disparity and non-disparity input defined by random** 666 **dots in dorsal visual areas**

667 Dorsal regions V3A/B, V5/MT+ and V7 showed no significant difference in pRF size for  
668 disparity when compared to the dot-defined luminance and motion conditions. There was,  
669 however, a reduction in pRF size compared to the checkerboard stimulus. This is consistent  
670 with previous work indicating that pRF mapping with isolated dot-defined bar stimuli resulted  
671 in larger pRF sizes compared to stimuli presented with a contrasting surround, either opposing  
672 motion or motion noise (Hughes et al. 2019). Thus, given the lack of difference between  
673 disparity-defined stimulus and other dot-defined stimuli, our finding is consistent with the  
674 conclusion from that paper that the pRF size in dorsal regions may depend on stimulus salience.  
675 While this result is also consistent with significant involvement of dorsal visual areas in  
676 disparity processing, most notably V3A/B (Poggio et al. 1988; Adams and Zeki 2001; Neri et al.  
677 2004; Minini et al. 2010; Ban and Welchman 2015), it does not indicate a special role for  
678 integration of disparity information across space.

679

#### 680           **6.4 Specialized processing for binocular disparity in lateral occipital cortex**

681 In a similar fashion to the results observed in V1, we detected a pattern of larger pRFs for  
682 disparity compared to other conditions in area LOC, typically considered a later ‘upstream’  
683 stage in visual cortical hierarchy processing (Grill-Spector et al. 2001). LOC is involved in the  
684 processing of 3D shape (Kourtzi and Kanwisher 2001; Kourtzi et al. 2003; Weigelt et al. 2007;  
685 Vernon et al. 2016), motion (Moutoussis et al. 2005; Krekelberg et al. 2005) and binocular  
686 depth (Chandrasekaran et al. 2006; Preston et al. 2008; Ban et al. 2012). While responsive to  
687 binocular disparity stimulation in isolation (Ip et al. 2014), LOC has been particularly  
688 associated with view-invariant representations of 3D shape which incorporate information  
689 about binocular depth (Welchman et al. 2005; Preston et al. 2009). The discrepancy between  
690 pRF sizes for disparity and other conditions may reflect the computational role for disparity  
691 information in LOC, not as the input to a binocular integration zone to generate a fused  
692 cyclopean representation, but instead as one component drawn upon to form view-invariant  
693 object representations. Preston et al., (2008) suggest that LOC represents depth position in a  
694 categorical manner, that is, as a coarse indicator of near vs. far position. As larger binocular  
695 disparities require larger receptive fields to capture the relevant retinal matches, it follows that  
696 coarseness in disparity tuning in LOC may be matched with a coarse spatial tuning in its pRFs.  
697 While the relationship between disparity tuning and receptive field size remains largely  
698 unknown in the human, in the macaque, electrophysiological studies have reported a  
699 multiplicative relationship between receptive field size and preferred disparity for V1 neurons  
700 (Prince et al. 2002b; Nienborg et al. 2004). Therefore, a coarse representation of both spatial  
701 and disparity tuning in LOC would be consistent with the tuning properties of disparity-  
702 selective cells.

703

704 An additional consideration is the source of disparity modulation. The dynamic random dot  
705 disparity stimulus presented here contains two sources of disparity information; absolute

706 disparity within the aperture field, and relative disparity at the edge between the aperture and  
707 the zero-disparity background. Unlike area V1, which is exclusively selective to absolute  
708 disparity (Cumming and Parker 1999), either component may drive responses in LOC. While  
709 LOC responses can be attributed to relative disparity (Welchman et al. 2005; Chandrasekaran  
710 et al. 2006; Preston et al. 2008; Read et al. 2010; Bridge et al. 2013), a direct coding of absolute  
711 disparity is possible and consistent with the similarity in tuning properties with area V1.

712

### 713 **6.5 fMRI estimates of binocular pRFs are in agreement with electrophysiological** 714 **priors**

715 This study presents the novel estimation of binocular receptive fields characteristics across  
716 human visual cortical areas, highlighting the discrepancies between disparity and non-  
717 disparity driven estimates of population-level receptive fields. While the estimates of pRF size  
718 for non-disparity modulated stimuli presented here are in broad agreement with previous fMRI  
719 studies (Wandell and Winawer 2015), no such baseline is available for disparity-defined pRFs.  
720 Furthermore, although direct comparisons to the electrophysiological literature may be  
721 informative, it is important to note the abstraction of these metrics from the behavior of single  
722 disparity-tuned cells. First, BOLD fMRI signals are measured from imaging voxels that contain  
723 many cells, both tuned and not tuned to disparity, which contribute to the observed signal.  
724 Second, imaged voxels encompass a large number of disparity-sensitive neurons that contain a  
725 variable distribution of spatial and depth preferences that are aggregated and averaged in the  
726 observed signal. Therefore, the BOLD signal reflects a population preference, which  
727 nevertheless reveals systematic variation in pRF size for disparity both within and across  
728 cortical visual regions.

729 Relating these findings to electrophysiology, we highlight two points. First, pRF size for  
730 disparity increased with eccentricity in all visual areas tested. Secondly, the scaling of pRF size

731 with eccentricity under disparity stimulation is consistent with the view of a binocular  
732 integration zone that obeys both local physiological constraints imposed by its component  
733 receptive fields, and imposing a limit on resolvable disparity (Banks et al. 2004; Nienborg et al.  
734 2004). Together, these observations reinforce the hypothesis that fMRI estimates of binocular  
735 receptive fields reflect the same mechanisms as those described in electrophysiological studies  
736 of disparity processing in animal models and provide the first characterization of the binocular  
737 integration zone in humans.

738

739 **7 Declarations**

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744 **Conflict of interest**

745 The authors declare no competing financial interests.

746 **Availability of data and material**

747 The datasets generated during and/or analysed during the current study are available from the  
748 corresponding author on reasonable request.

749 **Code availability**

750 The population receptive field modelling toolbox is available from  
751 <https://github.com/samsrf/samsrf>. The binocular energy modelling toolbox is available from  
752 <https://github.com/IvanAlvarez/BinocularEnergyModel>.

753 **Authors' contributions**

754 Conceptualization: IA, SAH, AJP, HB. Methodology: IA, SAH, AJP, HB; Formal analysis and  
755 investigation: IA. Writing - original draft preparation: IA; Writing - review and editing: IA, SAH,  
756 AJP, HB; Funding acquisition: AJP, HB.

757 **Ethics approval**

758 This study received ethical approval from the University of Oxford Central University Research  
759 Ethics Committee (MS-IDREC-C1-2015-040) and was conducted in accordance with the  
760 Declaration of Helsinki (2013 revision).

761 **Consent to participate**

762 Informed consent was obtained from all individual participants included in the study.

763 **Consent for publication**

764 The authors affirm that human research participants provided informed consent for  
765 publication of results based on data collected in this study.

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- 935

# Figures

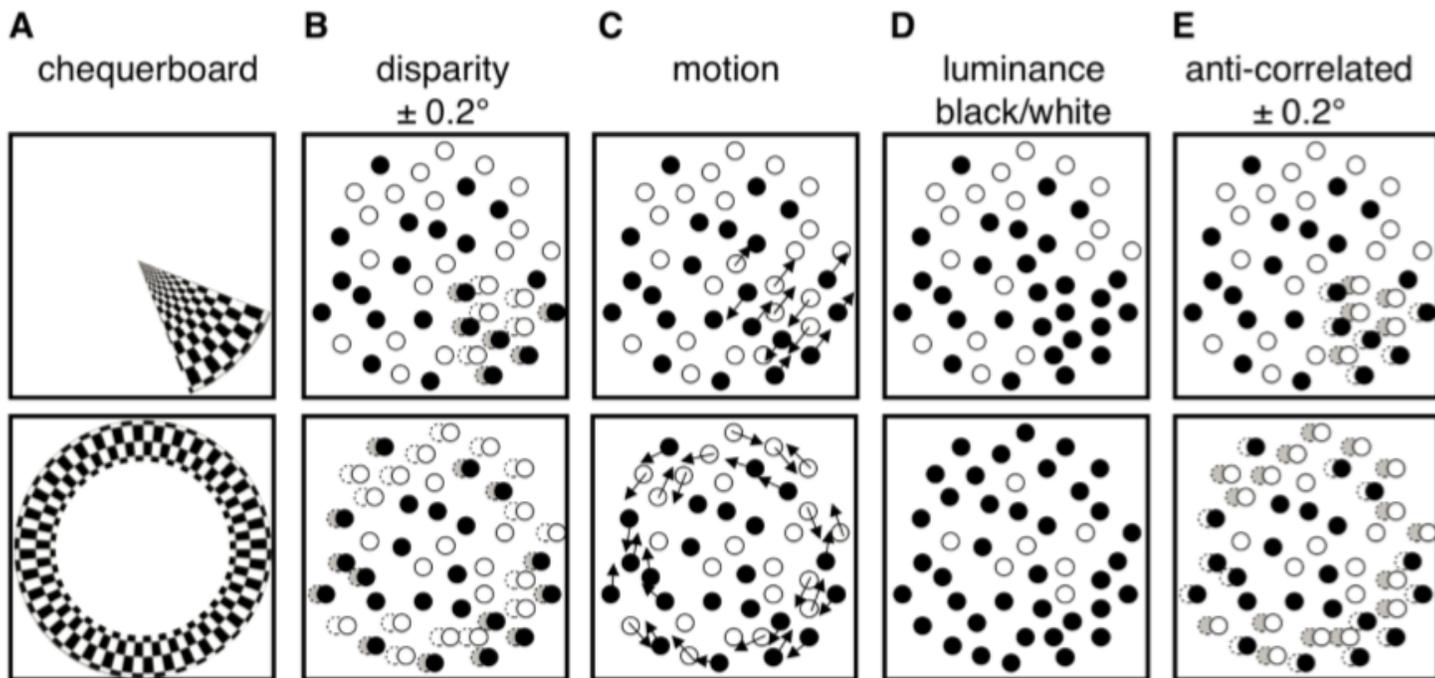
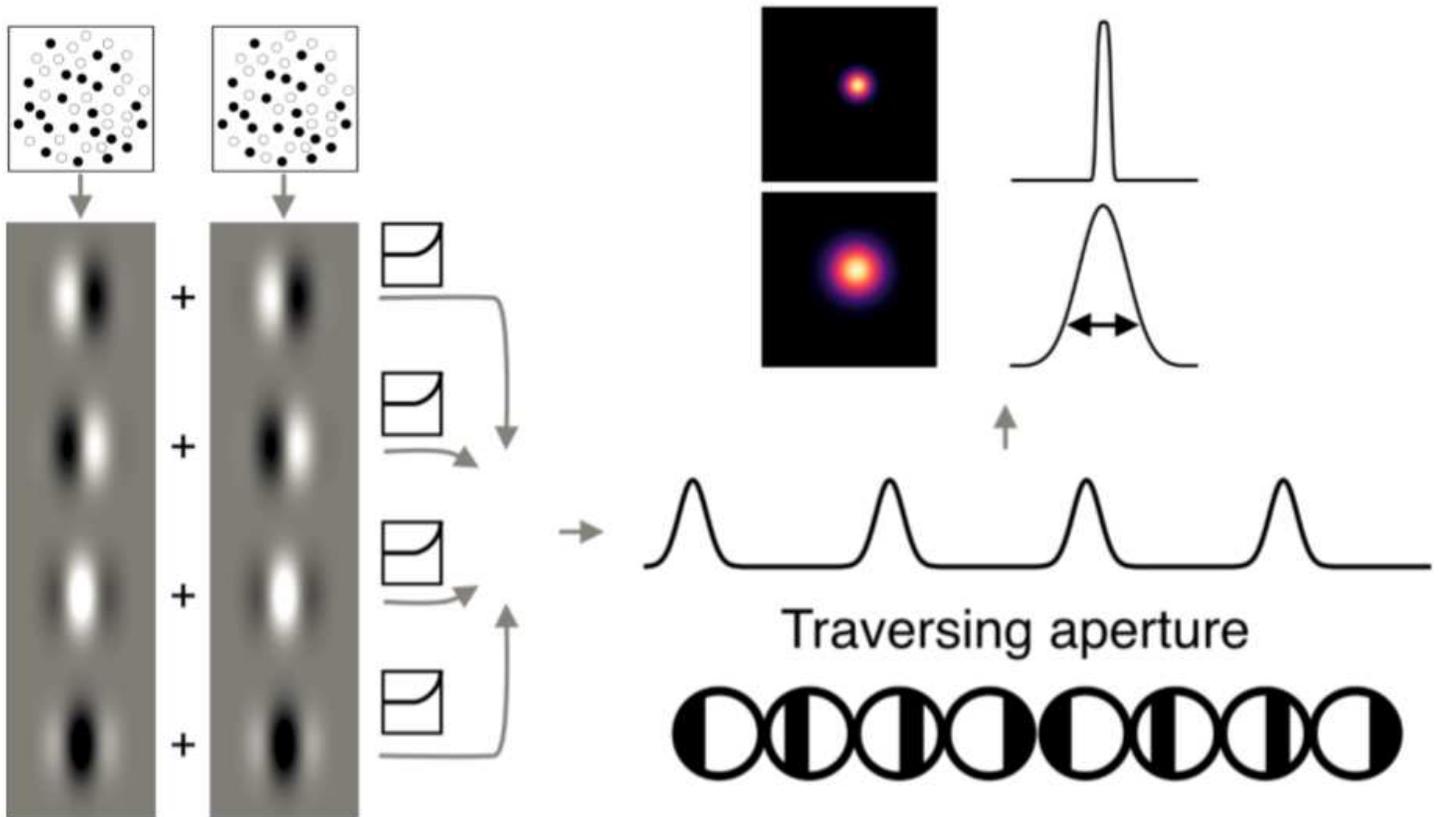


Figure 1

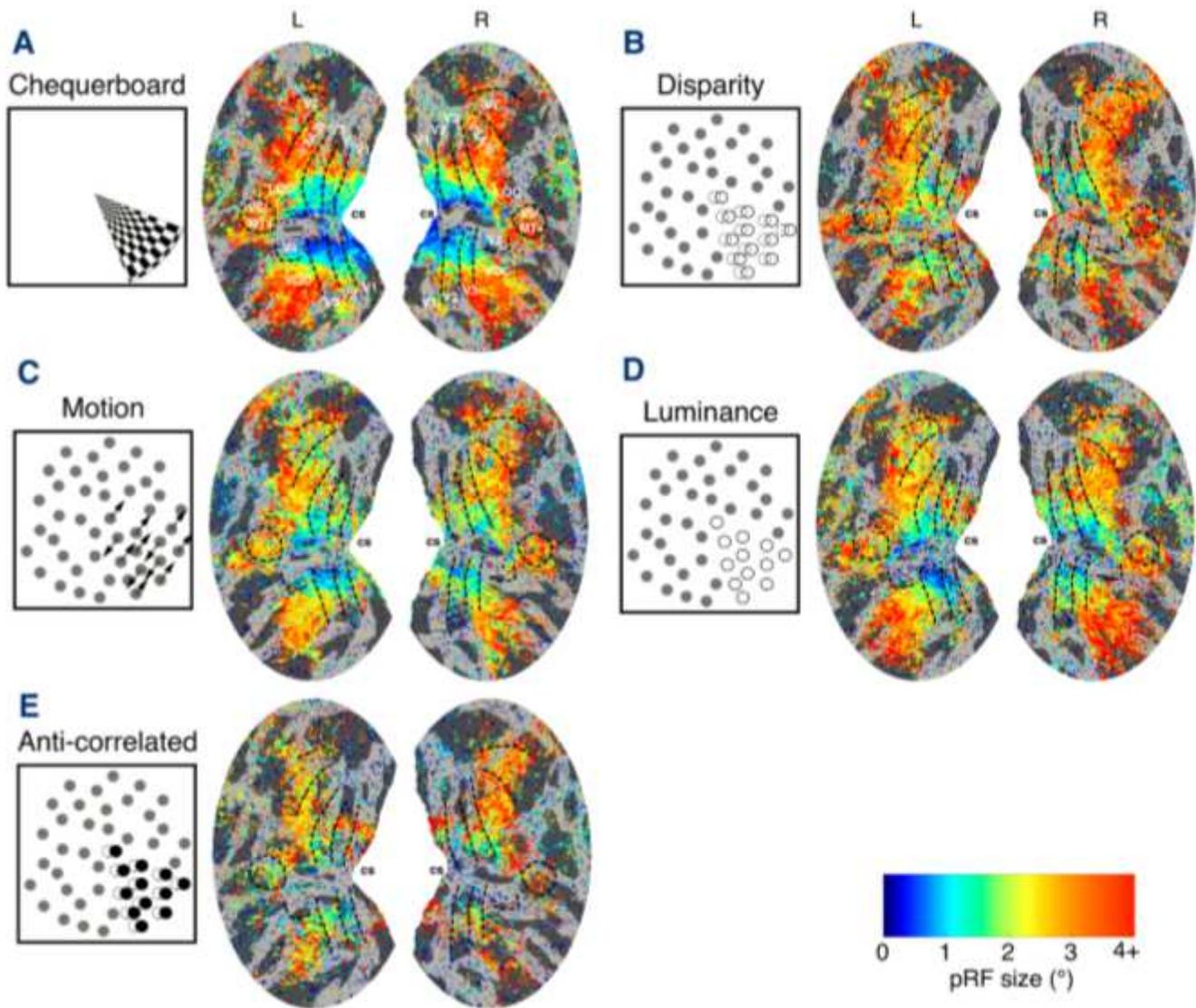
Experimental stimulus cartoon. Stimuli consisted of a contrast-reversing checkerboard (A) or dynamic random dot field (B-E) presented in a dynamically varied aperture of a wedge (upper row) or a ring (lower row). (A) Radial checkerboard reversing in contrast at 2Hz; (B) Disparity with random dot stimuli, dots inside aperture were binocularly correlated and changed in disparity ( $\pm 0.2^\circ$  from fixation); (C) Motion with clockwise and counter-clockwise components (dot speed =  $7^\circ/s$ ); (D) Luminance reversal between fully black and fully white (E) Anti-correlated binocular disparity ( $\pm 0.2^\circ$  from 182 fixation).





**Figure 3**

Binocular energy model implementation. Stimulus frames for the left and right eye were passed through a disparity-tuned Gabor filter bank, from which the monocular responses of each eye were linearly added, passed through a half-squaring non-linearity, and then pooled again by linear addition to produce the model complex cell response. The model cell responds periodically as the aperture defined by binocular correlation passes across its receptive field. The response timeseries of the population of RFs was fitted with the pRF model described. In the presence of a disparity-defined aperture, the width of the response is related to the area over which binocular information is integrated.



**Figure 4**

Group average estimates (N=7) of pRF size obtained under (A) checkerboard, (B) correlated disparity, (C) motion, (D) luminance and (E) anti-correlated disparity stimulation. pRF size estimates displayed on the normalized and flattened cortical surface, with cortical visual areas demarcated and calcarine sulcus (cs) labelled for reference. Vertices thresholded at  $CC_{norm} > 0.5$ .

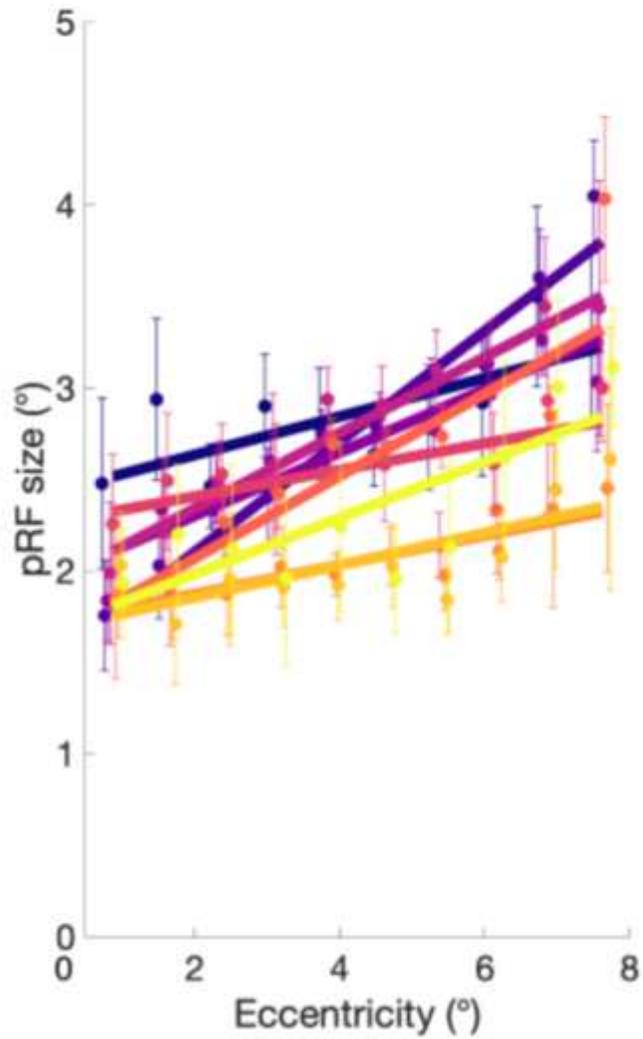
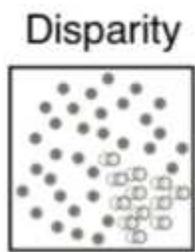
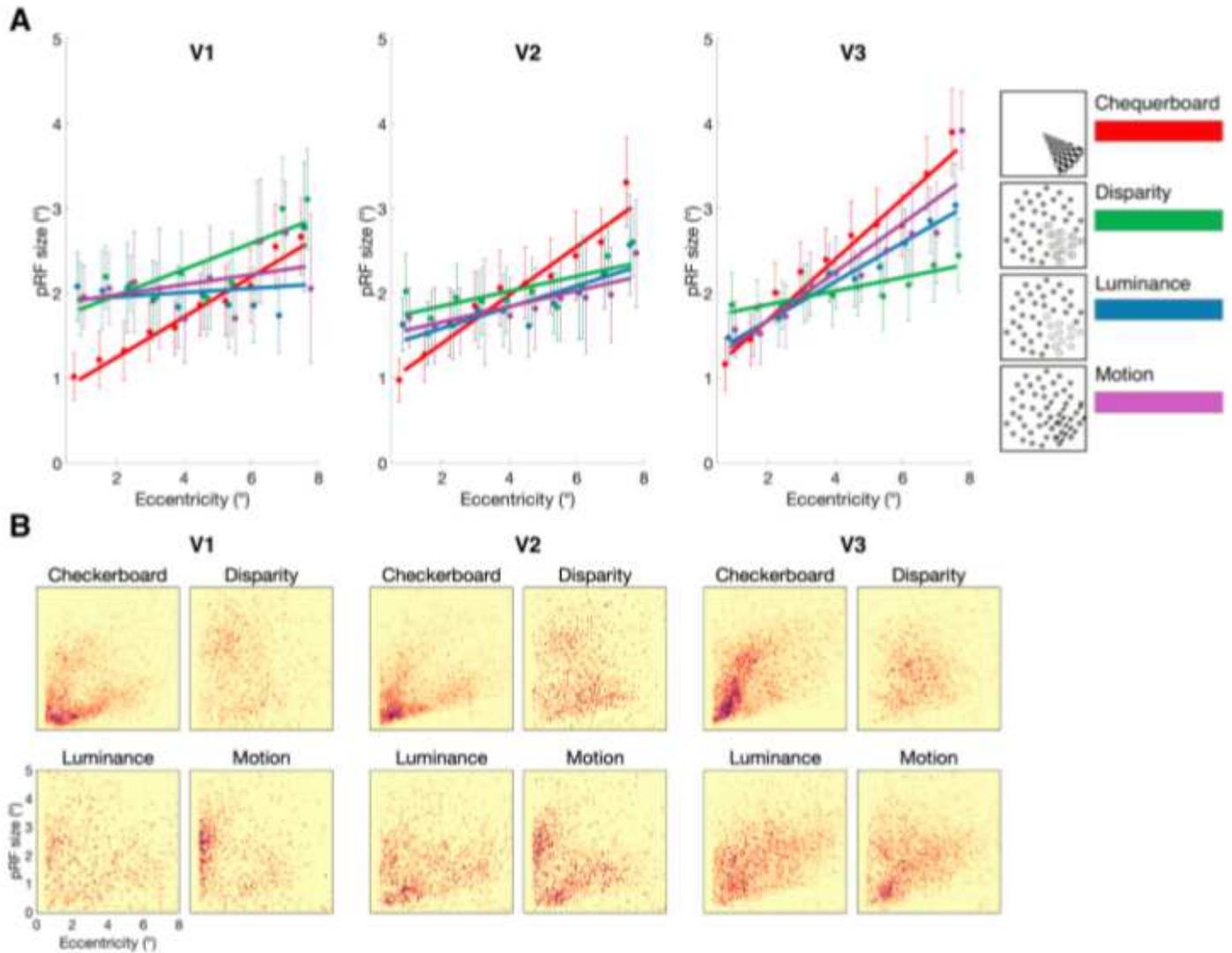


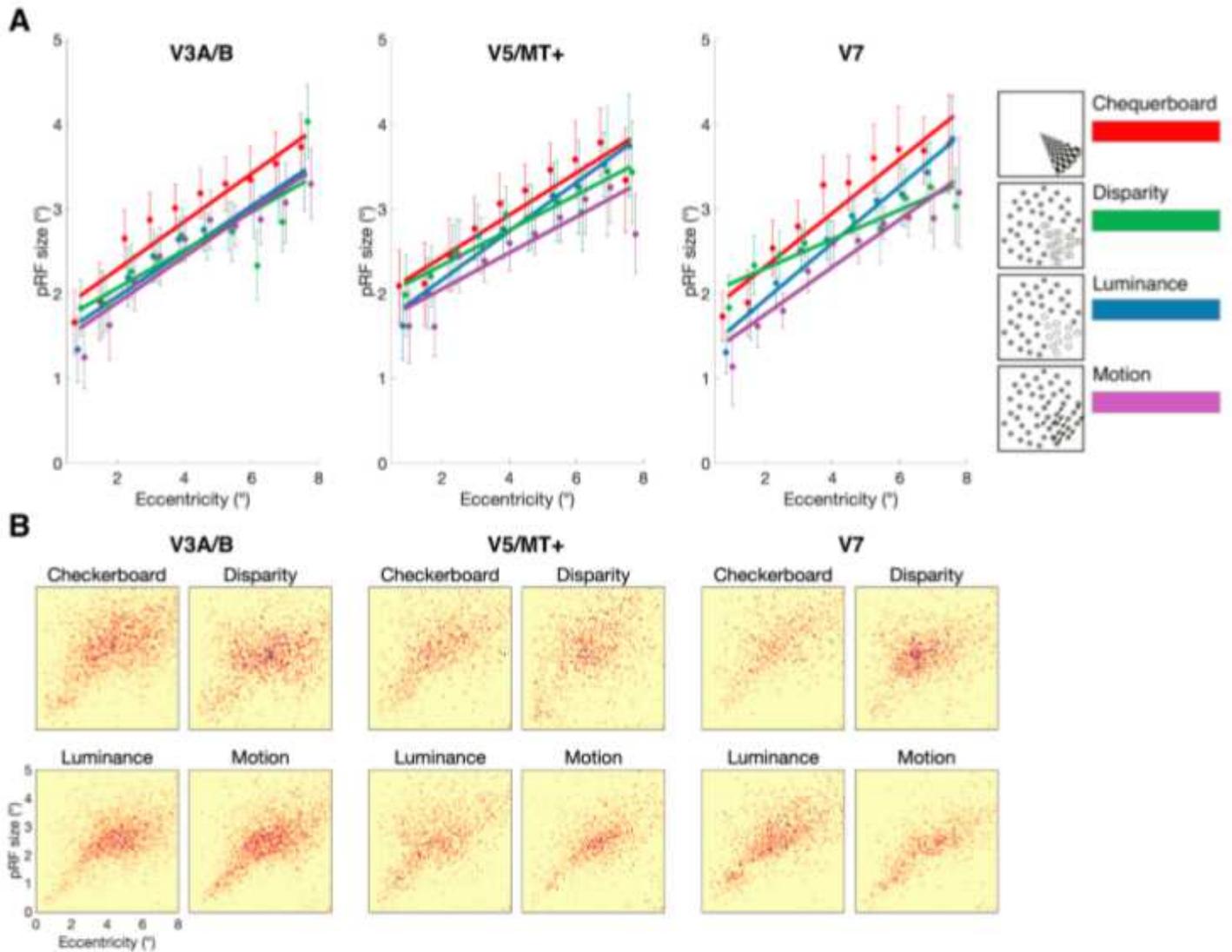
Figure 5

pRF size at different visual field eccentricities under disparity stimulation in the visual areas of interest. Estimates of stereoscopic pRF size were binned in 0.75° steps, with error bars indicating group SEM (N=7). pRF size increases both with eccentricity, and through the visual hierarchy. Vertices thresholded at CCnorm > 0.5. Small shift in eccentricity bin positions added to display differences between visual areas.



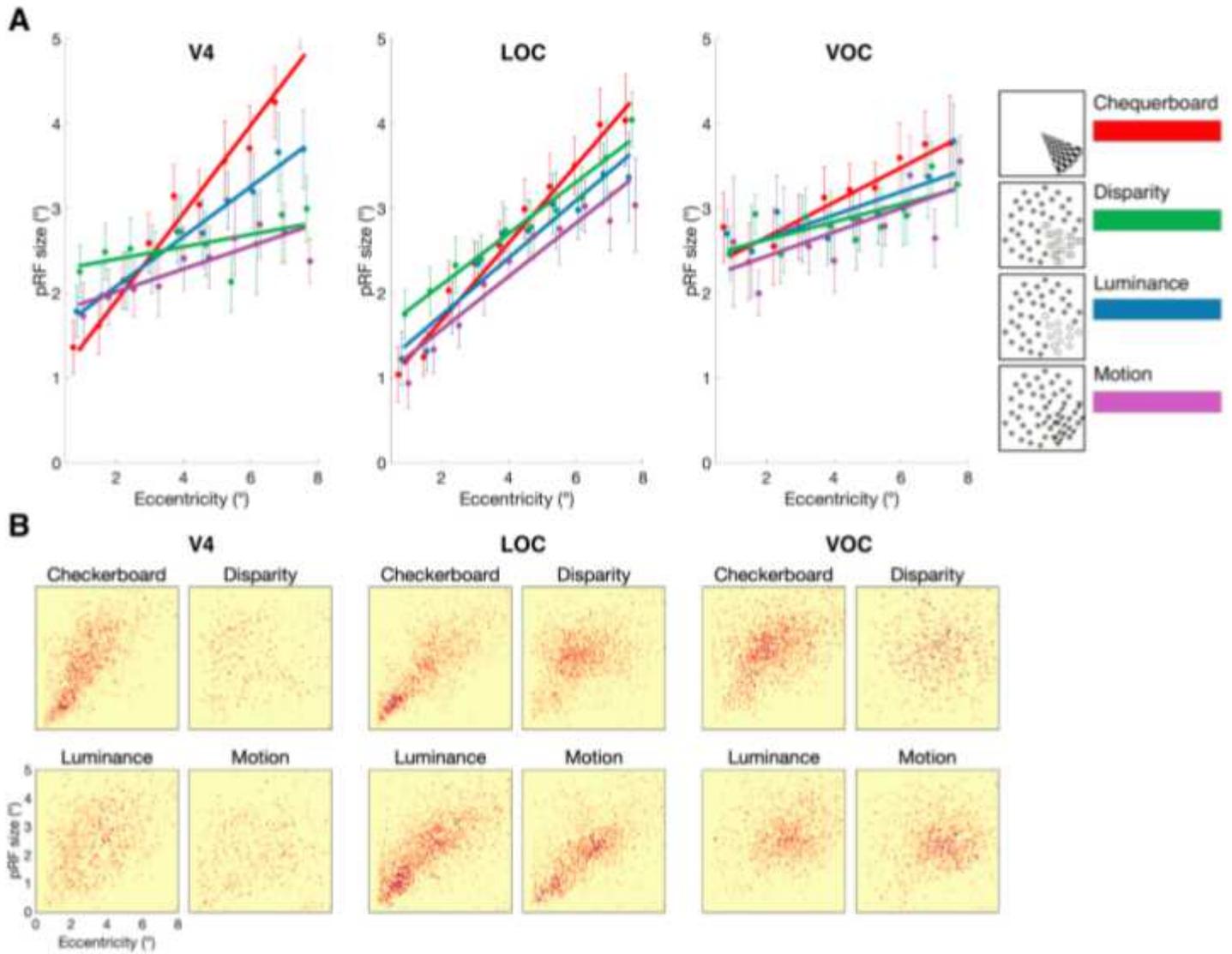
**Figure 6**

pRF size estimates across visual field eccentricity for checkerboard, disparity, luminance, and motion stimuli, across visual areas V1, V2 and V3. pRF size values were binned in 0.75° steps and fitted with a linear regression model. Error bars indicate mean standard errors across participants. (B) Distribution of pRF size against visual field eccentricity across cortical surface points in all (N=7) participants tested. 2D binned histogram with 100x100 equal size bins. Darker colors indicate higher density of significant vertices.



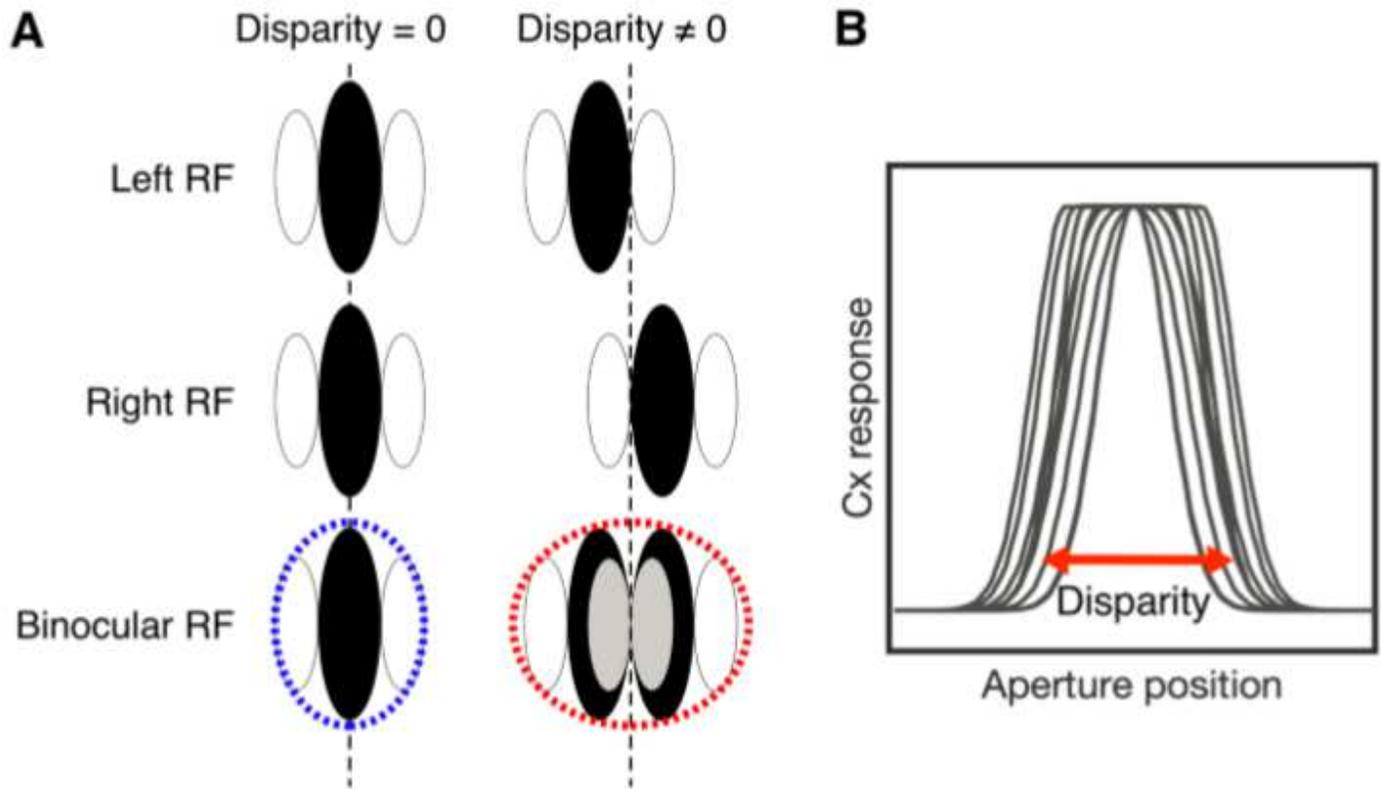
**Figure 7**

pRF size estimates across visual field eccentricity for checkerboard, disparity, luminance, and motion stimuli, across visual areas V3A/B, V5/MT+, V7. pRF size values were binned in 0.75° steps and fitted with a linear regression model. Error bars indicate mean standard errors across participants. (B) Distribution of pRF size against visual field eccentricity across cortical surface points in all (N=7) participants tested. 2D binned histogram with 100x100 equal size bins. Darker colors indicate higher density of significant vertices.



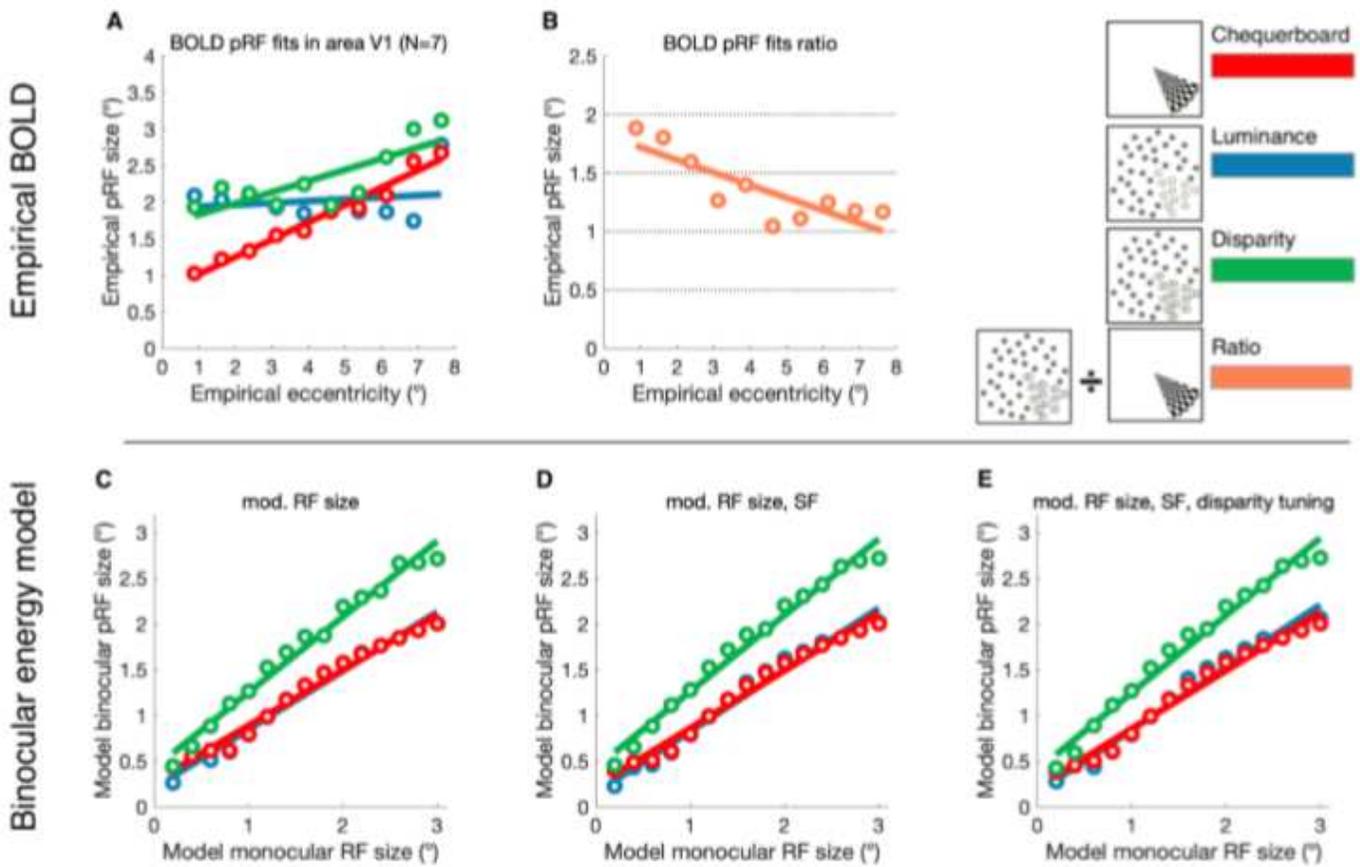
**Figure 8**

pRF size estimates across visual field eccentricity for checkerboard, disparity, luminance, and motion stimuli, across visual areas V4, LOC and VOC. pRF size values were binned in 0.75° steps and fitted with a linear regression model. Error bars indicate SEM. (B) Distribution of pRF size against visual field eccentricity across cortical surface points in all (N=7) participants tested. 2D binned histogram with 100x100 equal size bins. Darker colors indicate higher density of significant vertices.



**Figure 9**

Binocular energy model construction in the presence of a transient isparity aperture. (A) The monocular receptive fields for the left and right eye are combined to form a binocular receptive field. Tuning to non-zero disparity increases the size of the binocular receptive field, proportional to the horizontal displacement between the monocular receptive fields. (B) In the presence of a disparity-defined transient aperture, the window of response from a complex binocular cell is determined by the magnitude of the stimulus disparity, the cell's receptive field size and disparity tuning, i.e. the horizontal displacement between left and right monocular receptive fields. In the implementation presented here, both stimulus and model disparity are fixed at  $0.2^\circ$



**Figure 10**

BOLD pRF fits compared to binocular energy model predictions. (A) 565 Empirical BOLD pRF size increases with pRF eccentricity in area V1. pRFs measured under stimulation by disparity-defined RDS are larger than those measured contrast-defined checkerboard stimuli. Error bars omitted for clarity. (B) The ratio of pRF size for disparity over contrast is shown across eccentricities. (C-E) Binocular energy model predictions of simulated V1 cell populations show a similar pattern of pRF sizes, estimated by obtaining the model cell responses under disparity-, luminance- and contrast-defined stimulation and fitting the population-level responses with a pRF model. Varying model cell parameters across the model population in (C) receptive field (RF) size, (D) RF size and spatial frequency (SF) or (E) RF size, SF and disparity tuning, did not affect pRF size significantly under any type of stimulation.