fMRI Studies on the Human Brain
Mechanism of Visual Object Perception

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Bin WANG

The Graduate School of Natural Science
and Technology
(Doctor’s Course)
OKAYAMA UNIVERSITY
Abstract

The visual system is the part of the central nervous system which enables human to process visual information. The visual system is divided into central and peripheral vision. Central vision prefers for fine details, whereas, peripheral vision prefers for coarser information. To well understand the perception of object in human vision system, both central and peripheral vision should be investigated together. Functional magnetic resonance imaging (fMRI) has been used for over a decade to study human visual cortex. However, visual cortex functions for the object peripheral field are less well investigated because of technical difficulties in presenting large visual stimuli inside the bore of MRI scanner.

Moreover, attentional modulation in human visual areas has been demonstrated. The functional properties of visual cortical neurons are not fixed. Rather, they can be thought of as adaptive processors, changing their function according to the visual context, and their responses reflect the demands of the perceptual task being performed. It is described that attention enhances neural activities to object visual information in human visual cortex. Attention will increase retinotopic activities in human visual cortex, especially in the higher visual areas. The attention modulates the object processing in visual cortex also aroused our interested.

Firstly, in present study, we developed a simple method for wide-field stimulus presentation within the MRI environment. This system is advantageous in that the presented images have high resolution. We successfully applied this visual presentation system to studies of visual retinotopic mapping and object perception neural function in the peripheral visual field. Based on the wide-field mapping a result, this system was more effective at mapping checkerboard stimuli in V1-V3 from the central to peripheral visual fields. We located separate peripheral visual field representation areas (V1, V2, V3) and verified recent findings that human motion areas (V3A, MT+, V6). In higher-level visual areas, we also located several classical category-selective areas, including the face-selective area (FFA), occipital face area (OFA), house-selective area (PPA), transverse occipital sulcus (TOS), lateral occipital complex (LOC) and posterior fusiform area (pFs).

Secondly, using the wide-view visual presentation system and functional magnetic resonance imaging (fMRI), we studied the neural activity relationships between V1 and FFA or V1 and PPA within wide visual field. We found V1, FFA, and PPA showed significant different neural activities to faces and houses in 3 dimensions of eccentricity, meridian, and region. Most importantly, the RRV1s in FFA and PPA also exhibited significant differences in 3 dimensions. We proposed that
these differential RRV1s indicated FFA and PPA might have different processing strategies for encoding the wide field visual information from V1.

In addition, the receptive field of the human visual cortex pays important role in object processing. We also studied retinotopic representations and pRF maps for the wide-view field in human visual cortex. The visual areas maps had larger pRF on cortex representation for the peripheral visual field than central visual field. The V1-V3 had larger visual areas maps, and LO1 and LO2 likely to have response to central field. More differently, the pRF size is likely consisted with the size of macaque, but not with the central result of human.

Finally, we attempted to understand the retinotopy for the attention to the static object. In previous report, the neural activations and retinotopic activations in human visual cortex have been shown to be influenced by attention. Here, using images of static objects and the retinotopic mapping task, we estimated the retinotopy driven by attention and visual stimulation in the human visual cortex. We found the early visual areas showed neural response to whole stimulus with a slight attentional enhancement, while the higher visual areas exhibited mainly attention-driven retinotopy. In the higher visual areas, we found that the left hemisphere showed greater attention-driven retinotopic activity compared to the right hemisphere. The left hemisphere had a small attentional window and drove neurons with small receptive fields in visual areas, resulting in easy retinotopic activation, whereas the reverse was true for the right hemisphere. We proposed that the asymmetric retinotopic activity driven by attention to static object was possibly due to asymmetric attentional window for the attention to static object and weak influence of bottom-up attention.

In conclusion, we developed a simple method for wide-field stimulus presentation within the MRI environment, revealed out neural activity relationships between V1 and FFA or V1 and PPA within wide visual field, and firstly estimated the pRF maps of wide-view field. In addition, we found the higher visual area showed asymmetric retinotopic activation driven by attention to static object. According to the complexity of the neural mechanisms of visual system, future studies will focus on the peripheral object processing in human visual cortex, and the attention effect on the human visual cortex. Through studying the subsystems of visual cortex integration, we hope to clarify the mechanism for object perception, including the objects in central and peripheral field.
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Chapter 1

Introduction

1.1 The Human Visual System

1.1.1 Visual Fields

The visual field is the total area in which perception is possible while an individual is looking straight ahead. For a person with normal vision, the visual field usually extends outward over an approximately 90-degree angle on each side of the vertical midline of the face. But the angle is smaller above and below the midline, especially for a person whose eyes are deep-set or who has prominent eyebrows. Because the visual fields of the two eyes overlap to a large extent, a defect in the field of one eye may not be evident when both eyes are open. Thus, the visual field can be divided into the area that is visible only to the right eye, the area that is visible to the left eye, and the middle region of binocular vision.

All the light from the visual fields that are left of center of both eyes falls on the right sides of the retinas of both eyes. This information is transmitted by the optic nerves to the right visual cortex of the brain. Information about the right fields of vision is transmitted to the left cortex, and information about the region of binocular vision is transmitted to both the right and left cortex (Figure 1.1).

![Figure 1.1. The visual fields of human and visual information pathway](image-url)
The center of gaze, called the fovea, has a higher density of cones than anywhere else on the retina. In fact, at the fovea, there are no rods at all. The fovea evolved to have the highest possible visual acuity, and the cones are as small as they can possibly be and still function. Moreover, in the fovea, the retinal ganglion cells have smaller receptive fields, and in the periphery, they have much larger receptive fields (Figure 1.2) [1]. The central segments of the visual field, which falls on the retinal fovea, are processed with a higher resolution than the segments that fall in the periphery field. The fovea field is the central 5.2° in visual angle [2]. The parafovea field is defined to be a annulus visual field (5.2°~ 8.6°) and the perifovea field is defined to be a annulus visual field (8.6°~19°) outside the parafovea [3]. Here, we will refer to the central visual field roughly as that of the fovea, perifovea and perifovea (~ 19° visual field or 10° eccentricities) and peripheral vision for visual field as outside 19° visual field or 10° eccentricity.

The difference between central and peripheral vision becomes apparent when you understand the visual function of the eye. Inevitably, peripheral vision prefers for coarser information, whereas central vision prefers for fine details. Functionally, the peripheral vision is mainly concerned with motion processing [4-8], whereas the central vision is mainly concerned with form and color [9, 10]. To well understand the perception of vision in human vision system, both central and peripheral vision should be investigated together.

Figure 1.2. The distribution and density of cones and rods in retina.
The process of visual perception begins when an image of the external world forms on the retina in the back of the eye [1], and is projected to the visual cortex through the lateral geniculate nucleus. The human visual cortex is composed of 4–6 billion neurons that are organized into more than a dozen of distinct functional areas. There is a visual cortex in each hemisphere of the brain. The left hemisphere visual cortex receives signals from the right visual field and the right visual cortex from the left visual field. These areas include the gray matter in the occipital lobe and extend into the temporal and parietal lobes (Figure 1.3). Recently, the advance of neuroimaging allowed us to study noninvasively human vision. Especially, the functional magnetic resonance imaging (fMRI) technique of visual field mapping advances our understanding on the functional organization of human visual cortex. The technique revealed that there is a mosaic of orderly representations of the visual field on the human visual cortex, which is called retinotopy or visual field map and one of the hallmarks of mammalian visual systems[11-14]. Visual field map has advantages in that it facilitate spatial comparison of various visual attributes. This large domain can be divided into many discrete
visual areas that have been distinguished from one another on the basis of visual field maps (Figure 1.4), including several near medial occipital (V1, V2, V3), lateral occipital (LO-1, LO-2, hMT+), ventral occipital (hV4, VO-1, VO-2), dorsal occipital (V3A, V3B), and posterior parietal cortex (IPS-0 to IPS-4) [13, 14].

Figure 1.4. Visual field maps on a cortical surface. Currently identified visual field maps measured with our wide-view display system are shown from several views of the right hemisphere (see legend). The visual maps of V1, V2, and V3 are in the middle cortex. Maps in the dorsal cortex are denoted V3A/B and V6, whereas maps in the intraparietal sulcus are denoted IPS-x. Maps in the lateral occipital cortex are denoted LO-x and TO-x. Maps in the ventral occipital are named hV4, VO-x and PHC-x. The foveal, upper, and lower visual fields are indicated by *, +, and -, visual fields 120°.
The primary visual cortex (Brodmann’s area 17, V1) is the best-studied visual area in the brain[13, 14]. V1 is the first stage of cortical processing of visual information. V1 contains a complete map of the visual field covered by the eyes. It receives its main visual input from the lateral geniculate nucleus of the thalamus (LGN), and sends its main output to subsequent cortical visual areas. V1 has a very well-defined map of the spatial information in vision (Figure 1.4). Visual area V2, also called prestriate cortex, is the second major area in the visual cortex, and the first region within the visual association area (Figure 1.4). It receives strong feedforward connections from V1 (direct and via the pulvinar) and sends strong connections to V3, V4, and V5. It also sends strong feedback connections to V1. The term third visual complex refers to the region of cortex located immediately in front of V2 (Figure 1.4), which includes the region named visual area V3 in humans. Visual area V4 is one of the visual areas in the extrastriate visual cortex (Figure 1.4). V4 is tuned for orientation, spatial frequency, and color. Visual area V5, also known as visual area MT (middle temporal, Figure 1.4), is a region of extrastriate visual cortex that is thought to play a major role in the perception of motion, the integration of local motion signals into global percepts and the guidance of some eye movements.

1.2 Objects Processing in Human Visual Cortex

When a human looks at a number, letter or other shape, neurons in various areas of the brain's visual center respond to different components of that shape, almost instantaneously fitting them together like a puzzle to create an image that the individual then "sees" and understands.

The question of how the brain sees, recognizes and understands objects is one of the most intriguing in neuroscience. This may not even seem like a scientific question to some people, because seeing is so automatic and we are so good at it – far better than the best computer vision systems yet devised. That is because a large part of the human brain is devoted to interpreting objects in our world, so that we have the necessary information for interacting with our environment. Vision doesn't happen in the eye, it happens at multiple processing stages in the brain. Objects are signaled or encoded by large populations of neurons at higher-level stages in the object-processing part of the brain.”

Functional specializations for interpreting form, such as objects and faces, were measured using fMRI. Many such specializations were reported inlateral and ventral–occipital cortex (Figure 1.5), such as faces (fusiform face areas, FFA), houses and places (parahippocampal place area, PPA), words (visual word form areas, VWFA) and objects (lateral occipital complex, LOC) [15, 16]. These object-selective areas have been associated with preferential activation in specialised areas of
the cerebral cortex, leading to the suggestion that they may be produced separately in discrete neural regions.

The eccentricity organization of retinotopy (central and peripheral) is one of the most striking and robust organizational principles in the primate visual cortex [13, 14, 17]. Central vision prefers for fine details, whereas, peripheral vision prefers for coarser information. Functionally, the peripheral vision is mainly concerned with motion processing [4-8], whereas the central vision is mainly concerned with form and color [9, 10]. To well understand the perception of object in human vision system, both central and peripheral vision should be investigated together. fMRI offers an exciting opportunity to measure visual field maps in the human brain. To date, visual field maps for the central vision (~ 10° eccentricities) are well investigated by fMRI. However, visual field maps for the peripheral field (larger than 10° eccentricities) are less well investigated. This lack is mainly due to technical difficulties in presenting large visual stimuli inside the bore of MRI scanner.

![The location of object-selective areas](image)

Figure 1.5. The location of object-selective areas modulated from Wandell 2010.

The functional properties of visual cortical neurons are not fixed. Rather, they can be thought of as adaptive processors, changing their function according to the visual context, and their responses reflect the demands of the perceptual task being performed. Cortical neurons are subject to top-down influences of attention, expectation and perceptual tasks. Such influences represent a reversal of the central dogma of sensory information processing. The top-down signal carries a rich
amount of information that facilitates the interpretation of the visual scene and that enables the visual system to build a stable representation of the objects within it despite rapid and continuous eye movements. Attentional modulation has been demonstrated in human visual areas in several studies [18, 19]. Attention will increase retinotopic activities in human visual cortex, especially in the higher visual areas [20, 21]. It is described that attention enhances neural activities to object visual information in human visual cortex. The attention modulates the object processing in visual cortex aroused our interested.

1.3 The Purpose of the Present Dissertation

Over the past 10 years, the object processing in human visual cortex has been widely investigated using functional magnetic resonance imaging (fMRI). However, due to the technical limitations of visual presentation, the human visual cortex processing the object in the wide-view field is remand unknown. In addition, we also interested to invest the attention modulation in human visual cortex. In the present study, I will try to state the two issues using by fMRI. The framework of visual system studies in this thesis are shown in Figure 1.6.

Firstly, one aim of the present study is to develop a wide-view visual presentation system with a horizontal and vertical visual angle of 120° in MRI environment for vision research and visual retinotopic mapping. We will present the system design and the preliminary experimental testing of the system in this report. The experimental results suggest that the new system is safe and functional in the MRI environment and that it can be used for neuroimaging studies of the visual system.

Secondary, we also invested the neural activity relationships between V1 and FFA or V1 and PPA are still unclear. Using fMRI and wide-view present system, we tried to address this issue by measuring neural activities in V1, FFA and PPA for the images of faces and houses aligning in 4 eccentricities and 4 meridians. Then, we further calculated ratio relative to V1 as comparing the neural responses amplitudes in FFA or PPA with those in V1. We attempted to state processing strategies for encoding the object in wide field.

Thirdly, receptive field (RF) size is fundamental properties of visual cortex, and had important role on object processing. The periphery representation cortex has much larger receptive fields than the central representation cortex in primary area (V1). However, for human with more peripheral visual field, the visual areas maps and pRF maps is remained unknown. We tried to address this issue by pRF model developed by Dumoulin and Wandell.
Finally, retinotopic activity in the human visual cortex has been shown to be influenced by attention. When a subject is attending to a static object, the left hemisphere has a smaller attentional window than the right hemisphere. We further speculated that the human visual cortex has asymmetric retinotopy driven by attention to static objects. We attempted to estimate the retinotopy driven by attention and visual stimulation in the human visual cortex, and understand the attention modulation on static object processing.

1.4 The Contents of the Dissertation

Chapter 1: The concept of visual information processing in the brain were described, main including visual pathway, visual field and visual cortex. The summary previous studies, the study aim and contents of the thesis are also briefly described.

Chapter 2: A wide-view visual presentation system with a horizontal and vertical visual angle of 120° in MRI environment for vision study was developed. We will present the system design and the preliminary experimental testing of the system in this chapter. We developed a simple, effective
method for presenting wide-view visual stimuli within the MRI environment that can be applied to many kinds of fMRI studies of peripheral vision.

Chapter 3: In this chapter, using fMRI and wide-view present system, we tried to address this issue by measuring neural activities in V1, FFA and PPA for the images of faces and houses aligning in 4 eccentricities and 4 meridians. Then, we further calculated ratio relative to V1 (RRV1) as comparing the neural responses amplitudes in FFA or PPA with those in V1. We found V1, FFA, and PPA showed significant different neural activities to faces and houses in 3 dimensions of eccentricity, meridian, and region. Most importantly, the RRV1s in FFA and PPA also exhibited significant differences in 3 dimensions. In the dimension of eccentricity, both FFA and PPA showed smaller RRV1s at central position than those at peripheral positions. In meridian dimension, both FFA and PPA showed larger RRV1s at upper vertical positions than those at lower vertical positions. In the dimension of region, FFA had larger RRV1s than PPA.

Chapter 4: Using pRF model and wide-view presentation system with up to 60° of eccentricity, we tried to estimate the maps on visual cortex. We found retinotopic representations and pRF maps on temporal, occipital and parietal cortex. We further focused on the character of retinotopic representations and pRF size by wide-view field stimuli in V1-V3 and VO1/2. The visual areas maps consisted with the previous reported basing on central visual field. The V1-V3 had larger visual areas maps, and LO1 and LO2 likely to have response to central field.

Chapter 5: Using images of static objects and the retinotopic mapping task, we estimated the retinotopy driven by attention and visual stimulation in the human visual cortex. The early visual areas showed neural response to whole stimulus with a slight attentional enhancement, while the higher visual areas exhibited mainly attention-driven retinotopy. In the higher visual areas, we found that the left hemisphere showed greater attention-driven retinotopic activity compared to the right hemisphere.

Chapter 6: The general conclusions were drew form the present study. The future challenges related on the object processing in human visual cortex were also stated.
Chapter 2

Development of a Method to Present Wide-view Visual Stimuli in MRI for Peripheral Visual Studies

Summary

We developed a novel wide-view visual presentation method for fMRI studies. Computer-generated images were projected onto a hemispheric, translucent screen inside the MRI bore and were then back-projected onto a 52 mm diameter screen. To achieve a wide field view, a spherical screen with a curvature radius of 30 mm was placed 30 mm away from the subjects' eyes. The subjects wore contact lenses that enabled them to focus on the screen, and the resulting visual field reached 120°. To evaluate the clarity and quality of the MRI images, a signal-to-noise ratio valuation experiment was performed. In addition, we successfully applied this visual presentation system to studies of visual retinotopic mapping and object perception neural function in the peripheral visual field. Our study demonstrated that the system is compatible with the MRI environment. Based on the wide-field mapping results, this system were more effective at mapping checkerboard stimuli in V1-V3 from the central to peripheral visual fields. In higher-level visual areas, we successfully located several classical category-selective areas, including the face-selective area (FFA), occipital face area (OFA), house-selective area (PPA), transverse occipital sulcus (TOS), lateral occipital complex (LOC) and posterior fusiform area (pFs). In these areas, we found that the response amplitudes exhibited different decreasing trends with increasing eccentricity. In conclusion, we developed a simple, effective method for presenting wide-view visual stimuli within the MRI environment that can be applied to many kinds of fMRI studies of peripheral vision.

Key Words: visual presentation, wide-view, fMRI, visual cortex.
2.1 Background

Functional magnetic resonance imaging (fMRI) is widely used to measure brain activity and has become an important method for exploring the neural mechanisms behind the perceptual processing of vision [13, 22-24]. The fMRI technique has rapidly become the standard for inferring neuronal activity in human subjects due to its non-invasive nature, reliable response localization, and high spatial resolution [25, 26]. However, MRI employs intense magnetic fields that are easily disturbed by the presence of metallic objects and conductive materials. Such objects or electronic devices pose serious safety concerns for human subjects and decrease the quality of the images. In addition, the MRI scanner bore space is very narrow. Due to these shortcomings, a mode for presenting visual stimuli in the wide-view field remains a major problem. To date, the most commonly used method is the back-projection method, which implements a projector to project stimuli onto a rear-projection screen located outside the MRI scanner. Subjects then view stimuli reflected from the projection screen on an adjustable angled mirror (usually mounted on the head coil of the MRI). This method is limited in presenting wider-view stimuli, however, as it usually provides a visual field of only approximately 8-30° [17, 27, 28].

The visual cortex of the brain is the part of the cerebral cortex that is responsible for processing visual information. The visual cortex is divided into the central and peripheral parts. This central/peripheral organization is one of the most striking and robust organizational principles of the primate visual cortex. Due to the technical limitations of visual presentation, previous human visual retinotopic mapping studies have typically been limited to the central and/or pericentral visual fields [13, 22-24, 29-31]. Controversy still surrounds the patterning of visual representation in many areas of the visual cortex, and the peripheral organization is currently not well established.

Various visual stimuli presentation systems have previously been developed in an attempt to overcome the limitations of stimuli presentation within the MRI environment. Cheng et al. used smaller displays and lenses to achieve visual fields that reached up to 40° of eccentricity [32]. Recently, Pitzalis et al. and Stenbacka et al. placed a flat screen/mirror very close to the subject and reached a 110° visual field (horizontal meridian approximately 110°, vertical meridian approximately 80°) [33, 34]. In addition, stimuli presented using these systems are non-isotropic due to the scanner's small bore space and variation in the mirror's aspect ratio. In our previous study, we developed a 60° eccentricity wide-view visual presentation system using an optic fiber bundle and contact lenses [35]. This presentation system was applicable only for classical retinotopic mapping and dot motion experiments [35, 36]. The image resolution presented by this system was not high enough for presenting complex images, such as faces.
Figure 2.1. The overall wide-view visual stimulus presentation system. An LED projector with a zoom lens projects computer-generated stimuli onto a hemispheric translucent screen inside the bore of the MRI to produce small, high-resolution images on the hemispheric screen.

In the present study, we developed a simple method for wide-field stimulus presentation within the MRI environment. We created a large coverage space by projecting computer-generated stimuli onto a hemispheric screen. We adopted the conventions that the horizontal meridian of the visual field was at approximately 120°, and that the vertical meridian was at approximately 116°. This system is advantageous in that the presented images have high resolution, there is a higher signal-to-noise ratio (SNR) of the MRI images, and the system is lighter and easier to set up than other systems. In addition, the results from three visual experiments suggest that this new technique is safe for use in the MRI environment and that it can be used for many kinds of fMRI studies on peripheral vision.
Figure 2.2. The composition and mechanism of the presentation apparatus. (A) The visual stimulus presentation apparatus in the bore of the MRI scanner. The dashed line outlines the presentation apparatus. (B) Front view shows the components of the presentation apparatus, which include a hemispheric screen, screen fixture, mirror fixture and mirror. (C) The mechanism of the presentation apparatus. The mirror fixture was fixed onto the head coils of the MRI machine. The mirror angle could be adjusted from 40° to 50° by adjusting the two screws. When the distance between the screen and the subject's eyes was 30 mm, the screen field view was 120°. Subjects should wear contact lenses (Menicon soft MA; Menicon, Japan) with +20, +22, or +25 magnification in order to retain their focal length.

2.2 General Descriptions

2.2.1 Implementation

MRI involves the use of strong magnetic fields around the head of a subject within a narrow tunnel; therefore, any device used during MRI is required to be free of ferromagnetic elements, and should not interact with the magnetic field. Accordingly, non-magnetic materials were used to build the device used in this study. In general, the wide-view visual stimulus presentation system consists of a presentation apparatus, a projection apparatus and an operation computer (Figure 2.1). Computer-generated stimuli were projected onto a translucent hemispheric screen inside the MRI bore. The operator used a computer located in the operation room to control presentation of the stimuli.
2.2.2 Presentation Apparatus

The presentation apparatus was attached to the MRI head coil via the mirror stand placed on the head coil. The subject was able to directly view the stimuli when lying in the MRI scanner. The visual stimulus presentation apparatus included a hemispheric screen, a screen fixture and a mirror fixture. Figure 2.2 A shows the visual stimulus presentation apparatus inside the MRI core, and Figure 2.2 B shows a frontal view of the presentation apparatus. The mechanism of presenting the visual stimulus onto a hemispheric screen is shown in Figure 2.2 C.

Hemispheric screen

As shown in Figure 2.3A, a screen made from a transparent Poly (methyl methacrylate) column measuring 52 mm in diameter and 75 mm in length was used. On one of the column's extremities, a hemisphere measuring 52 mm in diameter with a curvature of 30 mm was made. Due to the size limitations of the head coil, the upper and lower edges of the hemisphere were cut by 2 mm to a final size of 48 mm. The inner surface of the hemisphere was coated with a thin layer of photographer’s dulling spray to make a translucent screen (Figure 2.3B).
Figure 2.4. Front view showing the design and size of the screen fixture. A screw was used to easily adjust and fix the screen.

Screen fixture

The screen fixture was made using a transparent Poly plant with a thickness of 10 mm. The position of the screen fixture could be regulated to match variations in the subjects' head sizes. Figure 2.4 shows the square outside and round inside design of the parts. The round interior had a diameter of approximately 60 mm, which was regulated by a screw. To keep the screen steady, a layer of 4 mm thick ethylene-vinyl acetate was pasted on the surface of the inner diameter.

Mirror fixture

A mirror fixture was used to fix the mirror and to support the screen fixture. The design and size of the mirror fixture are shown in Figure 2.5. A female screw and a male screw located on the mirror fixture were used to adjust the mirror angle from 40° to 50°. The completed part was pasted together using a-cyanoacrylate adhesive super glue. A 3D view of the assembled mirror fixture is shown in Figure 2.5C.

Screen View

Monocular (left or right eye) presentations were performed using the hemispheric screen. The
subject’s eye was fixed on the central axis, 3 mm distant from the screen. Due to the screens close proximity to the subjects' eyes, the subjects wore +20, +22, or +25 contact lenses (Menicon soft MA; Menicon, Japan) to retain their length of visual focus (Figure 2.2) [35]. Due to the size limitations of the head coil, the upper and lower edges of the screen were cut by 2 mm; thus, the final hemispheric screen size was 52 mm × 48 mm. The eye was located at the spherical center of the hemispheric screen. In this condition, the horizontal visual field was 120° and the vertical visual field was 116° (Figure 2.2). The distance between the eye and the center of the screen could not be directly measured. A tool and method were developed for determining the position of the hemispheric screen relative to the eye. A probe bar was used to position the surface of the hemispheric screen 30 mm from the eye and to make the axis of the hemispheric screen and the axis of the eye overlap.

![Diagram](image)

Figure 2.5. Front view showing the design and size of the mirror fixture. (A) The design of the support part used on both sides of the mirror fixture. A female screw and a male screw were used on this part to adjust the mirror angle. The two holes at the bottom of the component were used to fix the component during the machining process. (B) The bars linking the two support parts. (C) 3D view of the mirror fixture.
Figure 2.6. The images presented on the hemispheric screen. (A, B) Computer-generated images. (C, D) The image presented on the hemispheric screen. (C) The checkerboard stimuli had a size of 52 × 48 mm$^2$, contained 154,000 pixels, and covered the entire screen. (D) Within the same screen, a 150 × 150 pixel image of a face was presented and occupied a visual field of 40º.

2.2.3 Projection Apparatus

A Mitsubishi LVP-HC6800 projector (Mitsubishi Electric, Tokyo, Japan), configured to operate at 1600 × 1200 pixel resolution and a 60 Hz refresh rate, was used. The standard lens was replaced with a 70–300 mm focal length camera zoom lens (Nikon, Tokyo, Japan) in order to achieve small,
high-resolution images on a screen located inside the bore. The reconstituted projector presented 18 cm × 13.5 cm images at a distance of 4 m. In the present study, the projector was placed approximately 3 m away from the MRI scanner and approximately 4 m away from the hemispheric screen (Figure 2.1).

2.2.4 Projection to the Hemisphere

The spherical coordinate system is arguably the most natural choice of coordinate systems for the study of vision. A function \( f \), described by Equation [1], was used to generate “distorted” 2D images of geometrical shapes specified by spherical coordinates [37]. The function \( f(\lambda, \varphi) \rightarrow (x, y) \) is

\[
x = g(\text{ecc}(\lambda, \varphi)) \times \cos(\text{ang}(\lambda, \varphi)),
\]

\[
y = g(\text{ecc}(\lambda, \varphi)) \times \sin(\text{ang}(\lambda, \varphi))
\]  

[1]

where \( \lambda \) is the longitude of the point on the hemisphere, \( \varphi \) is the latitude of the point on the hemisphere, \( \text{ecc}(\lambda, \varphi) \) is the eccentricity, \( \text{ang}(\lambda, \varphi) \) is the polar angle in the polar coordinate system, and \( g(\text{ecc}(\lambda, \varphi)) \) is the eccentricity of the corresponding point on the projector’s image plane. The intensity of the distorted image was regulated based on the actual measurement intensity.

A beam of light is projected through the bore, reflected by an adjustable mirror (40°-50°), and ultimately focused onto the hemispheric screen. To maximize the precision of the method and to avoid geometric distortions, the central axis of the light beam was aligned with the central axis of the hemispheric screen. Example views of images presented on the hemispheric screen are shown in Figure 2.6. Both the checkerboard and face images were clearly presented. In the presently adopted convention, a 52 mm × 48 mm size image with a 460 × 425 pixel resolution was presented on the hemispheric screen. Due to the round shape of the hemispheric screen, approximately 154,000 pixels were presented on the screen. The luminance at the internal surface of the hemisphere on 6 level eccentricities (5°, 15°, 25°, 35°, 45° and 55°) in 8 directions was measured in a dimly illuminated room. The luminance values from the 8 directions were averaged. As the eccentricities increased, the mean luminance values of white were 143.3, 139.2, 146.2, 145.3, 137.2 and 138.4 cd/m², and the mean luminance values of black were 3.1, 3.1, 3.2, 2.8, 3.3 and 3.4 cd/m². The luminance values at each eccentricity were not different from the mean values of the whole screen (\( p \geq 0.5 \)). This allowed for a stimulus contrast of up to 95%.
2.3 Evaluation Experiments

2.3.1 Safety and Signal-to-Noise Ratio Tests

The presentation apparatus display located in the MRI bore was considered a potential source of MRI image interference. Therefore, to evaluate safety and image quality, a test was performed using an MRI Phantom. The wide-view visual presentation system was tested with the stimulus during this MRI scan (spin echo, TR/TE=3000/15 ms, 256×256 matrix, 15 continuous 5 mm slices without gap).

2.3.2 Functional MRI Evaluation Experiment

Subjects

8 healthy subjects without previous neurological or psychiatric disorders (age 21–26 years, mean 23 years; 2 women, 6 men) participated in the study. The subjects had normal or corrected-to-normal vision and were right-handed. We obtained written informed consent from all the subjects before the experiment began. Data used in the following analyses were obtained from seven subjects (data from one subject was excluded due to large head movements).

Retinotopic mapping experiments

To identify the retinotopic areas of the visual cortex, clockwise rotating wedge and expanding ring stimuli were employed [12, 22, 36]. The stimuli apertures contained high-contrast, black-and-white checkerboard patterns (Figure 2.6) that exhibited phase-reversing at a temporal frequency of 8 Hz, with eccentricity ranging from 2.4° to 60°. The wedge stimuli had boundaries of 22.5° and rotated clockwise at slow speed around a red fixation disk (approximately 1°) presented at the center of the screen. The wedge rotated at steps of 22.5° and remained at each position for 6 s before rotating to the next step. The eccentricity of the expanding rings ranged from 2.4° to 60°, and the width of the ring stimuli was applied in exponential increments ($y = 0.81e^{0.4x}$, $x=1-8$). The corresponding ring sizes were 1.2°, 1.8°, 2.7°, 4.0°, 6.0°, 9.0°, 13.4° and 20.0°. The expanding ring stimuli were moved in discrete steps (a total of eight steps) and remained at each position for 6 s before automatically expanding to the next position. Six complete rotation-expansion cycles of the checkerboard stimuli were conducted. All the experiments employed passive viewing, with subjects being required to maintain visual fixation on a red fixation disk that flickered at a temporal frequency of 4 Hz throughout the duration of the MRI scan.
Object localizer experiment

We also determined the object category-selective areas, according to object images, following conventional methods [16, 38-40]. Each subject participated in one localizer scan to define the selective areas for faces, houses and common objects (see Figure 2.7A). The stimuli consisted of 30 gray-scale images of faces, houses and objects and 30 phase-scrambled images of intact objects. Each scan contained 16 stimulus blocks of 10 s duration, four blocks for each category, separated by 10 s rest intervals. Two or three images in each block were repeated and the subjects were asked to perform a ‘one-back’ matching task while fixating on a central fixation point presented in the center of each image.

Figure 2.7. (A) Samples of images used in the object localizer experiment. (B) The size and position of the stimuli used in the position experiment.
Position experiments

As shown in Figure 2.7A, the gray-scale images of human faces and of houses were subtended by 12° at each position. The images were presented in 7×7 equally spaced positions (vertical × horizontal, respectively) on the display screen, for a total of 13 positions. The images were centered at the fixation point (foveal) and at positions 16°, 32° and 48° above, below, to the left and to the right of the fixation point. The object experiment contained 6 runs of single block-design experiments. In each 8 s block, different images from one category (faces or houses) were shown at a specific position. The images were shown at a rate of 1 Hz, and the image blocks were interleaved with baseline blocks lasting 8 s. Each run contained one block for each position and category combination. A total of 6 runs were performed for each subject. During scanning, the subjects were instructed to categorize each image while maintaining visual fixation on a red fixation point (a red disk, 1.8° in diameter, that was present throughout the entire experiment). Behavioral responses were collected during scanning using a magnet-compatible button box connected to the stimulus computer. To ensure that the subjects maintained fixation, they were instructed to respond within 1.2 s of a prompt provided by the dimming of the fixation disk. The dimming prompt occurred randomly, with a 1.8 to 3.8 s interval between prompts.

Image acquisition

Imaging was performed using a 3 Tesla MR scanner (Siemens MAGNETOM Trio). For the functional series, we continuously acquired 30 image slices using a standard T2 weighted echo-planar imaging (EPI) sequence (TR = 2 s; TE = 35 ms; flip angle = 85°; 64 × 64 matrices; inplane resolution: 2.3 × 2.3 mm; slice thickness: 2 mm, with a gap of 0.3 mm). The slices were manually aligned approximately perpendicular to the calcarine sulcus to ensure coverage of most of the occipital, posterior parietal and posterior temporal cortex. After the functional scans, a magnetization-prepared rapid gradient echo sequence (MP-RAGE; TR = 1800 ms; TE = 2.3 ms; matrix 256 × 256 × 224; 1 mm isotropic voxel size) was used to acquire high-resolution T1-weighted sagittal images that were used to generate a structural 3D scan.
Data analysis

Anatomical and functional images were analyzed using BrainVoyager QX 2.11 (Brain Innovation, Maastricht, The Netherlands). Anatomical scans were segmented to identify the white/gray matter boundaries and were then used for cortical surface reconstruction and inflating [41-43]. The functional data were subjected to correction, three-dimensional motion correction and high-pass temporal filtering (0.01 Hz) prior to statistical analysis [41]. Spatial smoothing was applied to the localizer and position scans, using a 4 mm full width at half maximum Gaussian kernel. No spatial smoothing was applied to the retinotopic mapping scans. The functional data were transformed into conventional Talairach space to yield a 4D data representation. To identify the retinotopic areas of the visual cortex, maps were created based on the cross-correlation values for each voxel, as determined by a standard hemodynamic box-car function ($r \geq 0.25$). Voxel-by-voxel statistical tests of the localizer scans and positions scans were conducted by computing contrasts based on a General Linear Model (GLM) and a double-gamma hemodynamic response function [44]. At the group level, a random effects analysis of variance was performed for the position scans of each subject. All the fMRI results are presented on a reconstructed cortical surface.
2.4 Results

2.4.1 Safety and Signal-to-Noise Ratio Tests

As shown in Figure 2.8, artifacts created by the radio frequency noise from the image of the phantom were not detected. The SNR was calculated using the following formula [2]:

\[ SNR = \left( \frac{2 - \frac{\pi}{2}}{N_{air}} \right) \times S_p \]  

[2]

where \( S_p \) is the mean of the signals in the Phantom and \( N_{air} \) is the standard deviation of the outside noise. The average SNR was calculated from ten MRI images for two conditions. The SNR was 187.50 without the device and 189.58 when the device was active. The digressive image rate with the device was 1.11%. we did not detect any artifacts created by the radio frequency noise from the image of the phantom.

2.4.2 Delineation of Retinotopic Areas by Wide-view Stimuli

As shown in Figure 2.9, the cortical surface of the left hemisphere of one subject was used to render the retinotopic mapping. The surface represents the boundary between the white and gray matter. Figures 10A and B show color maps of the responses to expanding rings on a medial view of the folded (Figure 2.10A) and unfolded (Figure 2.10B) cortical surface [12, 22, 36]. A systematic increase in eccentricity (red to navy) moving anteriorly along the medial wall of the occipital cortex was present. The color hue at each cortical surface point indicates the response phase, which was proportional to the eccentricity of the local visual field representation. As the expanding ring stimulus moved from the fovea to the periphery of the retina, the location of the responding areas varied from the posterior to anterior portions of the calcarine sulcus. The cortical surface was then flattened (Figure 2.9 C), and the surface region containing the activated area included the occipital lobe, the posterior parts of the parietal lobe and the temporal lobe. This surface map is referred to as the eccentricity dimension of the retinotopic map. The larger peripheral representation crossed to the fundus of the parietooccipital sulcus. Parallel treatment of the data from the rotating hemi-field stimulus is shown in Figure 2.9 D-F. The color indicates the periodic response phase, which was proportional to the polar angle of the local visual field representation. The locations of several visual areas were identified by measuring the angular visual field representations [12, 22, 36].
Figure 2.9 D–F shows angular visual field representations spanning most of the occipital lobe and the posterior parts of the parietal and temporal lobes on the folded (Figure 2.9 D), inflated (Figure 2.9 E) and flattened (Figure 2.9 F) cortical surfaces. The color at each location represents the angle of the rotating wedge that elicited an fMRI response.

Figure 2.9. Retinotopic maps of human visual areas. The top row shows a color-coded dipolar map [brown (fovea) - > orange - > blue - > cyan (periphery)] displayed on the original cortical surface (A), the unfolded cortical surface (B) and the cut and flattened cortical surface (C). The bottom row shows the polar angle (blue (upper vertical meridian) - > green (horizontal meridian) - > red (lower vertical meridian)) plotted on the same three surfaces (D–F).
2.4.3 Localization of Category-selective Areas

The localizer data were used to identify the bilateral extrastriate regions that were selective for faces, houses and objects. The subjects displayed high levels of accuracy (approximately 90%) during the ‘one-back’ task. Localization maps of the category-selective areas are shown in Figure 2.11. The face-selective area (FFA) and the occipital face area (OFA) were identified within a region that responds more strongly to faces compared to textures [16, 38, 45] (Figure 2.10 A). The house-selective area (PPA) and an area in the transverse occipital sulcus (TOS) were identified within a region that responds more strongly to houses than to textures [16, 39, 46] (Figure 2.10 B). Finally, the broadly object-selective areas that comprise the lateral occipital complex, namely, the LO and the posterior fusiform area (pFs) [16, 39, 46], were identified within a region that responds more strongly to common objects than to textures (Figure 2.10 C). All the areas were defined using an uncorrected contrast threshold of $P < 0.0001$.

2.4.4 Neural Activity Responses to Faces and Houses in Wide Fields

Numerous studies on the function of the face- and house-selective areas have been performed;
however, until now, there have been no reports regarding neural activation in response to stimuli in a wide-view field in these areas. The mean response magnitudes of the neural activity were averaged to the contralateral, upper and lower meridian images. This study had 13 hemisphere results from the FFA area and 14 hemisphere results from the OFA, PPA and TOS areas. These results were pooled together, and the averaged response magnitudes are shown in Figure 2.11. The neural activity decreased as a given image was viewed at a progressively greater distances from the center of the gaze. One-way ANOVAs with eccentricity as the repeated measure revealed significant main effects of eccentricity in all areas [F (3, 39) ≥ 40.02, p ≤ 0.001].

Figure 2.11. Neural activation in response to face and house stimuli in the ROIs. (A, B) Neural activation in response to face stimuli in the FFA (A) and OFA (B). (C, D) Neural activation in response to face stimuli in the PPA (C) and TOS (D). In both areas, neural activation decreased as the eccentricity of the presented image increased.
We normalized the response amplitude to each position by dividing the response amplitude by the central position. To compare this ratio relative to the central position, one-way ANOVAs with eccentricity (16°, 32° and 48°) as repeated measures revealed significant main effects of eccentricity in the FFA, OFA and PPA areas [F (2, 26) ≥ 10.65, p ≤ 0.001] and no main effect of eccentricity in the TOS [F (2, 26) = 0.59, p = 0.56]. Then, we performed two-way ANOVAs with areas (FFA, OFA, PPA and TOS) and eccentricity as the repeated measures and revealed that the ratios relative to the central position had main effects of area [F (3, 36) = 6.01, p = 0.002] and eccentricity [F (2, 24) = 23.51, p < 0.0001]. Moreover, pairwise comparisons for each cortical area showed that the value of the ratio was smaller than in the TOS in the other three areas (p ≤ 0.015). These differences were mainly found at the 16° and 32° positions (p ≤ 0.05). There was an interaction between category and eccentricity [F (9, 108) = 3.64, p = 0.04].

Figure 2.12. The ratio of neural activation relative to the central position in the face- and house-selective ROIs. (A, B) The ratio value of neural activation to face stimuli in the FFA (A) and OFA (B). (C, D) The ratio value of neural activation to house stimuli in the PPA (C) and TOS (D). The ratio in the TOS was smaller than in the other three areas.
2.5 Discussion and Conclusion

We developed a new method for presenting wide-view visual stimuli in the MRI environment. We used a projector with a zoom lens to project computer-generated stimuli onto a translucent hemispheric screen inside the bore of an MRI machine. Using the convention adopted in the present paper, we were able to generate visual stimuli at horizontal and vertical visual angles of approximately 120°.

Hemispheric screens have been found to be very useful for producing wide-view stimuli for visual studies; however, until now, only a wide-view system for electrophysiology had been developed using these screens [37]. The hemispheric screen used in this study was designed to suit common MRI coils. In the current system, the hemispheric screen was adopted for forward projection in the MRI room. This method is suited for both forward and backward projection systems, depending on the MRI room configuration. The presently described system utilized significantly less material in the MRI bore compared to the previous version of the system. In addition, the digressive rate of the images presented by the device was 1.11% (Figure 2.8); therefore, the Phantom's phase encoding was free of any artifacts created by radio frequency interference. More important, the described system presented images of common objects cleanly and with greatly improved resolution. All visual research programs can use this methodology or system to study peripheral vision. A large expansion of MRI-based peripheral vision studies would greatly improve our current understanding of the functions of human vision.

The wide-view visual presentation stimulus system can be used to define the retinotopic areas of the human visual cortex (the medial occipital lobe). Our retinotopic mapping results are consistent with previously described occipital visual areas [22, 47, 48]; however, our maps extend to the more peripheral fields, with an eccentricity of up to 60°. Compared to previous data [35], the described system was able to more effectively map the checkerboard stimuli in V1-V3 from the central and peripheral fields. Our results show that the larger peripheral representation achieved with the implemented system extended to the fundus of the parietooccipital sulcus. Previous fMRI studies have demonstrated that stimulus eccentricity up to 20° was likely to generate peripheral representation that reached the parietooccipital sulcus [17]. The receptive fields in the human visual areas increase in size with increasing stimulus eccentricity [13, 49-53]. Neurons in a peripheral visual area with large receptive fields have enlarged eccentric representations when small visual stimuli are used. Cortical distance, cortical area, cortical magnification and receptive fields are important parameters for visual studies and are greatly influenced by eccentricity. Compared to the use of central view stimuli only, the use of wide-view stimuli allows for more precise results.
According to the localizer test results, face-selective, house-selective and object-selective areas were found in the higher visual areas, which is consistent with previous studies using central stimuli [16, 38, 39, 45, 46]. Similar to the primary visual cortex, the high-order areas also demonstrated eccentric representation [54-58]. Moreover, the object representations were arranged according to a bias toward the central, rather than the peripheral, visual fields [45, 59, 60]. Although much work has been conducted to characterize the shape or category selectivity of these regions, very little is known about representations in higher areas. In the presently described system, we first revealed neural activation in response to face and house stimuli presented in a wide field with up to 54° eccentricity. We found that the face-selective areas produced much greater neural activation than the house-selective areas. The sizes and positions of the stimuli were consistent. Moreover, we normalized the response amplitude to each position by dividing the response amplitude by the response amplitude to the central position. We found that the ratios relative to the central position were not different in the FFA, OFA and PPA but that they were significantly different in the TOS (Figure 2.12). These functional areas lie either on the ventral temporal or lateral surfaces of the occipital cortex. The FFA and PPA lay on the ventral temporal cortical surfaces, and the OFA and TOS lay on the lateral occipital cortical surfaces [61]. The face- and house-selective areas on the ventral temporal cortical surfaces were not different, while the face- and house-selective areas on the lateral occipital cortical surfaces were significantly different. These results imply that the processing strategies in the face- and house-selective areas on the lateral occipital cortical surfaces are different but are not different on the ventral temporal cortical surfaces. We propose that this observation can be related to reports of a central-peripheral bias in the human object-selective area [45, 59, 60].

In conclusion, we successfully developed a novel method for the systematic presentation of high-resolution, wide-view images in the MRI environment. All visual research programs can adopt this method or system for the study of peripheral vision. The convention adopted in the present paper is suited for most MRI scanner head coils. The visual field size can be increased by using a larger hemispheric screen, and the image resolution can be increased by using a higher resolution projector. Moreover, we plan to continue the study to improve the optical properties and convenience of the system.
Chapter 3

Regional Neural Response Differences in the Determination of Faces or Houses Positioned in a Wide Visual Field

Summary

In human visual cortex, the primary visual cortex (V1) is considered to be essential for visual information processing; the fusiform face area (FFA) and parahippocampal place area (PPA) are considered as face-selective region and places-selective region, respectively. Recently, a functional magnetic resonance imaging (fMRI) study showed that the neural activity ratios between V1 and FFA were constant as eccentricities increasing in central visual field. However, in wide visual field, the neural activity relationships between V1 and FFA or V1 and PPA are still unclear. In this work, using fMRI and wide-view present system, we tried to address this issue by measuring neural activities in V1, FFA and PPA for the images of faces and houses aligning in 4 eccentricities and 4 meridians. Then, we further calculated ratio relative to V1 (RRV1) as comparing the neural responses amplitudes in FFA or PPA with those in V1. We found V1, FFA, and PPA showed significant different neural activities to faces and houses in 3 dimensions of eccentricity, meridian, and region. Most importantly, the RRV1s in FFA and PPA also exhibited significant differences in 3 dimensions. In the dimension of eccentricity, both FFA and PPA showed smaller RRV1s at central position than those at peripheral positions. In meridian dimension, both FFA and PPA showed larger RRV1s at upper vertical positions than those at lower vertical positions. In the dimension of region, FFA had larger RRV1s than PPA. We proposed that these differential RRV1s indicated FFA and PPA might have different processing strategies for encoding the wide field visual information from V1. These different processing strategies might depend on the retinal position at which faces or houses are typically observed in daily life. We posited a role of experience in shaping the information processing strategies in the ventral visual cortex.

Key Words: fusiform face area, parahippocampal place area, wide visual field, ventral visual cortex, fMRI
3.1 Background

The human visual cortex is organized hierarchically. The visual information from retinal ganglion cells is eventually processed in the visual cortex. In the hierarchy of visual cortical areas, the primary visual cortex (V1) is essential for visual information processing, as most or all of the input to the higher cortical areas passes through V1. A number of strategies are used for efficient information processing within this hierarchy, including linear and nonlinear filtering [62, 63]. These strategies are used with the aim of creating different compact visual and functional representations in the organization of the visual cortex [13-16].

The human visual system is divided into central and peripheral vision [64]. The visual system seems to represent central stimuli with a fair degree of fidelity, but it more crudely encodes stimuli in peripheral field. Even with such imprecise encoding, the visual stimuli from our peripheral vision are nonetheless important in determining eye movements [65, 66] and in object-motion perception [67], for example. Understanding the information available to the visual system in the peripheral visual field is the key to understanding our visual capabilities and limitations. Despite the importance of peripheral vision, there is little understanding of the information available to the visual system and of visual representation. Peripheral vision has mostly been characterized in terms of the reductions in resolution or contrast sensitivity as the eccentricity increasing [68, 69].

In the hierarchy of visual cortical areas, the ventral and lateral occipital-temporal cortex is responsible for the high-level visual object processing [13, 70-72]. Multiple cortical regions are characterized by their consistent preferential response to specific visual categories, such as faces (fusiform face areas, FFA) [38], houses and places (parahippocampal place area, PPA) [39, 73], words (visual word form areas, VWFA) [74, 75] and objects (lateral occipital complex, LOC) [40].

Central-peripheral organization of the category-selective areas is discovered in the human visual cortex [59, 60]. In the ventral visual cortex, the lateral regions, such as FFA and VWFA, represent foveal eccentricities and the medial regions, such as PPA, represent peripheral eccentricities [59, 60]. Since the discovery of central-peripheral organization, more differences have been found in these object-selective areas. For instance, FFA and LOC show a greater magnitude neural responses to lower field images than to upper field images [61, 76, 77], whereas PPA shows a significantly greater magnitude neural responses to upper field images than to lower field images [61, 78]. These differences in the high-order, category-selective areas imply uniform processing of objects at these different positions. However, Yue and his colleagues assumed that FFA only had a neural response to the local contrast corrected by the function of V1 and did not include any additional face-selective components in central visual field. They stated that the neural activity ratios between
V1 and FFA were constant as the eccentricities increasing in central visual field [77]. However, in wide visual field, the neural activity relationships between V1 and the ventral category-selective areas (FFA and PPA) are still unclear.

Here, we tried to address this issue by using functional magnetic resonance imaging (fMRI) and wide-view presentation system with up to 60° of eccentricity [71, 79]. The subjects were presented with a face and a house, both of which were centrally located along the left horizontal, right horizontal, upper vertical and lower vertical meridians, arranged in 4 levels of eccentricities (0°, 16°, 32°, 48°) at each meridian (Figure 1). V1 and the ventral category-selective areas (FFA and PPA) had different trends of decreased neural activity as the eccentricities of the images of the faces and houses increased. This study demonstrated that FFA and PPA had differences ratio relative to V1 (RRV1) for their neural response amplitudes in 3 dimensions. The differential RRV1s could be viewed as a processing strategy for encoding the images of the faces and houses with variations in eccentricity and meridian.

3.2 Materials and Methods

3.2.1 Subjects

MR imaging was performed at the Hospital of Okayama University. Eight subjects (6 males, 2 females), aged 22–25 years with a mean age of 23 years, participated in the study. All of the subjects were right-handed and had normal vision. Data from only 7 of the 8 subjects were included in the following analyses because one subject exhibited significant head movements during the scan. The experiments were performed with the written consent of each subject and were approved by the Ethics Committee of Okayama University Hospital.

3.2.2 Presentation of Stimuli

The stimuli were projected on a wide-view visual presentation system, which had been upgraded from a previous version [79, 80]. The subjects viewed the stimuli on a hemisphere 52 mm in diameter; the curvature radius of this hemisphere was 30 mm. The mean distance between the subjects’ eyes and the screen was 30 mm. The subjects wore contact lenses to focus on the stimulus, and the visual field of stimulus was 120° horizontal × 120° vertical, or 60° of eccentricity.
3.2.3 Position Experiments

The position experiments utilized grayscale images of human faces and houses. The face images were taken from the FEI face database (http://fei.edu.br/~cet/facedatabase.html), and the houses images were photos taken in Okayama City. The objects were presented at a variety of positions and grayscale backgrounds (Figure 1B). The position experiments utilized 48 unique images from each category. The images subtended a 12º visual angle at each position. We chose to use a constant image size because the magnification factors in the face- and house-selected areas were unknown, and the magnifications at the center and periphery were quite different. We wished to compare the neural activation corresponding to the images of the faces and houses at different positions throughout the central and peripheral visual fields. The images were centered at the fixation point (0º eccentricity) and were centered at 16º, 32º and 48º of eccentricities along 4 meridians: the left horizontal meridian, right horizontal meridian, upper vertical meridian and lower vertical meridian. A total of 13 positions were arranged in the 4 levels of eccentricities (0º, 16º, 32º and 48º) for each meridian (Figure 1A).

The position experiments included 6 runs of block design experiment. Each run contained one 8-s block for each position and category combination; thus, the session contained 26 blocks per run (2 categories × 13 positions). The image blocks were interleaved with 8-s baseline blocks (a grayscale screen with a central fixation point). In each image block, a series of images from one category (face or house) were shown at a specific position in random order. The images were shown at a rate of 1 Hz (800 ms per image, with a 200 ms inter-stimulus interval). During the scanning process, the subjects were instructed to categorize each image while fixating on a red point (a red disk 1.8º in diameter that was present for the duration of the experiment). When the red disk dimmed, the subjects reported their categorization with two buttons that corresponded to either a face or a house. The dimming prompts lasted 1.2 s, with a 1.8- or 3.8-s interval between the prompts, and it was not synchronized with the stimulus onsets. The button presses that occurred outside of the 1.2-s period following a prompt were ignored. The fixation task was primarily used to ensure that the subjects maintained their fixation during the scans. Before scanning, the subjects practiced this task to minimize false alarms and to maintain their focus on the fixation point. Behavioral responses were collected during the scanning using a magnet-compatible button box connected to the stimulus computer.
Figure 3.1. Stimulus configuration and example of stimulus images. (A) The images were either centered at the fixation point (0º) or centered at 16º, 32º or 48º for the left horizontal, right horizontal, upper vertical, or lower vertical meridians. The squares with the dashed lines indicate the stimulus positions in the spherical screen. The red dot indicates the fixation point. Within a given block, images of faces or houses were presented in one of the visual field positions. (B) Example images of a face and a house are shown.

3.2.4 Retinotopic Mapping Experiments

To identify the retinotopic areas of the visual cortex, the clockwise rotating wedge and expanding ring stimuli were employed [12, 22, 79, 81]. These stimulus apertures contained 100% contrast black-and-white checkerboard patterns, and they phase-reversed at a temporal frequency of 8 Hz at an eccentricity ranging from 2.4º to 60º. The wedge stimulus with boundaries of 22.5º was slowly rotated clockwise around a red fixation disk (approximately 1º) presented at the center of the stimulus. The wedge rotated at 22.5º steps, remaining at each position for 6 s before moving to the
next position. The eccentricity of the expanding rings ranged from 2.4º to 60º, and the width of the ring stimuli was expanded in exponential increments. The corresponding ring sizes were 1.2º, 1.8º, 2.7º, 4.0º, 6.0º, 9.0º, 13.4º and 20.0º. These expanding ring stimuli were moved in 8 discrete steps and remained at each position for 6 s before automatically expanding to the next position. All of the experiments involved passive viewing, and the subjects were required to maintain their gaze on the red fixation disk in the center of the screen that flickered at a temporal frequency of 4 Hz throughout the scan. Six complete cycles of rotations and checkerboard expansions were conducted.

3.2.5 Image Acquisition

The imaging was performed using a 3-Tesla MR scanner (Siemens Allegra, Erlangen, Germany). For the functional series, we continuously acquired images with 30 slices using a standard T2-weighted echo-planar imaging (EPI) sequence (TR = 2 s; TE = 35 ms; flip angle = 85º; 64 × 64 matrices; in-plane resolution: 2.3 × 2.3 mm; slice thickness: 2 mm with a gap of 0.3 mm). The slices were manually aligned approximately perpendicular to the calcarine sulcus to cover most of the occipital, posterior parietal and posterior temporal cortices. After the functional scans, high-resolution, sagittal, T1-weighted images were acquired using a magnetization-prepared rapid gradient echo sequence (MP-RAGE; TR = 1800 ms; TE = 2.3 ms; matrix 256 × 256 × 224; 1-mm isotropic voxel size) to obtain a 3D structural scan.

3.2.6 Data Preprocessing

The anatomical and functional images were analyzed using the BrainVoyager QX 2.11 (Brain Innovation, Maastricht, The Netherlands). The anatomical images were segmented for the identification of the white/gray matter boundaries and were then used for cortical surface reconstruction and inflation [41-43]. In each functional run, the first 2 volumes were discarded to ensure that the steady state had been reached. The functional data were preprocessed with motion and scan time corrections and high-pass temporal filtering (0.01 Hz) before statistical analysis [41]. Spatial smoothing, using a full-width, half-maximum Gaussian kernel of 4 mm, was applied to the position experiments data but not to the retinotopic mapping data. The functional data were transformed into the conventional Talairach space, yielding a 4D data representation [82].

3.2.7 General Linear Model

We applied a general linear model (GLM) to the position experiments data on a voxel-by-voxel basis. This boxcar function was convolved with a double-gamma hemodynamic response function
to account for the hemodynamic effects [44]. To combine the 6 runs of position experiments for each individual, a second-level analysis was performed using a fixed-effects model to estimate the blood oxygen level-dependent (BOLD) response amplitudes for each stimulus condition using a fixed effects analysis of variance (ANOVA). All statistical analyses used the statistical threshold of \( p < 0.05 \) with false discovery rate (FDR) correction and a cluster threshold of 20 mm\(^3\). The response maps were rendered on a cortical surface from a high-resolution structural MRI scan of a standard brain based on the Talairach coordinates.

3.2.8 Retinotopic Mapping Analysis

Our retinotopic mapping experiments employed a standard phase-encoded retinotopy design [12, 22, 79, 81]. For the polar angle and eccentricity mapping, the stimulation blocks were modeled by boxcar functions convolved with a double-gamma hemodynamic response function [44]. The stimulus-driven modulation of the BOLD response in each functional voxel was revealed via a linear correlation map analysis. This phase was mapped into physical units by identifying the stimulus parameter (polar angle or eccentricity) corresponding to the time. The color-coded cortical regions were classified based on an \( r \)-value threshold of 0.25. To aid in visualization, the retinotopic maps were projected onto computationally flattened representations of the cortical surface.

3.2.9 Region of Interest Analysis

In V1, as the stimulus positions moved from the fovea to the periphery of the retina, the locations of the response area varied from the posterior to the anterior areas of the calcarine sulcus. The regions of interest (ROIs) were individually defined for each participant based on the position experiments data and V1 mask obtained individually from retinotopic mapping. This method was performed by contrasting all the stimuli at one position with all the other positions using the contrast threshold of \( p < 0.05 \) corrected with the FDR and a spatial extent of at least 20 mm\(^3\) (Figure 3.2 A). For the positions of the face and house stimuli (Figure 1), 10 functional ROIs, corresponding to the 4 eccentricities and 3 meridians positions that occupied half of the visual fields, were defined in each hemisphere. The functional ROIs were defined separately for the images of the faces and houses and were referred to as Face-V1 and House-V1. The mean Talairach coordinates, cluster volume, and defined number of each ROI are shown in Table 3.1. Images faces and houses activated similar V1 extents at all the positions (all: paired t-test \( p > 0.2 \)). The neural activities in response to the images of the faces or houses at each stimulus position were assigned as the BOLD response amplitude in a matched ROI.
Figure 3.2. The locations of the ROIs on the visual cortex. (A) A central view of the inflated cortex shows V1 region, shown with dash lines. The 10 ROIs in V1 are indicated by the colored disks. The yellow disk corresponded to the central position. The red disks corresponded to the ROIs of the contralateral horizontal positions, the blue disks corresponded to the ROIs of the upper vertical positions, and the green disks corresponded to ROIs of the lower vertical positions. (B) The ventral view of the inflated cortex shows the locations of FFA and PPA. The face-selective area is shown by the red-yellow color, and the house-selective area is shown by the blue-cyan color.

Using the position experiments data, FFA and PPA were defined based on the combined activations from all 13 locations. The FFA ROIs were defined as a region that responded more strongly to images of faces than houses [16, 38, 45]; however, the FFA ROIs were identified as a region that responded more strongly to images of houses than faces [16, 39, 46] (Figure 3.2 B). The contrast threshold was $p < 0.05$, the data were corrected for FDR, and the spatial extent was 20 mm$^3$. The FFA ROIs were defined in the right hemisphere for all of the subjects and in the left hemisphere for 6 out of the 7 subjects. The PPA ROIs were defined in both hemispheres for all 7 subjects. We extracted the magnitude of the neural responses to the images of faces or houses in FFA or PPA for each position. Then, the statistical analyses were applied linear mixed model for repeated measures by using the SPSS software (version 16.0; SPSS Inc., Chicago, Ill).

### 3.2.10 Signal Intensity Mapping

To evaluate the quantities of MRI signal quality in V1 (calcarine sulcus), the signal intensity map (temporal signal-to-noise: the ratio of the average signal intensity to the signal standard deviation)
was measured for the EPI data [83]. The signal intensity values for the ROIs defined within V1 (Figure 2A) were also measured.

3.3 Results

3.3.1 Position Sensitivity in a Wide Field

In the position experiments, behavior performances at each position are listed in Table 3.2. Some subjects had no or less response to the images of faces or houses at the most peripheral positions, and then resulted in response times with miss values. In the 4 meridians, linear mixed models for repeated measures with factors of eccentricity (0º, 16º, 32º, and 48º) and category (faces or houses, 4 × 2) were applied. Neither the response times nor the accuracy was significantly affected by category, and there was no significant interaction between category and eccentricity (p > 0.05). We found a significant effect of eccentricity for the response times only at the lower vertical positions (p = 0.05) and for the accuracy at 4 meridian positions (p < 0.01). The detailed statistical values are listed in Table 3.3. To take the meridian effects into consideration, a linear mixed model for repeated measures with factors of eccentricity (16º, 32º, and 48º), meridian (left horizontal, right horizontal, upper vertical and lower vertical positions) and category (faces and houses, 3 × 3 × 2) revealed that both the response times and the accuracy were significantly affected by eccentricity and meridian (p ≤ 0.002), and there was significant interactions between meridian and eccentricity (p ≤ 0.004). The detailed statistical values are listed in Table 3.4. A pairwise comparison showed that the 48º positions had shorter response times and lower accuracy than the 16º and 32º positions. The right horizontal positions had shorter response times and lower accuracy compared to the other 3 meridians (p ≤ 0.002).

3.3.2 Neural Activity Maps for Images of Faces and Houses

In line with the behavior results, the neural activity in the visual cortex also had significant eccentricity and category effects. Figure 3.3 shows the mean neural activity maps of 7 subjects. We present the statistical maps at a threshold of p < 0.05 with FDR correction and a cluster threshold of 20 mm3. In the ventral visual cortex, the central positions had stronger neural activities compared with peripheral positions; the contralateral horizontal positions had stronger neural activities compared with the upper vertical positions and the lower vertical positions. The positions along the vertical meridian straddled each hemifield equally, thus, the stimuli sizes along the vertical meridian were about half of those along the horizontal positions, and then stronger neural activities
were found at the horizontal positions than the vertical positions. Generally, these results were consistent with the retinotopic organization of visual cortex [12, 22, 79, 81].

Figure 3.3. The mean neural responses of 7 subjects to images of faces or houses at the right horizontal, upper vertical, and lower vertical positions in ventral category-selective areas (FFA and PPA). (A) The neural responses to face images. (B) The neural responses to house images. Abbreviations: CHP, contralateral horizontal positions; UVP, upper vertical positions; LVP, lower vertical positions.
Figure 3.4. Mean response amplitudes in response to images of faces and houses at each of the 10 stimulus positions in V1 and ventral category-selective areas (FFA and PPA). Generally, the significant neural activities decreased as eccentricity increased in V1 (A, B) and ventral category-selective areas (FFA and PPA, C, D). There were significant effects of eccentricity and region for each meridian positions (all: $p \leq 0.02$), except for the upper vertical positions ($p = 0.18$) in V1. Significant interactions between eccentricity and region were found at the upper and lower vertical positions in V1 and in the upper vertical positions in the ventral category-selective areas (all: $p \leq 0.03$). Considering the dimension of meridian, there were significant main effects of meridian in V1 and ventral category-selective areas (FFA and PPA, $p < 0.001$). The abbreviations are the same as those used in Figure 3.3.
Figure 3.5. Mean RRCPs in V1 and ventral category-selective areas (FFA and PPA). The central position had an RRCP of 1. In general, similarly to the mean response amplitudes (Figure 4), the RRCPs decreased as the eccentricity increased in V1 (p < 0.001, A, B) and ventral category-selective areas (FFA and PPA, C, D). There were significant effects of eccentricity (p < 0.001) at each meridian positions and significant effects of region at the upper and lower vertical positions (p ≤ 0.01) in the ventral category-selective areas. Significant interactions between eccentricity and region were found (p = 0.002) only at the contralateral horizontal positions in the ventral category-selective areas. Considering the dimension of meridian, there were significant effects of meridian in V1 and ventral category-selective areas (FFA and PPA, p < 0.001). The abbreviations are the same as those used in Figure 3.3.
3.3.3 Mean Response Magnitude

We measured the mean magnitude of the response to the 10 positions, considering that one central position and 3 eccentricities in 3 meridians (contralateral horizontal, upper vertical, and lower vertical meridian) occupied half of the visual fields. In V1 and ventral category-selective areas, Face-V1 and FFA were the ROIs defined for the face images and House-V1 and PPA were the ROIs defined for the house images. Figure 4 shows the mean response magnitude in each ROI. Firstly, we considered each meridian separately, including the contralateral horizontal positions, upper vertical positions, and lower vertical positions. In V1, there were some missing values in the neural response magnitude that could not be defined by the contrast in each position (Materials and Methods). Linear mixed models for repeated measures with factors of eccentricity (0°, 16°, 32° or 48°) and region (for faces and houses, 4 × 2) were applied for V1 areas (Face-V1 and House-V1, Figure 3.4 A, B) and the ventral category-selective areas (FFA and PPA, Figure 3.4 C, D); the statistical values are listed in Table 3.5. Generally, there were significant main effects of eccentricity in V1 and the ventral category-selective areas (all: p < 0.001), which consisted of the behavior result (Table 3.2) and the neural activity on the visual cortex (Figure 3.3). In V1, the only significant main effects of region were found at the contralateral horizontal and lower vertical positions (p ≤ 0.02), and significant interactions between eccentricity and region were found at the upper vertical positions and lower vertical positions (p ≤ 0.03), except for V1 at the contralateral horizontal positions (p = 0.21). The faces had weaker neural response magnitudes than the houses at the contralateral horizontal positions, which resulted from the relatively smaller size of the face images compared to the house images. The faces were always shown as an ellipse shape, and the houses were always shown as a square shape. Moreover, the difference between the magnitudes of the neural response to the faces and houses became weaker at the upper vertical positions and lower vertical positions. In the ventral category-selective areas (Figure 3.4 C, D), we also found significant main effect of eccentricity at all three meridians positions (p < 0.001), which were similar as in V1. However, FFA had stronger neural response magnitudes than PPA, which contrasted with the results from V1. Significant main effects of region (p ≤ 0.02) were found at all the three meridians positions. A significant interaction between eccentricity and region was found only at the lower vertical positions (p = 0.01).

From the statistical results above, the meridian factor had effects on the neural response magnitude both in V1 (Figure 3.4 A, B) and the ventral category-selective areas (Figure 3.4 C, D). The neural response magnitudes at the peripheral 3 eccentric level positions were applied. Linear mixed models for repeated measures with factors of eccentricity (16°, 32° and 48°), meridian
(contralateral horizontal, upper vertical, and lower vertical positions), and region (3 × 3 × 2) were applied; the statistical values are listed in Table 3.6. Significant main effects of eccentricity, meridian, and region were found in V1 and ventral category-selective areas (all: p ≤ 0.03). There was a significant interaction between meridian and region (p = 0.03) in V1, while in FFA and PPA, there was a significant interaction between eccentricity, meridian, and region (p < 0.001). Pairwise comparisons showed that the neural response magnitude at 3 meridian positions were significantly different (p ≤ 0.01).

3.3.4 Relative to Central Position

We found differences in response magnitude of the neural activities in V1, FFA and PPA. The neural activities in response to the houses were stronger than those in response to the faces in V1, but FFA displayed much greater neural activities than PPA, especially for the central position. We normalized the neural response amplitude by calculating the ratio relative to central position (RRCP) for each position and ROI (RRCP = neural response amplitude at each position / neural response amplitude at central position). A ratio of 1 meant that the neural response amplitude of a position was the same as that of the central position. The mean results of the RRCPs are shown in Figure 3.5. The values of RRCPs were subjected to the same statistical analysis as the mean response magnitude above. The detailed statistical values are listed in Table 3.7. In V1 (Figure 3.5A, B), for each meridian, there were only significant effects of eccentricity (all: p < 0.001). Taking the meridian effect into consideration, the significant main effect of eccentricity and meridian were found (all: p < 0.001). In addition, no significant interactions were identified among eccentricity, meridian, and region (all: p > 0.1). These results indicated that the neural activities in V1 were affected by eccentricity and meridian but not by the category selectivity.

In the ventral category-selective areas (Figure 3.5 C, D), the statistical results were similar to those of the neural responses. For each meridian, there were significant main effects of eccentricity (all: p < 0.001) and region at the upper and lower vertical positions (all: p ≤ 0.01). In addition, significant interactions between eccentricity and region were found only at the lower vertical positions (p = 0.002). Taking the meridian effect into consideration, significant main effects of eccentricity, meridian and region were found (all: p ≤ 0.002). There was significant interaction between eccentricity, meridian and region (p = 0.02). The detailed statistical values are listed in Table 3.8. These results indicated that the neural activities in the ventral category-selective areas were affected by meridian and region, in addition to eccentricity.
3.3.5 Relative to V1

The results of the mean response amplitudes and RRCPs implied that the neural activities to the faces and the houses in V1 had a consistent effect of eccentricity and meridian. In contrast, there was a greater difference on the effect of eccentricity and meridian between FFA and PPA. We proposed that the neural representations of the images of faces and houses within a wide field included differences in V1 and ventral category-selective areas. To determine the conversion from V1 to FFA and PPA, we calculated the ratio relative to V1 (RRV1) for the neural response amplitude of each position and ROI (RRV1 = neural response amplitude in FFA or PPA / neural response amplitude in V1). When the neural response amplitude in FFA or PPA was greater than that in V1, the RRV1 was greater than 1, and when the amplitude was smaller, the RRV1 was smaller than 1. Only the positive response amplitudes were used for the final calculations. Figure 3.6 shows the mean RRV1s in each position for each ROI; the statistical values are listed in Table 3.9. Firstly, linear mixed models for repeated measures with factors of eccentricity and region (4 × 2) revealed main effects of eccentricity at the contralateral horizontal positions and upper vertical positions (p ≤ 0.03). An interaction between eccentricity and region was found only at the contralateral horizontal positions (p = 0.03). Pairwise comparisons of eccentricity reveal a different effect of eccentricity in each meridian positions and ROIs. At the contralateral horizontal positions, the 32º and 48º positions had bigger RRV1s than the 0º and 16º positions in FFA (p ≤ 0.05). Along the upper vertical median, the 32º and 48º positions had bigger RRV1s than the 0º positions in FFA, and the 48º positions had bigger RRV1s than the 0º positions in PPA (p < 0.05). In addition, there were main effects of region at the contralateral horizontal, upper vertical and lower vertical positions (p ≤ 0.05). The larger RRV1s in FFA than PPA were consisted with the results of mean response amplitudes; the faces elicited weaker neural activities in V1 area and stronger neural activities in the category-selective areas, comparing with house.
Figure 3.6. RRV1s in the ventral category-selective areas for images of faces and houses. (A) RRV1s in FFA for images of faces, and (B) RRV1s in PPA for images of houses. There were significant effects of region \((p \leq 0.05)\) for all 3 meridians and main effects of eccentricity at the contralateral horizontal and upper vertical positions \((p \leq 0.03)\). Moreover, considering the dimensions of meridian, there was a significant effect of meridian and region \((p < 0.001)\). Significant interactions between meridian and region were found \((p = 0.005)\). The abbreviations are the same as those used in Figure 3.3.

These two-factor statistical analysis results revealed that the RRV1s also had different effects of meridian in FFA and PPA (Figure 3.6). To analyze the meridian effect, a linear mixed model for repeated measures with factors of eccentricity, meridian and region \((3 \times 3 \times 2)\) revealed a main effect of meridian and region \((p < 0.001)\) and an interaction between meridian and region \((p = 0.005)\). The statistical values are listed in Table 3.10. In FFA, a pairwise comparison showed that the contralateral horizontal positions and upper vertical positions had a greater RRV1 than the lower vertical positions \((p < 0.001)\), and the contralateral horizontal positions caused no differences between the upper vertical positions \((p = 0.8)\), while in PPA, the upper vertical positions had a greater RRV1 than the contralateral horizontal positions and the lower vertical positions \((p \leq 0.04)\), and the contralateral horizontal positions caused no difference between the lower vertical positions \((p = 0.9)\).
Figure 3.7. Mean magnitudes of neural response to the images of faces (houses) and the checkerboard rings. (A) The combined magnitudes of neural response to the images of faces (houses) at the 3 meridian positions in FFA (PPA). The mean response magnitudes of the 3 meridians were consistent with the result described before (Figure 3.4). (B) The neural response magnitudes to the checkerboard rings in FFA and PPA. It is revealed that a significant effect of eccentricity and region \((p = 0.002)\) and an interaction between eccentricity and region \((p = 0.04)\). The two decreasing sections of the neural response magnitudes were the central 3 rings, which covered the visual field of \(8^\circ\) eccentricities \((p = 0.02)\), and the peripheral 5 rings, which covered the visual field of \(8-60^\circ\) eccentricities \((p = 0.004)\). A significant interaction was found between region and eccentricity for the central 3 rings \((p = 0.03)\). The \(x\)-axis of eccentricity is labeled on a base 2 logarithmic scale.

### 3.3.6 Neural Response to the Checkerboards Rings

We also measured the neural response magnitudes to the expending of checkerboard rings in the retinotopic mapping experiments (Materials and Methods). In Figure 3.7, we showed the mean magnitudes of the neural responses to the images of faces (houses) combined across all 3 meridians (Figure 3.7A) and the response magnitudes to the checkerboard rings (Figure 3.7 B) in FFA (PPA). Linear mixed models with repeated measure of eccentricity and region (FFA and PPA) were applied, and the statistical values are listed in Table 3.11. There were significant effects of eccentricity and region for both the images of faces (houses) and the checkerboards ring \((\text{all: } p \leq 0.01)\). The checkerboard had significantly stronger neural response magnitudes in PPA than FFA for all the 8
rings (p = 0.002), which was contrary to the neural responses to the images of faces and houses. As the widths of the rings were applied in exponential increments, the response magnitudes had peaks at the fourth or fifth rings, which mainly occupied the eccentricities of 8-18°. Then, there were two decreasing sections of the neural response magnitudes. One section was the central 3 rings, which covered the visual field of 8° eccentricities (p = 0.02), and the other one section was the peripheral 5 rings, which covered the visual field of 8-60° eccentricities (p = 0.004). An interaction between eccentricity and region was found between region and eccentricity for the central 3 rings (p = 0.03), but no interaction was found between region and eccentricity for the peripheral 5 rings (p = 0.12). In addition, there was no interaction between eccentricity and region on the response magnitudes to the faces and the houses (p = 0.42), which was consistent with the peripheral checkerboards.

### 3.3.7 Signal Intensity in V1

As demonstrated by the mean signal intensity mapping (temporal signal-to-noise: the ratio of the average signal intensity to the signal standard deviation) of the 7 subjects, the signal quality in the calcarine sulcus was very good, even in the anterior regions of calcarine sulcus (Figure 3.8 A). The simulations indicated that a TSNR of 40 (indicated in the map by light green) was the minimum to reliably detect the effects between the conditions in the EPI data [83]. Note that virtually all of the calcarine sulcus far exceeds this threshold, with many exceeding a TSNR of 200. The signal intensities in the ROIs for the Face-V1 and the House-V1 were also reported (Figure 3.8 B). Using linear mixed models for repeated measures, we found no differences between the ROIs of Face-V1 and ROIs of House-V1 (all: p ≥ 0.86); the statistical values for signal intensity are listed in Table 3.12. In the ROIs along the contralateral horizontal median, the signal intensities of the 4 eccentric positions (0˚, 16˚, 32˚, and 48˚) had no significant effect of eccentricity (p = 0.06). In the ROIs along the upper and lower vertical median, the signal intensities of the 3 eccentric positions (16˚, 32˚, and 48˚) had no significant effect of eccentricity (p ≥ 0.35). We found a significant effect of meridian on the signal intensities (p = 0.03, Table 3.13). Through pairwise comparison, the signal intensities in the upper and lower vertical median ROIs were no significant differences (p = 0.5) but significantly smaller than those in the contralateral horizontal positions ROIs (both: p < 0.05). The ROIs of the contralateral horizontal and central positions were mainly in the calcarine sulcus. However, the ROIs of the upper (lower) vertical positions were located at the gyrus ventral (dorsal) calcarine sulcus. The anatomical difference resulted in different signal intensities in the ROIs at the contralateral horizontal positions and vertical positions. Thus the results of signal intensity verified that the signal quality was not significantly different between the anterior and posterior regions of the calcarine sulcus.
Figure 3.8. Signal intensity of EPI. (A) Signal intensity maps showing EPI image quality in the calcarine sulcus. The color gradient indicates the mean signal intensity of the smoothed EPI time course data overlaid on the inflated cortex of the Talairach brain. The threshold of the color map was established at a TSNR of 40, and all the blue areas indicate a TSNR of at least 200. Simulations indicate that a TSNR of 40 (indicated in the map by light green) is the minimum necessary to reliably detect the effects between the conditions in the fMRI data [83]. (B) The signal intensities in the ROIs of V1. At the contralateral horizontal positions, the signal intensities in the 4 ROIs (0°, 16°, 32°, and 48°) were not significantly different (p = 0.06). At the upper and lower vertical positions, the signal intensities in the 3 ROIs (16°, 32°, and 48°) were not significantly different (p ≥ 0.35), but they were significant smaller than the signal intensities at the contralateral horizontal positions (p < 0.05). The abbreviations are the same as those used in Figure 3.3.
3.4 Discussion

Our study provides a broad-based survey of position information in FFA and PPA located in the ventral visual cortex. We measured the mean response amplitudes to 13 positions in a wide field and then calculated the values of the RRCPs and RRV1s. Important new findings were revealed concerning the different neural processing strategies in the dimensions of eccentricity, meridian and region.

3.4.1 Different Processing Strategies in the Dimension of Eccentricity

Human vision is divided into central and peripheral vision [64]. Peripheral vision has mostly been characterized in terms of the reductions in resolution or contrast sensitivity as eccentricity increases [84-86]. The ability of humans to detect movement is better in peripheral vision than foveal vision, but color discrimination is markedly worse [87, 88]. In the behavior data, lower accuracy was found at the peripheral positions. Consistent with the behavior performance, the mean response magnitudes in V1, FFA and PPA (Figure 3.4, 3.5) decreased as the visual stimuli (images of houses and faces) were presented at progressively greater distances from the center of the visual field. The neural response to the checkerboard rings also exhibited a decreasing trend as the eccentricities increased; the central 3 rings covered the visual field of 8º eccentricities, and the peripheral 5 rings covered the visual field of 8º-60º eccentricities (Figure 3.7 B). These results confirmed the central-peripheral organization in the primate visual cortex. After normalizing the neural response magnitudes by dividing the response magnitudes at the central position, the RRCP values decreased with the same trend in V1 and with different trends in ventral category-selective areas (FFA and PPA, Figure 3.5).

An important new finding was revealed by comparing the RRV1s. As shown in Figure 3.6, we found that the RRV1s in FFA and PPA had a significant effect of eccentricity (p ≤ 0.03) at the contralateral horizontal positions and upper vertical positions. Furthermore, the differences in eccentricity were mainly found at the contralateral horizontal and upper vertical positions for FFA and at the upper vertical positions for PPA. Measuring the signal intensity in V1 showed that the signal quality in the calcarine sulcus was very good. The signal intensities had no difference between the anterior and posterior regions of the calcarine sulcus (Figure 3.8). The consistent signal qualities confirmed that the differences in RRV1s were indeed the neural processing difference of the visual cortex but were not induced by dropping the signal quality. These results demonstrated that FFA and PPA had systematic neural variances from the central field to the peripheral field because the RRV1s increased with eccentricity, especially FFA. In the visual cortical areas, V1 is
essential for visual information processing. A number of strategies, including linear and nonlinear filtering, are used for efficient information processing in the higher level areas [63]. From our findings, we considered that FFA and PPA had different strategies in the dimension of eccentricity were adopted to process the information from V1, especially FFA.

In contrast, Yue and his colleagues reported that FFA produces neural activities that fit well with the model based on V1 function [77]. They analyzed neural responses along 4 meridians, including the ipsilateral horizontal positions. Their results suggest that the RRV1s of FFA in central visual field are a constant, which was approximately 1.3. In our study, within a wide visual field, the ipsilateral neural responses were weak or negative in V1 and PPA due to the contralateral main neural activities in the human visual cortex in response to stimuli, especially with regard to V1 [77, 89]. The RRV1s were not well suited to the ipsilateral neural responses, thus the ipsilateral neural responses were ignored. Combining all 3 meridians, our RRV1 results from FFA were compared with the results of Yue et al. (Figure 3.9). At the 0º and 16º positions, the RRV1s of FFA were consistent with Yue’s results (t-test, p ≥ 0.16), while in the peripheral positions (32º and 48º), our values were greater than those of Yue (t-test, p ≤ 0.03). Additionally, in our study, the RRV1s at the 32º and 48º positions were significantly greater than those at the central position (p ≤ 0.04), and the RRV1 at the 48º position was significantly greater than those at the 16 º position. The stimuli in Yue’s study covered the central visual fields, with approximately 12º of eccentricity. Obviously, the results from the central visual field did not represent the entire visual field. In combination with the report of Yue [77], it was confirmed that the neural activation in FFA adopted different processing strategies in the dimension of eccentricity, compared to the neural activation function of V1, which showed smaller RRV1s at the central positions and larger RRV1s at the peripheral positions. The human retina has much weaker visual information processing capabilities in the peripheral visual field than the central visual field [90, 91]. Remarkably, the greater RRV1s at the peripheral positions might reflect a compensation mechanism for the peripheral field on the higher visual cortex. In PPA, the 48º positions had greater RRV1s than the 0º positions only in the upper vertical meridian. We considered that the compensation mechanism for the peripheral field was weak in PPA.

3.4.2 Meridian Difference in Neural Processing

Previous studies demonstrated significant effects of meridian in the higher-level, category-selective areas. PPA showed a significantly greater response magnitude to the upper field images compared to the lower field images. In contrast, the FFA, EBA and LO exhibited opposite
effects and greater response magnitudes to the lower field images compared with the upper field images [58, 61, 92, 93]. In our study, the visual stimuli expanded approximately 54º of eccentricity and FFA and PPA exhibited greater neural activities and the RRCP values at the upper vertical positions than those at the lower vertical positions (p = 0.01). We considered that the result from the wide-field stimuli more accurately reflected this meridian bias.

There were stronger neural responses or RRCPs to the lower vertical positions compared to the upper vertical positions in V1 (Figure 3.4, 3.5), which were consistent with the previous reports of V1 [79, 94, 95] and were caused by the larger retinal ganglion density in the lower meridian [90, 91]. Generally, perception at the lower visual field is also superior to that in the upper visual field [96-98]. However, lower-biased neural responses were not found at the higher category-selective area, and the upper vertical positions had greater neural activities and RRCP values than the lower vertical positions. The RRV1 values at the upper vertical positions were also larger than those at the lower vertical positions (p ≤ 0.04, Figure 3.6). We inferred that the larger RRV1s in the upper vertical meridian might comprise a compensation mechanism for the lower vertical meridian biased retinal ganglion density and V1 neural activities. Moreover, in our study, the behavior performance was not different between the upper and lower vertical positions, which also supported this compensation mechanism.

Thus, according to this processing strategy model of a compensation mechanism based on meridian, approximately equal neural activities were observed for images of faces and houses at both the upper and lower vertical positions. Moreover, previous studies have reported lower biases in the FFA, EBA and LO [58, 61, 92, 93], which might be caused by the intense lower bias in V1. The upper biases in the PPA in the mean response amplitude results [58, 61, 92, 93] were justified, as the much stronger upper biases compensated for the lower biases in V1.

### 3.4.3 Difference between FFA and PPA

In present study, within wide visual fields of 60º eccentricities, the subject had no difference on the response time and accuracy for the face and house images. As the result, the images of both faces and houses elicited different neural responses magnitude for each position in V1 and ventral category-selective areas (FFA and PPA, Figure 3.4). Face images had significant smaller magnitude responses than house images in V1, and neural responses to face images in FFA were significantly greater than the neural responses to house images in PPA. We found smaller neural activities to checkerboards in FFA than that in PPA. It was implied that FFA and PPA had different strategies for processing images of faces and houses. Furthermore, the RRCPs had only significant difference
in ventral category-selective areas (FFA and PPA), but not in V1 (Figure 3.5). The RRV1s result also confirmed a difference between FFA and PPA (Figure 3.6). In FFA, face images generated much greater RRV1s than house images in PPA (p ≤ 0.05), especially in the contralateral horizontal meridian positions. These results demonstrate that different processing strategies were also employed in FFA and PPA. From the present results, greater RRV1s indicate that the neural responses had greater ratios added to V1 functions. In FFA, the RRV1 values at all positions were greater than 1 (t test, p < 0.0001), which means that FFA had an amplifying effect. However, in PPA, the RRV1 values at all the positions had no significant difference between value of 1 (t test, p = 0.37). In another word, there was no amplifying effect in PPA to processing house images. These results demonstrated that the larger RRV1s were associated with the central representation in FFA, and the smaller RRV1s were associated with the peripheral representation in PPA. The differences of RRV1s reflected more information about the different neural function between FFA and PPA, in addition to previous reports of the central-peripheral organization of the human category-selective areas [54, 59-61]. We hypothesized that the different neural processing strategies existed between face image processing in FFA and house image processing in PPA.

Figure 3.9. Comparison of our RRV1 results to the results obtained by Yue and colleagues. The stimuli in Yue’s study covered the central visual fields, approximately 12º of eccentricity. Our RRV1 results from FFA combined across all 3 meridians were compared to those of Yue. His results agreed with our RRV1 at 0º and 16º of eccentricity, and there was a significant difference with RRV1s at 32º and 48º. The asterisks denote significance (p < 0.05).
According to the central-peripheral organization for category-selective areas [59, 60], FFA is associated with center-biased representations in the cortex and PPA is associated with periphery-biased representations in the cortex [54, 59-61]. FFA had a stronger neural response to stimuli in the central fields than the peripheral fields, and PPA had stronger neural responses to stimuli in the periphery than the central fields. However, in the present results, we did not find the central-peripheral bias of neural activities in FFA and PPA. The neural response magnitudes and the RRCPs had similar decay trends at the contralateral horizontal and upper vertical positions. These differences between the present result and previous reports were clear in the comparison of the neural response to checkerboards. There was a significant interaction between region and eccentricity for the central 3 eccentric rings, covering the visual field of 8º eccentricities (p = 0.03), which meant that the FFA had a steeper decreasing trend compared to PPA. Within more peripheral fields, no interactions between region and eccentricity were found. The stimuli used in previous reports mainly covered visual fields with an eccentricity of 10º. The characteristics of the central-peripheral organization are limited [59-61]. In the present study, the stimuli covered a visual field with an eccentricity of 60º, and neural responses to images of faces, houses, and checkerboards had trend of decreasing as the eccentricities increased, but these data also exhibited differences (Figure 3.7).

At the contralateral horizontal positions, the FFA had significantly different RRV1s in eccentricity dimension (p ≤ 0.05) but PPA did not. Moreover, there was an interaction between region and eccentricity (p = 0.03). We considered that the compensation mechanisms for the peripheral field may be in FFA but not in PPA. The upper vertical positions had a main effect of eccentricity but the lower vertical positions did not. Furthermore, there was no interaction between region and eccentricity (p ≥ 0.35) at the upper and lower vertical positions, and we speculated that the difference in compensation mechanisms between FFA and PPA became weaker. The models of RRV1s relative to eccentricity and meridian factors were associated with region in the ventral category-selective areas.

3.4.5 The Influence of Perceptual Experiences on Human Visual Cortex

Processing consistent visual information from V1, FFA and PPA areas manifested different processing strategies in terms of eccentricity, meridian and region, which might imply compensation mechanisms for the peripheral field. These findings did not clearly support the resolution-need hypothesis [59, 72]. An alternative explanation for the different versions of the neural activity models for the face- and house-selective areas might appeal, instead, to the statistics based on experience. Through this experience hypothesis, the compensation mechanism for the peripheral field on the higher visual cortex may be comprehended [45].
As mentioned above, the different processing strategies for the eccentricity and meridian dimensions in the human visual cortex were adopted to compensate for the non-uniformity of the human retina and V1 [17, 90, 91], which resulted in weaker perceptual abilities in the peripheral field and the upper vertical positions [45, 96, 97]. We propose that the compensation mechanism is driven by visual perception needs. Moreover, specific modes for each category of stimuli correspond to the retinal location in which those objects are typically observed. Generally, the perception of face images is optimal with high-resolution foveal information [45, 59, 72]. However, faces may appear in the entire visual field. Thus, FFA exhibited RRV1s greater than 1.33 (Figure 3.6, 3.9), and the increasing RRV1s appear to have a role as a compensation mechanism for the peripheral faces. In contrast, house and sense perceptions provide more relevant visual information from the periphery in the everyday perceptual experience. Thus, PPA correspondingly exhibit smaller RRV1s (Figure 3.6, 3.9) and weaker or no compensation mechanisms for the peripheral houses. These associations might reflect how experience affects the locations of where these stimuli are typically observed in daily life. Moreover, natural selection may have also led to heritable differences between these areas [45].

3.5 Conclusion

From our results, the neural response amplitudes and the values of RRCPs demonstrated the significant differences for each position in V1, FFA, and PPA. Measuring the RRV1s, we found that the FFA and PPA process the visual information from V1 using different neural processing strategies. The first was the dimension of eccentricity, which the values of RRV1s at the central positions were smaller than those at the peripheral positions in FFA at the contralateral horizontal positions and upper vertical positions, and in PPA only at the upper vertical positions. The second was the dimension of meridian, which the RRV1s observed at the upper vertical positions were greater than those at the lower vertical positions. The third was the dimension of region, which the RRV1s in FFA were greater than those in the PPA, and the significantly increasing trends of RRV1s were observed in FFA. The findings reported here suggested that the ventral category-selective areas develop specific modes to process stimuli located at different positions, depending on the retinal locations of where the object is typically observed in daily life. Taken together, these different neural processing strategies of the ventral visual cortex might be shaped by experience.
Table List

Table 3.1. The mean Talairach coordinates, the cluster volumes, and the defined numbers of ROI in V1 for faces and houses at each position.

<table>
<thead>
<tr>
<th>Region</th>
<th>Position</th>
<th>Meridian</th>
<th>Eccentricity</th>
<th>Left Hemisphere</th>
<th>Cluster Size</th>
<th>Right Hemisphere</th>
<th>Cluster Size</th>
<th>Number Defined</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>x</td>
<td>y</td>
<td>z</td>
<td></td>
<td>x</td>
<td>y</td>
<td>z</td>
</tr>
<tr>
<td>Face-V1</td>
<td>Central</td>
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<td>-10.8</td>
<td>-91.4</td>
<td>-6.6</td>
<td>1720</td>
<td>7</td>
<td>6.1</td>
</tr>
<tr>
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<td></td>
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<td>-84.1</td>
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</tr>
<tr>
<td></td>
<td>Contralateral</td>
<td>16º</td>
<td>-9.2</td>
<td>-76.0</td>
<td>0.7</td>
<td>748</td>
<td>7</td>
<td>8.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-70.0</td>
<td>8.3</td>
<td>667</td>
</tr>
<tr>
<td></td>
<td>Horizontal Positions</td>
<td>32º</td>
<td>-14.7</td>
<td>-70.4</td>
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<td>478</td>
<td>7</td>
<td>14.7</td>
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<td></td>
<td></td>
<td>-61.1</td>
<td>7.6</td>
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<tr>
<td></td>
<td>Upper Vertical Positions</td>
<td>32º</td>
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<td>6</td>
<td>12.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td>-60.2</td>
<td>7.4</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>Lower Vertical Positions</td>
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<td>-78.0</td>
<td>5.7</td>
<td>435</td>
<td>6</td>
<td>3.9</td>
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<td>-73.1</td>
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<td>-81.1</td>
<td>-5.0</td>
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<td></td>
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<td>0.3</td>
<td>2519</td>
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<td>Contralateral</td>
<td>16º</td>
<td>-9.5</td>
<td>-76.4</td>
<td>1.3</td>
<td>863</td>
<td>7</td>
<td>7.8</td>
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<td></td>
<td></td>
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<td></td>
<td></td>
<td>-70.7</td>
<td>8.1</td>
<td>769</td>
</tr>
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<td></td>
<td>Horizontal Positions</td>
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<td>348</td>
<td>7</td>
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</tr>
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<td></td>
<td></td>
<td></td>
<td>-60.9</td>
<td>9.1</td>
<td>640</td>
</tr>
<tr>
<td>House-V1</td>
<td>Central</td>
<td>0º</td>
<td>-6.9</td>
<td>-66.3</td>
<td>-0.5</td>
<td>246</td>
<td>6</td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<td></td>
<td>-69.7</td>
<td>3.9</td>
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</tr>
<tr>
<td></td>
<td>Contralateral</td>
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<td>-8.3</td>
<td>-61.7</td>
<td>1.5</td>
<td>120</td>
<td>6</td>
<td>13.6</td>
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<td></td>
<td>-58.4</td>
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<td>-58.3</td>
<td>1.7</td>
<td>134</td>
<td>7</td>
<td>19.6</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-52.2</td>
<td>3.3</td>
<td>133</td>
</tr>
<tr>
<td></td>
<td>Upper Vertical Positions</td>
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<td>-6.1</td>
<td>-78.6</td>
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<td>367</td>
<td>7</td>
<td>3.6</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-74.4</td>
<td>12.6</td>
<td>317</td>
</tr>
<tr>
<td></td>
<td>Lower Vertical Positions</td>
<td>32º</td>
<td>-9.7</td>
<td>-63.4</td>
<td>6.3</td>
<td>182</td>
<td>7</td>
<td>8.0</td>
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<td></td>
<td></td>
<td></td>
<td>-65.2</td>
<td>10.6</td>
<td>77</td>
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<tr>
<td></td>
<td>Central</td>
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<td>-19.5</td>
<td>-63.4</td>
<td>6.8</td>
<td>135</td>
<td>7</td>
<td>16.5</td>
</tr>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>-57.3</td>
<td>8.2</td>
<td>61</td>
</tr>
</tbody>
</table>

Values are represented as the means ± SEM.

Table 3.2. Mean behavioral performance during object experiments.

<table>
<thead>
<tr>
<th>Position</th>
<th>Meridian</th>
<th>Response time (ms)</th>
<th>Percentage accuracy</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Faces</td>
<td>Houses</td>
</tr>
<tr>
<td></td>
<td></td>
<td>x±s</td>
<td>y±s</td>
</tr>
<tr>
<td>Central</td>
<td>0º</td>
<td>632 ±61</td>
<td>611 ±44</td>
</tr>
<tr>
<td>Left</td>
<td>16º</td>
<td>628 ±52</td>
<td>636 ±47</td>
</tr>
<tr>
<td>horizontal positions</td>
<td>32º</td>
<td>640 ±56</td>
<td>568 ±52</td>
</tr>
<tr>
<td>positions</td>
<td>48º</td>
<td>687 ±66</td>
<td>692 ±66</td>
</tr>
<tr>
<td>Right</td>
<td>16º</td>
<td>544 ±57</td>
<td>528 ±59</td>
</tr>
<tr>
<td>horizontal positions</td>
<td>32º</td>
<td>566 ±54</td>
<td>546 ±54</td>
</tr>
<tr>
<td>positions</td>
<td>48º</td>
<td>503 ±30</td>
<td>575 ±37</td>
</tr>
<tr>
<td>Upper</td>
<td>16º</td>
<td>557 ±54</td>
<td>581 ±59</td>
</tr>
<tr>
<td>vertical positions</td>
<td>32º</td>
<td>602 ±72</td>
<td>656 ±67</td>
</tr>
<tr>
<td>positions</td>
<td>48º</td>
<td>774 ±63</td>
<td>682 ±63</td>
</tr>
<tr>
<td>Lower</td>
<td>16º</td>
<td>559 ±39</td>
<td>619 ±38</td>
</tr>
<tr>
<td>vertical positions</td>
<td>32º</td>
<td>628 ±23</td>
<td>605 ±21</td>
</tr>
<tr>
<td>positions</td>
<td>48º</td>
<td>695 ±48</td>
<td>746 ±48</td>
</tr>
</tbody>
</table>

Values are represented as the means ± SEM.
Table 3.3. Linear mixed models for repeated measures with factors of eccentricity (0º, 16º, 32º and 48º) and category (faces and houses, 4 × 2) for the behavior performances.

<table>
<thead>
<tr>
<th>Response Time</th>
<th>Accuracy</th>
</tr>
</thead>
<tbody>
<tr>
<td>dfn, dfd</td>
<td>F</td>
</tr>
<tr>
<td>Left Horizontal Positions</td>
<td>Eccentricity</td>
</tr>
<tr>
<td>Category</td>
<td>1, 6</td>
</tr>
<tr>
<td>Eccentricity*Category</td>
<td>3, 16</td>
</tr>
<tr>
<td>Category</td>
<td>1, 15</td>
</tr>
<tr>
<td>Eccentricity*Category</td>
<td>3, 34</td>
</tr>
<tr>
<td>Right Horizontal Positions</td>
<td>Eccentricity</td>
</tr>
<tr>
<td>Category</td>
<td>1, 15</td>
</tr>
<tr>
<td>Eccentricity*Category</td>
<td>3, 34</td>
</tr>
<tr>
<td>Category</td>
<td>1, 15</td>
</tr>
<tr>
<td>Eccentricity*Category</td>
<td>3, 34</td>
</tr>
<tr>
<td>Upper Vertical Positions</td>
<td>Eccentricity</td>
</tr>
<tr>
<td>Category</td>
<td>1, 16</td>
</tr>
<tr>
<td>Eccentricity*Category</td>
<td>3, 34</td>
</tr>
<tr>
<td>Category</td>
<td>1, 16</td>
</tr>
<tr>
<td>Eccentricity*Category</td>
<td>3, 34</td>
</tr>
<tr>
<td>Lower Vertical Positions</td>
<td>Eccentricity</td>
</tr>
<tr>
<td>Category</td>
<td>1, 17</td>
</tr>
<tr>
<td>Eccentricity*Category</td>
<td>3, 32</td>
</tr>
</tbody>
</table>

dfn: degrees of freedom numerator, dfd: degrees of freedom denominator.

Table 3.4. A linear mixed model for repeated measures with factors of eccentricity (0º, 16º, 32º and 48º), meridian (left, right, upper, lower), and category (face and house 3 × 4 × 2) for the behavior performances.

<table>
<thead>
<tr>
<th>Response Time</th>
<th>Accuracy</th>
</tr>
</thead>
<tbody>
<tr>
<td>dfn, dfd</td>
<td>F</td>
</tr>
<tr>
<td>Eccentricity</td>
<td>2, 31</td>
</tr>
<tr>
<td>Category</td>
<td>1, 27</td>
</tr>
<tr>
<td>Eccentricity*Meridian</td>
<td>6, 74</td>
</tr>
<tr>
<td>Eccentricity*Category</td>
<td>2, 94</td>
</tr>
<tr>
<td>Meridian*Category</td>
<td>3, 72</td>
</tr>
<tr>
<td>Eccentricity<em>Meridian</em>Category</td>
<td>6, 54</td>
</tr>
</tbody>
</table>

Table 3.5. Linear mixed models for repeated measures with factors of eccentricity (0º, 16º, 32º and 48º) and region (for faces and houses, 4 × 2) for the neural responses in V1 and ventral category-selective areas (FFA and PPA).

<table>
<thead>
<tr>
<th>FFA and PPA</th>
</tr>
</thead>
<tbody>
<tr>
<td>dfn, dfd</td>
</tr>
<tr>
<td>Face-V1 and House-V1</td>
</tr>
<tr>
<td>Region</td>
</tr>
<tr>
<td>Eccentricity*Region</td>
</tr>
<tr>
<td>Region</td>
</tr>
<tr>
<td>Eccentricity*Region</td>
</tr>
<tr>
<td>Region</td>
</tr>
<tr>
<td>Eccentricity*Region</td>
</tr>
</tbody>
</table>
Table 3.6. A linear mixed model for repeated measures with factors of eccentricity (16°, 32° and 48°), meridian (contralateral horizontal, upper vertical, and lower vertical positions), and region (3 × 3 × 2) for the neural responses in V1 and ventral category-selective areas (FFA and PPA).

<table>
<thead>
<tr>
<th></th>
<th>Face-V1 and House-V1</th>
<th>Response in FFA and PPA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>dfn, dfd F Sig</td>
<td>dfn, dfd F Sig</td>
</tr>
<tr>
<td>Eccentricity</td>
<td>2.82 55.58 5.E-16</td>
<td>2.87 20.49 5.E-08</td>
</tr>
<tr>
<td>Meridian</td>
<td>2.54 21.63 1.E-07</td>
<td>2.92 18.52 2.E-07</td>
</tr>
<tr>
<td>Region</td>
<td>1.44 4.99 0.03</td>
<td>1.82 21.72 1.E-05</td>
</tr>
<tr>
<td>Eccentricity*Meridian</td>
<td>4.164 1.91 0.11</td>
<td>4.86 1.80 0.14</td>
</tr>
<tr>
<td>Eccentricity*Region</td>
<td>2.111 0.15 0.86</td>
<td>2.159 2.45 0.09</td>
</tr>
<tr>
<td>Meridian*Region</td>
<td>2.178 3.72 0.03</td>
<td>2.42 0.31 0.74</td>
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<tr>
<td>Eccentricity<em>Meridian</em>Region</td>
<td>4.60 0.53 0.71</td>
<td>4.51 8.36 3.E-05</td>
</tr>
</tbody>
</table>

Table 3.7. Linear mixed models for repeated measures with factors of eccentricity and region (4 × 2) for the RRCPs in V1 and ventral category-selective areas (FFA and PPA).

<table>
<thead>
<tr>
<th></th>
<th>Face-V1 and House-V1</th>
<th>FFA and PPA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>dfn, dfd F Sig</td>
<td>dfn, dfd F Sig</td>
</tr>
<tr>
<td>Contralateral Horizontal Positions</td>
<td>Eccentricity</td>
<td>2.35 28.25 5.E-08</td>
</tr>
<tr>
<td>Region</td>
<td>1.16 0.11 0.75</td>
<td>1.15 0.85 0.37</td>
</tr>
<tr>
<td>Eccentricity*Region</td>
<td>2.26 2.60 0.09</td>
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<tr>
<td>Region</td>
<td>1.17 2.89 0.11</td>
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<td>Eccentricity*Region</td>
<td>2.20 0.37 0.70</td>
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<tr>
<td>Region</td>
<td>1.34 1.24 0.27</td>
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<td>Eccentricity*Region</td>
<td>2.43 1.80 0.18</td>
<td>2.136 6.78 0.002</td>
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Table 3.8. A linear mixed model for repeated measures with factors of eccentricity, meridian, and region (3 × 3 × 2) for the RRCPs in V1 and ventral category-selective areas (FFA and PPA).

<table>
<thead>
<tr>
<th></th>
<th>Face-V1 and House-V1</th>
<th>FFA and PPA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>dfn, dfd F Sig</td>
<td>dfn, dfd F Sig</td>
</tr>
<tr>
<td>Eccentricity</td>
<td>2.68 38.23 6.E-12</td>
<td>2.83 20.57 6.E-08</td>
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<tr>
<td>Meridian</td>
<td>2.38 19.52 1.E-06</td>
<td>2.65 21.96 5.E-08</td>
</tr>
<tr>
<td>Region</td>
<td>1.36 1.90 0.17</td>
<td>1.60 10.83 0.002</td>
</tr>
<tr>
<td>Eccentricity*Meridian</td>
<td>4.165 1.55 0.19</td>
<td>4.148 1.12 0.35</td>
</tr>
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<td>Eccentricity*Region</td>
<td>2.142 2.15 0.12</td>
<td>2.100 0.19 0.82</td>
</tr>
<tr>
<td>Meridian*Region</td>
<td>2.171 1.90 0.15</td>
<td>2.166 0.70 0.50</td>
</tr>
<tr>
<td>Eccentricity<em>Meridian</em>Region</td>
<td>4.47 1.18 0.33</td>
<td>4.77 3.16 0.02</td>
</tr>
</tbody>
</table>
Table 3.9. Linear mixed models for repeated measures with factors of eccentricity and region (4 × 2) for the RRV1s.

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<tr>
<td>Eccentricity</td>
<td>3, 28</td>
<td>3.32</td>
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</tr>
<tr>
<td>Region</td>
<td>1, 43</td>
<td>21.54</td>
<td>3.E-05</td>
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<td>Eccentricity*Region</td>
<td>3, 26</td>
<td>3.62</td>
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<td>Eccentricity</td>
<td>3, 45</td>
<td>4.41</td>
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<td>1, 60</td>
<td>4.03</td>
<td>0.05</td>
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<td>Eccentricity*Region</td>
<td>3, 33</td>
<td>0.54</td>
<td>0.67</td>
</tr>
<tr>
<td>Eccentricity</td>
<td>3, 30</td>
<td>0.89</td>
<td>0.97</td>
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<tr>
<td>Region</td>
<td>1, 33</td>
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</tr>
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<td>Eccentricity*Region</td>
<td>3, 35</td>
<td>1.12</td>
<td>0.35</td>
</tr>
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</table>

Table 3.10. A linear mixed model for repeated measures with factors of eccentricity, meridian, and region (3 × 3 × 2) for the RRV1s.

<table>
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<td>2, 72</td>
<td>1.93</td>
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<td>Meridian</td>
<td>2, 77</td>
<td>9.16</td>
<td>3.E-04</td>
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<tr>
<td>Region</td>
<td>1, 66</td>
<td>17.25</td>
<td>1.E-04</td>
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<tr>
<td>Eccentricity*Meridian</td>
<td>4, 56</td>
<td>1.30</td>
<td>0.28</td>
</tr>
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<td>Eccentricity*Region</td>
<td>2, 50</td>
<td>2.05</td>
<td>0.14</td>
</tr>
<tr>
<td>Meridian*Region</td>
<td>2, 50</td>
<td>5.83</td>
<td>0.005</td>
</tr>
<tr>
<td>Eccentricity<em>Meridian</em>Region</td>
<td>4, 46</td>
<td>3.38</td>
<td>0.02</td>
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</table>

Table 3.11. Linear mixed models for repeated measures with factors of eccentricity and region (4 × 2) for the neural responses to the images of faces or houses, and checkerboards.

<table>
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</tr>
</thead>
<tbody>
<tr>
<td>Faces or Houses</td>
<td>Eccentricity</td>
<td>3, 45</td>
<td>73.19</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>1, 13</td>
<td>9.30</td>
</tr>
<tr>
<td></td>
<td>Eccentricity*Region</td>
<td>3, 39</td>
<td>0.97</td>
</tr>
<tr>
<td>Checkerboard</td>
<td>Eccentricity</td>
<td>7, 16</td>
<td>3.67</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>1, 28</td>
<td>12.53</td>
</tr>
<tr>
<td></td>
<td>Eccentricity*Region</td>
<td>7, 28</td>
<td>2.26</td>
</tr>
<tr>
<td>Central 3 rings</td>
<td>Eccentricity</td>
<td>2, 8</td>
<td>6.47</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>1, 24</td>
<td>2.99</td>
</tr>
<tr>
<td></td>
<td>Eccentricity*Region</td>
<td>2, 20</td>
<td>4.37</td>
</tr>
<tr>
<td>Peripheral 5 rings</td>
<td>Eccentricity</td>
<td>4, 12</td>
<td>6.43</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>1, 13</td>
<td>10.55</td>
</tr>
<tr>
<td></td>
<td>Eccentricity*Region</td>
<td>4, 22</td>
<td>2.04</td>
</tr>
</tbody>
</table>
Table 3.12. Linear mixed models for repeated measures with factors of eccentricity and region (4 × 2) for the signal intensity values in V1.

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<td>Eccentricity</td>
<td>3, 68</td>
<td>2.64</td>
</tr>
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<td></td>
<td>Region</td>
<td>1, 76</td>
<td>0.03</td>
</tr>
<tr>
<td>Upper Vertical Positions</td>
<td>Eccentricity*Region</td>
<td>3, 64</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>Eccentricity</td>
<td>2, 55</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>1, 18</td>
<td>0.01</td>
</tr>
<tr>
<td>Lower Vertical Positions</td>
<td>Eccentricity*Region</td>
<td>2, 22</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>Eccentricity</td>
<td>2, 65</td>
<td>1.06</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>1, 13</td>
<td>2.E-05</td>
</tr>
</tbody>
</table>

Table 3.13. A linear mixed model for repeated measures with factors of eccentricity, meridian, and region (3 × 3 × 2) for the signal intensity values in V1.

<table>
<thead>
<tr>
<th></th>
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<th>F</th>
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</thead>
<tbody>
<tr>
<td>Eccentricity</td>
<td>2, 63</td>
<td>0.56</td>
<td>0.58</td>
</tr>
<tr>
<td>Meridian</td>
<td>2, 61</td>
<td>3.55</td>
<td>0.03</td>
</tr>
<tr>
<td>Region</td>
<td>1, 18</td>
<td>4.E-04</td>
<td>0.98</td>
</tr>
<tr>
<td>Eccentricity*Meridian</td>
<td>4, 94</td>
<td>0.24</td>
<td>0.92</td>
</tr>
<tr>
<td>Eccentricity*Region</td>
<td>2., 132</td>
<td>0.59</td>
<td>0.56</td>
</tr>
<tr>
<td>Meridian*Region</td>
<td>2, 176</td>
<td>0.02</td>
<td>0.98</td>
</tr>
<tr>
<td>Eccentricity<em>Meridian</em>Region</td>
<td>4, 64</td>
<td>0.31</td>
<td>0.67</td>
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</table>
Chapter 4

Population Receptive Field Measurements for Human Peripheral Visual Field

Summary

Receptive field (RF) size is fundamental properties of visual cortex. Recently, using functional magnetic resonance imaging (fMRI), the maps for the population receptive field (pRF) were reported to the central visual field. However, with more peripheral visual field, the visual areas maps and pRF maps is remained unknown. Here, by pRF model developed by and wide-view presentation system with up to 60º of eccentricity, we tried to estimate the maps on visual cortex. We found the retinotopic representations and pRF maps of the wide-view visual field covered the temporal, occipital and parietal cortex. We further focused on the character of retinotopic representations and pRF size by wide-view field stimuli in V1-V3 and VO1/2. The visual areas maps consisted with the previous reported basing on central visual field. The V1-V3 had larger visual areas maps, and LO1 and LO2 likely to have response to central field. More differently, the pRF size is likely consisted with the size of macaque, but not with the central result of human. In conclusion, the present design successfully estimated the maps on the cortex with larger pRF size, but failed to estimate the maps for the cortex with smaller pRF size.

Key word: Visual cortex, Receptive field, wide-view, fMRI
4.1 Background

The human visual system is constantly solicited by stimuli appearing randomly in all parts of the visual field. Peripheral vision is weaker visual acuity than the central vision in humans. Peripheral vision is optimized for coarser information, compared that foveal vision is optimized for fine details. Because receptor cells on the retina are greater at the center and lowest at the edges. In addition, in the fovea, the retinal ganglion cells have smaller receptive fields, and in the periphery, they have much larger receptive fields. Peripheral vision provides critical wide field information about the environment, despite its low resolution and coarser information. The profiles of peripheral vision drove the motivation for measuring peripheral visual field map, and function of the visual cortex [64, 66, 99-103].

Using functional magnetic resonance imaging (fMRI), human visual area mapping has been widely investigated using the conventional traveling-wave method [11, 12, 31, 54, 56, 81, 104-106]. In addition, more peripheral visual field also commence being investigated using wide visual field representations apparatus [33-35, 79, 107]. Striate cortex areas, cortex magnification, and wedge dipole model for reconstruction of the retinotopic map were estimated by the stimuli ranged from central to peripheral field [79]. In peripheral field, the MT complex (MT1) may be specialized for the analysis of motion signals, whereas area V6 may be more involved in distinguishing object and self-motion [108].

Receptive field (RF) size is fundamental properties of visual cortex. The RF is a property of individual neurons, describing a limited part of the visual field visual field where a neuron responds to the visual stimulation. While the conventional traveling-wave method estimate only the most effective visual field location [11, 12, 81, 109]. The neuronal population within a voxel in fact responds to a range of visual field locations, and the stimuli may activate neurons whose receptive fields overlap but are not centered on the stimulus [109]. Thus, these approaches can give a rough estimate of map boundaries, and such measurements are not well suited for the description of a visual field map. pRF size influences the fMRI time course greatly [53, 56]. Phase-encoded retinotopic mapping can only capture the central tendency of many neuronal captive fields, the region of visual space that stimulates a voxel is referred to as the population receptive field (pRF) [109-111]. a quantitative framework was developed to model pRF properties and fit these models to the fMRI time series [109]. The periphery representation cortex has much larger receptive fields than the central representation cortex in primary area (V1) [49, 109]. However, with more peripheral visual field, the visual areas maps and pRF maps is remained unknown.
Here, we tried to address this issue by pRF model developed by Dumoulin and Wandell [109] and wide-view presentation system with up to 60° of eccentricity. We estimated the maps of the periphery visual field on temporal, occipital and parietal cortex. We further focused on the character of retinotopic representations and pRF size by wide-view field stimuli in V1-V3 and VO1/2.

4.2 Materials and Methods

4.2.1 Subjects

MR imaging was performed at the Hospital of Okayama University. 10 subjects, aged 22–27 years with a mean age of 23 years, participated in the study. All of the subjects were right-handed and had normal vision. Data from only ten of the eleven subjects were included in the following analyses because one subject exhibited significant head motions during the scan. The experiments were performed with the written consent from each subject and approved by the Ethics Committee of Okayama University Hospital.

4.2.2 Stimulus Presentation

Stimuli were projected on a wide-view visual presentation system, which was upgraded from a previous version [35, 79]. The subjects viewed the stimuli on a hemisphere 52 mm in diameter; the curvature radius of this hemisphere was 30 mm. The mean distance between the subjects’ eyes and the screen was 30 mm. The subjects wore contact lenses to focus on the stimulus, and the visual field of the stimulus was 120° horizontal × 120° vertical, or 60° eccentricity.

4.2.3 Visual Stimuli.

The stimuli included wedge and ring apertures that exposed a checkerboard pattern at 100% contrast (Figure 4.1). The aperture positions were displaced in discrete steps in synchrony with the functional magnetic resonance imaging (fMRI) volume acquisition, i.e., every 2 s. The wedge aperture subtended 45°(Figure 4.1 A)and widths of the rings apertures were one eighth of the stimulus radius (7.5°, Figure 4.1 A). These stimulus apertures contained black-and-white checkerboard patterns at 100% contrast, phase-reversing at a temporal frequency of 8 Hz. A full cycle of wedge and ring stimuli was 32 s, with a total of six cycles (192 s) per scanning run. The first five time frames (12 s) of each functional scan were discarded. Four scans (wedge, ring) were performed for each subject.
Figure 4.1 The sample of stimuli of checker board. (A) the wedge stimuli (B) the ring stimuli. The stimuli covered 60° eccentricity.

4.2.4 MRI Acquisition

Imaging was performed using a 3-Tesla MR scanner (Siemens Allegra, Erlangen, Germany). For the functional series, we continuously acquired images with 30 slices using a standard T2-weighted echo-planar imaging (EPI) sequence (TR = 2 s; TE = 35 ms; flip angle = 85°; 64 x 64 matrices; in-plane resolution: 2.3 x 2.3 mm; slice thickness: 2 mm, with a gap of 0.3 mm). The slices were manually aligned approximately perpendicular to the calcarine sulcus to cover most of the occipital, posterior parietal and posterior temporal cortices. After the functional scans, high-resolution sagittal T1-weighted images were acquired using a magnetization-prepared rapid gradient echo sequence (MP-RAGE; TR = 1800 ms; TE = 2.3 ms; matrix 256 x 256 x 224; 1 mm isotropic voxel size) to obtain a 3D structural scan.

4.2.5 Preprocessing of Anatomical and Functional Images.

FMRI analysis was performed in the mrVista software package for MATLAB, which is freely available at (http://white.stanford.edu/software/). T1-weighted anatomical scans were resampled to 1 mm3 resolution. The resulting anatomical image was automatically segmented using FSL [112] and then hand-edited to minimize segmentation errors [113]. The cortical surface was reconstructed at the gray–white matter border and rendered as a smoothed 3D surface [114]. Head movement and motion artifacts between and within functional scans were measured and corrected [115]. Functional data were then averaged across scans. Functional data were aligned to anatomical scans
and interpolated to the anatomical segmentation.

Visual field mapping and pRF analysis. We used a model-based method to estimate visual field maps and population receptive fields (pRFs) [109]. The BOLD response of each voxel was predicted using a two-dimensional Gaussian pRF model. This modeled the center location (x and y parameters) and spread (ơ) of the most responsive position of the voxels to the stimulus. The predicted fMRI time course was calculated by convolution of the modeled pRF, the stimulus sequence, and a canonical BOLD hemodynamic response function (HRF) [44, 116]. The pRF parameters for each voxel are determined by minimizing the sum of squared errors (RSS) between the predicted and observed fMRI time series. Further details of the pRF analysis are described in a previous study [109].

We estimate the visual field coverage from the full pRF. We first identify the pRF centers across all of the voxels within a visual field map. For each subject, we create a binary image showing whether a pRF center exists at each visual field location.

4.3 Result

By the method of pRF mapping, we successfully estimated the retinotopi maps and pRF maps. The retinotopic representations covered regions of temporal, occipital and parietal cortex, including the V1, V2, and V3, LO-1, LO-2, V3A/B, MT+, V6, IPS, hV4, VO-1, and VO-2 [13, 14, 17]. In present we focused on the character of retinotopic representations and pRF size by wide-view field stimuli in V1-V3 and VO1/2.

4.3.1 Visual Field Maps of V1, V2, V3

The visual areas maps clearly revealed three human hemifield maps near the calcarine sulcus in the occipital lobe V1 occupies the calcarine cortex (Figure 4.2). Encircling with V1, two additional maps (V2, V3) occupies a strip of cortex. V2 and V3 both contain discontinuous hemifield maps, which are divided along the horizontal meridian.

The V1, V2, V3 hemifield maps can be identified by the fMRI measurements of the eccentric and angular representations. The angular measurements divides this unified eccentricity representation into V1, V2, V3 hemifield maps. The vertical meridian representations of V1 and V2 are adjacent to one another. The horizontal meridian representations of V2 and V3 are adjacent to one another. V1 likely had activities to each angular of visual field equally (Figure 4.3). The expanding ring stimulus produces a single, large, and continuous eccentricity map. From the central
to the periphery, the location of the responding areas varied from the posterior to the anterior portions of the calcarine sulcus (Figure 4.1). V1 had representation of far peripheral stimuli (up to 60° eccentricity).

Figure 4.2 Visual field maps measured in the right hemisphere of a single subject participant using pRF mapping. (A) the polar angle representation, (B) the eccentricitic representation. The color overlay indicates the angle (left) or eccentricity (right) that produces the most powerful response at each cortical location. The stimuli covered 60° eccentricity.
4.3.2 Visual Field Maps of LO1 and LO2

Lateral occipital areas 1 (LO1) and 2 (LO2) were found in the human lateral occipital cortex between the dorsal part of visual area V3 and visual area V5/MT (Figure 4.2) [56]. The polar angle representation in LO1 extended from the lower vertical meridian (at the boundary with dorsal V3) through the horizontal to the upper vertical meridian (at the boundary with LO2) [56]. The polar angle representations in LO1 and LO2 are the mirror-reversals of each other. LO1 and LO2 overlap with the posterior portion of the object-selective lateral occipital complex and the kinetic occipital region [56, 58]. It is difficult to define the LO-1 and LO-2 border comes from lack of upper vertical meridian (3/11) or from the intermixed angle representations (2/11). The ability to identify these boundaries is consistent with a previous study that reports LO1 and LO2 is showed a pronounced lower visual field bias in which, more areas are devoted for in lower contralateral visual field (Figure 4.3). For the eccentricitic representation, LO1 and LO2 had representation for the central field, while had no representation for the peripheral field, especially the field out 20 degree of eccentricity (Figure 4.3).
4.3.3 The pRF Size in V1-V3 and LO1/2

Consisted with the maps visual field, the pRF size estimates from a 60° radius field of view are shown for eleven subjects in Figure 4.4. In V1-V3, there is a significant increase in pRF size as the increasing eccentricities. The quality of the pRF fit to the data is illustrated by the function of eccentricity (Figure 4.5). V1 and V2 had similar pRF size, and much smaller than V3. The present study, the checkboard ring moved from central peripheral field, with a speed of 3.75 degree per step. This design is not suite for estimated the cortex with small RF size, such as the V1. The small RF size will be enlarged after estimating.

In LO1 and LO2, significant increase in pRF size as the increasing eccentricities (Figure 4.4). There is a significant larger in pRF size at the same eccentricity comparing the responses in LO1 and LO2 with those in V1–V3 (Figure 4.4). LO1 and LO2 had pRF function only for the central field, but not for peripheral field (> 25 degree)
Figure 4.5. Averaged pRF size as a function of eccentricity for V1-V3 and LO1/2. (A) the pRF size for V1-V3. (B) the pRF size for LO1/2.

4.4 Discussion

In the present study, we estimated the visual field maps and pRF size maps to the wide-view field. These maps covered large region of visual areas, including the V1, V2, and V3, LO-1, LO-2, V3A/B, MT+, V6, IPS, hV4, VO-1, and VO-2 [13, 14, 17].

4.4.1 The Size of pRF in V1

In the medial visual cortices, The V1, V2, V3 hemifield maps can be identified by the fMRI measurements of the eccentric and angular representations [22, 81, 107, 117]. Consisted with phase-encoded retinotopic maps [35, 79, 80], the visual areas maps had large and continuous eccentricity map. From the central to the periphery, the location of the responding areas varied from the posterior to the anterior portions of the calcarine sulcus. V1 had representation of far peripheral stimuli, up to 60 eccentricities (Figure 4.2, 4.3).

We firstly reveal out the pRF maps to the peripheral field up to 60 degree eccentricity (Figure
4.5. In V1-V3, there is a significant increase in pRF size as the increasing eccentricities [49, 109]. The quality of the pRF fit to the data is illustrated by the function of eccentricity (Figure 4.6). V1 had much larger than the previous reported [49, 109]. Comparing with design of wandell’s reported [49, 109], the checkboard ring moved with a much higher speed, 3.75 degree per step, about 4 times of previous reports. This design is not suite for estimated the cortex with small RF size smaller than 4degree. In V2 and V3, the peripheral part of pRF size is consist with the report of macaque electrophysiological [118-120], but the central part of pRF size is much larger than previous studies including electrophysiological and human fMRI studies [49, 109]. Combining together, the pRF size in V1-V3 were not simple liner increasing, but had quite difference between central cortexes and peripheral cortexes.

![Figure 4.6](image)

**Figure 4.6.** A comparison between wide-view pRF (A) and previous studies (B)

### 4.4.2 The Visual Maps and pRF Maps in LO1 and LO2

The polar angle maps in LO1 and LO2 were consisted with the previous fMRI with central visual field [56]. The polar angle representations in LO1 and LO2 are the mirror-reversals of each other. LO1 and LO2 overlap with the posterior portion of the object-selective lateral occipital complex and the kinetic occipital region [56, 58]. LO1 and LO2 is showed a pronounced lower visual field bias in which, more areas are devoted for in lower contralateral visual field [56]. The rRF size is also consisted with the previous report [49, 109]. For the eccentricitic representation, LO1 and LO2 had representation for the central field, while had no representation for the peripheral field. The present reports shown that the higher visual areas (such as LO1 and LO2) had response limited to
the central visual field. However, from our result, the LO1 and LO2 and other higher visual field also had neural activities to the object at more peripheral position. We further proposed that the higher visual cortex is likely to be flexible for the eccentric presentation.

4.5 Conclusion

From our results, the visual areas maps and pRF maps were demonstrated with wide-view field, up to 60 degree eccentricity. The visual areas maps consisted with the previous reported basing on central visual field. The V1-V3 had larger visual areas maps, and LO1 and LO2 likely to have response to central field. More differently, the pRF size is likely consisted with the size of macaque, but not with the central result of human. Although, the present design successfully estimated the maps on the cortex with larger pRF size, and failed to estimate the maps for the cortex with smaller pRF size. A improving design should be carried in future.
Chapter 5

Hemispheric Asymmetries in the Retinotopy of Attention to Static Objects in the Human Visual Cortex

Summary

Retinotopic activity in the human visual cortex has been shown to be influenced by size of attentional window. When a subject is attending to a static object, the left hemisphere has a smaller attentional window than the right hemisphere. We further speculated that the human visual cortex has asymmetric retinotopy driven by attention to static objects. Here, using images of static objects and the retinotopic mapping task developed by Saygin and Sereno, we estimated the retinotopy driven by attention and visual stimulation in the human visual cortex. The early visual areas showed neural response to whole stimulus with a slight attentional enhancement, while the higher visual areas exhibited mainly attention-driven retinotopy. As predicted, in the higher visual areas, we found that the left hemisphere showed greater attention-driven retinotopic activity compared to the right hemisphere. The left hemisphere had a small attentional window and drove neurons with small receptive fields in visual areas, resulting in easy retinotopic activation, whereas the reverse was true for the right hemisphere. We proposed that the asymmetric retinotopic activity driven by attention to static object was possibly due to asymmetric attentional window for the attention to static object and weak influence of bottom-up attention.

Keywords– Retinotopy, Attention, Visual area, fMRI, Object
5.1 Background

A mosaic of orderly representations of the visual field exist in the human visual cortex; this phenomenon is called retinotopy and is one of the hallmarks of the mammalian visual systems [13, 17, 105, 121]. Retinotopy provides detailed information about the correspondence between the visual field and its cortical representation in individuals. Functional magnetic resonance imaging (fMRI) and phase-encoding retinotopic mapping has been used for over a decade to study cortical retinotopic maps in the human brain, and multiple retinotopic maps have been defined [12, 13, 22, 105]. The human visual cortex is thought to contains early visual areas (V1, V2 and V3), and other higher visual areas are located in the dorsal, lateral, and ventral visual cortex [13, 14, 17].

Attentional modulation in human visual areas has been demonstrated in several studies [18, 19, 54, 122, 123]. Attention might affect the retinotopic activity in the human visual cortex by two main features: the size of attentional window and enhancement of retinotopic activity. The attentional window is a visual region selected by attention for further detailed processing [124, 125]. The attentional window varies in size and may be under top-down control [126-129]. Indeed, the influence of the attentional window on retinotopic activity is comparable to that of the receptive field because the attentional window can selectively drive neurons in the visual cortex [130]. A small window of attention would cause a top-down attentional bias for neurons in the visual cortex with small receptive fields, while a large attentional window would result in a bias for neurons with large receptive fields [131, 132]. The size of the receptive fields greatly influences retinotopic activity [49, 53, 109]. A cortex with smaller receptive fields responds only to a narrow range of wedge positions, and the retinotopic response modulation is larger; conversely, a cortex with large receptive fields responds at least partially to the entire field, and the retinotopic response modulation is smaller [49, 109]. Thus, a small attentional window would show strong retinotopic activity, a larger attentional window would have weak retinotopic activity.

In addition, attention on the retinotopic stimuli increases retinotopic activity in the human visual cortex, especially in the higher visual areas [19-21, 122, 133, 134]. It has been noted that attention enhances neural activity to process visual information in human visual cortex [18, 54, 122, 123, 135]. Thus, attended retinotopic stimuli arouse greater neural activity than unattended retinotopic stimuli [20, 54, 122, 133]. Increased neural activity in response to retinotopic stimuli results in an improving reliability of the retinotopy [20].

Based on the enhancement of retinotopic activity by attention, Saygin and Sereno [122] presented a seminal experiment design and successfully estimated multiple retinotopic representation regions.
driven by attention and biological motion stimuli in the visual areas. They found that bilateral higher visual areas showed almost equal, mainly attention-driven retinotopy, while early visual areas showed mainly stimulus-driven retinotopy. Moreover, it appeared as though this retinotopic activity was not specifically driven by biological motion and was similarly activated by other coherent motion stimuli [122].

However, visual processing of static objects and motion are considered to be different; for example, compared with static objects, moving objects are advantageously processed for recognition, depth perception, and memory [136-140]. From functional neuroimaging studies, the lateral occipital complex and fusiform gyrus are functionally specialized for static objects, and cortical area MT+ is functionally specialized for motion [124, 141-144].

More importantly, attending static visual objects and motion might rely on different visual processing mechanisms that are related to the attentional window. Top-down control over visual selection can be accomplished by endogenously varying the size of attentional window [128, 129]. Attending to global versus local aspects of a static object’s shape rely on distinct cerebral hemispheres of the brain [145-152]. The right hemisphere was reported to have a larger attentional window compared to the left hemisphere [153-156]. Nevertheless, attending to global versus local aspects of motion produces no such hemispheric asymmetries [157, 158]. For motion stimuli, the size of the attentional window is likely to be similar between the bilateral hemispheres. These reports imply that attending a static object and attending a motion stimulus rely on asymmetric and symmetric attentional windows, respectively. As mentioned above, retinotopic activity in the human visual cortex is affected by the size of the attentional window. Therefore, we further speculated that rather than the nearly symmetric retinotopic activity, attention to static objects drives asymmetric retinotopic activity in the human visual areas.

In the present study, to address this issue, we used images of static objects (faces and houses) and the retinotopic mapping task developed by Saygin and Sereno [122] to estimate the retinotopy driven by attention and visual stimuli in the human visual cortex. As predicted, compared with biological motion, static objects produced quite different attention- and stimulus-driven retinotopic activity in the visual cortical areas. Most importantly, we found asymmetric retinotopic activity in the higher visual areas, which was mainly driven by attention, but not by stimulation with visual objects. In the early visual areas, the retinotopic activity from attention and stimuli were found to be weak, and slightly modulated by attention.
5.2 Materials and Methods

5.2.1 Subjects

Ten male subjects (aged 20 –26 years) participated in this study, which was approved by the Ethics Committee of the Hospital of Okayama University. All of the subjects were in good health with no history of psychiatric or neurological disorders and gave their informed written consent. The subjects had normal or corrected-to-normal visual acuity. Any scans exhibiting excessive head motion were excluded from additional analyses. There were 8 subjects who participated in the main face and house experiment. In addition, these subjects also participated in two more experiments: a canonical retinotopic mapping experiment and a localizer experiment for defining object-selective regions. Before starting experiments, the subjects were trained and familiarized with the stimuli and tasks outside the scanner.

5.2.2 Visual Display

The stimuli were generated on a computer using Presentation software (Neurobehavioral Systems, Albany, CA, USA). The stimuli were projected from an LED display projector located outside of the scanner room onto a translucent screen located at the end of the scanner bore. The subjects viewed the screen at a total path length of 30 cm through a mirror attached to the head coil. The screen subtended 16° of visual angle in both the horizontal and vertical dimensions. A trigger pulse from the scanner synchronized the beginning of the image acquisition to the onset of the stimulus presentation.

5.2.3 Experimental Stimuli

Two types of classic objects, i.e., faces and houses, were selected to examine the retinotopy driven by attention and static object visual stimulation. Twelve images of faces or houses and their corresponding scrambled images were used; each image was outlined with a colored circle (red, blue, green, yellow, light blue, purple; Figure 5.1 A). The images were randomly presented in each position. The composite stimulus was a circular area populated with 9 images arranged around a central fixation cross. The stimulus covered 16 ° of visual angle in diameter (Figure 5.1 B). In the inner ring, 3 images subtending 2 ° were centrally positioned with a distance of 2.8° from the central fixation cross; the angle between each image was 120 °. In the outer rings, 6 images subtending 3.6 ° were centrally positioned with a distance of 6.3 ° from the central fixation cross; the angle between each image was 60 °. These images aligned in three wedges. The three wedges
were 120° apart. The target wedge contained two face or house images in each condition. There were 2 additional “wedges” in the background that also contained the two images. The background contained images of faces (houses) or their scrambled images in the following experiment conditions.

For the retinotopic mapping stimuli, the images changed every 1 s with an interval of 0.2 s. The wedge rotated at steps of 30°, remaining at each position for 6 s before rotating to the next step, and one cycle lasted 72 s. The rotation always started with the retinotopic wedge at the upper vertical meridian of the visual field (12 o’clock). Each run contained six complete cycles of rotations, starting and ending with a 12-s baseline block (a grayscale screen with a central fixation point). For each subject, the rotation direction was clockwise in half of the runs and counter-clockwise in the other half.

5.2.4 Experimental Conditions

We used a phase-encoded retinotopic mapping and experimental design similar to that used by Saygin and Sereno [122], which allowed us to examine retinotopic activity primarily driven by stimuli or attention. Consistent with the previous designs, there were three conditions named: Attention + Stimulus, Attention, and Stimulus.

In the Attention + Stimulus condition, the target wedge contained face or house images, whereas the background contained a scrambled version of the same image (Figure 5.1 B, left column). The subjects were asked to fixate upon the central fixation cross, maintain their attention on the rotating target wedge, and monitor for trials in which the two images in the wedge were identical or not. When the two images were not identical, the subjects were asked to report by button pressing with their right hand. Thus, there was subtle stimulus and attention contrast between the target wedge and the background. Thus, retinotopic activity could be driven by static object stimulation and spatial attention of those objects.

In the Attention condition, a face or house image was presented in both the wedge and the background (Figure 5.1 B, middle column). As in the Attention + Stimulus condition, the subjects attended the target wedge while fixating on the central cross and were asked to respond when the two figures in the wedge were not identical. Because the object stimuli were consistent between the target wedge and the background, there was only attentional contrast between the target wedge and the background. Accordingly, this condition mainly evoked neural activity from attention to the objects in the target wedge. To help the subjects track the wedge, a color cue was used: instead of using a random color for each circular outline, a light blue outline was consistently presented in the
wedge. The circular outlines in the background were shown in another color.

In the Stimulus condition, the stimuli were identical to the Attention + Stimulus condition, in which face or house images appeared in the wedge and scrambled images were shown in the background (Figure 5.1 B, right column). The only difference was the fixation cross, which also changed color once per 1.2 s. The colors lasted for 0.4 s, with a 0.8 s interval. The color change of the fixation cross did not correlate with the stimulus rotating frequency. The subjects were asked to ignore all peripheral stimuli and carry out a one-back working memory task with the color of the fixation cross. This task requires sustained attention on the central cross; therefore, the peripheral stimuli were given minimal attention. Thus, there was only stimulus contrast between the target wedge and the background, and retinotopic activity was mainly evoked by the stimulation with static objects.

5.2.5 Retinotopic Mapping Experiments

To identify the retinotopic maps of the visual cortex, clockwise rotating wedge and expanding ring stimuli were employed [12, 22, 79, 81]. These stimulus apertures contained 100% contrast, black-and-white checkerboard patterns, were phase-reversing at a temporal frequency of 8 Hz, and had eccentricity ranging from 0.3° to 8°. The wedge stimulus had boundaries of 30° and was slowly rotated clockwise around a red fixation disk (approximately 0.2°) presented at the center of the stimulus. The wedge rotated at steps of 30° and remained at each position for 4 s before rotating to the next step. These expanding rings ranged in eccentricity from 0.3° to 8°, with six steps of rings with consistent widths. These expanding ring stimuli were moved in discrete steps (with a total of 6 steps) and remained at each position for 4 s before automatically expanding to the next position. All of the experiments employed passive viewing, and the subjects were required to maintain their gazes on a red fixation disk throughout the period of the scan. Eight complete cycles of rotations and expansions scans were conducted.

5.2.6 Localizer Experiments

The subjects participated in a localizer scan to define the area selective for faces and houses. The stimuli were 30 grayscale images of faces, houses and objects. The control nonsense patterns were 30 phase-scrambled images of the intact objects. Each scan began and ended with 12 s of rest and contained 16 stimulus blocks with a 10-s duration, with four blocks for each category separated by 10-s rest intervals. For each block of the localizer scan, 10 images from a stimulus class were centrally presented subtending 16°×16° (800 ms per image, with a 200-ms interstimulus interval).
Two or three images in each block were repeated, and the subjects were asked to perform a ‘one-back’ matching task while fixating on a central fixation point (approximately 1 °) presented in the center of each image.

5.2.7 Image Acquisition

Imaging was performed using a 3-Tesla MR scanner (Siemens Allegra, Erlangen, Germany). For the functional series, we continuously acquired images with 32 slices using a standard T2-weighted echo-planar imaging (EPI) sequence (TR = 2 s; TE = 35 ms; flip angle = 85°; 6 4 × 6 4 matrices; in-plane resolution: 3 × 3 mm; slice thickness: 3.5 mm with no gap). After the functional scans, high-resolution sagittal T1-weighted images were acquired using a magnetization-prepared rapid gradient echo sequence (MP-RAGE; TR = 1800 ms; TE = 2.3 ms; matrix 256 × 256 × 224; 1 mm isotropic voxel size) to obtain a 3D structural scan.

5.2.8 Data Analysis

We acquired 2 volumes of whole brain T1-weighted anatomical data for each subject. These images were averaged and re-sampled into a 1 × 1 × 1 mm resolution three-dimensional anatomical volume that was corrected for inhomogeneity and linearly transformed. We applied inhomogeneity correction and rotation to the ac-pc plane (FMRIB, University of Oxford, http://www.fmrib.ox.ac.uk/fsl/). The gray and white matter was segmented from the anatomical volume using custom software and hand-edited to minimize segmentation errors. Data analysis was restricted to the gray matter. The surface at the white/gray boundary was rendered as a smoothed three-dimensional surface using VTK software (http://www.vtk.org/). Data from all gray layers were mapped to this surface, and the maximum value was assigned to each triangle on the surface.

The functional data were processed and analyzed using the mrVista-Toolbox (Stanford University, Stanford, CA, USA; http://white.stanford.edu/software/). The data from each fMRI session were analyzed voxel-by-voxel with no spatial smoothing. The raw data were pre-processed in several steps. The data were slice-time corrected to compensate for the difference in the time of acquisition across slices within each 2-s frame. Head movements across scans were examined by comparing the mean value maps of the BOLD signals, and a motion correction algorithm was applied; most scans had minimal head motion. Motion artifacts within each scan were also corrected. All of the scans in the final analysis had less than one voxel of motion.
Figure 5.1. The experimental stimuli. (A) A sample of the face and house images and the scrambled image of each. The images were shown with a colored circular outline. (B) A sample of the stimuli used in the retinotopic experiment for object attention. The target wedge contained face (upper row) or house (lower row) images and was positioned at one o’clock in each condition. Here, the wedge has been marked with dashed lines for ease of identification; in the actual stimuli, no such marking was present. Note that although two image were in the target wedge, there were 2 additional such “wedges” that also contained the two scrambled images (120° apart, shown here at approximately 5 o’clock and 9 o’clock). In the Attention + Stimulus condition (left column), the wedge contained face and house images, and the background contained scrambled images. In the Attention condition (middle column), faces and houses were displayed in the wedge and in the background. The images in the wedge were presented with an identically colored circle (here, light blue), a subtle cue to help the subjects determine to which wedge they needed to attend. The visual stimuli in the Stimulus condition (right column) were identical to the Attention + Stimulus condition, except the fixation cross also changed color once every 1.2 seconds. The colors lasted for 0.4 s with a 0.8 s interval. The color of the fixation cross does not correlate with the stimulus frequency. The two rows of sample stimuli also show the image positions of the two adjacent rotating steps.
For retinotopic data of object, we combined data from the “clockwise rotation” and “counter-clockwise rotation” scans by time shifting the time series at each voxel to remove the hemodynamic delay [159]. We then time-reversed the counter-clockwise scans and averaged across the time-shifted and time-reversed scans, separately for each subject, across the scanning sessions. Thus, the resulting mean time series reflected the timing of clockwise scans, in which targets progressed through the right hemifield in the first part of each cycle and through the left hemifield field in the second half of the cycle. For the retinotopic mapping data, we only collected clockwise rotating scans and expanding scans. The time series of these scans were subjected to time shifting to remove the hemodynamic delay [159].

We used cyclic stimulation protocols in the retinotopic experiments of object and retinotopic mapping experiments, and a fast Fourier transform (FFT) procedure was used to estimate the retinotopic activity in human visual areas [12, 22, 81]. Briefly, for each voxel, the FFT is computed and a coherency value is determined by taking the ratio between the power at the stimulation frequency and the summed power across all frequencies. The retinotopic location eliciting activity in each voxel was then determined from the phase value at the stimulus frequency, and only voxels with a powerful response at a coherence ≥ 0.25 were selected. This is a standard technique for retinotopic mapping that we choose because it has proven to be simple, robust, and sensitive.

For the localizer data analysis, the data analysis was performed with a general linear model (GLM). Square-wave functions matching the time course for each condition were convolved with a standard hemodynamic response model [159]. The data were not spatially smoothed. Contrast maps were computed as voxel-wise t-tests between the weights of the predictors of the relevant experimental conditions and the voxels that passed the threshold (p < 10^{-4}, uncorrected). Face-selective areas, the fusiform face area (FFA) and occipital face area (OFA), were identified using the contrast of houses > faces, objects, and phase-scrambled images [16, 38]. House-selective areas, the parahippocampal place areas (PPA) and transverse occipital sulcus (TOS), were identified using the contrast of houses > faces, objects, and phase-scrambled images [16, 39].

5.3 Results

5.3.1 Behavioral Performance

In the Attention + Stimulus and Attention conditions, the subjects maintained their attention on the rotating target wedge; while in the Stimulus condition, the subjects’ attention was directed away from the retinotopic stimuli. For the three conditions, the behavioral performance results of the
clockwise and counter clockwise runs were averaged because no significant difference was observed between the two rotating directions [all: F (1, 9) < 0.5, p > 0.5]. Table 1 shows the mean response times and accuracy. We ran a 2 × 3 repeated-measures analysis of variance (ANOVA) with category (faces or houses) and condition (Attention + Stimulus, Attention, Stimulus) as factors for accuracy and response time. For accuracy, there were no significant main effects of factor category [F (1, 9) = 2.56, p = 0.14] or condition [F (2, 18) = 0.44, p = 0.65]. The accuracy results indicate that the task performance dealing with faces and houses in each condition were well balanced. However, for the mean response time, there were significant main effects of factor category [F (1, 9) = 5.35, p = 0.05] and condition [F (2, 18) = 120, p < 0.001]. Subjects were slower to perform face discrimination than house discrimination, a result that is likely due to face discrimination being more difficult than house discrimination. A pairwise comparison showed that the Attention + Stimulus condition and the Attention condition had no difference in response times (p = 0.6), but were both slower than the stimulus condition (both, p < 0.001). The response time results reflect that the subjects performed the wedge attention task with similar difficulty in the Attention + Stimulus and Attention condition, but found that the Stimulus condition was much easier.

Table 5.1. The behavioral performance in the three conditions with faces and houses

<table>
<thead>
<tr>
<th>Condition</th>
<th>Percent Accuracy (%)</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Faces</td>
<td>Houses</td>
<td>Faces</td>
<td>Houses</td>
</tr>
<tr>
<td>Attention + Stimulus</td>
<td>80 ±4</td>
<td>90 ±3</td>
<td>722 ±18</td>
<td>667 ±15</td>
</tr>
<tr>
<td>attention</td>
<td>82 ±3</td>
<td>86 ±4</td>
<td>719 ±19</td>
<td>669 ±17</td>
</tr>
<tr>
<td>stimulus</td>
<td>81 ±4</td>
<td>85 ±4</td>
<td>547 ±25</td>
<td>529 ±22</td>
</tr>
</tbody>
</table>

Values are the mean ±SEM
Figure 5.2. Retinotopic activity in retinotopic visual areas produced by checkerboard, face, and house stimulation in the Attention + Stimulus condition. Flattened surface reconstructions of the visual cortex of one representative subject (Sub 5). (A) Retinotopy induced by checkerboards. (B, C) Retinotopy driven by faces (B) and houses (C) in the Attention + Stimulus condition. The area boundaries were determined using standard retinotopic maps with checkerboards (Figure 5.2 A). For the polar angle component, the upper visual field is denoted in blue, the horizontal meridian in green,
and the lower visual field in red. The upper and lower/vertical meridian are indicated with dotted and dashed lines, respectively, and the horizontal meridian is indicated with a solid line; white circles, approximate location of foveal representation in V1-V3. CaS, calcarine sulcus; IPS intraparietal sulcus, ITS, inferior temporal sulcus; OTS, Occipitotemporal sulcus.

5.3.2 Retinotopy in the Attention + Stimulus Condition

In the Attention + Stimulus condition, in which the rotating target wedge contained static objects (face or house) and the background was filled with scrambled images, the subjects were asked to attend to the target wedge. Retinotopic activity in the human visual cortex that was driven by attention and stimuli was estimated. Similar retinotopic activity was found in 8 subjects for two of the static object categories (faces and houses). Individual activation of retinotopic activity in the visual cortex is shown overlaid on flattened surface reconstructions (Figures 5.2, 5.3). Retinotopic activity induced by faces and houses in the Attention + Stimulus condition (Figures 5.2 B-C, 5.3 A, 5.4 A) was similar compared with the retinotopic activity driven by checkerboards (Figure 5.2 A). The upper visual field is denoted in blue, the horizontal meridian in green, and the lower visual field in red. The boundaries of the retinotopic maps were determined using checkerboards (Figure 5.2 A).

The early visual areas included V1, V2, and V3; the retinotopic higher visual areas included V3A/B, LO-1, LO-2, hV4, VO-1, and VO-2 [13, 14, 17].

In contrast with the retinotopic activity induced by checkerboards, the retinotopic activity driven by static objects was very weak in the bilateral early visual areas, especially in V1 (Figures 5.2 A, 2B-2C, 5.3). From V1 to V3, the area of retinotopic activation became stronger. Notably, there were 3 wedges in the inner positions and 6 images in the outer positions. We further analyzed retinotopic data of object with 3 or 6 times the base rotation frequency and found retinotopic activity mainly in the early visual areas (Figure 5.5). The retinotopic activity that was 3 times the base rotation frequency was more posterior than the retinotopic activity that was 6 times the base rotation frequency. Similar retinotopy was found for the two static object categories: faces and houses. The early visual areas had nearly equally neural activities to the entire stimulus in the field.

In the retinotopic higher visual areas, similar retinotopy was found for the two object categories: faces and houses. The retinotopic activity driven by static objects (Figures 5.2 B-C, 5.3 A, 5.4 A) and the activity driven by checkerboards (Figure 5.2 A) were similar in phase but not in intensity. The checkerboard stimulus induced similar retinotopic activity between the bilateral hemispheres...
while the face and house stimuli produced stronger retinotopic activity in the left hemisphere compared to the right (Figures 5.2 B-C, 5.3 A, 5.4 A). In the left hemisphere, retinotopic activity covered regions of the temporal, occipital and parietal cortex. Furthermore, we consistently found six distinct topographically organized cortical areas including V3A/B, LO-1, LO-2, hV4, VO-1, and VO-2 in each subject [13, 56, 105, 160]. Some of the subjects had intensive retinotopic activity extending into the intraparietal sulcus (IPS) motion-selective areas (MT+) and other non-retinotopic regions of the lateral and ventral visual cortex, for example Sub 8 in Figure 5.4 A. However, in the right hemisphere, the wedges of faces and houses extracted much less retinotopic activity compared to the left visual cortex in these retinotopic visual areas: V3A/B, LO-1, LO-2, hV4, VO-1, and VO-2 (Figures 5.2 B-C, 5.3 A, 5.4 A).

5.3.3 Retinotopy in the Attention and Stimulus Conditions

The retinotopic activity results in the Attention + Stimulus condition suggested that the activity driven by static objects may be driven by visual stimuli and (or) attention [122, 161]. Further experimental conditions, the Attention and Stimulus conditions, allowed us to identify which patterns of activation were primarily driven by attention or stimulus.

In the Attention condition, face or house images were presented in both the wedge and in the background, and the subjects were asked to attend to the target wedge. Retinotopic activity driven by attention in the human visual cortex was estimated. Generally, for faces and house, the retinotopic activity in the Attention condition was similar as compared to that observed in the Attention + Stimulus condition (Figures 5.3 B, 5.4 B). In the bilateral early visual cortex, we also found weaker retinotopic activity (Figures 5.3 B, 5.4 B) and intense retinotopic activation with 3 or 6 times the base rotation frequency (Figure 5.5 B). In the retinotopic higher visual areas, there was significant retinotopic activity in the left visual areas and much weaker activation in the right visual areas.

In the Stimulus condition, the presented stimuli were identical to the Attention + Stimulus condition. The only difference was that the subject ignored all of the peripheral stimuli and carried out a one-back working memory task with the color of the fixation cross. This task requires sustained attention on the central cross and resulted in minimal attention on the peripheral stimuli. This condition aims to induce stimulus-driven retinotopic activity. In the Stimulus condition (Figures 5.3 C, 5.4 C), the faces and houses evoked weak or no retinotopic activity in the bilateral visual areas, including the early visual areas and the retinotopic higher visual areas. In addition, we identified retinotopic activity with 3 or 6 times the base rotation frequency in the early visual areas.
Figure 5.3. Retinotopic activity driven by faces in the three conditions. Flattened surface reconstructions of the visual cortex of one representative subject (Sub 3). (A) The Attention + Stimulus condition. (B) The Attention condition. (C) The Stimulus condition. The conventions are the same as in Figure 5.2.
Figure 5.4. Retinotopic activity driven by house stimuli in the three conditions. Flattened surface reconstructions of the visual cortex of one representative subject (Sub 8). (A) The Attention + Stimulus condition. (B) The Attention condition. (C) The Stimulus condition. The conventions are the same as in Figure 5.2.
Figure 5.5. Maps of retinotopic activity with 3 or 6 times the base rotation frequency in the early visual areas. Flattened surface reconstructions of the visual cortex of one subject (Sub 3). (A and B) Maps of retinotopic activity with 3 times the base rotation frequency in the early visual areas (V1-V3). As shown by the spatial position encoded with color, the early visual cortex also had intense retinotopic activity driven by the three wedges 120° apart. This activity is consistent with the results showing a percent signal change to the target and background wedges. (C and D) Retinotopic activity with 6 times the base rotation frequency in the early visual areas (V1-V3). Because of the smaller cortical magnification factor and the larger receptive fields in the peripheral visual field of areas higher areas (V2 and V3), it is difficult to use the blood oxygenation level dependency (BOLD) activity to form variances of 6 times the base rotation frequency; thus, we found much weaker retinotopic activity in V1. The activity is more anterior than that of 3 times the base rotation frequency, which is consistent with the retinotopic activity of the visual areas. The voxels with a powerful response at a coherence ≥ 0.25 are colored.
Figure 5.6. The mean area of retinotopic activity in the retinotopic visual areas. (A) The mean area of the face and house activation in the Attention + Stimulus condition. (B) The mean area of the face and house activation in the Attention condition. (C) The mean area of the face and house activation in the Stimulus condition. (D) The mean area of the retinotopic activity induced by checkerboard stimulation.
5.3.4 Mean Cortical Areas of Retinotopy

We measured the cortical areas of retinotopic activity in the visual areas (V1-V3, V3A/B, LO-1, LO-2, hV4, VO-1, and VO-2) for the two object categories in the three conditions. The mean areas of the eight subjects are shown in Figure 5.6. The area results were consistent with the individual retinotopic maps (Figures 5.2-5.4).

In the early visual areas, the mean area of retinotopic activity was examined with a 4-way (2 × 3 × 3 × 2) repeated-measures (ANOVA), with hemisphere (left and right), region (V1-V3), condition (Attention + Stimulus, Attention, Stimulus) and category (face and house) as factors. There were significant main effects of region [F (2, 6) = 26.73 p = 0.001] and condition [F (2, 6) = 26.25 p < 0.001], but no effects of hemisphere [F (1, 7) = 0.93 p = 0.37] or category [F (1, 7) = 1.58 p = 0.25]. In addition, there was a significant interaction between area and condition [F (4, 28) = 5.95 p = 0.02]. Bonferroni’s pairwise comparison revealed that the area in the Attention + Stimulus condition and the Attention condition were not different (p = 0.16), but the area in these two conditions was larger compared to the Stimulus condition (p < 0.005).

In addition, to compare with the area of retinotopic activity induced by checkerboard, we ran 2 × 3 repeated-measures ANOVAs with category (checkerboards and objects) and region (V1-V3) as factors for the three conditions, two static objects and two hemispheres. We found that the area of the face- or house-induced retinotopic activity was significantly smaller than the area resulting from checkerboard stimulation [all: F (1, 7) ≥ 276.5 p < 0.0001]. There was a significant interaction between stimuli and area [all: F (2, 14) = 15.2, p < 0.001].

To generally compare cortex areas in the retinotopic higher visual areas, we ran a 4-way (2 × 6 × 3× 2) repeated-measures ANOVA with hemisphere (left and right), region (V3A/B, LO-1, LO-2, hV4, VO-1, and VO-2), condition (Attention + Stimulus, Attention, and Stimulus) and category (face and house) as factors. We found that the area in the retinotopic higher visual areas had significant main effects of hemisphere [F (1, 7) = 15.21 p = 0.006], region [F (5, 35) = 7.12, p = 0.007] and condition [F (2, 14) = 46.87, p < 0.001], but no main effect of category [F (1, 7) = 0.286, p = 0.61]. Furthermore, we also found a significant interaction between hemisphere and condition [F (2, 14) = 5.51, p = 0.44] and an interaction between hemisphere and region [F (5, 35) = 2.97, p = 0.024]. According to Bonferroni’s pairwise comparison, the left hemisphere had a significantly larger mappings area compared to the right hemisphere, mainly in 3A/B, LO-1, LO-2, hV4, VO-1, and VO-2 for faces and houses in the Attention + Stimulus and Attention conditions; significant differences (all: p < 0.05) are indicated with an asterisk in Figures 5.6A, 6B. However, we did not
find a significant difference between the two hemispheres in the Stimulus condition (all: p > 0.16). These statistical results imply that asymmetric retinotopy is limited in the Attention + Stimulus and Attention conditions. Furthermore, the area of retinotopic activation in the Attention + Stimulus and Attention conditions was not different (p ≥ 0.36), but the area in these conditions was much larger than that of the Stimulus condition (p < 0.0001).

Compared with the retinotopic activity area induced by checkerboard stimulation, the area resulting from the face or house stimuli was smaller, especially for the right hemisphere and in the Stimulus condition. For the three conditions, two static objects and two hemispheres, a two-way (2 × 6) repeated-measures ANOVAs with category (checkerboards, faces or houses) and region (V3A/B, LO-1, LO-2, hV4, VO-1, and VO-2) as factors revealed that the area was significantly smaller compared to the area induced by checkerboard stimulation [all: F (1, 7) ≥ 21.65 p ≤ 0.002]. In addition, a two-way (2 × 6) repeated-measures ANOVA with hemisphere (left and right) and region as factors revealed no significant difference between the two hemispheres [F (1, 7) = 0.76 p = 0.42].

5.3.5 ROI Analysis of Retinotopic Activity

To further examine the differences between each condition and hemisphere, we examined the neural response amplitudes to wedge of faces and houses in V1, LO-1 and VO-1. ROIs were represented by disks with a radius of 3 mm that were placed on the surface near the horizontal meridian in V1 (denoted by the light blue disk), LO-1 (denoted by the purple disk), and VO-1 (denoted by the purple disk) (Figure 5.7A). The locations of these ROIs were determined by the retinotopic maps from checkerboard stimulation, including retinotopic maps of the wedge and ring. In each ROI, object, and condition, the six cycles of neural activity were averaged into one cycle, which lasted 72 s. The mean percent change in the signal of the 8 subjects is shown in Figures 5.7B-5.7D. The light yellow bars show the time of wedge duration at the right horizontal meridian, and the light pink bars show the time wedge duration at the right horizontal meridian. We averaged the percent change in signal to these horizontal wedges, while accounting for a hemodynamic delay of 6 s [159], and further compared the neural activity in the left ROIs to the right horizontal wedges with those in the right ROIs to the left horizontal wedges.
Figure 5.7. The mean neural response amplitude to faces and houses in the three conditions. (A) The location of V1, LO-1, and VO-1 ROIs in the cortex. These ROIs were adjacent to the representation of the horizontal meridian. (B-D) The mean neural response amplitude to faces and houses within the ROIs of V1, LO-1, and VO-1 in the Attention + Stimulus condition (B), Attention
condition (C), and Stimulus condition (D). The light red columns indicate when the wedge appeared in the right horizontal meridian, and light blue columns indicate when the wedge was over the left horizontal meridian. In V1, the neural activity evoked by faces and houses has three peaks, which are consistent with the inner image numbers. In left LO-1 and VO-1, the neural activity evoked by faces and houses has one peak, while in right LO-1 and VO-1, the neural activity evoked by faces and houses has no obvious peak.

Generally, the V1 neural activity evoked by faces or houses in the three conditions had three obvious peaks (Figure 5.7), which was consistent with the number of wedges. In the more anterior cortical region that was responsive to the outer images (Figure 5.5), we found six peaks of neural activity (results not shown). Although the early visual areas had neural activities to the entire stimulus in the field, we noticed the early visual areas exhibited slight attentional enhancement. The neural activity driven by the target wedges was greater than in the other two background wedges (p < 0.05) in the Attention + Stimulus and Attention conditions. However, the neural activity induced by the target wedges was equal to that of the two background wedges when the subject paid no attention to the peripheral stimuli in the Stimulus condition, (p ≥ 0.25). Furthermore, we found no difference in neural activity between left and right V1 (paired t-test: t7 ≤ 1.72, p ≥ 0.12).

In the retinotopic higher visual areas, neural activities evoked by the target wedge of faces or houses in the Attention + Stimulus and Attention conditions had one peak in the ROIs of left LO-1 and VO-1 and no obvious peak in the ROIs of right LO-1 and VO-1. The neural activity in left LO-1 and VO-1 were significantly larger than that of right LO-1 and VO-1 (all: paired t-test: t7 ≥ 2.4, p ≤ 0.05). However, in the Stimulus condition, we found no obvious peaks of neural activity in bilateral LO-1 and VO-1. The neural activity in LO-1 and VO-1 were no different between left and right (paired t-test: t7 ≤ 0.85, p ≥ 0.4).

5.3.6 Retinotopy in Object-selective Regions

The lateral and ventral visual cortex is known to contain multiple visual areas activated by several categories of object stimuli [16, 38, 39]. As shown in Figure 5.8, the face-selective areas, including FFA and OFA, were defined by the contrast of faces > houses, common objects, and phase-scrambled images [16, 38]. The houses-selective areas, including PPA and TOS, were defined by houses > faces, common objects, and phase-scrambled images [16, 39]. Consistent with the retinotopic activity in the retinotopic higher visual areas (Figures 5.2-5.5), we found retinotopic activity in the face- and house- selective areas in the Attention + Stimulus condition (Figure 5.8),
especially in areas OFA and TOS that are located in the lateral visual field. The phase-encoding mappings in these object-selective regions also exhibited a difference between the two hemispheres. Similar retinotopic activity was also found in the Attention condition, but much weaker retinotopic activity was observed in the Stimulus condition.

Figure 5.8. Retinotopic activity induced by faces and houses in the Attention + Stimulus condition in object-selective regions. Flattened surface reconstructions of the visual cortex of two representative subjects (Sub 8). (A) Retinotopic activity driven by faces. (B) Retinotopic activity induced by houses. The orange lines show the face-selective areas (FFA and OFA). The pink lines show the house-selective areas (PPA and TOS). The other conventions are the same as in Figures 5, 3.
Figure 5.9. The mean area of retinotopic activity in the object-selective regions. (A) The mean area of the activity driven by faces and houses in the Attention + Stimulus condition. (B) The mean area of the face- and house-induced activation in the Attention condition. (C) The mean area driven by faces and houses in the Stimulus condition. (D) The mean area of the object-selective regions.
We measured the area of retinotopic activation in these object-selective regions in the three conditions (Figure 5.9). A 4-way (2 × 4 × 3 × 2) repeated-measures ANOVA with hemisphere (left and right), region (FFA, PPA, OFA, TOS), condition (Attention + Stimulus, Attention, and Stimulus), and category (face and house) as factors revealed significant main effects of hemisphere \[ F(1, 7) = 22.9, p = 0.002 \] and condition \[ F(2, 14) = 48.26, p < 0.0001 \], but no main effect of category \[ F(1, 7) = 1.67, p = 0.24 \]. Bonferroni’s pairwise comparison revealed that maps on the left hemisphere were significantly larger than the right hemisphere, mainly in FFA, OFA, and TOS for faces and houses in the Attention + Stimulus and Attention conditions (p < 0.05, indicated by asterisks in Figure 5.9).

We ran two-way (2 × 4) repeated-measures ANOVAs with category (ROI size and faces or houses) and object-selective regions (FFA, PPA, OFA, TOS) as factors, and we found that the area of retinotopic activity in each hemisphere, visual area, condition, and object was significantly smaller than the area of the object-selective ROIs, especially in the right hemisphere and in the Stimulus condition \[ F(1, 7) ≥ 7.65, p ≤ 0.05 \]. Moreover, to compare the bilateral object-selective regions, we used a 2-way (2 × 4) repeated-measures ANOVA with hemisphere (left and right) and region (FFA, PPA, OFA, TOS) as factors, and we found no difference between the bilateral hemispheres \[ F(1, 7) = 2.2, p < 0.18 \].

5.4 Discussion

Using two categories of static objects (faces and houses) and the retinotopic mapping task developed by Saygin and Sereno [122], we further estimated retinotopic activity during spatial attention to two categories of classic objects in human visual areas. Early visual areas had weak or no retinotopic activity, and showed neural activities to entire stimulus in field with a slight attentional enhancement. Most importantly, we found that asymmetric retinotopic activity is mainly driven by attention in higher visual areas, including the retinotopic higher visual areas and object-selective regions. The asymmetric retinotopic was quite different from the retinotopic activationes of induced by biological motion [122].

5.4.1 Hemispherical Asymmetries in Retinotopic Activity Driven by Attention

When the subjects attended the target wedge in the Attention + Stimulus and Attention conditions, we found that the retinotopic activity induced by static objects exhibited hemispherical asymmetries in the higher visual areas, including the retinotopic higher visual areas (V3A/B, LO-1, LO-2, hV4, VO-1, and VO-2) and the object-selective regions FFA, PPA, OFA, and TOS (Figures 5.2-5.5, 5.8,
However, in the Stimulus condition, we found that retinotopic responses in the bilateral higher visual areas was absent or reduced. These hemispherical asymmetries in retinotopic activation are mainly driven by attention to the visual object, not by stimulation with the visual objects themselves.

In some studies using static object images, such as faces, the standard retinotopic method revealed that the bilateral visual cortex shows intense retinotopic activity [31, 162]. Because both stimuli and attention are always at the same position during retinotopic tasks, retinotopic activity in the visual areas might be driven by two components of visual stimuli: one is the stimulation of the visual stimulus, and the other is the attention to the visual stimulus [122]. In particular, we found that the left higher visual cortex had much more intense retinotopic activation than the right higher visual area, an effect that was mainly driven by attention. The present results imply that only the spatial attention to objects contributes to asymmetric retinotopic activity in the higher visual areas.

However, while comparing retinotopy in the visual cortex, it was difficult to determine the cause of the asymmetric retinotopic activation. We further analyzed the neural activity in the bilateral LO-1 and VO-1. The neural activity in left LO-1 and VO-1 had one obvious peak, which corresponded to the target wedge, while the neural activity in right LO-1 and VO-1 had no obvious peak (Figure 5.7). The neural activity in left LO-1 and VO-1 were much larger compared to that of right LO-1 and VO-1. Our results were consistent with previous reports on the size of the attentional window. When subjects attend to static objects, the left hemisphere is likely to have a smaller attentional window than the right hemisphere [153-156, 163]. The size of the attentional window plays an important role in visual processing [130, 164-166]. Although the subjects were asked to pay attention to the target wedge during the scanning, the small attentional window in the left hemisphere would cause a top-down attentional bias for neurons with small receptive fields in the visual cortex; conversely, the large attentional window in the right hemisphere would cause a top-down attentional bias for neurons with large receptive fields in the visual cortex [131, 132]. Furthermore, receptive field size influences retinotopic activity in the visual cortex [49, 53, 109]. The regions of cortex with smaller receptive fields respond only to a narrow range of wedge positions, and the retinotopic response modulation is larger, while areas with large receptive fields respond at least partially to the entire field, and the retinotopic response modulation is smaller [49, 109]. Therefore, when attending to static objects, the left hemisphere with its small attentional window would show strong retinotopic activation, while the right hemisphere, possessing a large attentional window, would have weak retinotopic activation.
5.4.2 Different Retinotopic Activity between Static Object and Biological Motion

Using static objects, retinotopic activation driven by attention exhibited hemispherical asymmetries (Figures 5.2-5.4, 5.6, 5.8, 5.9). However, using biological motion stimuli, attention-driven bilateral retinotopic activation was found in the higher visual areas, including the motion areas (MT+) and the traditional retinotopic areas [122]. One explanation is that attention to motion does not have such hemispherical asymmetries for the attentional window as in the static object condition [158]. The bilateral visual areas, having almost equally sized attentional windows, show similar neural activity to the attended wedge and result in similar retinotopic activation. However, another explanation is that retinotopic activity is influenced by bottom-up (stimuli-based) attention. To visually process multiple objects, the visual cortex can be modulated by both bottom-up (stimulus-driven) and top-down (voluntary) control, such as selective attention [129, 167-171]. For example, observers employ bottom-up attention to extract essential visual cues from biological motion (Saenz, Buracas et al. 2002; Maunsell and Treue 2006; Tyler and Grossman 2011). Compared to static objects, coherent motion is likely to have much more bottom-up attentional modulation in addition to top-down attention [129, 172, 173]. The bottom-up attention of biological motion may restrict the large attentional windows of the right hemisphere and induce retinotopic activity equal to that of the left hemisphere. However, attention to static objects is likely to not have such bottom-up attention, or at least the influence is not strong enough to affect retinotopic activity. Basing on both explanations, asymmetric retinotopy induced by static object might because of asymmetric size of attentional window and weak bottom-up attention effect; nearly symmetric retinotopy induced by biological motion was possibly due to symmetric size of attentional window and weak bottom-up attention effect.

In the Stimulus condition, where there was an absence of attention to the peripheral stimuli, we found that retinotopic activity to the static object was reduced or non-existent (Figure 5.6). In contrast, retinotopic activity to biological motion was found mainly in the motion-selective areas (MT+) [122]. We thought that retinotopic activity induced by biological motion might be driven by the bottom-up attention mentioned above (Saenz, Buracas et al. 2002; Maunsell and Treue 2006; Tyler and Grossman 2011). With bottom-up attention, biological motion might evoke retinotopic activity in the higher visual areas; in contrast, with absent or diminished bottom-up attention, static objects might induce little to no retinotopic activities.

5.4.3 Common Attentional Modulation in the Higher Visual Areas

Although static object and biological motion stimuli produced quite different retinotopic activity
in the same tasks, we also confirmed common attentional modulation driven by static objects and biological motion. When the subjects paid attention to the target wedge for both static object and biological motion stimuli, spatial attention drove intense retinotopic activity in the lateral and ventral visual areas as well as the intraparietal sulcus, [122]. The retinotopic activity became weaker, especially for static objects, when the subjects did not attend to the peripheral stimuli. In the higher visual areas, spatial attention contributed mainly to the modulation of retinotopic activity while the stimulus provided a minimal contribution. Moreover, the retinotopic activity evoked by faces, houses and biological motion was likely to encompass common areas in the higher visual regions, including V3A/B, LO1, LO2, hV4, VO1, and VO2. Furthermore, our results show that both faces and houses produced similar retinotopic activity in object-selective regions, for example OFA and TOS, activity that occasionally expanded along the lateral visual cortex into the motion-selective areas (MT+). Correspondingly, biological motion also produced retinotopic activity in FFA [122].

### 5.4.4 Retinotopy in the Early Visual Areas

In all three conditions, both faces and houses induced weakly retinotopic activity, especially in V1 (Figures 5.2-5.5), which is consistent with the results from biological motion stimulation in the Attention condition. The present signal changes in V1 had three obvious peaks in each condition (Figure 5.7). Additionally, we further analyzed retinotopic data of static object with 3 or 6 times the base rotation frequency, and intense retinotopic activity was found in the early visual areas (Figure 5.5). Human fMRI studies in the early visual cortex have shown no selective neural activation to images of static objects compared with their scrambled pattern [16, 38, 39]. These results implied that the early visual areas respond not only to the image in the target wedge but also to the other image in the background, confirming that the early visual areas are mainly driven by stimuli.

Moreover, we noticed significant attentional enhancement of the neural response amplitude to the target wedge compared with the other two wedges (p < 0.05) when the subjects attended the target wedge (Figure 5.7). In contrast, the target wedges and the two other wedges induced neural responses with equal amplitude (p ≥ 0.25) when the subjects paid no attention to the peripheral stimuli in the Stimulus condition. The present data suggest that neural activation in the early visual areas reflects modulation by attention, albeit weaker than that of the higher areas [174, 175].

### 5.5 Conclusion

In the present study, we used static objects and the retinotopic mapping task estimated the retinotopy in visual cortical areas driven by attention and visual stimulation with static objects.
Early visual areas had weak or no retinotopic activity, and showed neural activities to entire stimulus in field with a slight attentional modulation, while the higher visual areas were mainly driven by attention, not by visual object stimulation. In the higher visual areas, intense retinotopic activity was found in the left hemisphere, while much weaker activity was observed in the right hemisphere. The left hemisphere has a small attentional window, which drives neurons with small receptive fields in the visual areas and results in easy retinotopic activation. We further proposed that the asymmetric retinotopic activity driven by attention to static object was possibly due to asymmetric attentional window for static object attention and weak influence of bottom-up attention.
Chapter 6

General Conclusion and Future Challenges

6.1 Summaries of Important Findings

1) We successfully developed a novel method for the systematic presentation of high-resolution, wide-view images in the MRI environment. All visual research programs can adopt this method or system for the study of peripheral vision. The convention adopted in the present paper is suited for most MRI scanner head coils. The visual field size can be increased by using a larger hemispheric screen, and the image resolution can be increased by using a higher resolution projector. Moreover, we plan to continue the study to improve the optical properties and convenience of the system.

2) From our results, the neural response amplitudes and the values of RRCPs demonstrated the significant differences for each position in V1, FFA, and PPA. Measuring the RRV1s, we found that the FFA and PPA process the visual information from V1 using different neural processing strategies. The first was the dimension of eccentricity, which the values of RRV1s at the central positions were smaller than those at the peripheral positions in FFA at the contralateral horizontal positions and upper vertical positions, and in PPA only at the upper vertical positions. The second was the dimension of meridian, which the RRV1s observed at the upper vertical positions were greater than those at the lower vertical positions. The third was the dimension of region, which the RRV1s in FFA were greater than those in the PPA, and the significantly increasing trends of RRV1s were observed in FFA. The findings reported here suggested that the ventral category-selective areas develop specific modes to process stimuli located at different positions, depending on the retinal locations of where the object is typically observed in daily life. Taken together, these different neural processing strategies of the ventral visual cortex might be shaped by experience.

3) From our results, the visual areas maps and pRF maps were demonstrated with wide-view field, up to 60 degree eccentricity. The visual areas maps consisted with the previous reported basing on central visual field. The V1-V3 had larger visual areas maps, and LO1 and LO2 likely to have response to central field. More differently, the pRF size is likely consisted with the size of macaque, but not with the central result of human. Although, the present design successfully estimated the maps on the cortex with larger pRF size, and failed to estimate the maps for the...
cortex with smaller pRF size. A improving design should be carried in future.

4) In the present study, we used static objects and the retinotopic mapping task estimated the retinotopy in visual cortical areas driven by attention and visual stimulation with static objects. Early visual areas had weak or no retinotopic activity, and showed neural activities to entire stimulus in field with a slight attentional modulation, while the higher visual areas were mainly driven by attention, not by visual object stimulation. In the higher visual areas, intense retinotopic activity was found in the left hemisphere, while much weaker activity was observed in the right hemisphere. The left hemisphere has a small attentional window, which drives neurons with small receptive fields in the visual areas and results in easy retinotopic activation. We further proposed that the asymmetric retinotopic activity driven by attention to static object was possibly due to asymmetric attentional window for static object attention and weak influence of bottom-up attention.

6.2 Future Challenges

According to the complexity of the neural mechanisms of visual system, future studies will focus on the peripheral object processing in human visual cortex, and the attention effect on the human visual cortex. For example, we will exam the eccentricitic function and the pRF maps in object-selective areas the attention modulation in human visual areas, and so on. Through studying the subsystems of visual cortex integration, we hope to clarify the mechanism for object perception, including the objects in central and peripheral field.
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Appendix

Appendix A — A simple introduction to functional magnetic resonance imaging

A.1 What is fMRI?

Functional magnetic resonance imaging (fMRI) concept builds on the earlier MRI scanning technology and the discovery of properties of oxygen-rich blood. MRI brain scans use a strong, permanent, static magnetic field to align nuclei in the brain region being studied. Another magnetic field, the gradient field, is then applied to kick the nuclei to higher magnetization levels, with the effect depending on where they are located. When the gradient field is removed, the nuclei go slowly back to their original states, and the energy they emit is measured with a coil to recreate the positions of the nuclei. MRI thus provides a static structural view of brain matter. The central thrust behind fMRI was to extend MRI to capture functional changes in the brain caused by neuronal activity. Differences in magnetic properties between arterial (oxygen-rich) and venous (oxygen-poor) blood provided the link between magnetic resonance and neural activity. This blood oxygenation level dependent (BOLD) effect is the basis for most of the fMRI studies to map patterns of activation in the working human brain. The scanners used in our experiment are shown in Figure A.1.

Figure A. 1. The SIEMENS MRI scanner used in our experiment
A.2 BOLD signal and fMRI data

FMRI is a non-invasive method since it uses blood as its intrinsic contrast agent (BOLD-contrast) to assess neural activity in the brain. In detail, the iron in blood hemoglobin is nature’s own intrinsic contrast agent, because it can change the blood’s magnetic susceptibility. Oxygenated arterial blood contains oxygenated hemoglobin, which is diamagnetic and has about the same magnetic susceptibility as other brain tissue. Therefore it does not alter the regional magnetic field and does not affect tissue T2* much. Deoxygenation of hemoglobin produces deoxyhemoglobin, which is a paramagnetic compound and disturbs the local magnetic field, relative to the surrounding tissue water, leading to the large observed magnetic susceptibility effect. The difference in magnetic susceptibility creates a local magnetic field gradient, consequently inhomogeneities in the magnetic field. The local T2*, critical in fMRI contrast, is thus determined by the balance of deoxygenated to oxygenated hemoglobin in blood within a voxel.

![Diagram of BOLD signal and fMRI process](image)

Figure A. 2. Illustration stimulus to fMRI BOLD. Neural activity increases the blood flow in the active region to provide the neurons with more oxygen and decreased deoxyhemoglobin in concentrations. Reduced field inhomogeneities lead to a longer T2* and therefore to an increased MRI signal.
In the normal awake brain about 40% of the oxygen delivered to the capillary bed in arterial blood is extracted and metabolized. Thus there is a large amount of deoxyhemoglobin in the venous vessels. When the brain is activated, as illustrated in Figure A.2., the local blood flow increases substantially, but oxygen metabolism increases only a small amount. As a result, the venous blood is more oxygenated. The reduction in deoxyhemoglobin concentration leads to a longer T2* and thus a signal increase (a few percent). This signal increase depends on the magnetic field strength and is higher at higher field strength. Nevertheless, one can never see the activation in a reconstructed fMRI with the naked eye. Statistical analysis is necessary to reliably detect these activations [A.1]

Since the discovery that brain activation can be detected and localized through the BOLD effect, a number of imaging approaches have been used to measure this activation. The prototype brain mapping experiment consists of alternating periods of a stimulus task and a control/rest task and this cycle is repeated several times. During these cycles of stimulus and control, echo planar images (EPI) are collected covering all or part of the brain. This is achieved by dividing the brain into several slices and imaging them consecutively with EPI. EPI is a very fast imaging method, requiring about 100 ms to acquire one slice, hence, about one to three seconds to cover the whole brain, and has a high signal to noise ratio (SNR). Series of images of the brain can be collected throughout stimulus/control cycles. The price paid for the speed is that the images have a lower spatial resolution than conventional MR images. But also the BOLD effect itself imposes an intrinsic resolution limit for the fMRI, since oxygenation changes can be detected several mm downstream in the venous system from the site of neuronal activity. The set of resulted images can be interpreted as a four dimensional data set, three spatial dimensions and time [A.2]. The image examples are shown in Figure A.3.

![Figure A. 3. Image examples of fMRI and MRI scanning. T2* image is the functional image with low resolution; T2 image and T1 image are structural images with higher resolution.](image-url)
A.3. BOLD hemodynamic response

The change in the MR signal from neuronal activity is called the hemodynamic response (HDR). It lags the neuronal events triggering it by 1 to 2 seconds, since it takes that long for the vascular system to respond to the brain's need for glucose. From this point it typically rises to a peak at about 5 seconds after the stimulus. If the neurons keep firing, say from a continuous stimulus, the peak spreads to a flat plateau while the neurons stay active. After activity stops, the BOLD signal falls below the original level, the baseline, a phenomenon called the undershoot. Over time the signal recovers to the baseline. There is some evidence continuous metabolic requirements in a brain region contribute to the undershoot (Figure A.4).

The mechanism by which the neural system provides feedback to the vascular system of its need for more glucose is partly the release of glutamate as part of neuron firing. This glutamate affects nearby supporting cells, astrocytes, causing a change in calcium ion concentration. This, in turn, releases nitric oxide at the contact point of astrocytes and intermediate-sized blood vessels, the arterioles. Nitric oxide is a vasodilator causing arterioles to expand and draw in more blood. A single voxel's response signal over time is called its time course. Typically, the unwanted signal called the noise, from the scanner, random brain activity and similar elements, is as big as the signal itself. To eliminate these, fMRI studies repeat a stimulus presentation multiple times.

![Figure A.4. The model of HRF.](image-url)
A.4. Important parameter of fMRI scanning

**TR:** repetition time, the time interval between successive excitation pulse usually expressed in seconds.

**TE:** echo time, the time interval between an excitation pulse and data acquisition (defines as the collection of data from the center of k-space), usually expressed in milliseconds.

**Flip Angle:** the change in the precession angle of the net magnetization following excitation.

**Field of view:** the extent of the imaging volume within a slice and is generally expressed in centimeters.

**Matrix size:** how many voxels in each direction. Matrix used in fMRI are generally powers of 2, such as 64, 128, or 256, to facilitate use of the FFT for image construction.

**Voxel Size:** provides the size of each voxel on each slice (e.g., $2 \times 2 \text{ mm}^2$).

**Slice thickness:** provides the third dimension (through-plane) and is generally the same or larger than the in-plane voxel size (e.g., 3mm).

A.5. Advantages and disadvantages of fMRI

In fMRI applications to functional mapping of the brain, BOLD signal acquisition with gradient echo is most popular because of its relatively high sensitivity (0.5-3% signal change by neural activation) and the simplicity of measurement. BOLD signal acquired by gradient echo measurement, however, has a limited spatial resolution because the signal includes contributions from veins draining the sites of activation. It has been reported that the orientation column structure, in the primary visual area in the cat brain, can be resolved in CBV-based fMRI but cannot be seen with the gradient echo BOLD signal. A further disadvantage of BOLD measurements is the often-observed contamination with large surface vessel signals. Activation-induced signal changes in these can reach very large value of 10-20%, especially when nearby activated areas send their more oxygenated venous blood to a draining surface vessel.

In intra-vascular signals, the BOLD effect is present regardless of the size of the vessel in both gradient and spin echo acquisitions and the signals contribute to the voxel signal (unless they decay out at a long value of echo-time). The intra-vascular signal is the major component at 1.5 T MRI. The BOLD effect with spin echo, in the extra-vascular space around capillaries, is relatively small.
but becomes important at super-high field MRI. Since the capillary area signal has better functional specificity, it can be advantageous to use such high fields (e.g., above 7T) where BOLD-fMRI at higher spatial resolution can also be performed.

Another main disadvantage of BOLD signals, which is common to all measurements based on vascular changes, is the slow response time (i.e., seconds). If the neural events to be measured are happening slowly, they can be tracked with fMRI since the measurement is in real time. When events occur in short time scales relative to the fMRI response time, the overlap of evoked fMRI signals make it difficult to resolve individual events. With the slow response of fMRI, it is difficult to study fast dynamics of neural processing which proceeds in tens to hundreds of milliseconds.
Appendix B — fMRI data processing and analysis with BrainVoyager

B1. Preprocessing the fMRI data

The functional data was loaded and converted into BrainVoyager’s internal “FMR” data format. Slice scan time correction was performed using sinc interpolation based on information about the TR (2000 msec) and the order of slice scanning (ascending, interleaved). 3-D motion correction was performed to detect and correct for small head movements by spatial alignment of all volumes of a subject to the first volume by rigid body transformations. Estimated translation and rotation parameters were inspected and never exceeded 2 mm or 2 degrees. Following a linear trend removal, low-frequency nonlinear drifts of 7 cycles (0.015 Hz) for the design time series were removed by temporal highpass filtering. Since event-related responses have more energy at higher frequencies, we could apply a higher cutoff, making the filtering of low-frequency content (linear and nonlinear drifts) more effective. Modest spatial smoothing was applied Gaussian filter (FWHM, 4 mm).

Figure B. 1. The horizontal view of the 3D brain before transforming talairach standard space. B. The horizontal view of the 3D brain transformed into talairach standard space. C. Visualization of the segmented cortex as a reconstructed mesh representation; gyri is colored in light gray, sulci is colored in darker gray. D. Visualization of an inflated representation of the cortex mesh.
The anatomical data of each subject was loaded and converted into BrainVoyager’s internal “VMR” data format (Figure B.1). Transformed into AC-PC and Talairach standard space. In order to perform a cortex-based data analysis, the gray/white matter boundary was segmented using largely automatic segmentation routines. The white/gray matter border was segmented with a region-growing method using an analysis of intensity histograms. Fully automatic 3D morphing algorithm, the resulting meshes were transformed into inflated cortex representations.

B2. Normalization of Functional Data

To transform the functional data into Talairach space, the functional time series data of each subject was first coregistered with the subject’s 3-D anatomical dataset, followed by the application of the same transformation steps as performed for the 3-D anatomical dataset (see above). This step results in normalized 4-D volume time course (“VTC”) data.

B3. GLM analysis

In order to account for hemodynamic delay and dispersion, each of the predictors was derived by convolution of an appropriate box-car waveform with a double-gamma hemodynamic response function. After fitting the GLM and accounting for the effects of temporal serial correlation (using AR(1) modeling[22], Activation maps for stimuli characters and figure individual voxels threshold of p<0.001, corrected with false discovery rate (FDR) was adopted.
Publications

Journal papers:


International conference papers


5) Tianyi Yan, Bin Wang, Jinglong Wu, Bing Yu, Qiyong Guo. Multiple cortical representation


Oral Presentation


Chapters in books

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