

1 Spatial sampling in human visual cortex is
2 modulated by both spatial and feature-based
3 attention

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12 *Conflict of interest*

13 The authors declare no competing financial interests.

14 *Acknowledgements:*

15 This study was supported in part by an Open Research Area grant (ORA; #464-11-
16 030) issued by the Netherlands Organisation for Scientific Research (NWO) to JT.

Abstract

17

18 Spatial attention changes the sampling of visual space. Behavioral studies suggest that
19 feature-based attention modulates this resampling to optimize the attended feature's sam-
20 pling. We investigate this hypothesis by estimating spatial sampling in visual cortex while
21 independently varying both feature-based and spatial attention.

22 Our results show that spatial and feature-based attention interacted: resampling of
23 visual space depended on both the attended location and feature (color vs. temporal fre-
24 quency). This interaction occurred similarly throughout visual cortex, regardless of an
25 area's overall feature preference. However, the interaction did depend on spatial sampling
26 properties of voxels that prefer the attended feature. These findings are parsimoniously
27 explained by variations in the precision of an attentional gain field.

28 Our results demonstrate that the deployment of spatial attention is tailored to the
29 spatial sampling properties of units that are sensitive to the attended feature.

Introduction

30
31 The resolution of the visual system is highest at the fovea and decreases gradually with
32 increasing eccentricity. But the visual system's resolution is not fixed. Attention can be
33 directed to a location in space and/or a visual feature, which temporarily improves percep-
34 tual sensitivity (Posner et al., 1980; Rossi and Paradiso, 1995; Found and Müller, 1996;
35 Carrasco and Yeshurun, 1998; Yeshurun and Carrasco, 1999; Kumada, 2001; Saenz et
36 al., 2003; Wolfe et al., 2003; Theeuwes and van der Burg, 2007) at the cost of reduced
37 sensitivity for non-attended locations and features (Kastner and Pinsk, 2004; Pestilli and
38 Carrasco, 2005; Wegener et al., 2008).

39 Attending a location in space increases activity in units representing the attended lo-
40 cation, as shown by both electrophysiological (Luck et al., 1997; Reynolds et al., 2000) and
41 fMRI studies (Tootell et al., 1998; Silver et al., 2005; Datta and DeYoe, 2009). In addition,
42 spatial receptive fields were shown to shift toward an attended location in macaque MT+
43 (Womelsdorf et al., 2006) and V4 (Connor et al., 1997). Using fMRI to measure popula-
44 tion receptive fields (pRFs; Dumoulin and Wandell, 2008; Dumoulin and Knapen, 2018),
45 it was found that pRF shifts induced by spatial attention occur throughout human visual
46 cortex (Klein et al., 2014; Kay et al., 2015; Sheremata and Silver, 2015; Vo et al., 2017), a
47 process thought to improve visual resolution at the attended location (Anton-Erxleben
48 and Carrasco, 2013; Kay et al., 2015; Vo et al., 2017). Such *spatial resampling* is under-
49 stood as the result of an interaction between bottom-up sensory signals and a top-down
50 attentional gain field (Womelsdorf et al., 2008; Klein et al., 2014; Miconi and VanRullen,
51 2016).

52 Feature-based attention, for example directed toward color or motion, selectively in-
53 creases activity in those units that represent the attended feature, as evidenced by electro-
54 physiological (Treue and Maunsell, 1996; Treue and Trujillo, 1999; McAdams and Maun-
55 sell, 2000; Maunsell and Treue, 2006; Müller et al., 2006; Zhang and Luck, 2009; Zhou
56 and Desimone, 2011), fMRI (Saenz et al., 2002; Serences and Boynton, 2007; Jehee et al.,
57 2011), and behavioral reports (Saenz et al., 2003; White and Carrasco, 2011). These stud-
58 ies consistently show that feature-based attention modulates processing irrespective of
59 the attended stimulus's spatial location. In addition, feature-based attention also appears

60 to shift featural tuning curves toward the attended value, as reported by both electrophys-
61 iological (Motter, 1994; David et al., 2008) and fMRI studies (Çukur et al., 2013).

62 The similarity in the effects of feature-based and spatial attention on affected neu-
63 ral units suggests a common neural mechanism for both sources of attention (Hayden
64 and Gallant, 2005; Cohen and Maunsell, 2011). Yet spatial attention necessitates retino-
65 topically precise feedback (Miconi and VanRullen, 2016), while feature-based attention
66 operates throughout the visual field (Maunsell and Treue, 2006). Studies investigating
67 whether one source of attention potentiates the other generally find that interactions are
68 either nonexistent or very weak at the earliest stages of processing (David et al., 2008; Hay-
69 den and Gallant, 2009; Patzwahl and Treue, 2009; Zhang and Luck, 2009), but emerge at
70 later stages of visual processing (Hillyard and Munte, 1984; Handy et al., 2001; Bengson et
71 al., 2012; Ibos and Freedman, 2016), and ultimately influence behavior (Kingstone, 1992;
72 Kravitz and Behrmann, 2011; Leonard et al., 2015; White et al., 2015; Nordfang et al.,
73 2017). In addition, the effects of feature-based compared to spatial attention arise earlier
74 in time (Hopf et al., 2004; Hayden and Gallant, 2005; Andersen et al., 2011). This supports
75 the idea that feature-based attention can direct spatial attention toward or away from
76 specific locations containing attended or unattended features (Cohen and Shoup, 1997;
77 Cepeda et al., 1998; Burnett et al., 2016). Especially when attention is endogenously cued,
78 feature-based attention has been argued to influence the spatial resampling induced by
79 spatial attention in order to optimize sampling of visual features for behavior (Yeshurun
80 and Carrasco, 1998, 2000; Yeshurun et al., 2008; Barbot and Carrasco, 2017). Together,
81 these studies suggest that feature-based attention can influence the spatial resampling re-
82 sulting from spatial attention.

83 To investigate this hypothesis directly, we measured pRFs under conditions of differ-
84 ential spatial attention (i.e. toward fixation or the mapping stimulus) and feature-based
85 attention (i.e. toward the mapping stimulus's motion or color content). We first char-
86 acterize how spatial attention influences the sampling of visual space, and subsequently
87 investigate how feature-based attention modulates this spatial resampling. An explicit
88 gain-field interaction model allowed us to formally capture the pRF position changes re-
89 sulting from our attentional manipulations (Klein et al., 2014).

90 In brief, our results show that pRF changes are stronger when attending the stimulus's

91 color compared to temporal frequency content. These modulations occurred similarly
92 throughout the visual system, regardless of an area's bottom-up feature preference (such
93 as areas MT+ for temporal frequency and areas VO and hV4 for color (Liu and Wandell,
94 2005; Brouwer and Heeger, 2009, 2013)). We suggest that the larger degree of spatial
95 resampling when attending color is related to finer spatial sampling in relatively color
96 preferring voxels. In addition, we show that these feature-based attentional modulations
97 can be explained by changes in the precision of the attentional gain field.

98 *Results*

99 We first characterize the pattern of pRF parameter changes that resulted from the differen-
100 tial allocation of spatial attention (i.e. either toward fixation or the moving bar stimulus).
101 We explain this pattern of results from an attentional gain field perspective. Then, we
102 investigate how feature-based attention (i.e. either toward color or temporal frequency
103 changes in the bar) modulated the pRF changes, and how this modulation relates to
104 bottom-up feature preference.

105 *Region of interest definition*

106 Figure 1A shows voxels' *Attend Fixation* location preferences, by depicting color-coded
107 polar angle coordinates on an inflated cortical surface for one example participant's right
108 hemisphere. We examined the relation between pRF eccentricity and size within each
109 of the retinotopic regions, and performed further analyses on those regions that showed
110 clear progressions of polar angle on the surface as well as positive size-eccentricity rela-
111 tions in all participants, as shown in Figure 1B (and Supplementary Figure 1). In addition,
112 we created a *combined* ROI that pooled voxels across selected ROIs in order to evaluate
113 pRF changes across the visual system.

114 *pRF changes induced by spatial attention*

115 In order to quantify pRF changes resulting from differential allocation of spatial atten-
116 tion we created an *Attend Stimulus* condition by averaging pRF parameters between the

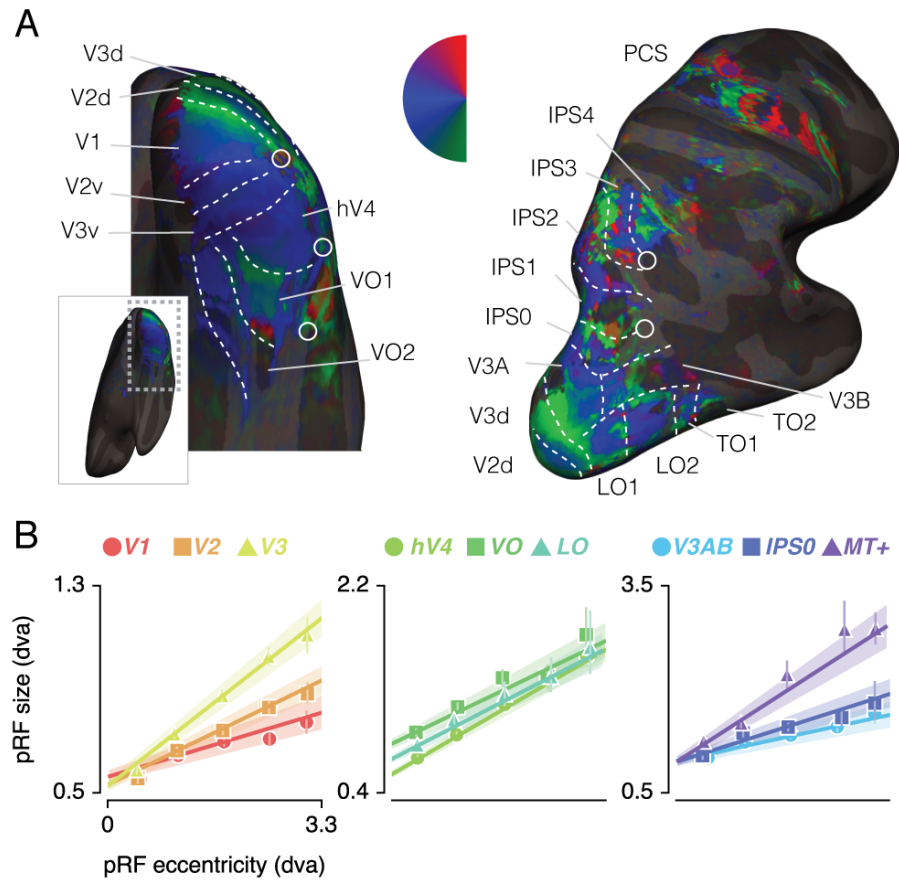


Figure 1: ROI definition A. *Attend Fixation* pRF polar angle maps for an example participant with retinotopic areas up to the intra-parietal sulcus defined by hand. B. *Attend Fixation* pRF size as a function of eccentricity for all areas that showed robust relationships across all participants. All error bars and shaded error regions denote 95% CI of data and linear fits respectively across voxels.

117 *Attend Color* and *Attend Temporal Frequency* (henceforth: *Attend TF*) conditions. To in-
118 spect how spatial attention affected pRF positions, we plotted a vector from the *Attend*
119 *Fixation* to the *Attend Stimulus* pRF position (Figure 2A and B and Supplementary Figure
120 2). Visual inspection of these pRF position shifts shows both increasing shift magnitude
121 up the visual hierarchy and shifts occurring mainly along the radial dimension (i.e. toward
122 or away from the fovea).

123 *pRF shift direction*

124 This latter observation seems at apparent odds with a recent study reporting pRFs to
125 mainly shift in the horizontal direction (Sheremata and Silver, 2015). To quantify the ob-
126 served direction of pRF shifts we computed the ratio of shifts in the radial, horizontal, and
127 vertical directions (see Figure 2C and Supplementary Figure 3). In line with the data of
128 Sheremata and Silver (2015), we find that changes of pRF horizontal location consistently
129 better describe the overall shifts than do changes of pRF vertical location in all ROIs ex-
130 cept V1/2/3 (p 's < .05, see Supplementary Tables 1 and 10). We also find that pRF shifts
131 are described even better by shifts in the radial dimension (i.e. changes in eccentricity)
132 compared to shifts in the horizontal direction in all ROIs (p 's < .01, see Supplementary Ta-
133 bles 1 and 11). Figure 2D is intended to ease interpretation of these results. It depicts how
134 different hypotheses regarding the underlying directionality of pRF shifts (i.e. horizontal,
135 vertical, or radial - i.e. foveopetal/foveofugal) translate into changes in measured pRF x ,
136 y , and eccentricity as a function of quarter visual field polar angle (i.e. from vertical to
137 horizontal meridian). For example, if pRFs shift primarily in the radial direction (right
138 hypothesis column, Figure 2D), this would result in strongest pRF x -direction changes
139 close to the horizontal meridian and strongest pRF y -direction changes close to the ver-
140 tical meridian. pRF eccentricity changes however, would show no dependence on polar
141 angle. Figure 2D, right column, shows that the data (*combined* ROI) corresponds most
142 to the radial shift hypothesis. To quantify this visual intuition, we compared the slopes
143 of the change in pRF x and y over polar angle by binning polar angle into three bins and
144 comparing the first and last bins (i.e. horizontal and vertical meridian respectively). This
145 showed that, compared to the slope of pRF y change over polar angle, the slope of pRF
146 x change was more negative (p < .001, cohen's d = 0.677, N = 11946, see Supplementary

147 Figure 4). This pattern of results can only be explained by pRFs shifting in the radial direc-
 148 tion. Visual field coverage is known to be non-uniform such that the horizontal meridian
 149 is overrepresented at both subcortical (Schneider et al., 2004) and cortical (Swisher et al.,
 150 2007; Silva et al., 2017) levels and was also clearly present in our data (Rayleigh tests for
 151 non-uniformity in ROIs separately, p 's < .001, see Supplementary Tables 2, 12 and 13).
 152 This means that shifts that occur exclusively in the radial dimension appear as a domi-
 153 nance of horizontal compared to vertical shifts when averaging over the visual field.

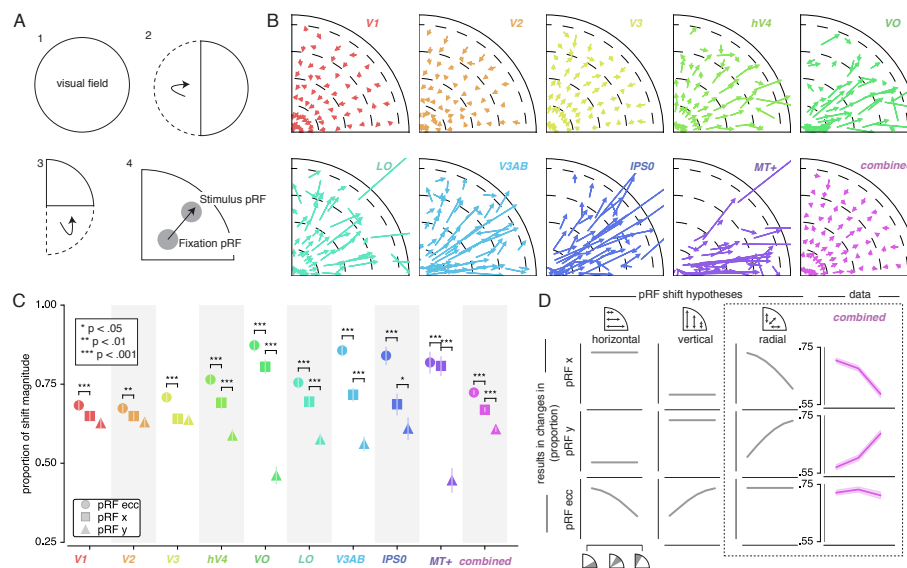


Figure 2: Effect of attention on pRF position. A. Plotting strategy. For pRF shift visualizations, all pRF positions are mirrored into one quadrant of the visual field. Then, vectors representing the shift of pRF centers between conditions were drawn from the *Attend Fixation* to the *Attend Stimulus* pRF position. B. Shift vectors as described in A. pRF shift magnitude increased up the visual hierarchy, and shifts appear to occur mainly in the radial direction (i.e. changes in pRF eccentricity). Dotted lines demarcate eccentricity bins used in subsequent analyses. C. Changes in pRF position in the horizontal, vertical, and radial directions as a proportion of the length of the shift vectors, as depicted in B. The magnitude of pRF shifts is consistently best described by changes in pRF eccentricity. D. pRF x, y and eccentricity position shifts plotted as a function of polar angle, for different shift direction hypotheses. The data closely matches the radial shift direction hypothesis, showing strongest pRF x shifts close to the horizontal meridian, strongest pRF y shifts close to the vertical meridian and strong pRF eccentricity changes across all polar angles. In C single, double, and triple asterisks indicate significant differences with FDR corrected $p < .05$, $< .01$ and $< .001$ respectively.

154 *pRF changes across eccentricity*

155 To further inspect the attention-induced radial shifts described above, we plotted the
156 difference between *Attend Stimulus* and *Attend Fixation* pRF eccentricity for each of four
157 *Attend Fixation* pRF eccentricity bins (Figure 3A and Supplementary Figure 5). The *com-*
158 *bined* ROI shows that overall, parafoveal pRFs shifted away from the fovea, while periph-
159 eral pRFs shifted toward the fovea. These outward shifting parafoveal pRFs are found in
160 all other ROIs except V1 and V2, whereas the inward shifting peripheral pRFs are also
161 present in V1, V2 and V3 (see Supplementary Tables 3, 4, and 14-17).

162 In addition to pRF position changes, we also inspected changes in pRF size induced by
163 differences in spatial attention as a function of *Attend Fixation* pRF eccentricity (Figure
164 3B and Supplementary Figure 6). Overall, parafoveal pRFs increased in size, while periph-
165 eral pRFs decreased in size. These expanding parafoveal pRFs were present in all ROIs
166 except V2/3, whereas shrinking peripheral pRFs were found in all ROIs except V1, MT+
167 and IPS0 (see Supplementary Tables 5, 6, and 18-21). Overall, this pattern of results is
168 strikingly similar to the changes in pRF eccentricity described above. In fact, the changes
169 in pRF size and eccentricity were strongly correlated in all ROIs (Figure 3C; Supplemen-
170 tary Figure 6; Pearson R over 20 5-percentile bins between .74 and .99, p 's < .001, see
171 Supplementary Tables 7 and 22). Together, these results show that attention to the stim-
172 ulus caused parafoveal pRFs to shift away from the fovea and increase in size, whereas
173 peripheral pRFs shifted toward the fovea and decreased in size.

174 *Formal account for observed pattern of pRF shifts*

175 In order to provide a mechanistic explanation for the complex pattern of pRF shifts
176 described above, we modeled our results using a multiplicative Gaussian gain field model
177 (Womelsdorf et al., 2008; Klein et al., 2014). We adapted this framework to work in condi-
178 tions where attention shifted over space as a function of time (see Methods). In brief, this
179 modeling procedure used the *Attend Fixation* pRF, one attentional gain field at fixation
180 and another convolved with the stimulus in order to predict the *Attend Stimulus* pRF posi-
181 tion. We determined optimal attentional gain field sizes by minimizing the difference be-
182 tween observed and predicted *Attend Stimulus* pRF positions in the quadrant visual field
183 format of Figure 2B. Figure 4A (and Supplementary Figure 7) illustrates that model pre-

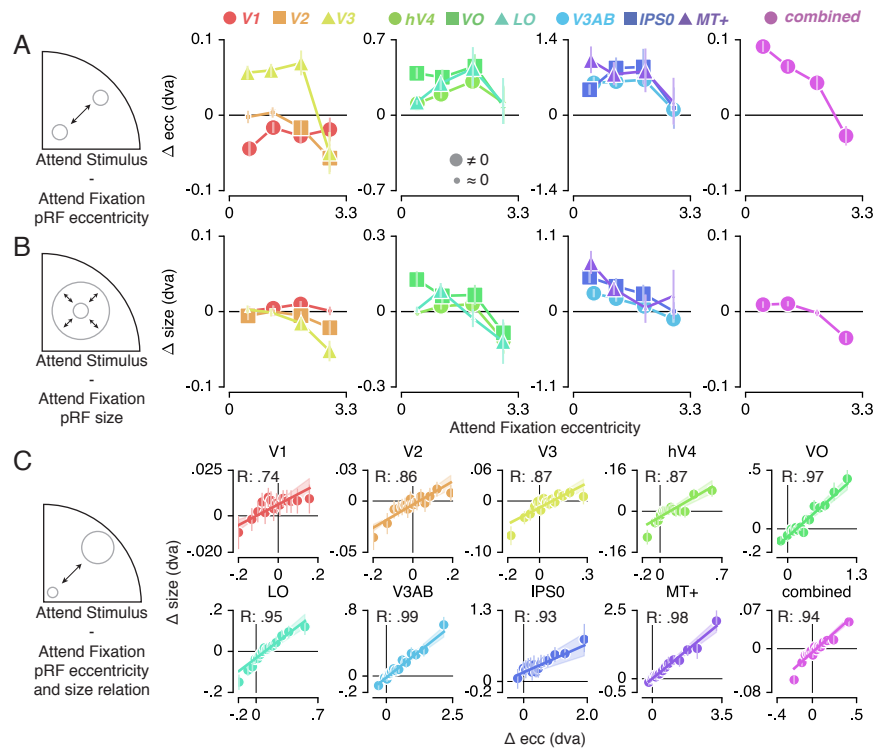


Figure 3: Effect of attention on pRF eccentricity and size. Difference between *Attend Stimulus* and *Attend Fixation* pRF eccentricity (A) and size (B) as a function of *Attend Fixation* eccentricity. Overall, parafoveal pRFs tend to shift away from the fovea and increase in size, while peripheral pRFs tend to shift toward the fovea and decrease in size. C. Changes in pRF eccentricity and size were strongly correlated in all ROIs. In A and B, markers are increased in size when bootstrapped distributions differ from 0 with FDR corrected $p < .05$. In C markers' errorbar denotes 95% CI of data over voxels and shaded error regions denote 95% CI of linear fit parameters over bins.

184 ductions closely followed the data, thereby accurately reproducing radially shifting pRFs.
185 Examining the predicted change in pRF eccentricity as a function of eccentricity (i.e. the
186 dominant pRF shift direction; Figure 4B and Supplementary Figure 8) showed that the
187 model was able to capture widely varying eccentricity change profiles across ROIs using
188 very similar attentional gain field sizes (Figure 4C). This shows that a common attentional
189 influence can result in very different pRF shift patterns, which then necessarily depend
190 on differential spatial sampling properties across ROIs (i.e. distribution of pRF sizes and
191 positions). In sum, these results show that the attentional gain field model provides a
192 parsimonious and powerful account for the variety of pRF shift patterns across ROIs.

193 We further investigated how the model was able to reproduce the eccentricity-
194 dependent eccentricity changes we reported above. For this, we inspected pRF shifts
195 induced by attending either fixation or the stimulus relative to the stimulus drive (i.e. the
196 pRF outside the influence of attention derived from the model). For illustrative purposes,
197 we here display results for V2, V3 and IPS0 as these areas showed marked differences in
198 their eccentricity change profile (Figure 4D-F). The left panels of each figure reveal the
199 effects of attending fixation and the stimulus separately. This shows that both sources of
200 spatial attention pull the measured pRFs toward the fovea, albeit with differing relative
201 magnitudes across eccentricity. The right panel of each figure shows that the resulting
202 difference between attending fixation and the stimulus constitutes the eccentricity
203 dependent patterns observed in the data (Figure 4B).

204 Together, these analyses show that existing multiplicative gain field models of atten-
205 tion can be extended to predict pRF shifts in situations where spatial attention shifts over
206 time. Additionally it confirms, extends, and quantifies earlier reports showing that the
207 precision of the attentional gain field is similar across the visual hierarchy (Klein et al.,
208 2014).

209 *Feature-based attentional modulation*

210 Having established (1) the pattern of changes in spatial sampling (i.e. changes in pRF size
211 and eccentricity) resulting from differential allocation of spatial attention and (2) a mech-
212 anistic explanation of these changes, we next examined how this pattern was modulated

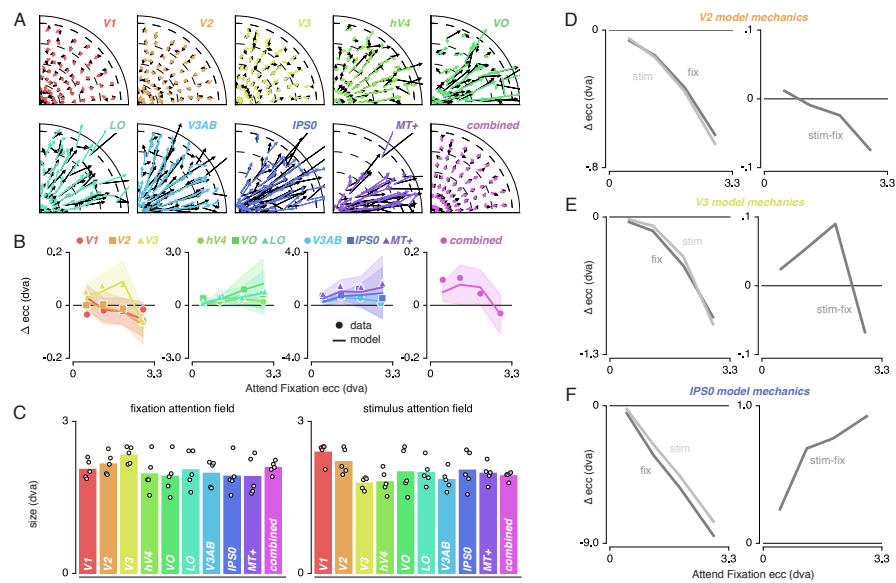


Figure 4: An attentional gain field model showed that the changes in pRF position can be described by a Gaussian interaction process. A. Observed (black) and predicted (color) pRF shifts. B. Observed and predicted changes in pRF eccentricity (the main pRF shift direction) as a function of eccentricity. Markers depict data and lines the corresponding attentional gain field model fit. C. Fitted fixation and stimulus attentional gain field sizes. Dots depict individual subjects, and the bar the average across subjects. D-F. Left panels depict changes in eccentricity induced by attending fixation (dark gray lines) and by attending the stimulus (light gray lines). Although both sources of attention cause a pull toward the fovea in all ROIs, relative shift magnitude differs across eccentricity. The right panels show how the difference between both spatial attention conditions results in the patterns as observed in B. In B, Error bars denote 95% CIs over subjects. Plotting conventions as in Figure 2.

213 by differences in feature-based attention. Figure 5A (and Supplementary Figure 9) shows
214 how pRF eccentricity and size are differentially affected by attending color or temporal
215 frequency within the stimulus for the *combined* ROI. This illustrates that while both tasks
216 caused similar pRF changes, these effects were generally more pronounced when attend-
217 ing color.

218 In order to quantify the modulation of feature-based attention per voxel we first setup
219 a single robust index of the of the degree to which spatial attention resampled visual space,
220 combining changes in pRF eccentricity and size (as these were highly correlated, see Fig-
221 ure 3C). This Attentional Modulation Index (AMI, see Methods) is depicted in Figure 5B
222 for the *combined* ROI when attending color and TF. We then quantified the difference in
223 this attentional modulation index between attending color and temporal frequency as a
224 feature-based Attentional Modulation Index (feature AMI, see Methods). Positive values
225 of feature AMI indicate that attending color induced greater pRF changes, while negative
226 values indicate that attending TF lead to stronger pRF changes. Figure 5C shows that this
227 feature AMI was positive across eccentricity in the *combined* ROI. Inspecting the average
228 feature AMI across voxels within each ROI (Figure 5D) reveals that attending changes
229 in color compared to TF in the bar stimulus produced stronger spatial resampling in all
230 ROIs (p 's < .01, see Supplementary Tables 8 and 23).

231 *Feature AMI and feature preference*

232 The feature-based modulations we describe above are possibly related to differences
233 in bottom-up preference for the attended features. Feature-based attention is known to
234 increase activity of neurons selective for the attended feature, regardless of spatial lo-
235 cation (Treue and Maunsell, 1996; Treue and Trujillo, 1999; McAdams and Maunsell,
236 2000; Maunsell and Treue, 2006; Müller et al., 2006; Zhang and Luck, 2009; Zhou and
237 Desimone, 2011). If voxels contain on average more color-preferring compared to TF-
238 preferring neurons, attending color should therefore activate a greater amount of neu-
239 rons, potentially leading to a greater apparent shift of the aggregate pRF. To test this hy-
240 pothesis, we estimated the difference in response amplitude to the presence of color and
241 temporal frequency within a full-field stimulus (in a separate experiment, see Methods).
242 We then summarized each voxels' relative preference for color and temporal frequency

243 by means of a feature preference index. Higher values of this feature preference index in-
244 dicate greater preference for color compared to TF. Figure 5E (and Supplementary Figure
245 10) displays the feature AMI as a function of feature preference, for each ROI. Note that
246 feature preference was negative on average in most ROIs, suggesting that our TF manip-
247 ulation (7 vs 0 Hz grayscale Gabors) caused stronger response modulations compared to
248 our color manipulation (colored vs grayscale Gabors). Although this induced an offset
249 across the brain, variations in this measure across ROIs replicate known specializations of
250 the visual system with high precision (Liu and Wandell, 2005; Brouwer and Heeger, 2009,
251 2013): while areas MT+ and V1 show the strongest preference for TF compared to color,
252 areas V4 and VO show the strongest preference for color compared to TF. Importantly,
253 regardless of these large variations in feature preferences between MT+/V1 and VO/hV4,
254 average feature AMI was nearly equal in these ROIs. In addition, there was no correla-
255 tion between feature preference and feature AMI across all ROIs ($R = .20$, $p = .608$, $N =$
256 9 , $\rho = .37$, $p = .332$, $N = 9$). These results show that the feature-based attentional mod-
257 ulations we observe occur globally across the brain, and do not depend on bottom-up
258 feature preference.

259 *Feature preference and spatial sampling*

260 What could then explain the fact that attending color in the stimulus induced greater
261 changes in spatial sampling? Behavioral studies have suggested that the influence of spa-
262 tial attention should be adjusted by feature-based attention in order to improve sampling
263 of attended visual features (Yeshurun et al., 2008; Barbot and Carrasco, 2017). One of the
264 factors that influences required spatial resampling is pRF size. Smaller pRFs need to shift
265 a greater distance in order to bring a stimulus into their responsive region. This means
266 that if color-preferring voxels are relatively small, this creates a requirement of greater
267 shifts when attending color. Indeed, both pRF size (Dumoulin and Wandell, 2008) and
268 color compared to TF preference (Curcio et al., 1990; Azzopardi et al., 1999; Brewer et al.,
269 2005) are known to be strongly eccentricity dependent such that foveal voxels have rela-
270 tively small pRFs and are relatively color sensitive. We also clearly observe both effects
271 in our data (see Figure 1B and Supplementary Figure 1; and Figure 6 and Supplementary
272 Figure 11, correlation between feature-preference and eccentricity is negative except in

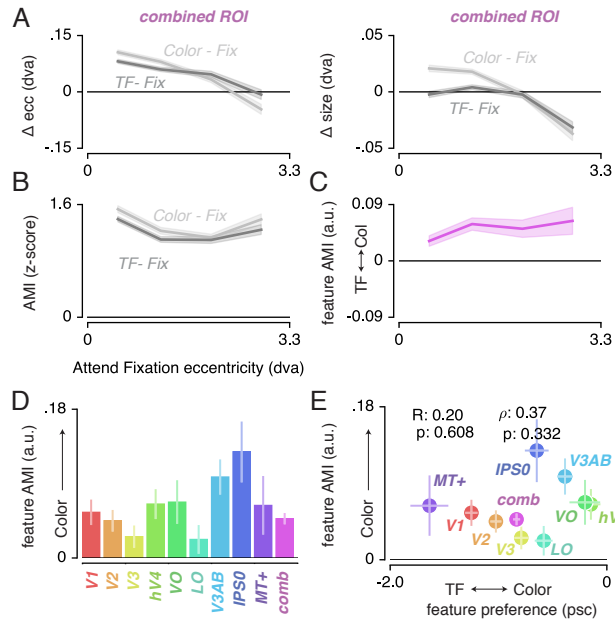


Figure 5: Feature-based attentional modulation across ROIs. A. Differences in pRF eccentricity and size relative to the *Attend Fixation* condition, for both the *Attend Color* and *Attend TF* condition. The changes in both eccentricity and size are more pronounced when attending changes in color versus TF changes in the bar. B. The Attentional Modulation Index (AMI) combines eccentricity and size changes to form one robust index of spatial attention and is greater when attending color compared to TF. C. The feature AMI quantifies this difference. Positive values of this feature AMI across eccentricity confirm stronger pRF modulations when attending color compared to TF. D. Average feature AMI for each ROI, extending greater observed pRF modulations when attending color compared to TF to all individual ROIs. E. Average feature AMI as a function of average feature preference across ROIs. Feature preference increases with higher color compared to TF preference. Although hV4 and VO are relatively sensitive to color and MT+ is relatively sensitive to TF, feature AMI is comparable in these areas. Errorbars denote 95% CI over voxels.

273 LO and VO, see Supplementary Tables 9 and 24). This means that the greater amount of
 274 spatial resampling when attending color can be parsimoniously explained by color being
 275 sampled by relatively smaller pRFs.

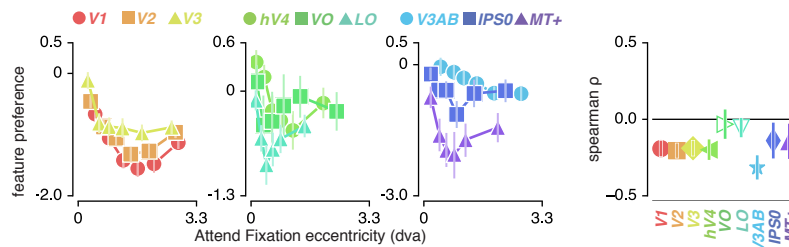


Figure 6: Feature preference and eccentricity. Preference to color compared to TF is greatest near the fovea. Errorbars denote 95% CI over voxels.

276 *Feature-based attention influences attentional gain field precision*

277 Smaller pRFs also require a more precise attentional gain field to shift a given distance
 278 (a property of the multiplication of Gaussians). Combining this with our observation that
 279 pRFs experience greater shifts when attending color, we predict that attentional gain fields
 280 should be more precise in this condition. In order to test this, we repeated the attentional
 281 gain field modeling procedure described above, replacing the *Attend Stimulus* data with
 282 the *Attend Color* and *Attend TF* data in two separate fit procedures. Indeed, this returned
 283 smaller fitted stimulus attentional gain field sizes in the *Attend Color* compared to the
 284 *Attend TF* fit procedure (Figure 7 left panel) both in the *combined ROI* (0.094 dva smaller
 285 over subjects when attending color, $t(4) = 9.021$, $p = .001$, cohen's $d = 4.511$) and across
 286 ROIs (median over ROIs on average 0.061 dva smaller over subjects when attending color,
 287 $t(4) = 4.243$, $p = .013$, cohen's $d = 2.121$). As the *Attend Fixation* data was used as input
 288 in both modeling procedures, we verified that the estimated fixation attentional gain field
 289 was not different between procedures (Figure 7 right panel; p 's of .693 and .224 and cohen's
 290 d of -0.213 and -0.719 for across ROIs and *combined ROI* respectively). These analyses
 291 show that the stronger influence of spatial attention when attending color is realized by a
 292 more precise attentional gain field located at the stimulus. In sum, our results suggest that
 293 (1) the attentional system adjusts its influence in accordance with the spatial sampling

294 characteristics of units that prefer the attended feature and (2) that it does this equally
295 across visual regions regardless of their bottom-up feature preference.

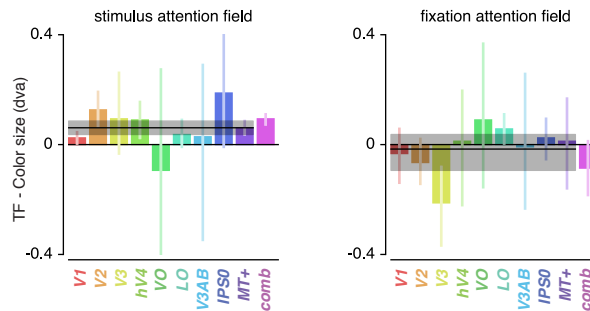


Figure 7: Feature-based attentional modulation of attentional gain field sizes. The greater effects of attention to color compared to TF are caused by more precise attentional gain fields toward the stimulus. Error bars represent 95% CI over subjects. Black horizontal lines indicates median attentional gain field size difference over ROIs, with shaded area representing 95% CI over subjects.

296 *Task and Fixation Performance*

297 Finally, we verified that the pRF results were not affected by differences in fixation accu-
298 racy or behavioral performance (see Figure 8). To provide evidence in favor of these null
299 hypothesis, we performed JZL Bayes factor analyses (using JASP; Love et al. (2015)). We
300 rotated recorded eye position to the direction of bar movement and computed the me-
301 dian and standard deviation of position along this dimension across bar passes per bar
302 position (Figure 8B). We next setup a model including the factor of attention condition
303 (3 levels), bar position (24 levels), and their interaction. We found that when predicting
304 gaze position, the evidence was in favor of the null hypothesis with a Bayes Factor (BF)
305 of 18620. When predicting gaze variability however, we found evidence against the null
306 hypothesis with a BF of 5.980. Evidence for including each of the factors (condition, bar
307 position, and their interaction) into the model returned BFs of 0.713, 547.193 and 0.017
308 respectively. The BF of 0.713 for the factor of condition means that we cannot determine
309 whether gaze variability was different between conditions. However, even if this would
310 be the case, this could only lead to an offset in pRF size and not to changes in pRF posi-

311 tion (Levin et al., 2010; Klein et al., 2014; Hummer et al., 2016). As we observe a complex
312 pattern of both pRF size and eccentricity in- and decreases, a difference in gaze variability
313 cannot explain the attentional modulations of pRF parameters we observed. More impor-
314 tantly, these analyses also showed that although bar position influenced gaze variability
315 (BF of 547.193), it did not do so differently between attention conditions (BF of 0.017).
316 Using a similar approach, we then tested whether a model including attention condition
317 (3 levels) and stimulus eccentricity (3 levels) influenced behavioral performance (Figure
318 8A). This returned evidence for the null hypothesis with a BF of 6.25. Together, these
319 results show that differences in pRF parameters between conditions cannot be explained
320 by either fixation accuracy or behavioral difficulty.

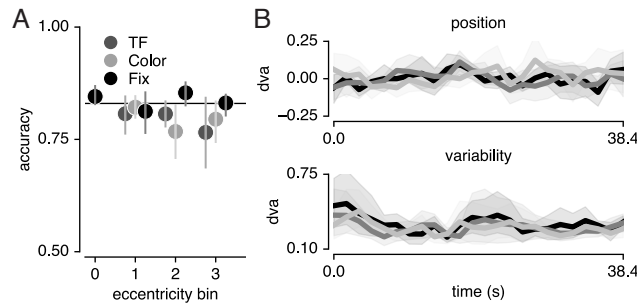


Figure 8: Task and fixation performance A. Behavioral accuracy per attention condition and per bar stimulus eccentricity bin. Horizontal line denotes Quest target of 83%; chance level was 50%. B. Median (top panel) and standard deviation (bottom panel) gaze position in the direction of bar movement per bar position. Error bars denote 95% CI across 5 participants.

Discussion

321
322 We investigated how spatial and feature-based attention jointly modulate the sampling
323 of visual space. We find that directing covert spatial attention toward a moving bar stim-
324 ulus altered the eccentricity and size of pRFs in concert. These changes in spatial sam-
325 pling were parsimoniously explained by an attentional gain field model. Attending color
326 changes within this stimulus induced stronger pRF changes compared to attending tem-
327 poral frequency changes. These feature-based attentional modulations occurred globally
328 throughout the brain, irrespective of a visual region's average feature preference. We sug-

329 gest that the greater degree of spatial resampling when attending color is related to smaller
330 pRF sizes in relatively color preferring voxels. In addition, we show that the greater de-
331 gree of spatial resampling when attending color is caused by a more precise attentional
332 gain field on the stimulus.

333 The average changes in pRF size and eccentricity for each visual region are largely
334 consistent with previous studies where attention was devoted to a peripheral stimulus
335 versus fixation (Kay et al., 2015; Sheremata and Silver, 2015). More specifically, we sys-
336 tematically investigated the spatial structure of the complex pattern of pRF changes that
337 resulted from such differential spatial attention. The resulting characterization details
338 how the sampling of visual space by single voxel pRFs is affected by spatial attention,
339 which is of specific relevance for future studies that determine spatial selectivity for voxel
340 selections. First, we show that attending the stimulus compared to fixation caused pRFs
341 to shift radially. Although a previous study reported a dominant horizontal shift direc-
342 tion (Sheremata and Silver, 2015), we suggest that the overrepresentation of the horizon-
343 tal meridian (Schneider et al., 2004; Swisher et al., 2007) made radially shifting pRFs to
344 appear as predominantly horizontal changes. Second, we report closely coupled pRF ec-
345 centricity and size changes that depended on pRF eccentricity. Specifically, we found
346 that parafoveal pRFs shifted toward the periphery and increased in size while peripheral
347 pRFs shifted toward the fovea and decreased in size. This finding supports the resolution
348 hypothesis of attention (Anton-Erxleben and Carrasco, 2013), which posits that spatial
349 attention acts to reduce resolution differences between the fovea and periphery. We note
350 that the functional implication of pRF size changes was recently questioned, as stimulus
351 encoding fidelity was shown to be unaffected by pRF size changes (Vo et al., 2017). How-
352 ever, the exact functional significance of changes in pRF size bears no consequence for
353 the conclusions currently presented. Due to the strong correlation we observed between
354 pRF eccentricity and size changes, we combined both measures into a single robust index.
355 Our relevant quantifications are therefore agnostic to the potentially separable functional
356 implications of changes in pRF size and eccentricity.

357 The pattern of pRF shifts we observe is well described by an attentional gain field
358 model (Reynolds and Heeger, 2009; Klein et al., 2014). First, this highlights that a simple
359 and well-understood mechanism underpins the apparent complexity of the observed pat-

360 tern of pRF changes. Second, it extends the utility of such attentional gain field models to
361 situations where attention is dynamically deployed over space and time during the map-
362 ping of the pRF (Kay et al., 2015). In agreement with earlier reports (Klein et al., 2014;
363 Puckett and DeYoe, 2015), we found that the best-fitting model implemented comparable
364 attentional gain field sizes across visual regions. This strongly points to spatial attention
365 being implemented as a global influence across visual cortex. We conclude that differ-
366 ences in pRF shift patterns between different visual regions depended primarily on differ-
367 ences in visual sampling (i.e. differences in pRF center and size distributions) rather than
368 on differing attentional influences. Despite the broad correspondence between model
369 fits and data, the model did not capture the observed decreases in pRF eccentricity of the
370 most foveal pRFs in V1. Two recent studies showed that in early visual areas, spatial at-
371 tention shifted pRFs away from the attended location, but toward the attended location
372 in higher visual areas (de Haas et al., 2014; Vo et al., 2017). Other studies showed that in
373 precisely these visual regions, both the pRF and the attentional gain field are composed of
374 a suppressive surround in addition to their positive peak (Zuiderbaan et al., 2012; Puck-
375 ett and DeYoe, 2015). We leave the question whether these suppressive surrounds could
376 explain such repulsive shifts in lower visual cortex for future research. As a more general
377 aside, gain fields have been shown to influence visual processing at the motor stage (van
378 Opstal et al., 1995; Snyder et al., 1998; Trotter and Celebrini, 1999). Thus, our results
379 further establish the close link between attentional and motor processes (Rizzolatti et al.,
380 1987; Corbetta et al., 1998).

381 Of particular interest, we showed that the changes in visual space induced by spa-
382 tial attention were stronger when attending color compared to when attending temporal
383 frequency. This occurred throughout the brain, irrespective of visual regions' preference
384 for the attended features. In other words, while MT+ and V4 differed greatly in their
385 relative feature preference, both areas showed comparable pRF changes resulting from
386 differences in feature-based attention. This stands in apparent contrast with previous
387 studies reporting that feature-based attention selectively enhances responses in cortical
388 areas specialized in processing the attended feature (Corbetta et al., 1990; Chawla et al.,
389 1999; O'Craven et al., 1999; Schoenfeld et al., 2007; Baldauf and Desimone, 2014). How-
390 ever, attending a stimulus consisting multiple features was shown to spread attentional

391 response modulations of one of the object's feature dimensions to other constituent fea-
392 ture dimensions (Katzner et al., 2009; Çukur et al., 2013; Kay and Yeatman, 2017), albeit
393 somewhat later in time (+/- 60ms; Schoenfeld et al., 2014). This could mean that the
394 global pattern of pRF shifts we observed is caused by such an object-based attentional
395 transfer mechanism. In addition, changing the sampling of visual space globally through-
396 out the brain enhances stability in the representation of space. Different modifications
397 of visual space per visual region would require an additional mechanism linking differ-
398 ent spatial representations. Instead, the global nature of spatial resampling we observe
399 supports a temporally dynamic but spatially consistent adaptation of visual space.

400 The greater degree of spatial resampling when attending color can be explained by
401 differences in spatial sampling in voxels that prefer color compared to temporal fre-
402 quency. Behavioral studies have suggested that feature-based attention should modulate
403 the strength of spatial resampling in order to improve sampling of attended features
404 (Yeshurun et al., 2008; Barbot and Carrasco, 2017). One of the factors that determines
405 the required degree of spatial resampling is receptive field size. Specifically, smaller pRFs
406 need to shift a greater distance in order to bring a stimulus into their responsive region.
407 Both our data and previous findings show that pRF size (Dumoulin and Wandell, 2008)
408 and color compared to temporal frequency preference (Curcio et al., 1990; Azzopardi
409 et al., 1999; Brewer et al., 2005) vary across eccentricity such that foveal voxels have
410 smaller pRFs and are more color sensitive. This means that color is sampled by smaller
411 pRFs than temporal frequency. Attending color in the stimulus therefore required a
412 greater degree of spatial resampling in order to optimally sample the attended feature. In
413 addition, gain field models of attention predict that smaller pRFs require a more precise
414 attentional gain field in order to shift a given distance. Indeed, our results showed that
415 attending color versus temporal frequency resulted in more precise attentional gain fields
416 directed toward the bar stimulus. Together, this shows that the larger degree of spatial
417 resampling we observed when attending color can be parsimoniously explained by
418 smaller pRF size in voxels that prefer color over temporal frequency. Yet, as pRF size is so
419 strongly related to pRF eccentricity, we can not exclude an influence of pRF eccentricity
420 above and beyond pRF size. However, receptive field size is suggested to be crucial in
421 the eccentricity dependence of attentional influences observed in behavior (Yeshurun

422 and Carrasco, 1998, 1999; Anton-Erxleben and Carrasco, 2013). Therefore, although
423 differential influences of attention across eccentricities have been observed before in
424 the brain (e.g. Roberts et al., 2007; Bressler et al., 2013), these are likely brought about
425 by differences in pRF size. In sum, our results confirm the notion that the endogenous
426 attentional system is able to take into account the spatial sampling properties of units that
427 prefer the attended feature, and that it adjusts the strength of its influence accordingly
428 (Yeshurun et al., 2008; Barbot and Carrasco, 2017).

429 Electrophysiological studies on the interaction between feature-based and spatial at-
430 tention generally measure overall response amplitudes instead of changes in spatial sam-
431 pling. This showed that interactions between feature-based and spatial attention are weak
432 to non-existent in relatively early stages of processing (David et al., 2008; Hayden and Gal-
433 lant, 2009; Patzwahl and Treue, 2009; Zhang and Luck, 2009), but develop at later stages
434 of visual processing (Hillyard and Munte, 1984; Handy et al., 2001; Andersen et al., 2011;
435 Bengson et al., 2012; Ibos and Freedman, 2016, but see Egnér et al. (2008)). We add to
436 this (1) that feature-based attention modulates the effects of spatial attention on spatial re-
437 sampling and (2) that these interactions occur globally throughout the brain, manifesting
438 themselves even in the earliest cortical visual regions. Interactions between spatial and
439 feature-based attention in early stages of processing could be concealed when focusing
440 on changes in response amplitude instead of changes in spatial sampling. However, it is
441 important to note that measuring spatial sampling at the level of voxels does not allow us
442 to determine whether observed changes in spatial sampling are due to changes in spatial
443 sampling of individual neurons, or rather due to differential weighting of subpopulations
444 of neurons within a voxel. Nevertheless, it has been shown that spatial attention does
445 influence spatial sampling of individual neurons (Connor et al., 1997; Womelsdorf et al.,
446 2006). Yet, future studies are required to extend our conclusions regarding the interac-
447 tions between feature-based and spatial attention to the single neuron level.

448 Another important remaining question pertains to the source of the interactions be-
449 tween feature-based and spatial attention. Signals of spatial selection are thought to orig-
450 inate from a network of frontal and parietal areas, identified using fMRI (Shulman, 2002;
451 Silver et al., 2005; Jerde et al., 2012; Sprague and Serences, 2013; Szczepanski et al., 2013;
452 Kay and Yeatman, 2017; Mackey et al., 2017), and electrophysiology (Moore and Arm-

453 strong, 2003; Gregoriou et al., 2009). As we focused on careful measurement of spatial
454 sampling in feature sensitive visual cortex with a relatively small stimulus region, we did
455 not include the frontoparietal regions containing large receptive fields into our analyses.
456 A recent study suggested a central role for the ventral prearcuate gyrus for conjoined
457 spatial and feature-based attentional modulations (Bichot et al., 2015). Correspondingly,
458 signals of feature selection in humans have been localized to a likely human homologue
459 of this area, the inferior frontal junction (IFJ; Zanto et al., 2010; Baldauf and Desimone,
460 2014). This region is therefore a possible candidate for controlling the interactions be-
461 tween feature-based and spatial attention.

462 In sum, we show that visuospatial sampling is not only affected by attended locations
463 but also depends on the spatial sampling properties of units that prefer attended visual
464 features. The global nature of these modulations highlights the flexibility of the brain's
465 encoding of sensory information in order to meet task demands (Rosenholtz, 2016).

466 *Materials and Methods*

467 *Participants*

468 Five participants (2 female, 2 authors, aged between 25 - 37) participated in the study.
469 All gave informed consent, and procedures were approved by the ethical review board of
470 the University of Amsterdam, where scanning took place.

471 *Apparatus*

472 *MRI acquisition*

473 All MRI data was acquired on a Philips Achieva 3T scanner (Philips Medical Systems),
474 equipped with a 32-channel head coil. T1 weighted images were acquired for each par-
475 ticipant with isotropic resolution of 1 mm³, repetition time (TR) of 8000 ms, TE of 3.73
476 ms, flip angle of 8°. Functional T2* weighted data consisted of 30 2D slices of echo pla-
477 nar images (EPI) with isotropic resolution of 2.5 mm², with a 0.25 mm slice gap, TR of
478 1600 ms, TE of 27.62 ms, and a flip angle of 70°. Each participant completed between
479 6 to 8 Attention-pRF Mapping runs (20 min each) and 2-3 Feature preference and HRF

480 Mapping runs (10 min each), spread over 2 (N = 1) or 3 (N = 4) sessions within a 2 week
481 period (see Experimental Design).

482 *Gaze recording*

483 During all functional runs, gaze position was recorded using an Eyelink 1000 (SR Re-
484 search, Osgoode, Ontario, Canada), sampled at 1000 Hz. A 9-point calibration-validation
485 procedure was run at the start of each session.

486 *Stimulus presentation*

487 Visual stimuli were created in PsychoPy (Peirce, 2008) and run on a 15 inch 2013 Mac-
488 Book Pro Retina. Participants viewed a 32 inch BOLD screen (resolution: 1920 x 1080,
489 refresh rate: 100 Hz; Cambridge Research Systems), at 156 cm distance of the partici-
490 pants' eyes at the end of the bore, via a helmet-mounted front-silvered mirror. Auditory
491 stimuli were presented through headphones using the MRConfon system.

492 *Experimental Design*

493 *Attention-PRF Mapping Stimulus*

494 A bar stimulus of 0.9 degrees of visual angle (dva) width traversed a circular aperture
495 of 7.2 dva in one of eight directions (cardinal and diagonal orientations in both direc-
496 tions, see Figure 9A), completing a full pass in 38.4 s by stepping 0.34 dva every 1.6 s, and
497 pausing 4.8 s between each bar pass. One run contained 24 bar passes in total (3 for every
498 direction), plus four blank periods of 38.4 s when no bar stimulus was shown. Through-
499 out the experiment, a gray disk of 9.6 arcmin (60 cd/m²), with a 4.2 arcmin black rim (0
500 cd/m²) was present on the screen as a fixation mark. The bar stimulus was composed of
501 1500 Gabor elements (4.34 cycle/dva spatial frequency, 9 arcmin sd, average luminance
502 of 60 cd/m²) projected over a dark-gray background (15 cd/m²). Three times per bar
503 location (i.e. every 533 ms), Gabor element parameters were updated to a new random
504 location (uniformly distributed over the spatial extent of the bar at full width), a random
505 orientation (uniformly drawn between 0 - 360°), a random color combination (either
506 blue-yellow (BY), or cyan-magenta (CM)) and a random new temporal frequency (TF;
507 either high or low). The high and low temporal frequencies were chosen per participant

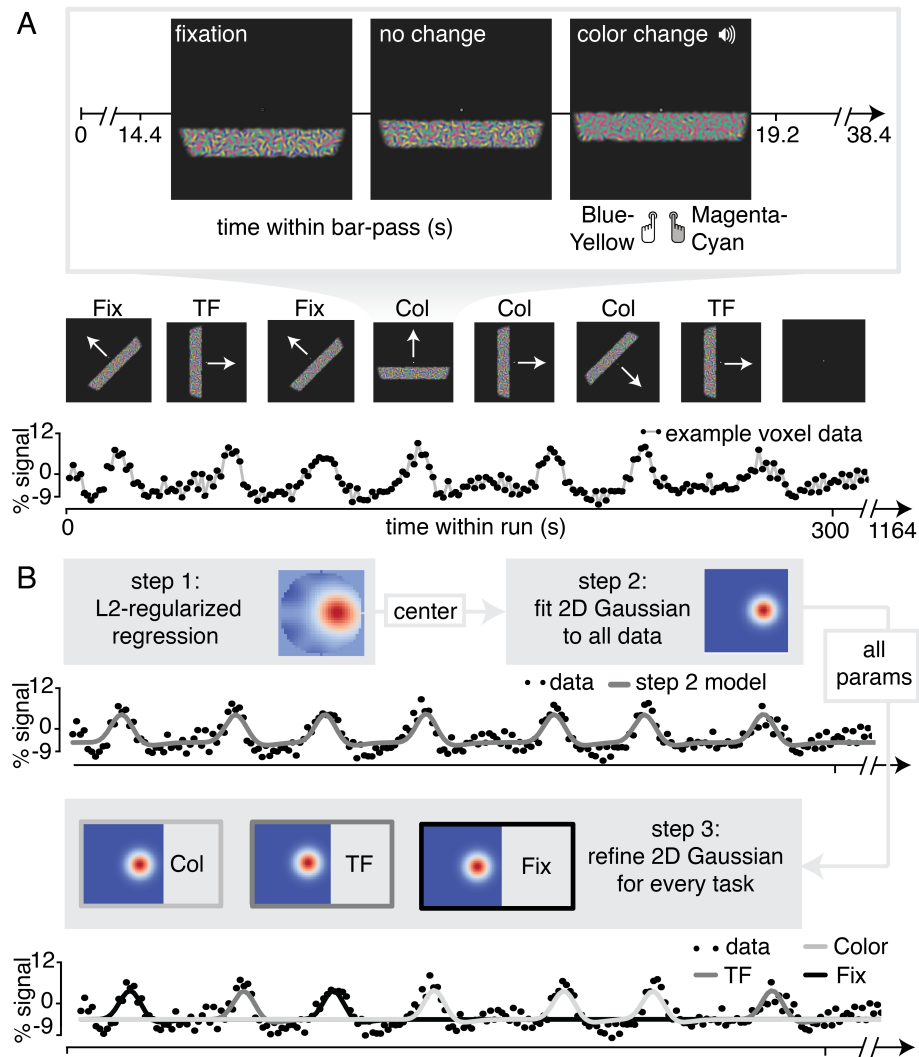


Figure 9: Experimental Design and pRF Fitting procedure. A. Experimental Design. Throughout a bar pass participants reported either changes in color (*Attend Color*) or temporal frequency (*Attend TF*) of Gabor elements within the moving bar stimulus, or changes in fixation mark luminance (*Attend Fixation*), while maintaining accurate fixation. Participants were informed auditorily about the upcoming task 2 s before each bar pass. B. Overview of pRF fitting procedure. pRF parameters were estimated from each voxel's BOLD signal time course in a three step procedure. First, a design matrix was constructed based on 31x31 pixels' visual stimulation time course of the entire experiment, which was convolved with a participant-specific HRF (derived from separate data, see *Feature preference and HRF Mapper*). L2-regularized regression was used to find the position of the spatial response profile's peak of each voxel. Second, to find precise estimates of pRF center location and size we used a more finegrained 101x101 design matrix and gradient descent to fit a single parameterized 2D Gaussian pRF model to data from all attention conditions combined, initialized at the L2-regression derived peak location. Third, 2D Gaussian pRF models were fitted to data from the different attention conditions separately, initialized with the parameters resulting from step 2.

508 to facilitate their ability to distinguish TF changes (6 and 4 Hz in 3 participants, 7 and 3
509 Hz in 2 participants). The overall color and/or TF composition of the bar was transiently
510 altered on some of these parameter updates, by changing the ratio of Gabor elements
511 assigned either color combination or either TF (as targets for the behavioral tasks, see
512 below). The temporal predictability of these events was minimized by randomly drawing
513 occurrences according to an exponential distribution (mean 4 s, minimum 2 s). Addition-
514 ally, the fixation mark central disk luminance either increased or decreased, with proba-
515 bility and duration of these occurrences identical to those of changes in the bar stimulus
516 composition. These three types of transients (fixation mark luminance, bar color and TF
517 composition) were independent, meaning they were randomly interleaved and could be
518 combined on the screen. Importantly, this design ensured that physical stimulation was
519 equated across all three attention conditions, which we describe below.

520 *Attention-PRF Mapping Task*

521 For an overview of the stimulus and behavioral task, see Figure 9A. Before each bar
522 pass an automated voice (Apple OSX Dictation voice ‘Kathy’) informed participants to
523 perform a 2-alternative forced-choice task (2AFC) on one of the three stimulus parameter
524 deviations. Task-relevant visual stimulus changes were accompanied by an auditory pure
525 tone (440 Hz). This auditory cue alerted the participant to respond, while task-irrelevant
526 stimulus changes occurred independently and without warning tone. This ensured that
527 all task-related information was conveyed to the participant by auditory means, with-
528 out concurrent changes in visual stimulation. The different stimulus changes (i.e. color,
529 TF and fixation luminance) occurred independently and thus sometimes simultaneously,
530 rendering the auditory tone not reliably predictive of the stimulus dimension to attend.
531 Therefore, participants needed to stably maintain condition-specific top-down attention
532 throughout the duration of a bar pass. In the *Attend Color* condition, participants judged
533 the relative predominance of Blue-Yellow or Cyan-Magenta Gabor elements in the bar
534 stimulus, while in the *Attend TF* condition, participants judged the relative predominance
535 of high compared to low TF Gabor elements in the bar stimulus. We chose color and TF
536 as these features are known to be processed markedly differently in the visual system.
537 While color is preferentially processed by the ventral visual areas V4 and VO, temporal

538 information is known to be processed preferentially by area MT+ (Liu and Wandell, 2005;
539 Brouwer and Heeger, 2009, 2013). We specifically chose TF and not coherent motion, as
540 coherent motion signals have been shown to influence pRF measurements (Harvey and
541 Dumoulin, 2016). Both color and TF have been shown to be able to capture attention
542 (Wolfe and Horowitz, 2004; Cass et al., 2011). In the *Attend Fixation* condition, partici-
543 pants judged whether the central disk of the fixation mark increased or decreased in lumi-
544 nance. The magnitude of the stimulus changes was titrated by means of a Quest staircase
545 procedure (Watson and Pelli, 1983), set to approximate 83% correct performance. In or-
546 der to equate task difficulty across not only conditions but also bar stimulus eccentricity,
547 we used separate Quest staircases at three different bar stimulus eccentricities in each of
548 the attention conditions. Additionally, there was a separate staircase for the *Attend Fixa-*
549 *tion* task when no bar stimulus on screen. This made for a total of 10 separate staircases
550 during the experiment. Participants extensively practiced the task outside the scanner
551 and staircases were reset before scanning. Each experimental run contained one bar pass
552 per task condition, per direction, in random order (total of 24 bar passes per run).

553 *Feature preference and HRF Mapper*

554 We performed a separate randomized fast event-related fMRI experiment in order to
555 (1) determine each voxels' relative preference for color and TF, and (2) to find the pa-
556 rameters that best described each participants' HRF, to be used in the pRF estimation
557 procedure (see below). Full-field stimuli consisted of 8000 Gabor elements, uniformly
558 distributed throughout the full circular aperture traversed by the pRF mapping stimulus
559 ensuring identical density compared to the pRF mapping stimulus. Also, every 533 ms,
560 all Gabor elements were assigned a new random orientation and location. These stimuli
561 were presented for 3.2 s, with an inter-trial interval of 3.2 s. In a full factorial 2 x 2 de-
562 sign, we varied the color and TF content of the stimulus in an on-off fashion. That is, the
563 TF of the Gabor elements was either 0 or 7 Hz, and the elements were either grayscale
564 or colored (balanced BY/CM). Trial order was determined based on an M-sequence (Bu-
565 račas and Boynton, 2002), with no-stimulus (null) trials interspersed as a fifth category
566 of trials. During this experiment, participants performed the same 2-AFC fixation-point
567 luminance task as in the Attention-pRF Mapping Task (*Attend Fixation*), using a separate

568 staircase. A single HRF was determined per participant using the R1-GLM approach (Pe-
569 dregosa et al., 2015), on data from all conditions. The median HRF from the 1000 most
570 responsive voxels (highest beta-weights in the colored high TF condition) was used as the
571 participant specific HRF.

572 *Data analysis*

573 *MRI Preprocessing*

574 T1-weighted images were first segmented automatically using Freesurfer, after which
575 the pial and grey/white matter surfaces were hand-edited. Regions of interest (ROIs) were
576 defined on surface projected retinotopic maps using Freesurfer without the use of spatial
577 smoothing. For every participant, one session's EPI image was selected as the target EPI,
578 which was registered to his/her Freesurfer segmented T1-weighted image using the bbg-
579 ister utility, after which the registration was hand-adjusted. Then, all EPI images were first
580 motion corrected to their middle volume using FSL (Jenkinson et al., 2012) MCFLIRT to
581 correct for within run motion. Then, all EPI images were registered both linearly (using
582 FLIRT) and non-linearly (using FNIRT) to the mean-motion corrected target EPI to cor-
583 rect for between run and session motion and inhomogeneities in B0 field. Low frequency
584 drifts were removed using a 3rd order savitzky-golay filter (Savitzky and Golay, 1964)
585 with a window length of 120s. Arbitrary BOLD units were converted to percent-signal
586 change on a per-run basis.

587 *pRF fitting procedure*

588 pRF fitting and (statistical) parameter processing was performed using custom-
589 written python pipeline available at [https://github.com/daanvanes/pRF_attention_](https://github.com/daanvanes/pRF_attention_analyses)
590 [analyses](https://github.com/daanvanes/pRF_attention_analyses). Links to the data files required to reproduce the figures and analyses can be
591 found in the readme of this repository. The fitting routines heavily relied on the scipy and
592 numpy packages. We approximated the pRF by a two-dimensional isotropic Gaussian
593 function. For an overview of our pRF fitting procedure, see Figure 9B. A predicted
594 timecourse for a given Gaussian function can be created by first computing the overlap
595 of this function with a model of the stimulus for each timepoint, and then convolving
596 this overlap with the participant-specific HRF (Dumoulin and Wandell, 2008). It is

597 possible to find these Gaussian parameter estimates using a minimization algorithm,
598 but such an approach is at risk of missing the global optimum when parameters are
599 not initialized at appropriate values. Recently, a model-free reverse-correlation-like
600 method was developed, generating a pRF spatial profile without requiring any pre-set
601 parameters (for details see Lee et al. (2013)). Briefly, we employed this method using L2
602 regularized (Ridge) regression on a participant-specific-HRF convolved design matrix
603 coding the stimulus position in a 31x31 grid for each timepoint, predicting data from all
604 attention conditions together. Using a high regularisation parameter ($\lambda = 10^6$), we used
605 this procedure not to maximize explained signal variance, but to robustly determine
606 the pRF center, which was defined as the position of the maximum weight. Having
607 determined these approximate initial values for the pRF center, we next initialized
608 a minimization procedure (Powell (1964) algorithm) at these location values, fitting
609 position (x, y), size, baseline and amplitude parameters of an isotropic 2D Gaussian to
610 data from all conditions together using a design matrix with size 101x101 for enhanced
611 precision. Then, all resulting Gaussian parameters were used to initialize a second
612 minimization procedure which fitted a Gaussian for each attention condition separately
613 at the same time (all parameters independent except for one shared baseline parameter).
614 This approach allowed us to recover fine-grained differences in pRF parameters under
615 conditions of differential attention.

616 *pRF selection*

617 We discarded pRFs that were either at the edge of the stimulus region (above 3.3 dva
618 in the *Attend Fixation* condition), or had size (standard deviation) larger than our stim-
619 ulus diameter (7.2 dva) in any of the tasks. Additionally, each voxel's contribution to all
620 analyses was weighted according to the quality of fit of the pRF model, which was defined
621 as 1 minus the ratio of residual to observed variance:

$$R^2 = 1 - \frac{\sum_i (m_i - p_i)^2}{\sum_i (m_i - \bar{m}_i)^2} \quad (1)$$

622 where i , m and p refer to voxel index, measured BOLD time-course and predicted
623 time-course respectively. We disregarded voxels with an $R^2 < .1$.

624 *pRF parameter analyses*

625 The statistical approach used to combine pRF results across participants was similar
626 to that of two recent and comparable studies (Klein et al., 2014; Kay et al., 2015), that
627 adopted a ‘dense sampling of individual brain approach’ (Poldrack, 2017). This approach
628 favours careful measurement of individual brains at the expense of large sample sizes in
629 terms of the number of subjects. After defining visual ROIs per participant using standard
630 retinotopic mapping procedures (Dumoulin and Wandell, 2008), this entailed pooling
631 voxels for each ROI across participants. Statistics are then computed over this collection
632 of voxels, much akin to the way in which neurons are often pooled across monkeys. In
633 order to provide additional estimates of stability across participants, we also performed all
634 analyses for each participant separately, the results of which can be found in the Statistical
635 Appendix.

636 Except for the Rayleigh tests (Supplementary Table 2) p-values and confidence inter-
637 vals were computed using 10^5 fold bootstrap procedures. To test whether bootstrapped
638 distributions differed from a certain threshold, p-values were defined as the ratio of boot-
639 strap samples below versus above that threshold multiplied by 2 (all reported p-values
640 are two-tailed). In order to provide maximally robust estimates of central tendency and
641 variance of parameter estimates, we excluded outliers using a threshold of five two-sided
642 median absolute deviations. As this outlier rejection was performed for each analysis
643 separately, this resulted in slightly different number of voxels included in each analysis
644 (see Ns in statistics tables). Outlier rejection was performed either per visual field bin
645 (cf. Figure 1B, 2B/D, 3A/B, 4A/B/D/E/F, 5A/B, scatters in Figure 6), per percentile bin
646 (cf. Figure 3C), or per ROI (cf. Figures 2C, 5D/E). When analyses are performed across
647 participants outliers were again rejected at the voxel level per participant, but all partici-
648 pants were always included (cf. 4A/B/C/D/E/F and 7). When comparing correlations to
649 0, correlations were Fisher transformed using the inverse hyperbolic tangent function.

650 *Feature attention modulation index*

651 We computed a per-voxel index to quantify how strongly feature-based attention
652 modulated the effects of spatial attention on spatial sampling (feature-based attention
653 modulation index, or feature AMI). This measure combined pRF eccentricity and size

654 parameters, as our results showed that spatial attention affected these parameters in con-
655 cert (see Figure 3). Per voxel and per attention condition to the bar stimulus, (*Attend*
656 *Color* and *Attend TF*) we set up a two-dimensional vector containing difference in pRF
657 eccentricity and size relative to the *Attend Fixation* condition. pRF size and eccentricity
658 differences were normalized respective to their variance in the *Attend Stimulus* condition
659 to ensure that both measure contributed equally to the feature AMI. We then computed a
660 feature AMI by dividing the difference between the norms of these vectors by their sum.
661 This way, positive values of feature AMI indicate greater spatial attention effects on pRF
662 parameters in the *Attend Color* condition than in the *Attend TF* condition and vice versa.
663 Note that this measure abstracted out both the affected pRF parameter (i.e. eccentricity
664 and size) and the sign of these changes (i.e. shifts toward the fovea or periphery and in-
665 creases or decreases in size).

666 *Attentional Gain Field modeling*

667 To provide a parsimonious mechanistic account for how attention to the moving bar
668 stimulus changed pRF position, we adapted an existing attentional gain model of atten-
669 tion (Womelsdorf et al., 2008; Reynolds and Heeger, 2009; Klein et al., 2014). This model
670 conceptualizes the measured Gaussian pRF as the multiplication between a Gaussian
671 stimulus-driven pRF (*SD*, i.e. the pRF outside the influence of attention), and a Gaussian
672 attentional gain field (*AF*). Following the properties of Gaussian multiplication, the nar-
673 rower the *AF* the stronger the influence on the *SD*, and the narrower the *SD* the smaller
674 the resulting shift. An overview of model mechanics is shown in Figure 10. We estimated
675 the *SD* by dividing the measured *Attend Fixation* pRF by an *AF* at fixation (AF_{fix} , Figure
676 10A). As attention to the stimulus shifted the locus of attention as the bar moved across
677 the screen, we modeled the effect of attention for each bar stimulus position separately
678 (Figure 10B). Each unique bar stimulus (24 bar positions for each of 8 directions) was
679 convolved with a Gaussian kernel (AF_{stim}) and multiplied with the estimated *SD*. This
680 yielded one predicted pRF per bar position. These predicted pRFs were then scaled to a
681 maximum of 1 and averaged over the different bar positions. This averaged profile essen-
682 tially represented the pRF ‘smeared’ across visual space as spatial attention moved along
683 with the bar stimulus throughout the recording. The peak of this averaged profile was

684 then designated as the predicted pRF center location in the *Attend Stimulus* condition
685 (Figure 10C). Thus, the modeling procedure consisted of two separate AFs, one at fixa-
686 tion (AF_{fix}) and one convolved with the bar stimulus (AF_{stim}), which were estimated at
687 the same time. The input to the model was the *Attend Fixation* pRF, and the output was
688 the predicted position for the *Attend Stimulus* pRF. Formally, this is given by:

$$pRF_{stimpos} = argmax \left(\frac{1}{n} \cdot \sum_{t=0}^n \left(\frac{(dm_{(t)} * AF_{stim}) \cdot (pRF_{fix}/AF_{fix})}{max((dm_{(t)} * AF_{stim}) \cdot (pRF_{fix}/AF_{fix}))} \right) \right) \quad (2)$$

689 where $(dm_{(t)} * AF_{stim})$ represents the stimulus design matrix at timepoint t convolved
690 with the AF toward the stimulus, (pRF_{fix}/AF_{fix}) represents the estimation of the SD, and
691 the denominator ensures scaling to a maximum of 1. To estimate how well a set of AF pa-
692 rameters fit the data across the entire visual field, we minimized the L2 distance between
693 the predicted and measured *Attend Stimulus* pRF positions of the 64 vectors derived from
694 the quadrant visual field format of Figure 2B. AF sizes were determined at an ROI level,
695 thus assuming that attention influenced all pRFs within an ROI similarly, while possibly
696 varying between ROIs. The model was evaluated for a 50 x 50 evenly spaced grid of AF
697 sizes, where the AF at fixation varied between 1.5-2.5 dva, and the AF convolved with the
698 stimulus varied between 0.6-1.6 dva (i.e. 0.02 dva precision). The convolution between
699 the stimulus and the AF_{stim} resulted in effective AF size to be 0.9 (bar stimulus width)
700 larger than the AF_{stim} itself. These parameter ranges therefore result in equal effective AF
701 sizes. Reported sizes are the standard deviation of the 2D Gaussians, with 0.9 (the bar
702 width) added to AF_{stim} sizes. Modeling was performed for each participant separately.

703 *Gaze data processing*

704 Gaze data was cleaned by linearly interpolating blinks detected by the EyeLink soft-
705 ware. Transient occasions in which the tracker lost the pupil due to partial occlusion by
706 the eyelid leading to high-frequency, high-amplitude signal components were detected
707 and corrected as follows. Pupil size was first high-pass filtered at 10 Hz (the pupil im-
708 pulse response function is a low-pass filter with a cutoff below 10 Hz (Knapen et al., 2016;
709 Korn and Bach, 2016)), after which those time-points in which the acceleration of pupil

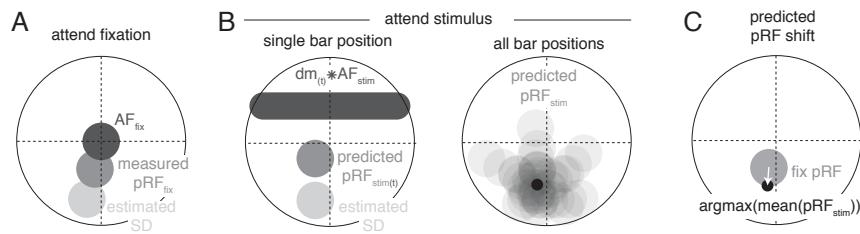


Figure 10: Schematic overview of modeling procedure. A. The Stimulus Drive (SD) was estimated by dividing the measured Attend Fixation pRF by an AF at fixation (AF_{fix}). B. Attention toward the bar stimulus at a given timepoint t was modeled as the multiplication of the estimated SD with the bar stimulus at that timepoint ($dm_{(t)}$) convolved with another AF (AF_{stim}). These predicted Attend Stimulus pRFs were averaged over all timepoints. The maximum position of this profile was taken as the predicted Attend Stimulus pRF position. C. The predicted pRF shift ran from the measured Attend Fixation pRF toward the predicted Attend Stimulus position.

710 size was greater than 10^5 mm/s, and their neighbours within 5 s, were replaced with NaN
 711 values. Drift correction was performed within each bar-pass by subtracting the median
 712 gaze position. All gaze positions were rotated to the direction of bar movement, after
 713 which we analyzed the median and variance (standard deviation) of the component in
 714 the direction of bar movement (i.e. the component relevant for the pRF measurement).

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Supplementary Material

Introduction

This document contains figures and analyses performed for individual subjects. Results are reported using different methods. The ‘super subject’ method pools voxels across subjects and computes p-values and confidence intervals using bootstrapping across voxels. Resulting p-values were FDR corrected for multiple comparisons. This corresponds to what is reported in the main text. The ‘per subject’ method computes these same analyses, but for each subject individually. We report in how many of the subjects these bootstrap tests over voxels are significant with uncorrected $p < .05$. The ‘over subjects’ method takes the average over the ‘per subject’ results, and computes confidence intervals and t-tests over these 5 values. Statistical tables for all analyses are found at the bottom of this document.

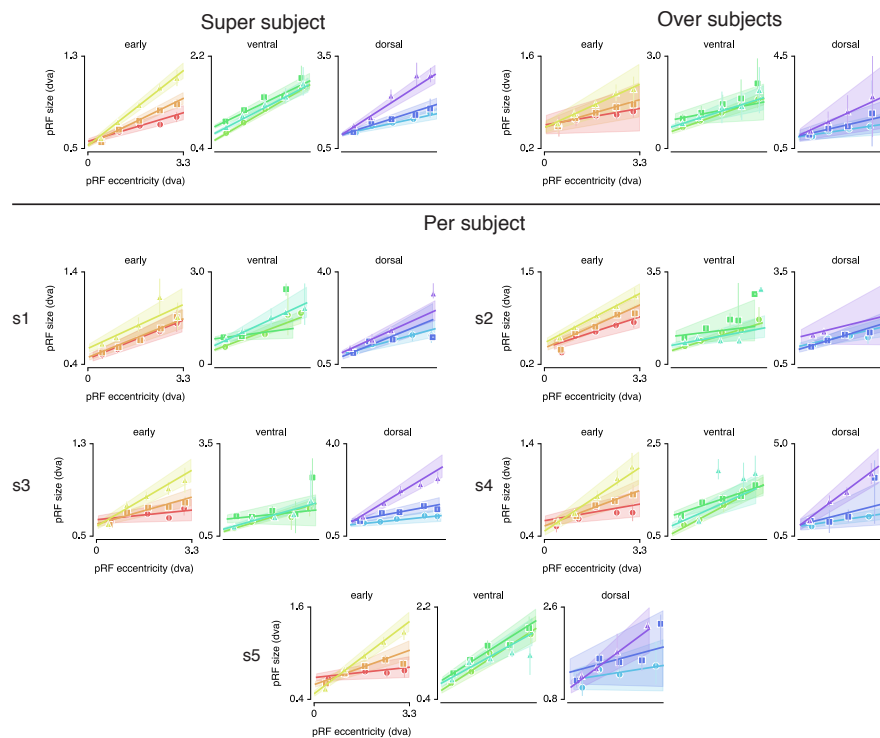


Figure 1: Eccentricity-size relations for all statistical methods.

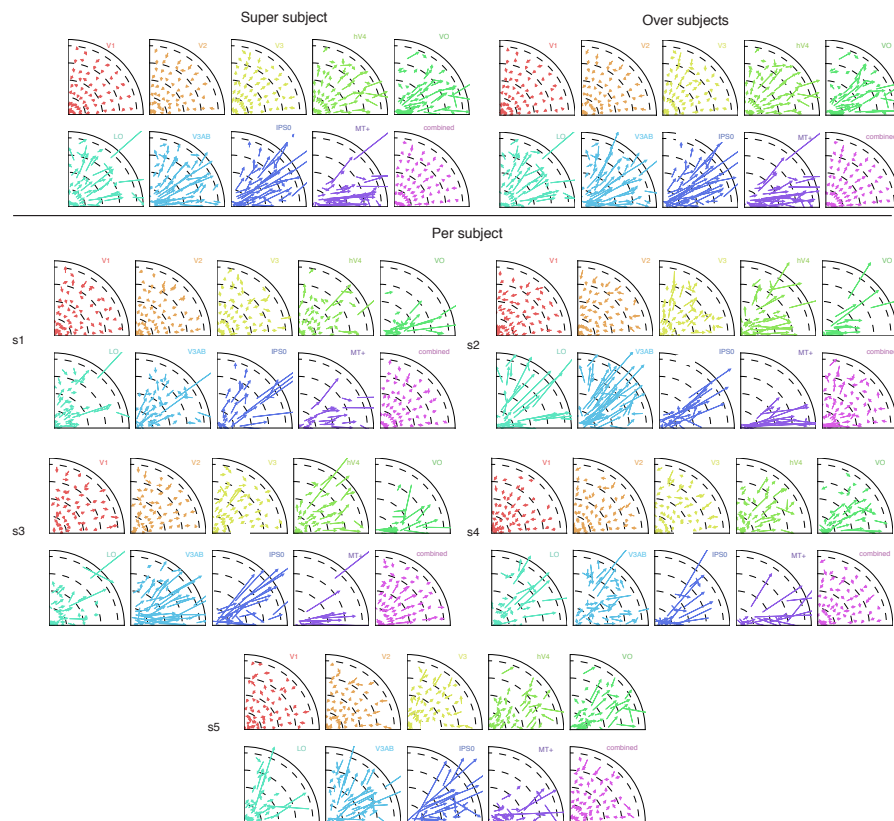


Figure 2: pRF shift plots for the different statistical methods. Shift vectors run from the *Attend Fixation* to the *Attend Stimulus* pRF location. This figure indicates that the shift patterns seen in the super subject are almost identical to the over subjects method, and highly agree with the individual subject figures. Note the radial shift direction that is readily apparent in all ROIs in all subjects. Also note how the *combined* ROI clearly shows paravoveal pRFs shifting toward the periphery and peripheral pRFs shifting toward the fovea across subjects. Finally, the absence of pRFs near the vertical meridian in data from all subjects in VO, IPS0 and MT+ highlight the overrepresentation of the horizontal meridian that is found in all ROIs (see Tables 2, 12 and 13).

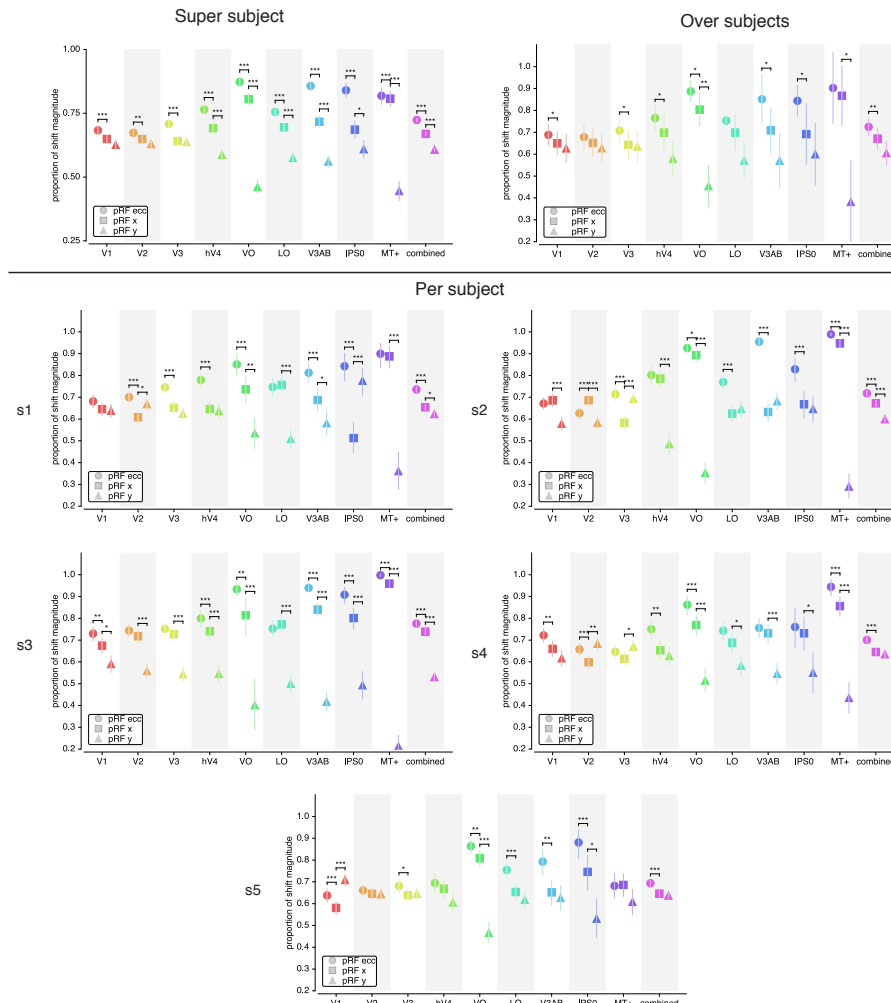


Figure 3: pRF shift directions for the different statistical methods. The ‘over subject’ panel replicates the ‘super subject’ results, namely that shifts are best explained by eccentricity changes, followed by changes in pRF x and finally in pRF y in all ROIs. The dominance of eccentricity over x changes was significant in all individual subjects (‘per subject’ method) in the *combined* ROI, and in at least 2 (but often 5) subjects in all other ROIs (see Table 10). The individual subject evidence also replicated the finding that pRFs shifted more in the x compared to y directions in hv4/VO/LO/V3AB/IPS0/MT+ and in the combined ROI (see Table 11). The dominance of x over y shifts was explained from a non-uniformity in the distribution of pRF polar angle (i.e. overrepresentation of horizontal meridian, see Table 2). This was also found in most individual subjects for most ROIs (see Tables 12 and 13). Single, double and tripple asterisks indicate significant differences at $p < .05$, $.01$ and $.001$ respectively.

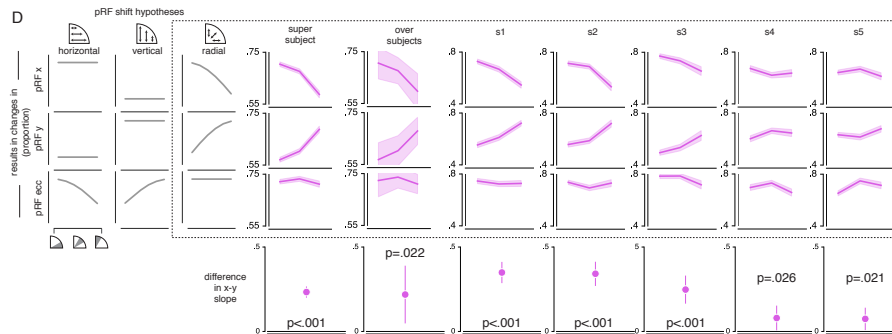


Figure 4: pRF x, y and eccentricity position shifts plotted as a function of polar angle, for different shift direction hypotheses. The data from all statistical methods closely matches the radial shift direction hypothesis, showing strongest pRF x shifts close to the horizontal meridian, strongest pRF y shifts close to the vertical meridian and no polar angle dependence of pRF eccentricity shifts. This is evidenced by a more positive slope of y change over polar angle compared to slope of x change over polar angle in the 'super subject' method (see main text for statistics), for the 'over subjects' method (slope difference = 0.219, $t(4) = 3.616$, $p = 0.022$, Cohen's $d = 1.808$), and was significant in every individual subject. Error bars reflect 95% CIs across voxels in the 'super subject' and 'per subject' method, and across subjects in the 'over subjects' method.

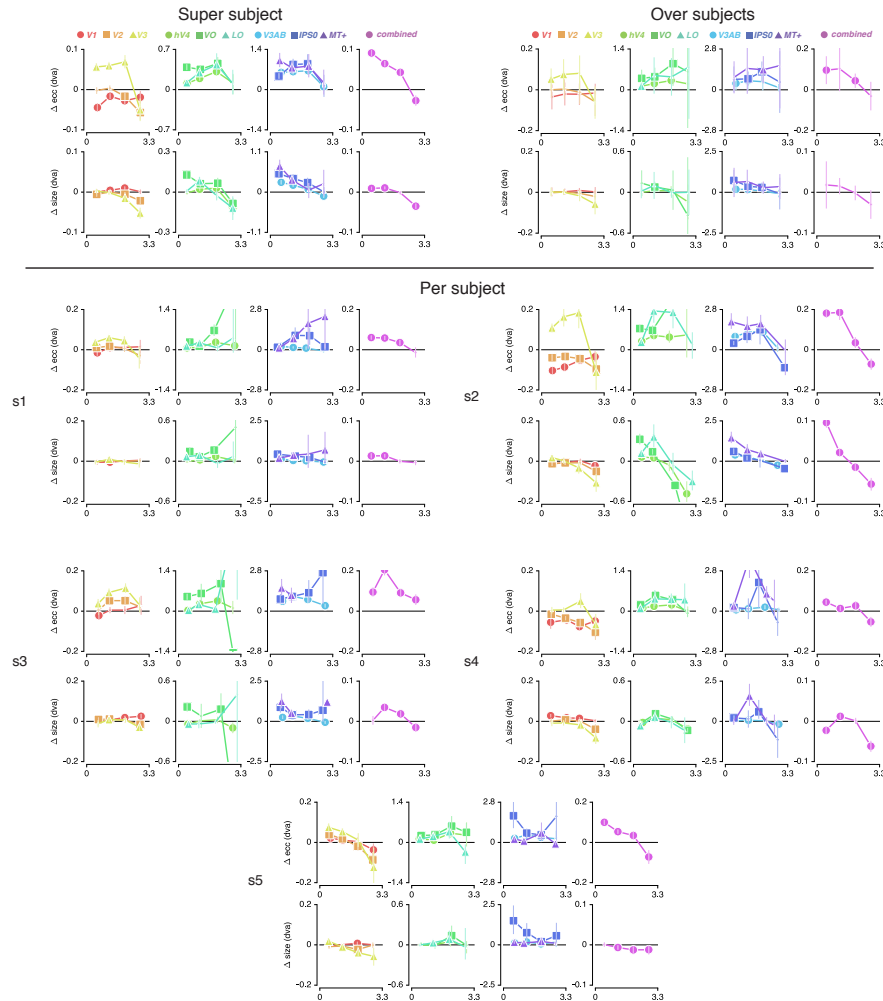


Figure 5: Difference between *Attention to Stimulus* and *Attention to Fixation* pRF eccentricity and size as a function of *Attention to Fixation* eccentricity (see Tables 3-6 and 14-21). The data shows a transition from inwards to outwards shifts across the visual hierarchy in all subjects. Additionally, the progressions of change over eccentricity are similar within ROIs across subjects. Finally, data from the *combined* ROI in most subjects reveals that parafoveal pRFs tend to shift away from the fovea and increase in size, while peripheral pRFs tend to shift toward the fovea and decrease in sizes. In the 'super subject' and 'per subject' methods markers' errorbar denotes 95% CI of data over voxels; in the 'over subjects' method, errorbar denotes 95% CI over subjects. Increased marker size indicates significance with $p < .05$ (FDR corrected for 'super subject').

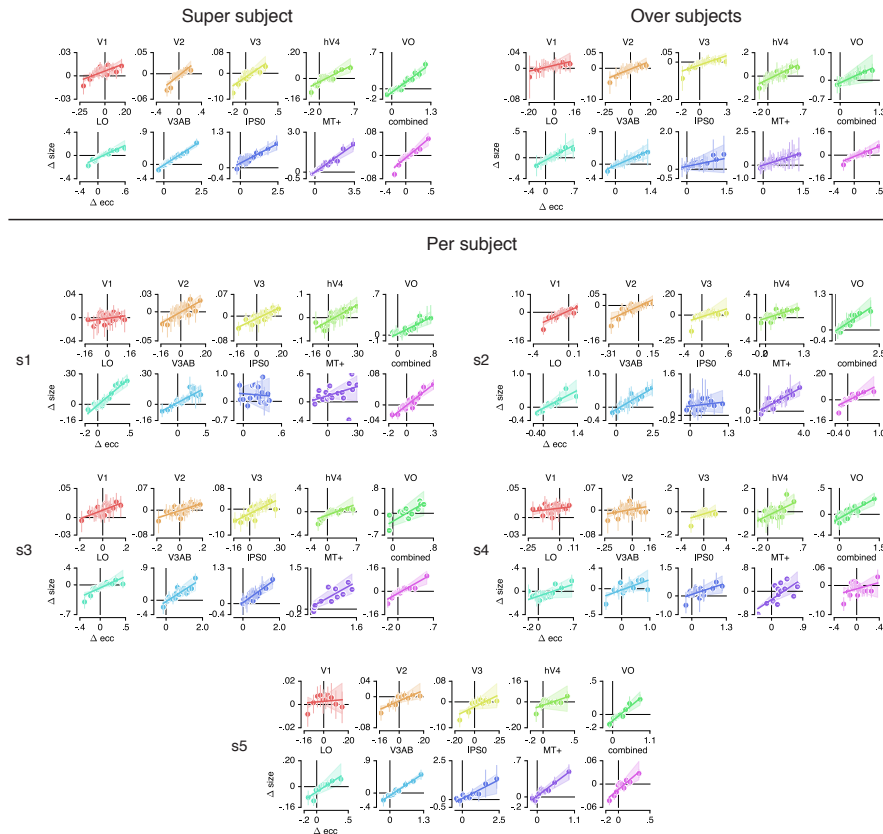


Figure 6: Changes in pRF eccentricity and size were strongly correlated in all ROIs. In the 'over subjects' method, we find that pRF eccentricity and size changes are significant in all ROIs except IPSO (although $p = .070$). In the 'per subject method', we find such a significant correlation in at least 2 (but often 5) subjects (see Table 22). In the 'super subject' and for 'per subjects' figures, markers' errorbar denotes 95% CI of data over voxels; in the 'over subjects' figure, errorbar denotes 95% CI over subjects.

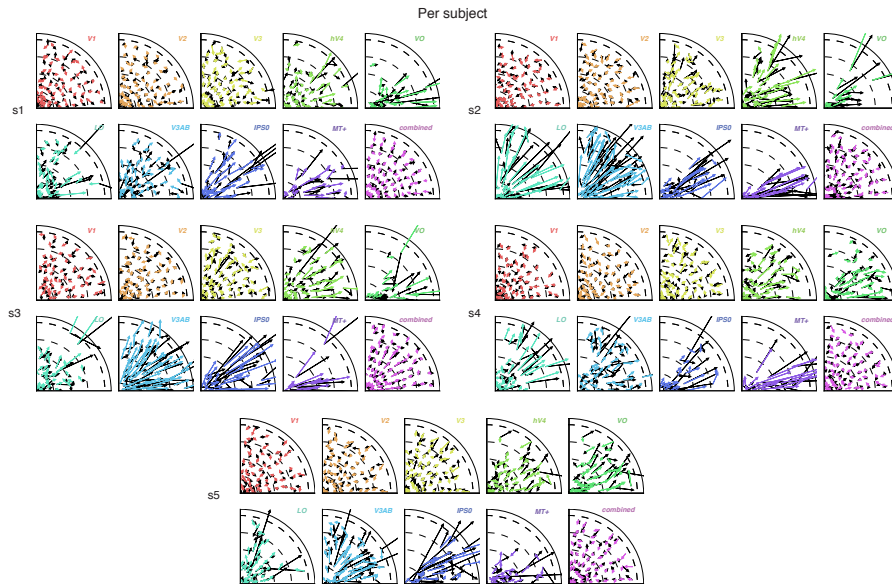


Figure 7: Attentional gain field modeling results for each subject. Arrows depict observed (black) and predicted (color) pRF shifts. This shows that the model closely captured the data in all individual subjects.

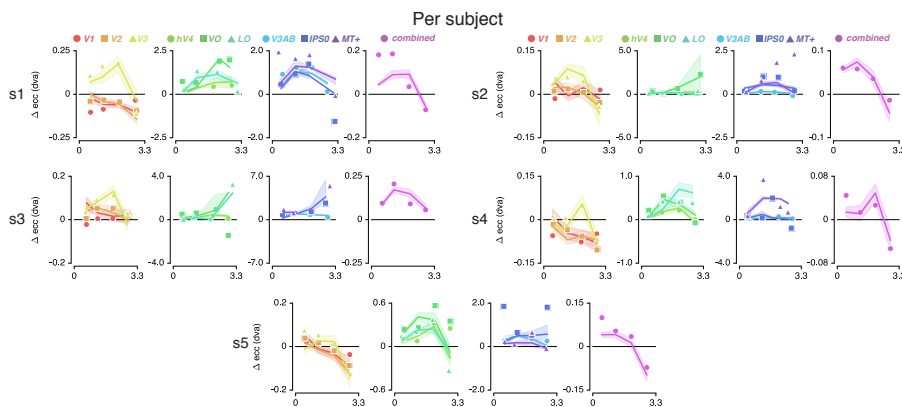


Figure 8: Attentional gain field modeling results for each subject. Observed (markers) and predicted (solid lines) pRF eccentricity difference between *Attend Fixation* and *Attend Stimulus* conditions for each subject. Shaded areas indicate 95% CI over voxels. This shows that the model was able to capture between subject variance with a high accuracy.

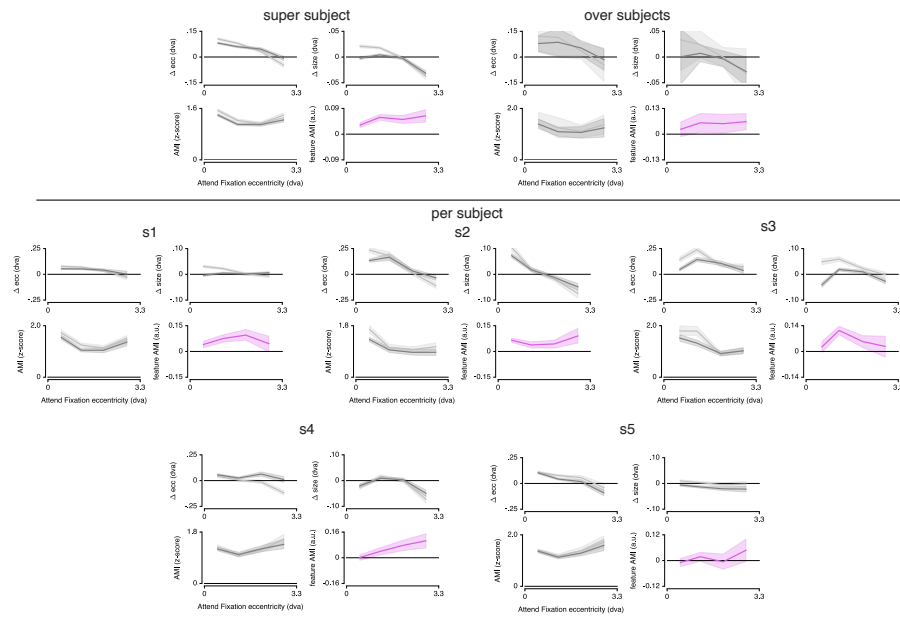


Figure 9: Differences in pRF eccentricity and size relative to the *Attention to Fixation* condition, for both the *Attention to Color* and *Attention to TF* condition separately. The changes in both eccentricity and size are more pronounced when attending changes in color versus TF in the bar. This pattern is most clear in the 'super subject' and 'over subjects' method (albeit with larger variance), and is present in most individual subjects. In the 'super subject' and 'per subject' figures, error bars denote 95% CI over voxels, in the 'over subject' method error bars indicate 95% CI over subjects.

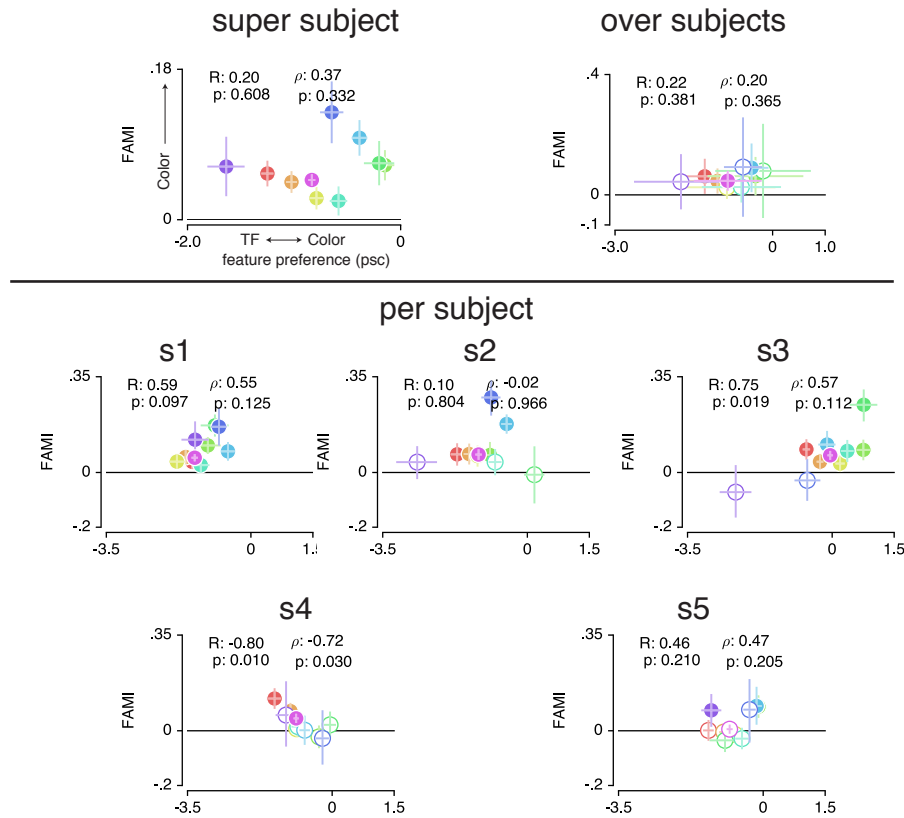


Figure 10: Feature AMI compared to feature preference for each ROI, for each statistical method. The y-axis displays feature AMI, which increases when pRF modulations (size and eccentricity changes combined, see Methods) are greater when attending color compared to TF. The x-axis displays feature preference, which increases with higher color compared to TF preference. pRF modulations were greater when attending color in all ROIs in the ‘super subject’ method, and was unrelated to feature preference (see Table 8). In the ‘over subjects’ method, we confirm that feature AMI was not different between ROIs over subjects (RM ANOVA, factor of ROI: $F(8,4) = 1.108$, $p = 0.384$, $\eta^2 p = 0.225$), and that it was on average 0.064 over ROIs across subjects, $t(4) = 4.654$, $p = 0.010$, cohen’s $d = 2.081$). Additionally, we found that feature AMI was significantly positive in at least 2 (but often 4) out of 5 subjects in each ROI (see Table 23). Finally, we also found no correlation with feature preference in the ‘over subjects’ method ($t(4) = 0.655$, $p = .549$, cohen’s $d = 0.33$).

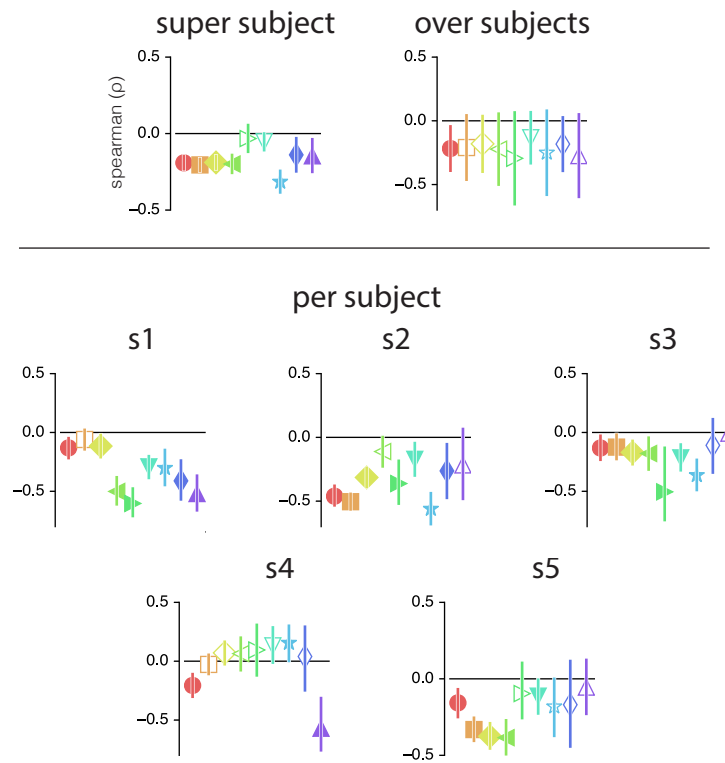


Figure 11: Color compared to TF preference versus eccentricity correlations. The 'super subject' method shows negative correlations in all ROIs except VO and LO. The 'over' subjects method shows that this correlation is negative on average and does not vary across ROI (RM ANOVA with main factor of ROI $F(8,4) = 0.354$, $p = .937$, $\eta^2 p = .030$, on average -0.218 over ROIs, $F(1,4) = 15.630$, $p = .017$, $\eta^2 p = .641$). When looking at individual subjects, we find that correlations are positive in at least two but often in the majority of subjects across ROIs (see Table 24).

Statistical Tables - Main Text

Table 1: Statistics corresponding to Figure 2C on pRF shift direction ratios. P-values reflect proportion of bootstrapped differences that are different from 0. Single, double and triple asterisks indicate FDR corrected significance of <.05, <.01 and <.001 respectively. FDR correction performed over all p-values in this table simultaneously.

ROI	x>y				ecc>x			
	N	p	Δ ratio	cohen's d	N	p	Δ ratio	cohen's d
V1	2176	.098	.02	.04	2176	<.001***	.03	.09
V2	2752	.102	.02	.03	2752	.002**	.02	.06
V3	2320	.773	.00	.01	2318	<.001***	.07	.18
hV4	1201	<.001***	.10	.18	1201	<.001***	.07	.20
VO	582	<.001***	.34	.67	573	<.001***	.08	.37
LO	1397	<.001***	.12	.20	1394	<.001***	.06	.16
V3AB	880	<.001***	.16	.27	873	<.001***	.15	.46
IPS0	313	.023*	.08	.14	313	<.001***	.16	.61
MT+	325	<.001***	.36	.68	306	<.001***	.04	.28
combined	11946	<.001***	.06	.10	11940	<.001***	.05	.15

Table 2: Statistics corresponding to Figure 2 on uniformity of polar angle distributions. P-values test whether pRFs are distributed non-uniformly over polar angle (Rayleigh test). Triple asterisks indicate FDR corrected significance of <.001. FDR correction performed over all p-values in this table simultaneously.

ROI	N	z	p
V1	2176	66.848	<.001***
V2	2754	51.904	<.001***
V3	2322	63.704	<.001***
hV4	1201	50.418	<.001***
VO	582	116.563	<.001***
LO	1405	40.995	<.001***
V3AB	883	32.554	<.001***

ROI	N	z	p
IPSO	316	56.946	<.001***
MT+	328	119.052	<.001***
combined	11967	463.382	<.001***

Table 3: Statistics corresponding to Figure 3A on pRF eccentricity changes. P-values reflect whether bootstrapped distribution is different from 0, for each ROI and each eccentricity bin (bin 3 and 4 in table below). Single, double and triple asterisks indicate FDR corrected significance of <.05, <.01 and <.001 respectively. FDR correction performed over all p-values in this table simultaneously.

ecc bin	1				2				
	ROI	N	p	Δ ecc	cohen's d	ROI	N	p	Δ ecc
V1	509	<.001***	-.044	-.44	749	<.001***	-.016	-.20	
V2	862	0.504	-.002	-.02	931	.204	.004	.04	
V3	920	<.001***	.056	.49	747	<.001***	.059	.58	
hV4	693	<.001***	.109	.67	359	<.001***	.194	.64	
VO	313	<.001***	.389	1.04	162	<.001***	.352	.85	
LO	1047	<.001***	.121	.62	263	<.001***	.295	.60	
V3AB	220	<.001***	.600	.86	348	<.001***	.623	.87	
IPSO	170	<.001***	.473	.91	86	<.001***	.876	1.05	
MT+	186	<.001***	1.015	.68	103	<.001***	.759	.66	
combined	4920	<.001***	.091	.45	3748	<.001***	.065	.37	

Table 4: Statistics corresponding to Figure 3A on pRF eccentricity changes. P-values reflect whether bootstrapped distribution is different from 0, for each ROI and each eccentricity bin (bin 1 and 2 in table above). Single, double and triple asterisks indicate FDR corrected significance of <.05, <.01 and <.001 respectively. FDR correction performed over all p-values in this table simultaneously.

ecc bin	3				4				
	ROI	N	p	Δ ecc	cohen's d	ROI	N	p	Δ ecc

ecc bin	3				4			
V1	595	<.001***	-.028	-.30	323	.010*	-.019	-.15
V2	616	<.001***	-.017	-.16	343	<.001***	-.057	-.36
V3	427	<.001***	.069	.43	226	<.001***	-.050	-.24
hV4	110	<.001***	.313	.91	39	0.046	.115	.27
VO	71	<.001***	.455	1.05	36	.325	.081	.14
LO	56	<.001***	.434	.64	31	.260	.108	.17
V3AB	199	<.001***	.657	.93	113	.017*	.102	.21
IPSO	36	<.001***	.896	1.01	21	.470	.135	.17
MT+	18	<.001***	.818	1.04	18	.249	.240	.27
combined	2128	<.001***	.043	.22	1150	<.001***	-.027	-.14

Table 5: Statistics corresponding to Figure 3B on pRF size changes. P-values reflect whether bootstrapped pRF size difference distribution is different from 0, for each ROI and eccentricity bins 1 and 2 (bin 3 and 4 in table below). Single, double and triple asterisks indicate FDR corrected significance of <.05, <.01 and <.001 respectively. FDR correction performed over all p-values in this table simultaneously.

ecc bin	1				2			
ROI	N	p	Δ size	cohen's d	N	p	Δ size	cohen's d
V1	509	.624	.001	.02	749	<.001***	.004	.15
V2	862	.007*	-.006	-.09	931	.870	.000	.01
V3	920	.237	.003	.04	747	.613	-.001	-.02
hV4	693	.040	-.007	-.08	359	<.001***	.021	.24
VO	313	<.001***	.128	.51	162	<.001***	.063	.34
LO	1047	.060	.008	.06	263	<.001***	.084	.36
V3AB	220	<.001***	.268	.76	348	<.001***	.189	.65
IPSO	170	<.001***	.501	.99	86	<.001***	.369	.79
MT+	186	<.001***	.711	.68	103	<.001***	.332	.77
combined	4920	<.001***	.009	.10	3748	<.001***	.010	.16

Table 6: Statistics corresponding to Figure 3B on pRF size changes. P-values reflect whether bootstrapped pRF size difference distribution is different from 0, for each ROI and eccentricity bins 3 and 4 (bin 1 and 2 in table above). Single, double and triple asterisks indicate FDR corrected significance of <.05, <.01 and <.001 respectively. FDR correction performed over all p-values in this table simultaneously.

ecc bin	3				4			
	N	p	Δ size	cohen's d	N	p	Δ size	cohen's d
V1	595	<.001***	.010	.33	323	.663	.001	.03
V2	616	.012*	-.005	-.10	343	<.001***	-.021	-.31
V3	427	<.001***	-.015	-.19	226	<.001***	-.052	-.54
hV4	110	.012*	.029	.24	39	<.001***	-.114	-.72
VO	71	<.001***	.066	.41	36	<.001***	-.085	-.98
LO	56	.108	-.026	-.21	31	.006**	-.119	-.45
V3AB	199	<.001***	.075	.37	113	<.001***	-.111	-.62
IPS0	36	<.001***	.260	.78	21	.988	.003	.01
MT+	18	.541	.056	.14	18	.128	.227	.31
combined	2128	.252	-.002	-.03	1150	<.001***	-.035	-.38

Table 7: Statistics corresponding to Figure 3C on correlations between eccentricity and size changes. P-values are two-tailed tests whether bootstrapped distribution of pRF eccentricity and size change correlations across bins is different from 0. Triple asterisks indicate FDR corrected significance of <.001. FDR correction performed over all p-values in this table simultaneously.

ROI	R	N	p
V1	0.74	20	<.001***
V2	0.86	20	<.001***
V3	0.87	20	<.001***
hV4	0.87	20	<.001***
VO	0.97	20	<.001***
LO	0.95	20	<.001***
V3AB	0.99	20	<.001***

ROI	R	N	p
IPS0	0.93	20	<.001***
MT+	0.98	20	<.001***
combined	0.94	20	<.001***

Table 8: Statistics corresponding to Figure 5D on feature-based attentional modulation. P-values are uncorrected two-tailed tests whether bootstrapped feature attentional modulation index distribution is different from 0. Double and triple asterisks indicate FDR corrected significance of <.01 and <.001 respectively. FDR correction performed over all p-values in this table simultaneously.

ROI	N	mean diff	p	cohen_d
V1	1605	0.05	<.001***	0.170
V2	2165	0.04	<.001***	0.146
V3	1762	0.03	<.001***	0.105
hV4	860	0.05	<.001***	0.197
VO	451	0.08	<.001***	0.290
LO	1009	0.02	0.008**	0.085
V3AB	703	0.11	<.001***	0.364
IPS0	237	0.14	<.001***	0.486
MT+	252	0.08	<.001***	0.270

Table 9: Statistics corresponding to Figure 6 on correlation between feature preference and eccentricity. P-values are uncorrected two-tailed tests whether bootstrapped correlation value of feature preference and pRF eccentricity differs from 0. Single and triple asterisks indicate FDR corrected significance of <.05 and <.001 respectively. FDR correction performed over all p-values in this table simultaneously.

ROI	N	corr	p
V1	2154	-0.191	<.001***
V2	2718	-0.205	<.001***
V3	2274	-0.189	<.001***

ROI	N	corr	p
hV4	1169	-0.199	<.001***
VO	567	-0.033	0.475
LO	1365	-0.054	0.052
V3AB	877	-0.315	<.001***
IPS0	313	-0.139	0.012*
MT+	325	-0.146	0.007*

2

Statistical Tables - Supplementary Material

Table 10: Statistics corresponding to Supplementary Figure 3 on pRF x versus y shift ratios. P-values result from t-tests over the 5 subject values. Single, double and triple asterisks indicates uncorrected p-value < .05, .01 and .001 respectively. The last two columns reflect in how many out of 5 subjects these differences were different from 0 with uncorrected bootstrapped p-values of <.05 over voxels.

ROI	N	p	t	Δ ratio	cohen's d	x>y	y<x
V1	5	.614	0.546	.02	.27	2	1
V2	5	.638	0.508	.02	.25	2	2
V3	5	.882	0.158	.01	.08	1	2
hV4	5	.100	2.128	.12	1.06	2	0
VO	5	.004**	5.858	.35	2.93	5	0
LO	5	.091	2.216	.13	1.11	3	0
V3AB	5	.165	1.699	.14	.085	3	0
IPS0	5	.411	0.918	.09	.46	3	1
MT+	5	.014*	4.162	.48	2.08	4	0
combined	5	.151	1.773	.07	.89	3	0

Table 11: Statistics corresponding to Supplementary Figure 3 on pRF eccentricity versus x shift ratios. P-values result from t-tests over the 5 subject values. Single, double and triple asterisks indicates uncorrected p-value < .05, .01 and .001 respectively. The last two columns reflect in how many out of 5 subjects these differences were different from 0 with uncorrected bootstrapped p-values of <.05 over voxels.

ROI	N	p	t	Δ ratio	cohen's d	ecc>x	ecc<x
V1	5	.049*	2.797	.04	1.40	3	0
V2	5	.350	1.057	.03	.53	2	1
V3	5	.036*	3.094	.06	1.55	3	0
hV4	5	.037*	3.072	.07	1.54	3	0
VO	5	.013*	4.240	.08	2.12	5	0
LO	5	.153	1.764	.06	.88	2	0
V3AB	5	.037*	3.084	.14	1.54	4	0
IPS0	5	.047*	2.845	.15	1.42	4	0
MT+	5	.080	2.335	.03	1.17	3	0
combined	5	.003**	6.707	.05	3.35	5	0

Table 12: Rayleigh test for non-uniformity for subjects 1-3. Single, double and triple asterisks indicates uncorrected p-value < .05, .01 and .001 respectively.

ROI	s1			s2			s3		
	N	z	p	N	z	p	N	z	p
V1	469	3.221	.040*	558	26.131	<.001***	333	11.823	<.001***
V2	592	0.659	.518	605	9.986	<.001***	411	48.090	<.001***
V3	533	1.021	.360	463	22.909	<.001***	389	12.275	<.001***
hV4	335	18.664	<.001***	183	0.626	.535	228	32.801	<.001***
VO	97	37.899	<.001***	136	46.282	<.001***	36	11.037	<.001***
LO	271	2.255	.105	367	25.638	<.001***	268	37.663	<.001***
V3AB	169	4.560	.010*	176	23.160	<.001***	233	43.613	<.001***
IPS0	67	0.101	.905	77	17.517	<.001***	78	38.176	<.001***
MT+	43	14.066	<.001***	71	17.095	<.001***	43	27.463	<.001***

	s1			s2			s3		
combined	2576	12.585	<.001***	2636	119.207	<.001***	2019	208.441	<.001***

Table 13: Rayleigh test for non-uniformity for subjects 4-5. Single, double and triple asterisks indicates uncorrected p-value < .05, .01 and .001 respectively.

	s4			s5		
ROI	N	z	p	N	z	p
V1	369	3.891	.020*	447	40.575	<.001***
V2	563	4.195	.015*	583	20.792	<.001***
V3	504	22.465	<.001***	433	27.032	<.001***
hV4	218	0.995	.370	237	30.059	<.001***
VO	146	24.882	<.001***	167	28.314	<.001***
LO	195	4.618	.010*	304	24.695	<.001***
V3AB	176	3.471	.031*	129	18.098	<.001***
IPS0	49	12.339	<.001***	45	11.335	<.001***
MT+	47	26.131	<.001***	124	50.139	<.001***
combined	2267	51.292	<.001***	2469	163.225	<.001***

Table 14: Statistics corresponding to Supplementary Figure 5 on pRF eccentricity changes in eccentricity bin 1. P-values reflect whether t-test showed that subject average values were different from 0, for each ROI. Single, double and triple asterisks indicate uncorrected significance of <.05, <.01 and <.001 respectively. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of < .05.

ROI	N	p	t	Δ ecc	cohen's d	pos in	neg in
V1	5	.172	-1.663	-0.035	-0.831	1	4
V2	5	.998	0.003	0.000	0.001	2	2
V3	5	.042*	2.953	0.053	1.477	4	0
hV4	5	.052	2.729	0.124	1.365	5	0
VO	5	.017*	3.903	0.393	1.952	5	0

ROI	N	p	t	Δ ecc	cohen's d	pos in	neg in
LO	5	.030*	3.309	0.125	1.655	5	0
V3AB	5	.047*	2.843	0.442	1.422	5	0
IPS0	5	.080	2.335	0.715	1.167	5	0
MT+	5	.089	2.237	0.858	1.119	5	0
combined	5	.015*	4.067	0.096	2.033	5	0

Table 15: Statistics corresponding to Supplementary Figure 5 on pRF eccentricity changes in eccentricity bin 2. P-values reflect whether t-test showed that subject average values were different from 0, for each ROI. Single, double and triple asterisks indicate uncorrected significance of <.05, <.01 and <.001 respectively. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of < .05.

ROI	N	p	t	Δ ecc	cohen's d	pos in	neg in
V1	5	.348	-1.063	-0.021	-0.532	2	2
V2	5	.822	0.240	0.004	0.120	3	2
V3	5	.045*	2.884	0.075	1.442	4	0
hV4	5	.049*	2.805	0.216	1.402	5	0
VO	5	.014*	4.151	0.444	2.075	5	0
LO	5	.087	2.252	0.491	1.126	5	0
V3AB	5	.047*	2.837	0.623	1.419	5	0
IPS0	5	.009**	4.674	0.753	2.337	4	0
MT+	5	.075	2.391	1.463	1.195	5	0
combined	5	.056	2.671	0.103	1.335	5	0

Table 16: Statistics corresponding to Supplementary Figure 5 on pRF eccentricity changes in eccentricity bin 3. P-values reflect whether t-test showed that subject average values were different from 0, for each ROI. Single, double and triple asterisks indicate uncorrected significance of <.05, <.01 and <.001 respectively. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of < .05.

ROI	N	p	t	Δ ecc	cohen's d	pos in	neg in
V1	5	.296	-1.202	-0.022	-0.601	0	2
V2	5	.556	-0.642	-0.012	-0.321	1	3
V3	5	.057	2.651	0.081	1.326	4	0
hV4	5	.001**	8.314	0.319	4.157	5	0
VO	5	.028*	3.355	0.897	1.678	5	0
LO	5	.120	1.969	0.444	0.985	4	0
V3AB	5	.053	2.714	0.557	1.357	5	0
IPS0	5	.007**	5.103	1.234	2.551	5	0
MT+	4	.016*	4.896	1.378	2.827	4	0
combined	5	.019*	3.799	0.044	1.900	5	0

Table 17: Statistics corresponding to Supplementary Figure 5 on pRF eccentricity changes in eccentricity bin 4. P-values reflect whether t-test showed that subject average values were different from 0, for each ROI. Single, double and triple asterisks indicate uncorrected significance of <.05, <.01 and <.001 respectively. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of < .05.

ROI	N	p	t	Δ ecc	cohen's d	pos in	neg in
V1	5	.369	-1.011	-0.016	-0.506	0	3
V2	5	.071	-2.442	-0.059	-1.221	0	3
V3	5	.085	-2.273	-0.063	-1.136	0	3
hV4	5	.082	2.308	0.202	1.154	1	0
VO	5	.417	0.904	0.623	0.452	3	1
LO	5	.285	1.234	0.782	0.617	2	1
V3AB	5	.122	1.960	0.154	0.980	1	0
IPS0	5	.516	0.711	0.533	0.356	2	1

ROI	N	p	t	Δ ecc	cohen's d	pos in	neg in
MT+	4	.187	1.590	1.662	0.795	2	1
combined	5	.273	-1.270	-0.031	-0.635	1	3

Table 18: Statistics corresponding to Supplementary Figure 5 on pRF size changes in eccentricity bin 1. P-values reflect whether t-test showed that subject average values were different from 0, for each ROI. Single, double and triple asterisks indicate uncorrected significance of <.05, <.01 and <.001 respectively. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of < .05.

ROI	N	p	t	Δ ecc	cohen's d	pos dif	neg pos
V1	5	.768	0.315	0.002	0.158	1	1
V2	5	.511	-0.721	-0.003	-0.361	1	1
V3	5	.777	0.304	0.002	0.152	2	0
hV4	5	.934	-0.088	-0.002	-0.044	1	2
VO	5	.109	2.056	0.134	1.028	3	0
LO	5	.671	0.457	0.016	0.228	2	2
V3AB	5	.041*	2.977	0.184	1.489	4	0
IPS0	5	.031*	3.267	0.725	1.633	5	0
MT+	5	.124	1.943	0.603	0.971	4	0
combined	5	.426	0.884	0.018	0.442	2	1

Table 19: Statistics corresponding to Supplementary Figure 5 on pRF size changes in eccentricity bin 2. P-values reflect whether t-test showed that subject average values were different from 0, for each ROI. Single, double and triple asterisks indicate uncorrected significance of <.05, <.01 and <.001 respectively. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of < .05.

ROI	N	p	t	Δ ecc	cohen's d	pos dif	neg pos
V1	5	.572	0.614	0.003	0.307	2	1
V2	5	.697	0.418	0.002	0.209	2	1
V3	5	.937	0.085	0.000	0.042	2	1

ROI	N	p	t	Δ ecc	cohen's d	pos dif	neg pos
hV4	5	.082	2.308	0.024	1.154	3	0
VO	5	.037*	3.089	0.078	1.544	3	0
LO	5	.214	1.475	0.101	0.738	4	0
V3AB	5	.033*	3.211	0.175	1.605	5	0
IPSO	5	.027*	3.419	0.367	1.709	4	0
MT+	5	.058	2.631	0.656	1.316	5	0
combined	5	.088	2.250	0.015	1.125	4	1

Table 20: Statistics corresponding to Supplementary Figure 5 on pRF size changes in eccentricity bin 3. P-values reflect whether t-test showed that subject average values were different from 0, for each ROI. Single, double and triple asterisks indicate uncorrected significance of <.05, <.01 and <.001 respectively. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of < .05.

ROI	N	p	t	Δ ecc	cohen's d	pos dif	neg pos
V1	5	.061	2.579	0.009	1.290	3	0
V2	5	.373	-1.001	-0.005	-0.501	0	1
V3	5	.111	-2.041	-0.017	-1.020	0	3
hV4	5	.376	0.995	0.022	0.498	1	0
VO	5	.773	0.308	0.031	0.154	3	1
LO	5	.800	-0.271	-0.007	-0.135	1	0
V3AB	5	.085	2.280	0.068	1.140	3	0
IPSO	5	.034*	3.164	0.297	1.582	4	0
MT+	4	.076	2.662	0.285	1.537	2	0
combined	5	.800	-0.270	-0.002	-0.135	1	2

Table 21: Statistics corresponding to Supplementary Figure 5 on pRF size changes in eccentricity bin 4. P-values reflect whether t-test showed that subject average values were different from 0, for each ROI. Single, double and triple asterisks indicate uncorrected significance of <.05, <.01 and <.001 respectively. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of < .05.

ROI	N	p	t	Δ ecc	cohen's d	pos dif	neg pos
V1	5	.800	0.270	0.002	0.135	1	1
V2	5	.122	-1.959	-0.021	-0.979	0	3
V3	5	.028*	-3.386	-0.058	-1.693	0	4
hV4	5	.188	-1.587	-0.141	-0.793	0	3
VO	5	.329	-1.110	-0.338	-0.555	0	3
LO	5	.997	-0.004	0.000	-0.002	0	1
V3AB	5	.352	-1.052	-0.075	-0.526	0	4
IPSO	5	.827	-0.233	-0.079	-0.117	2	1
MT+	5	.257	1.322	0.349	0.661	2	0
combined	5	.071	-2.447	-0.030	-1.223	0	4

Table 22: Statistics corresponding to Supplementary Figure 6 on correlations between eccentricity and size changes. P-values are uncorrected two-tailed tests whether t-test of over subject pRF eccentricity and size change correlations is different from 0. Single and triple asterisks indicate uncorrected significance of <.01 and <.001 respectively. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of < .05.

ROI	R	N	t	p	pos in	neg in
V1	0.461	5	2.888	.045*	2	0
V2	0.704	5	6.411	.003**	4	0
V3	0.704	5	7.219	.002**	5	0
hV4	0.749	5	10.609	<.001***	5	0
VO	0.886	5	12.673	<.001***	5	0
LO	0.847	5	8.074	.001**	5	0
V3AB	0.861	5	6.954	.002**	5	0

ROI	R	N	t	p	pos in	neg in
IPS0	0.500	5	2.450	.070	3	0
MT+	0.745	5	6.261	.003**	4	0
combined	0.799	5	5.431	.006**	4	0

Table 23: Statistics corresponding to Supplementary Figure 10. Astrisk indicate whether the average feature AMI over subjects was different from 0 with $p < .05$. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of $< .05$.

ROI	N	mean diff	t	p	cohen d	pos in	neg in
V1	5	0.065	4.008	.016*	2.004	4	0
V2	5	0.040	4.195	.014*	2.097	4	0
V3	5	0.028	1.985	.118	0.992	2	0
hV4	5	0.055	3.235	.032*	1.618	4	0
VO	5	0.079	1.594	.186	0.797	2	0
LO	5	0.026	1.122	.325	0.561	2	1
V3AB	5	0.111	3.243	.032*	1.621	4	0
IPS0	5	0.113	2.218	.091	1.109	2	0
MT+	5	0.060	1.531	.201	0.766	3	0

Table 24: Statistics corresponding to Supplementary Figure 11. Astrisk indicate whether the spearman correlation between feature preference and eccentricity over subjects was different from 0 with $p < .05$. Right most columns indicate in how many out of 5 subjects the bootstrap test over voxels was different from 0 with uncorrect p-value of $< .05$.

ROI	N	corr	p	pos in	neg in
V1	5	-0.218	.031*	0	5
V2	5	-0.210	.090	0	3
V3	5	-0.181	.084	0	4
hV4	5	-0.222	.095	0	3
VO	5	-0.294	.088	0	3

ROI	N	corr	p	pos in	neg in
LO	5	-0.133	.138	0	4
V3AB	5	-0.250	.105	1	3
IPS0	5	-0.183	.076	0	2
MT+	5	-0.273	.085	0	2