High-resolution population receptive field mapping of human high-level visual areas

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Abstract:

The retinotopic organization of the visual system in specialized visual processing areas provides an account of the resolution of visual input that is available in these areas. Given that the resolution of the visual information that is available within the parahippocampal place area is contested due to previous assumptions of its peripheral bias, we utilized Benson et al's (2018) retinotopy dataset and the Human Connectome Project dataset to determine eccentricity and retinal field size and their anatomical organization within the parahippo campal place area. We also contrast our findings by comparing them to other specialized processing areas, namely, the fusiform face area, the occipital place area and the lateral occipital complex. We find a correlation of retinal field size and eccentricity along the anterior-posterior axis as well as a contralateral field bias across the viewing plane within each of the four regions of interest. The apparent foveal representation and spatial organization indicates that high-resolution visual information is represented within the parahippocampal place area.

Keywords: retinotopy; 7T fMRI; population receptive fields; retinal field size; eccentricity; PPA; OPA; LOC; FFA

Introduction

Decades of research have confirmed that early stages of visual processing within the visual system, from the lateral geniculate nuclei to V3 in striate cortex, show retinotopic organization. The organization of the receptors relative to the visual field is indicative of their spatial resolution, where greater receptive field size and greater eccentricity is considered to have relatively low spatial resolution. Conversely, small eccentricity, or near foveal representation has been shown to represent higher acuity representation of the visual plane. Previous studies have concluded that the parahippocampal place area (PPA) is sensitive to the peripheral field as shown by Arcaro, McMains, Singer and Kastner (2009), and Hasson et al. (2002) who mapped eccentricity and receptive field size. The PPA, in particular, has been shown to exhibit a peripheral field bias, which is commonly interpreted as the PPA lacking sensitivity to high spatial frequencies (Rovamo, Virsu, & Näsänen, 1978).

In addition to the peripheral bias, behavioural studies have suggested that low-spatial resolution information allows for a speed and accuracy trade-off, where scene information at a low spatial resolution can activate category-level information rapidly and accurately using only low-resolution, or low-spatial frequency information. It is thought that the low-spatial frequency information provides a coarse global representation of the scene, which is sufficient for basic-level scene categorization. More recent evidence, however, suggests the opposite. High-spatial frequency visual information, such as line drawings of scenes, suffice to form scene category representations in the PPA (Walther et al., 2011). Additionally, neuroimaging studies have shown that the PPA is activated more strongly by high than low spatial frequencies (Rajimehr, Devaney, Bilenko, Young, & Tootell, 2011) and that scene content in the PPA is more efficiently conveyed by high than low spatial frequencies (Berman, Golomb, & Walther, 2017). In fact, the PPA seems to be sensitive to a wide range of visual features, as long as they convey scene content.

Besides the PPA, other visual processing areas that have specialized visual processing are the occipital place area (OPA), the fusiform face area (FFA), which specializes in faces, and in the lateral occipital complex (LOC), which is sensitive to objects. In this study, we mapped the spatial organization of the receptive field sizes and eccentricity in each of the four regions of interest (ROIs) using the high field strength (7T) retinotopic dataset from Benson et al. (2018).

Methods

In total, 158 participants from the Human Connectome Project dataset, which includes both 7T and 3T scans were utilized to fit the population receptive fields across subjects (Benson et al., 2018). The 7T scan included 6 runs of retinotopic scans using stimuli that were designed to stimulate high-level visual cortex. Whole-brain data were collected at a 1.6mm isotropic resolution with a 1s TR. The 3T scan included a working memory task, which used stimuli from several categories, such as places, faces, tools, and body parts. We used those as a face-place-object localizer in order to functionally localize four high-level regions of interest: two scene-selective areas, the PPA, and the OPA; one face-selective area, the FFA, and one object-selective area, the LOC. We utilized retinotopy data from Benson et al. (2018), that was computed using a population receptive field model by Kay, Winawer, Mezer, and Wandell (2013), in order to map out the visual field within each of these ROIs. We analyzed the population receptive fields for all voxels falling within the functionally localized ROIs in individual subject space.

We computed a mixed-effects model with participants as the random factor in order to compute the correlation of the voxel location along each of the cardinal axes in the Cartesian coordinate system. We also calculated the field of view relative to the viewing plane for each voxel in order to measure any biases relative to the viewing plane that might be present within each hemisphere of the ROI. Additionally, the slope of the linear model that computed the correlation between eccentricity and retinal field size by participant was compared across ROIs.

Results

The resulting hemifield bias within each of the 4 ROIs supported previous findings for the contralateral hemifield bias within the viewing plane (Table 1). The results also indicated that both hemispheres of the PPA, the right OPA, and the left FFA showed evidence of an upper-field bias. Consistent with previous studies (Silson, Groen, Kravitz, & Baker, 2016), the LOC had a significant bias towards the lower half of the viewing plane (Figure 1).

Table 1: Viewing plane hemifield bias

ROI	F-score interaction effect	p-value
PPA	50.085	< .001
OPA	58.718	< .001
LOC	41.228	< .001
FFA	5.381	0.021

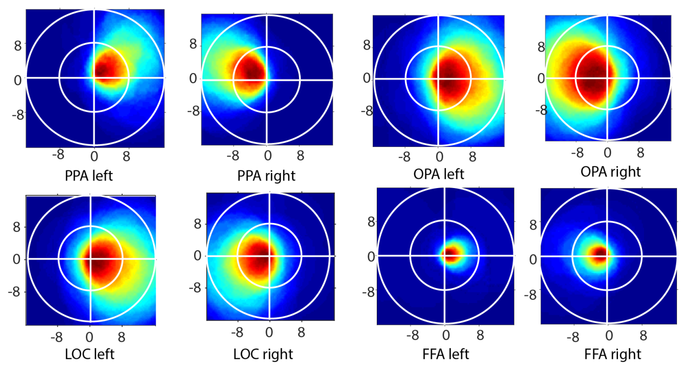

Figure 1. Hemifield bias

The normalized histograms of the distributions also showed that the mean distribution of the eccentricity and retinal field size were skewed further away from the fovea in the PPA and the OPA relative to the FFA and the LOC (Figure 2, Figure 3).

The slope of each of these linear models of eccentricity and retinal field size indicated significant differences across the ROIs (Figure 4) through a repeated measures ANCOVA, $F = 36403.4$, $p < 0.001$.

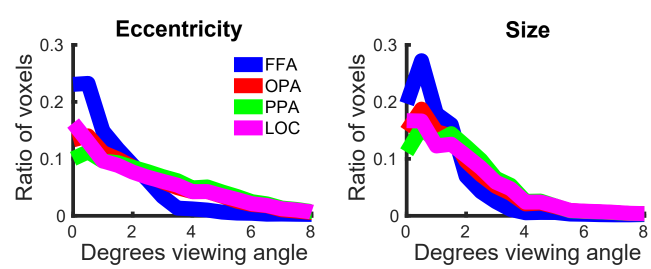

Figure 2. Normalized distribution of eccentricity (right) and retinal field size (left) across participants

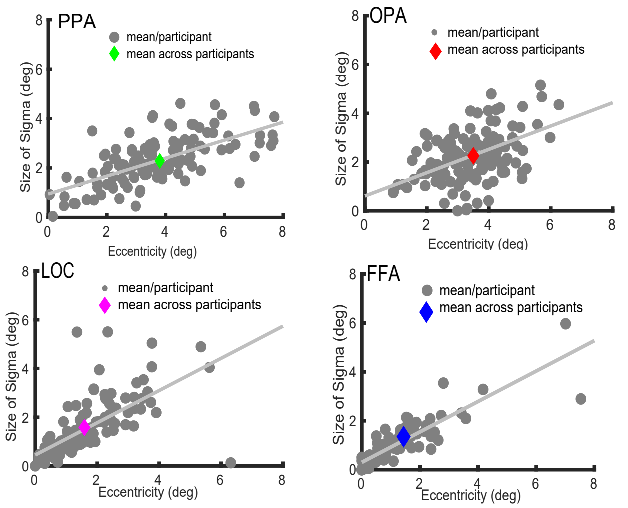

Figure 3. Mean eccentricity and retinal field size across participants

Table 2: Mixed effects model fit estimation.

PPA	Size			Eccentricity		
axis	L►M	P►A	I►S	L►M	P►A	I►S
left	0.017	0.077	0.082	-0.088	0.051	0.178
right	-0.046	0.052	0.046	0.092	n.s.	0.121
OPA						
left	0.027	0.057	0.055	-0.085	0.004	0.087
right	-0.076	-0.081	0.057	0.055	n.s.	0.067
LOC						
left	0.060	0.024	0.055	0.045	-0.007	0.082
right	-0.048	0.045	0.045	-0.047	0.011	0.063
FFA						
left	-0.014	0.027	-0.003	-0.038	0.020	0.007
right	n.s.	0.028	-0.012	0.037	0.010	-0.009

All estimations are significant unless specified otherwise

The results from a correlation of eccentricity and size along the y axis indicated that receptive field size and eccentricity increase from posterior to anterior, with the exception of the left hemisphere of the LOC, which indicated more foveal representation in the anterior regions relative to the posterior regions along the AP axis (Table 2). The foveal representation in the posterior regions of the PPA, OPA and FFA and right

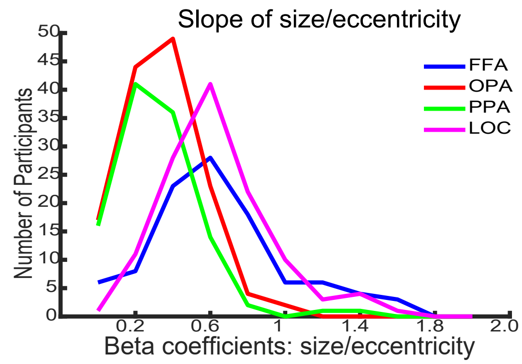

Figure 4. Slope of eccentricity correlated with retinal field size across participants

LOC, suggests that as the visual information is passed from low-level to high-level visual areas, the visual field is increasingly more low-resolution within these regions.

Regression of eccentricity with the lateral-medial axis, on the other hand, showed more foveal representation laterally than medially in each ROI. This relationship was inverted within the PPA and the OPA for the correlation of size of the retinal field, that is, the direction change of retinal field size flipped, such that retinal field size increases from medial to lateral within the PPA and the OPA. Along the z-axis, eccentricity and retinal field size both showed a positive correlation across PPA, OPA and LOC, such that both eccentricity and size of retinal field increased from inferior to superior.

Discussion

The organization of receptive field size and eccentricity within the four ROIs, PPA, OPA, LOC, and FFA seems to follow a retinotopically defined organization similar to that of early visual cortex. A contralateral hemifield bias within the viewing plane is in line with the contralateral organization of the visual system that is present at the early visual processing layers in V1 and V2. The continuation of the contralateral bias at the higher-level visual processing areas suggests that the visual system maintains the retinotopic organization at higher levels of the visual system. The upper field bias that was found within the PPA is in line with previous findings (Silson et al., 2015). An upper field bias was also found within the right hemisphere OPA and the left hemisphere of the FFA, suggesting that these ROIs also have a specialization for the upper field. The LOC was found to have a lower-field bias, which is consistent with previous findings for this ROI (Silson et al., 2016).

Considering that the LOC specializes in object feature processing, a lower hemifield bias could account for the typical location of objects, as they are usually located in lower areas within the field of view due to their relatively smaller size and often located resting on the ground or on elevated surfaces.

Anatomical spatial organization

The retinotopic organization within the PPA is not only evident via the viewing-plane contra-lateral hemifield bias, it is also evident via the organization of eccentricity and retinal field size within the ROI along all 3 cardinal axes. The significant positive correlation between the anterior-posterior axis indicates that low-resolution information is processed in more anterior regions of the PPA and high-resolution information is processed within the more posterior regions of the PPA. This is also true for the other ROIs for both eccentricity and retinal field size, except for the LOC, which showed a negative correlation within the left hemisphere for eccentricity with the AP-axis. The OPA and PPA showed a significant positive correlation within both left hemispheres for eccentricity. Both hemispheres in the OPA and PPA indicated that size increases from posterior to anterior. The small retinal field size in the posterior indicates high resolution visual information is present within the PPA and the OPA. More anterior parts of the brain areas show a preference for the periphery.

Conclusion

Although the results suggest that retinotopic organization maintains a similar organization to that of the early visual areas within cortex, it is unknown how features that are extracted within these ROIs are passed along them internally.

The foveal representation within the PPA indicates that the PPA is receiving both high spatial resolution and low spatial resolution visual input. These findings suggest that the PPA receives visual information from early visual cortex to allow for processing fine-grained details as well as global features of scenes.

Acknowledgments

Thank you to our sponsors and to Noah Benson for his assistance with Npythy toolbox.

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