SEEING DIFFERENTLY IN NEAR AND FAR

By

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Abstract

Based on evidence from studies involving animal single cell recording, animal brain lesion, and human brain damage, researchers have suggested that there may be differential visual representations for objects in near (*peripersonal,* within arm's reach) and far (*extrapersonal,* beyond arm's reach) space in the human visual system. The findings in Chapter 2 and Chapter 3 of the present thesis provide the first behavioural evidence suggesting that healthy human observers prefer to rely on different visual mechanisms in processing information in near and far spaces. The different performance in detecting visual targets presented in near and far space indicates that the brain can actively modulate the information processing either in parvocellular and magnocellular pathways or in ventral and dorsal streams.

To determine the loci of the neural modulation regarding near and far viewing, visual identification tasks were employed in Chapter 4. In four experiments, visual stimuli were presented in either isoluminant green or achromatic white in order to decouple the neural processing in parvocellular and magnocellular pathways. The different patterns of the visual performance in the four experiments suggest that the change to near or far viewing distance results in altered information transmission in parvocellular and magnocellular pathways. Thus, the data in the present thesis provide the first behavioural evidence indicating that the LGN serves as a gatekeeper for regulating and redistributing visual information for later cortical analysis.

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Preface

This thesis consists of studies that each investigated the visual mechanisms of how human observers perceive information in near and far viewing distances. Each of the following empirical chapters is either currently submitted for review in a scientific journal, or in under preparation for submission.

Chapter 2 is a manuscript currently submitted for publication in Neuropsychologia, by Li, T., Watter. S., and Sun, H-J. entitled “Differential visual processing for equivalent retinal information from near versus far space”. The author of the current thesis is the first author of this work whose contributions include the development of the original idea and experimental design, data collection and analysis, and manuscript preparation. The second author contributed on the experimental design and manuscript preparation. The last author is the thesis supervisor.

Chapter 3 and Chapter 4 are manuscripts in preparation to submit for publication in Psychological Science and Neuropsychologia. The author of the current thesis is the first author of these works whose contributions include the development of the original idea and experimental design, data collection and analysis, and manuscript preparation.

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Chapter 1

General Introduction

1. Neural mechanisms of visual perception

When our eyes are open, the visual system experiences a coherent picture of the world. Objects we see have shape and color, are located at positions in space, and may move or stay relative to other objects. Different types of information from the visual world are extracted and integrated by neurons in different parts of the brain, so that we can perceive a meaningful world. Although visual information is initially encoded in a 2-dimensional fashion in the retina, the brain can still perceive the visual world in a 3-dimensional way. This can be done by analyzing information of various depth cues such as accommodation, convergence, binocular disparity, linear perspective, and texture gradient amongst many others. While different features (e.g., shape, colour and motion etc.) of the visual world are analyzed by various structures in the brain, it is possible that visual information from near space and far space can also be processed in different visual subsystems in order to be optimally used to meet ecological demands. The present thesis investigates the visual system's performance in dealing with near and far space, and intends to reveal different neural processes the brain employs when viewing the world in near versus far distance. In this chapter, neural characteristics and functions of the subsystems in some early stages of visual processing will be reviewed, in order to understand how the visual information from near and far space is processed by the complex visual system.

1.1. Visual information in the eye

Light is absorbed and detected by the photoreceptors, i.e. rods and cones on the retina. This information is propagated to bipolar cells and then further to ganglion cells. The ganglion cells generate action potentials in response to light, and these impulses are transmitted through their axons towards the visual cortex. In addition to the direct path through bipolar cells to the ganglion cells, information from photoreceptors can also travel laterally to the surrounding photoreceptors, bipolar cells and ganglion cells through horizontal cells and amacrine cells (Wassle & Boycott, 1991). The retina cells are organized in layers, which are seemingly backwards: light must pass through the ganglion cells and bipolar cells before it reaches the photoreceptors. Image distortion is minimal when light passes through these layers of cells because they are relatively transparent. This arrangement makes the photoreceptors more effective in responding to light because the pigmented epithelium that lies below the photoreceptors plays a critical role in the maintenance of the photoreceptors and photopigments (Dowling, 1987).

1.2. Photoreceptors

The conversion of the light signal into neural signals occurs in the photoreceptors at the back of the retina. There are two types of photoreceptor in the human eye, rods and cones, which are named by the shape of the outer segments of the cells. Compared to cones, rods have higher number of disks (cell membrane folds) and higher density of photoreceptive pigment (rhodopsin) on each disk. Most importantly, the activation of rhodopsin can cause an enzyme cascade of chemical changes that hyperpolarize the membrane of the rod upon receiving just a single photon of light (Stryer, 1987). Therefore, rods respond very well to extremely dim lights, over 1000 times more sensitive than cones. Consequently, the human eye depends entirely on rods in darker environments. However, rods will respond as much as they can when the light is still quite dim, so they are saturated in full daylight and become completely useless. Actually, under daylight, cones are the source for vision (Wandell, 1995). Another difference between rods and cones is that all rods contain the same photopigment in their outer segments, which is called rhodopsin. In rods, the peak absorbance for light is at a wavelength of 498 nm. There are three types of cones. The long-wave cones contain a photopigment that is most sensitive to the wavelength of 558 nm. The middle-wave cones contain another kind of photopigment which is most sensitive to the wavelength of 531 nm. The smallest number is the short-wave cones which contain the photopigment most sensitive at 419 nm wavelength. Thus, how we perceive color depends only on the work of cones, but not the rods (Brown & Wald, 1964).

The distribution of cones and rods varies from the fovea to the peripheral area of retina (Curcio et al., 1990). Cones are heavily concentrated in the fovea, which is the center of the projected image on the retina. Rods are completely absent at the center of the fovea, and are most densely packed at the eccentricity of 12º to 15º from the center fovea. There are many rods that converge on a single retinal ganglion cell but the ratio between cone and ganglion cell is much lower and nearly 1 to 1 (Kolb & Dekorver, 1991). The combined effect of this arrangement is that the peripheral retina is more sensitive to weak light, because rods are specialized for low luminance light, and each ganglion cell receives signals from more rods compared with cones (Watanabe & Rodieck, 1989). These characteristics enable the peripheral retina to detect faint light, but the resolution is poor in both daylight and nightlight. The region of retina most highly specialized for high-resolution vision is the fovea, which contains only cones and no rods at the center (Cohen, 1992).

1.3. Bipolar cells

Bipolar cells provide a direct route for information transmission from photoreceptors to ganglion cells. Each bipolar cell receives its direct input either from rods or from cones (Rodieck, 1998). Input for each rod bipolar cell is typically supplied by 15 to 45 photoreceptors. One type of cone bipolar cell, the midget bipolar cell, receives its input from a single cone (Kolb & Dekorver, 1991). Midget bipolar cells are found in the fovea, and connecting to specialized ganglion cells. Other bipolar cells receive inputs from a cluster of 5 to 20 adjacent cones. The receptive field of a bipolar cell is the area of retina that when stimulated with light, the response of the bipolar cell can be influenced. Depending on the receptive field, bipolar cells can be categorized into two fundamental classes, the ON-center and OFF-center bipolar cell. When a small spot stimulus is positioned in the receptive field center of an ON-center bipolar cell, the corresponding photoreceptors will be triggered and their hyperpolarization will cause the depolarization of the bipolar cell. The OFF-center bipolar cell hyperpolarizes when a light spot is positioned at its receptive field center. On the other hand, illumination of the surround would cause hyperpolarization of the ON-center bipolar cell and depolarization of the OFF-center bipolar cell (Nelson & Kolb, 1983). Although bipolar cells create the direct pathway from the photoreceptors to ganglion cells, horizontal cells feed information laterally in the outer plexiform layer of the retina to influence the activity of neighboring photoreceptors and therefore other bipolar cells. In other words, bipolar cells also are connected via horizontal cells to a ring of surrounding photoreceptors. In addition, certain amacrine cells, which receive inputs from bipolar cells, send synapses back to other bipolar cells as well as to ganglion cells (Wassle & Boycott, 1991). The above mentioned arrangement of lateral inputs to bipolar cells leads to a center-surround receptive field. At the central circular area of this receptive field, the bipolar cells provide direct photoreceptor inputs to ganglion cells. Photoreceptor information at the area surrounding the central field is provided to bipolar cells via horizontal cells and amacrine cells that are then transmitted to ganglion cells.

1.4. Ganglion cells

Ganglion cells receive visual information from bipolar cells and amacrine cells, and project mainly to several regions of the thalamus. Enroth-Cugell and Robson (1966) provided the first evidence that two distinct retinal ganglion cell populations project to the lateral geniculate body. Testing cat ganglion cells with stationary sinusoidal grating patterns, they found that some cells had a “null position” where contrast reversal of the sinusoidal grating pattern gave no response. At the null position, spatial summation of the receptor elements in the center and surround of the cell’s receptive field cancelled in a linear fashion. These units were termed “X” cells. Another class of retinal ganglion cells lacked a null position and hence demonstrated nonlinear spatial summation and were called “Y” cells. In general, X cells had smaller receptive fields and gave more sustained, tonic responses to visual stimulation. Y cells had larger receptive fields and more transient, phasic responses.

In primate retina, “midget” cells and “parasol” cells are two most common and distinctive types of ganglion cells (Polyak, 1957). Midget cells were named on the basis of their diminutive size, uniformity, and small dendritic trees. Parasol cells were identified by their larger cell bodies and more generous, umbrella-like dendritic arbors. The primate midget cells and parasol cells resemble X and Y cells in the cat retina, except for their responses to colored stimuli (Leventhal, Rodieck, & Dreher, 1981). Midget cells in the primate retina have color-opponent receptive fields. The field center and the surround receive input from different cone types, for example, red on-center and green off-surround. Parasol cells have broad-band fields that share a mixed cone input to the field center and surround (De Monasterio & Gouras, 1975). Because midget ganglion cells project to the four dorsal layers in lateral geniculate nucleus (LGN) which contain smaller cells, i.e. parvocellular cells, they are known as P ganglion cells. Parasol ganglion cells project to the two ventral layers (magnocellular layers) of LGN that contain larger cells, i.e. magnocellular cells, therefore the parasol ganglion cells are called M ganglion cells. P cells constitute about 80% of the ganglion cell population, M cells constitute about 10%, and the remaining 10% is made up of a variety of other types of ganglion cells (Perry , Oehler, & Cowey, 1984). P ganglion cells have small receptive field centers, are sensitive to color, and have high spatial resolution. They provide information about fine detail at high contrast. M cells have larger receptive fields than P cells and are more sensitive to small differences in contrast and to movement. They fire at higher frequencies and conduct impulses more rapidly along their larger-diameter axons (De Monasterio & Gouras, 1975). The P cells show the highest density in the fovea of the retina. Beyond the fovea, the density of both M and P type of ganglion cells decline with the increase of the eccentricity. However, they do not decline at the same rate. From the fovea to the periphery, the density of P cells decline much more steeply than that of the M cells. This was observed in both non-human primates (Tychsen, 1992) and humans (Dacey & Petersen, 1992).

Similar to bipolar cells, ganglion cells can also be classified into two groups based on their receptive fields (Kuffler, 1953). For ganglion cells with ON-center receptive field, light produces the most vigorous response if it completely fills the center of the receptive field. Whereas in order to most effectively inhibit the firing of a ganglion cell, light must cover the entire ring-shaped surround. An OFF-center ganglion cell has a converse organization of the receptive field, with inhibition arising with center stimulation. The size of the receptive field of a ganglion cell depends on its location in the retina. The receptive fields of cells situated in the central areas of the retina have much smaller centers than those at the periphery (Dacey & Petersen, 1992).

1.5. Lateral Geniculate Nucleus (LGN)

In the nervous system afferent information from every sensory system except olfaction passes through the thalamus before reaching the cerebral cortex. The lateral geniculate body is often called a thalamic “relay station” as if its function were merely to transmit a faithful copy of the retinal output to the visual cortex. However, some recent studies and also Chapter 4 of the present thesis argue that the LGN must have some functions more important than merely providing a simple conduit for information passing from the eye to the occipital lobe.

Receptive field organization: Neurons in the lateral geniculate body share with retinal ganglion cells the same basic centre-surround arrangement of their receptive fields (Hubel & Weisel, 1961; Weisel & Hubel, 1966). On-center cells respond with a burst of spikes when a small spot of light stimulates the field center. The maximal response is obtained by choosing a spot size equal to the diameter of the receptive field center. If the spot is larger than the field center, the cell’s response is attenuated, indicating antagonism between the center and the surround subfields. A light annulus suppresses spontaneous activity and produces a brisk “off” response. The monkey on-center cells are slightly more numerous than off-center cells found in the retina and the lateral geniculate body. Diffuse light is a mediocre stimulus for neurons with center-surround receptive field organization because the field center and the surround have offsetting effects upon the cell's discharge rate. It appears that as receptive field requirements become more stringent in the hierarchy from retina to lateral geniculate body to visual cortex, diffuse light becomes progressively less effective as a stimulus. Information about absolute light intensity is generally not important for the visual system, except perhaps for the small subclass of retinal ganglion cells that drive the pupil light reflex. Information about spatial discontinuities in patterns of light energy is more useful for image analysis. Cells with center-surround receptive field organization are ideally suited for detecting such contrasts. Their best responses are elicited by contours illuminating just a portion of their receptive field.

Magno- versus parvo-: There is a striking difference in the morphology of neurons in the dorsal laminae and the ventral laminae of the primate lateral geniculate body. The two ventral laminae contain loosely packed cells with giant somas that exceed 30 μm in diameter. They are commonly referred to as the "magnocellular" laminae. The four dorsal laminae are comprised of much smaller neurons and hence are known as the "parvocellular" laminae (Reid, 1999). This anatomic dichotomy provides a powerful hint that neurons in dorsal and ventral laminae of the lateral geniculate body play different functional roles in the processing of visual information. In the LGN, approximately 80% of cells are in the parvocellular layers, 10% in the magnocellular layers, and the remaining 10% in the ventral portion of these major layers.

Functional specificity of geniculate laminae: In the primate lateral geniculate body, the parvocellular laminae receive input from the midget retinal ganglion cells, and the magnocellular laminae receive input from the parasol cells. This pattern of innervation implies that the color-opponent and broad-band retinal channels remain segregated at the level of the lateral geniculate body (Perry, Oehler, & Cowey, 1984).

In the parvocellular laminae, the majority of cells have color-selective responses. Wiesel and Hubel (1966) described three principal types of parvocellular units. The most common cell (Type I) has a standard center-surround receptive field arrangement. The center and surround have different spectral sensitivities because they are fed by different cone systems. A typical cell might give an “on” response to a red spot and an “off” response to a green annulus. Type I cells account for about 80% of parvocellular units. A much less common cell class (Type II) lacks center-surround receptive field organization. Type II cells are comprised of only a field center that is supplied by input from antagonistic cone populations with different spectral sensitivity. Such cells have chromatically but not spatially opponent receptive fields. They give an “on” response to one color and an “off” response to another color anywhere in the receptive field. Finally, a small group of parvocellular units (Type III) demonstrate center-surround field organization but no color selectivity. The field center and surround receive undifferentiated input from all cone types. These cells account for less than 10% of parvocellular units.

The magnocellular laminae are populated with “color blind” broad-band cells that have center-surround receptive fields. The majority of these cells resemble the Type III cells found in the parvocellular laminae. Another variety of cell (Type IV), unique to magnocellular laminae, has a broad-band (all three types) cone input to the field center and tonic suppressive surround supplied by long wavelength cones. These cells respond with dramatic, prolonged silence to a large red spot. This characteristic of the subset of magnocellular cells was used by some vision studies to suppress the activity in magnocellular pathway by presenting a large red field to the observer (Chapman, Hoag, & Giaschi, 2004; Edwards, Hogben, Clark, & Pratt, 1996).

Parvocellular cells and magnocellular cells differ in other important receptive field parameters besides their color responses. At any given eccentricity, the receptive fields of magnocellular cells are several times larger than the fields of parvocellular cells. Magnocellular axons conduct action potentials to striate cortex more rapidly than parvocellular axons. Furthermore, magnocellular cells have higher contrast sensitivity than parvocellular cells (De Monasterio & Gouras, 1975). When visually stimulated, magnocellular cells give rapid, phasic responses whereas parvocellular cells give slow, tonic responses (Schiller, & Malpeli, 1978). In these various respects a parallel can be drawn between X and Y cells in the cat and parvocellular and magnocellular cells in the monkey.

The response properties of geniculate cells are remarkably similar to those of their retinal inputs. A single excitatory post-synaptic potential from a ganglion cell is usually sufficient to evoke a discharge from a geniculate neuron (Lee, Virsu, & Creutzfeldt, 1983). There is little divergence or convergence in the transmission of information through the lateral geniculate body. In all of these respects, the lateral geniculate body appears to behave as a relay nucleus.

The lateral geniculate body receives a massive feedback projection from neurons in layer 6 of the primary visual cortex (Gilbert & Kelly, 1975). This reciprocal corticogeniculate projection might be expected to influence profoundly the receptive fields of geniculate cells since the shapes of the receptive field of most cells in V1 are quite different from those in LGN and the receptive field sizes are gradually larger within the hierarchy of cortical areas (Hubel & Wiesel, 1968; Smith, et al., 2001). Potentially, the neural feedback offers an anatomical substrate for modulation of retinal inputs at the geniculate level before transfer to visual cortex. However, reversible inactivation of the corticogeniculate input by cooling striate cortex produces only slight effect upon the response properties of cells in the lateral geniculate body (Baker & Malpeli, 1977). In addition, the receptive fields of the cells in LGN layers are almost identical to those of the ganglion cells of the retina that provide afferent input. Considering that feedback inputs outnumber the feed-forward inputs received by LGN cells, it is surprising that the information coming from the visual cortex, which has much larger receptive field compared with LGN and ganglion cells in retina, does not alter the response properties of the cells in LGN which are similar to those of ganglion cells in the retina. This surprising result left researchers without a clear understanding of the role of the lateral geniculate body.

1.6. The primary visual cortex

Primary visual cortex is located in the occipital lobe of the primate brain. It is defined as Brodmann's area 17 and is the major synaptic target of the LGN. It is also known as V1 or the striate cortex.

Retinotopic mapping: The projections from the retina to the LGN and V1 retain the basic mapping of the retinal surface: Adjacent regions on the retina project to adjacent regions in LGN and V1. In turn, the pattern of retinal stimulation is geometrically related to the layout of objects in space. However, retinotopical organization is distorted, because the neural sampling of each level is not uniformly distributed. For example, the density of the ganglion cells is much higher at the fovea than at the periphery of the retina. As a result, the central few degrees of the visual field are overrepresented or magnified in V1 representation (Goebel, Muckli, & Kim, 2003).

Orientation selectivity: Cells in LGN and their target cells in layer 4C of the primary visual cortex have circular receptive fields and respond greatly to light that falls on the center of the receptive field. However, outside of layer 4C in V1, most cells exhibit orientation selectivity. Hubel and Wiesel (1968) found that these cells respond best when presented with a bar of light at a particular orientation moving across their receptive fields. Bars perpendicular to that orientation elicit much weaker firing responses. The orientation selective neurons have a highly ordered organization over V1, both perpendicular to the cortical surface and parallel to it. For the cells perpendicular to the primary visual cortex surface, from layer 2 down through layer 4, the preferred orientation remains the same. However, the orientation selectivity for the cell on the horizontal neighbor changes systematically with the distance.

Direction selectivity: For the cells in V1 that show orientation selectivity, a subset of them also show direction selectivity. These cells respond when a bar of light at the optimal orientation moves to one direction perpendicular to the orientation of the bar but not when moving to the opposite direction (Goodwin, Henry, & Bishop, 1975; Schiller, Finlay, & Volman, 1976). Cells showing direction selectivity normally receive inputs from the magnocellular layers of the LGN. Direction selective cells are thought to be specialized for the analysis of object motion.

Binocular receptive fields and ocular dominance: Before V1, visual information from each eye is transmitted separately in visual neurons, for example in different layers of LGN. The first stage at which binocular integration of the neural signals occurs is in V1. Cells in V1 have binocular receptive fields, one for the ipsilateral eye and the other for the contralateral eye. The cortical neurons can be excited by appropriate stimulation of either eye, although one eye will generally have a greater influence over the other. This aspect of eye preference represents another horizontal organization over the surface of V1: Neighboring orientation columns tend to have the same eye preference. However, at intervals of about 0.5 mm across the surface of V1, eye preference changes abruptly to the other eye. (Hubel & Wiesel, 1968).

Layers in V1: The cells in the primary visual cortex are arranged into about six layers. Receiving most visual inputs from the LGN, layer 4 is further divided into 4 layers, labeled 4A, 4B, 4Cα, 4Cβ. The magnocellular stream projects from layer 4Cα into layer 4B while the parvocellular stream projects from layer 4Cβ mainly to layer 3. Basically, there are three functionally distinct pathways that go from the retina to V1 and then V2 (Merrigan & Maunsell, 1993).

Magnocellular pathway: The cells in the magnocellular layers of LGN project to layer 4Cα of the V1, which in turn projects to layer 4B and then to extrastriate cortical areas such as middle temporal area (MT), medial superior temporal area (MST), etc. The pyramidal cells in layer 4B of striate cortex are orientation selective, with many also being direction selective. Continuing with neural characteristics of the magnocellular pathway, neurons in the layer 4B of V1 show transient responses, relatively large receptive fields and poor wavelength sensitivity. Cells in layer 4B of V1 are thought to be involved in the analysis of object motion and the guidance of motor actions.

Parvo-interblob pathway: Some cells in the parvocellular layer of LGN sends axons to layer 4Cβ and then to both blob (Cytochrome-oxidase darker region) and interblob areas in layer 2 and 3 of striate cortex, which then project to extrastriate cortical areas V2, V4 and inferiotemporal area (IT), etc. Many of these neurons in layer 2 and 3 are binocular and generally insensitive to colour. Compared with other pathways, the orientation-selective receptive fields are small for these neurons, suggesting that they are involved in the fine analysis of object shape.

Blob pathway: A small portion of retinal ganglion cells which are non-magnocellar and non-parvocellar types project to the koniocellular layers of LGN, which are ventral to each of the magnocellular and parvocellular layers. Cells in the koniocellular layers of LGN project directly to the cytochrome oxidase blobs in layer 2 and 3 of V1, which then go to extrastriate cortical areas such as V2 and V4. These blobs also receive convergent input from parvocellular, magnocellular and koniocellular layers of LGN via layer 4C. Cells in the blobs have receptive fields typically center-surround, color-opponent and monocular. Their orientation selectivity is poor whereas wavelength sensitivity is high, indicating the blob pathway is specialized in color analysis.

V1 outputs: In Monkeys, V1 projects to about ten visual areas in the brain, with around 50% of projections to V2, 20% to V3, and 10% to MT. For feedback connections, layer 6 also send axons back to the LGN. Layer 5 pyramidal cells send axons to the superior colliculus and pons (Casagrande & Kaas, 1994).

After primary visual cortex: There are more than two dozen distinct areas in visual cortex, each of which represents some aspects of the visual world (Felleman & Van Essen, 1991). Anatomically, these visual areas can be grouped into two largely independent cortical streams of visual processing, one passes dorsally from V1 to the posterior parietal areas of the cortex and the other project ventrally to the inferotemporal cortex. Ungerleider and Mishkin (1982) called these the dorsal stream and ventral stream. They suggested that the ventral stream is specialized for object perception, e.g. to identifying what an object is, whereas the dorsal stream is specialized for spatial perception, e.g. locating where an object is.

1.7 Ventral stream

The ventral visual-processing stream consists of the areas of the occipital, occipitotemporal and temporal regions that are solely devoted to processing visual stimuli and are unresponsive to information from other modalities or to multimodal information.

Area V4 receives input from V2, which continues the parvo-interblob pathway and the blob pathway from LGN via V1. Cells in area V4 have receptive fields normally 16 to 30 times larger than that in V1 (Van Essen & Zeki, 1978). Many of the cells in V4 are both orientation selective and color selective (Desimone, & Schein, 1987; Zeki, 1978), which made researchers consider this area as important for shape and color perception. Perceptual deficits in shape and color were observed in monkeys with lesions in V4 area (Walsh et al., 1992, 1993; Wild et al., 1985). The retinotopic map of the visual field is continued from V1 to V4, although distorted, but after V4, the visual field is no longer mapped retinotopically (Van Essen, 2004).

Area IT is in the inferior temporal lobe which contains neurons with complicated spatial receptive fields. A major output of V4 projects to area IT. Cells in area IT were found to be sensitive to a wide variety of colors and abstract shapes. Along the ventral stream, the cells are sensitive to gradually more complicated visual stimuli. For example, while cells in V2 are likely to respond to one or more simple stimulus qualities (e.g. color, texture, length, width, orientation, direction of motion, spatial frequency), the cells in area IT fire only in response to much more complex visual stimuli. For example, cells in IT of monkeys can be tuned to specific forms, such as hands (Gross, Bender, & Rocha-Miranda, 1969) or faces (Gross, Rocha-Miranda, & Bender, 1972). In addition, the response of cells in IT area is unaffected by changes in retinal position, retinal size, and orientation (Desimone, Albright, Fross, & Bruce, 1984). This allows us to recognize objects from various perspectives. Cells in IT area have large receptive fields that can encompass as much as 130 degrees of the field of view in front of the head. This allows an object to be identified regardless of where it is located in space and regardless of its size.

The **lateral occipital complex (LOC)** is located at the posterior portion of the fusiform gyrus. In neuroimaging studies, the response of the LOC to an object is the same regardless of the size, location, viewpoint and illumination of the object (Grill-Spector et al., 1998). In addition, neural activation in the LOC area exhibits a similar response to both line drawings and photographs of the same object (Kourtzi & Kanwisher, 2000). Additionally, another area in the ventral stream is the fusiform face area which is on the fusiform gyrus. Neurons in this area showed specific response for faces (Kanwisher, McDermott, & Chun, 1997). Furthermore, there is also an area called the extrastriate body area that responds preferentially to human bodies and body parts rather than inanimate objects and object parts (Downing et al., 2001).

The ventral visual stream also exhibits a **lateralized processing preference**. The right hemisphere of the ventral stream appears to preferentially process global information, whereas the left hemisphere preferentially processes local information. For example, a task invented by David Navon (1977) would display a big letter which was composed of many small letters. Patients with lesions of the left hemisphere showed poor ability to perceive local but not global aspect of the letters; whereas patients with lesions on the right hemisphere showed better performance on local rather than global aspect of form (Delis, Robertson, & Efron, 1986). The lesions most likely to cause such global/local effects are those in the temporal region, consistent with the idea that the regions in the ventral visual stream are specialized for object recognition (Robertson, Lamb, & Knight, 1988)

1.8 Dorsal stream

Area MT (middle temporal), also known as area V5, is a small but important region in the dorsal stream. There are multiple pathways that provide input to area MT with differing contributions from the magnocellular, parvocellular and koniocellular pathways. There is a specific link between the magnocellular pathway and the dorsal stream. That is, the neurons in V1 that project directly to area MT are innervated predominantly by inputs from magnocellular layers of the LGN (Yabuta, Sawatari, & Calaway, 2001). Area MT also receives inputs from area V2 and V3, which are largely innervated by cells in layer 4B of V1 receiving information mainly from magnocellular pathway. Some neurons in layer 4B of V1 project to the thick stripes in V2, then either directly connect to MT or via V3 to MT. This pathway receives most inputs from magnocellular cells of LGN, whereas small amount of the neurons in layer 4B of V1 also receive inputs from layer 4Cβ of V1 which is innervated by parvocellular cells in LGN (Nassi & Callaway, 2006). Nearly all the cells in area MT are selective for motion direction, which is not seen in earlier levels of the dorsal stream or in any level of the ventral stream. Similar to the cells in layer 4B of V1, neurons in MT have large receptive fields and are sensitive to stimulus movement in specific directions. Cells in MT are most likely to be activated by motion of objects rather than their structure (Albright, 1984). Cells sensitive to similar directions of motion are grouped into direction-of-motion columns in area MT, similar to the repeated arrangement of the orientation columns in V1.

Beside MT, there is a region known as **MST** in the parietal area. In addition to the sensitivity for linear motion that is characteristic of neurons in MT, cells in MST are also sensitive to radial motion (inward or outward from the center) and circular motion (clockwise or counterclockwise) (Tanaka & Saito, 1989).

Area 7 is an important part in the dorsal stream for processing spatial information. The receptive field of the cells in Area 7 generally encompasses almost all of the contralateral visual space as well as a large portion of ipsilateral space. Thus, it enables the visual system to obtain information about the location of an object in a large expanse of space. Many cells in Area 7 respond to a specific direction of motion, either inward or outward from the center of the visual field. Also, some cells in this area fire optimally when the object moves at a specific relative velocity compared with the movement of the animal in locomotion (Motter & Mountcastle, 1981). Similarly, some cells in Area 7 are responsive to the retinal location of an object relative to an animal's eyes and/or head (Andersen & Mountcastle, 1983). This allows for the creation of a stable spatial map of the world, with the perceived object at a stable spatial location in this map, independent of the movement of the animal's head and body. Unlike cells in the ventral visual stream, cells in parietal area are not particularly sensitive to form or colour, making them ill-suited to detecting the visual properties from which shape can be derived (Van Essen & Maunsell, 1983). Moreover, they are not particularly sensitive to items positioned in the center of visual field, where acuity is the highest in V1 and V2, a fact that serves as additional evidence that these cells do not play a large role in object recognition (Baizer, Ungerleider, & Desimone, 1991).

1.9 Ventral/Dorsal distinction

Some researchers suggest that the distinction between dorsal and ventral visual streams can be described as the distinction between "what" and "where" (Ungerleider & Mishkin, 1982). This is based on some observations that damage to parietal regions does not interfere with object discrimination. In such study, monkeys are shown two food wells that have identical covers. A small tower, which acts as a landmark, is situated closer to one of the covers than the other. The position of the landmark changes from trial to trial. For instance, sometimes the landmark is closer to the right food well and sometimes it is closer to the left food well. However, this landmark is always positioned closer to the well containing the food. Thus, the animal must be able to encode its relative position to know that the reward is hidden under the well nearer to the landmark. Monkeys with parietal lobe lesions are impaired on this task as it requires the computation of the spatial relations among items (Pohl, 1973). In another study (Mishkin, Ungerleider, & Macko, 1983), the monkey was familiarized with an object placed in a central location (e.g., an elongated, striped pyramid). This object was then placed over one food well, whereas another object (e.g., a checkered, three-dimensional rectangle) was placed over the other food well. In each trial, the reward was hidden under the object with which the animal was not familiarized (i.e., the novel object), in this case, the checkered, three-dimensional rectangle. Monkey with temporal lobe lesion found this task difficult even though they could perform the spatial-location task with ease.

However, some other researchers suggest that the distinction between the dorsal and ventral visual systems is better described as the distinction between "what" and "how" rather than "what" and "where" (Goodale & Milner, 1992). They argued that the role of the dorsal system is to know how motor acts must be performed to manipulate an object, for example, how the hands and fingers must be positioned to grasp an object. In one case study, a patient with bilateral parietal damage could recognize line drawings of common objects but couldn't adjust the gap between her index finger and thumb to grasp items, even though she could correctly move her hand to the region in space where the item was located (Jakobson, et al., 1991). In contrast, patients with damage to ventral extrastriate regions showed impairments in discriminating the size, shape, and orientation of visual objects, yet they can accurately guide both the hand and fingers to these same objects (Milner et al., 1991).

The notion that parietal regions are involved in spatial aspects of motor control is also supported by studies of single-cell recordings in monkeys and neuroimaging results in humans. Neurons in the inferior parietal lobe of monkeys are active when the animal directs motor acts to particular locations, such as reaching, or tracking an item with the eyes. Because these cells exhibit both sensory- and movement-related activity, some researchers have suggested that these areas of the brain are important for integrating external information about space along with commands for motor actions in extrapersonal space (Lynch et al., 1977; Mountcastle et al., 1975). Moreover, some cells in parietal regions are sensitive to the visual qualities of an object that influence how the hand and fingers should be positioned in order to grasp the object (Taira et al., 1990). Neuroimaging studies also reveal that posterior parietal cortex is activated when individuals are engaged in visually guided movements (Matsumura et al., 1996).

Some researchers suggest that the two views about the function of dorsal visual streams may be reconciled. The visual processing about "where" may rely more on inferior regions of posterior parietal cortex whereas the "how" function may rely more on superior posterior parietal regions (Creem & Proffitt, 2001).

1.10. Feedback system in lower level visual processing

In cats, only 25 percent of the total number of synaptic inputs of the interneurons in lateral geniculate nucleus (LGN) are from retinal afferents, whereas 37 percent of the synaptic contacts come from the cortex (Montero, 1991). For the LGN relay cells, only 12 percent of the inputs comes from the retina whereas 58 percent from the cortex.

Sherman and Guillery (1998, 2001) distinguished the input connections to the LGN into two different types: drivers and modulators. The drivers are from ganglion cells that connect to the retina and which are relayed to cortex. The modulators are cells conducting information from other parts of the brain. The researchers define the corticothalamic input to the LGN as modulators because the elimination of these inputs could not alter the basic center/surround organization of the LGN relay cells and had only subtle effect on their receptive fields. The firing modes determined two types of neural response in the LGN relay cells. Bursting is arrhythmic and easily seen during sleep or pathological states. Tonic firing is more similar to relay information and thus is better for faithful, detailed reconstruction of the stimulus from the retina. Sherman (2001) believed that the modulators from cortex serve to switch the information transmission from burst to tonic or from tonic to burst mode. The influence of feedback on the performance of LGN cells was illustrated by removing the feedback from V1. In the absence of feedback, the sensitivity to the difference in orientation alignment for the inner and outer on/off receptive field was greatly reduced in LGN cells (Sillito, Cudeiro, & Murphy, 1993). That seems to suggest that the processing efficiency in LGN can be affected by the feedback signals from the visual cortex.

2. Visual Attention and Neural Modulation

Visual perception is one of the most important ways for a human being to know the world. When looking at the environment, many stimuli converge on the senses and the more important ones must be attended to for successful performance. Due to limitations of the amount of information the brain can process at a given time, the neural system must be able to enhance some forms of processing while inhibiting others in order to properly analyze the most important information.

2.1. Modulation of neural processing

Different attributes of visual information are processed by various neural substrates. When attention is focused on one attribute, the corresponding neural processing should be enhanced in order to better analyze specific information. This kind of active modulation in neural processing was observed in some neuroimaging studies. In a combined PET and ERP study, increased neural activity in the contralateral part of extrastriate (V2-V4) visual regions was observed when a visual target appeared in the attended location as compared to an unattended location (Heinze et al., 1994). ERP studies indicate that this space-based attentional modulation occurs relatively early on, approximately 100 ms after stimulus presentation. Moreover, attention can influence specific neural processing based on the attributes of the attended items. In a PET study, participants decided whether two successive displays of moving colored shapes were identical or not. Individuals were told to base their decision on one of the attributes (e.g. color) and to ignore others (e.g. speed and shape) (Corbetta et al., 1991). Thus the perceptual information was equivalent across conditions, with variations only in what attribute should be attended to. When the person attended to color, ventral visual regions sensitive to color, such as V4, were most active. When the person attended to shape, greater activation was found in portions of the ventral visual-processing stream. When the person attended to speed, activation was greatest in area MT, the portion of the dorsal processing stream that is sensitive to motion. ERP data suggested that selection on the basis of stimulus attributes, such as color and shape, occurs around 250-300 ms after stimulus presentation (Anilo-Vento, Luck, & Hillyard, 1998). Attentional selection can also be object-based. In one study, displays included both faces and houses. When attention was directed to an attribute that was associated with faces, increased activation was observed in the fusiform face area. In contrast, when attention was directed to an attribute associated with houses, increased activation was observed in the parahippocampal place area (O'Craven, Downing, & Kanwisher, 1999). This object-based attention was also confirmed by MEG data (Downing, Liu, & Kanwisher, 2001), which showed that the amplitude of M170' (a peak in scalp magnetoencephalography at a latency of 170 ms after image onset) is greater when individuals attended to faces as compared to houses. From the above evidence we can see that attention acts to influence the neural processing in distinct brain modules, ramping up their activity if they are processing information that is attentionally relevant. Some evidence suggests that attention may also decrease the activation of brain regions processing information that is task-irrelevant (Rees, Frith, & Lavie, 1997).

2.2 Spatial neglect and brain damage

Hemineglect, sometimes referred to as hemi-inattention, is a syndrome in which an individual ignores, or does not pay attention to, the side of space contralateral to the lesion. Neglect is usually observed after vascular damage to the parietal region of the brain, especially the right part of the parietal lobe (e.g., Ogden, 1985). Hemineglect not only affects attention along the horizontal plane (i.e., left and right), but also has effect on the vertical plane and the near-far plane. One case study showed that the neglect patient could detect a single stimulus in all four quadrants of her visual field. However, when shown two objects, one above the horizontal meridian and one below, the individual always ignored the one below. When required to find the midpoint of vertically oriented sticks of wood, she estimated the midpoint to be above the true midpoint of the rod (Rapcsak, Cimino, & Heilman, 1988). Another case study showed the opposite pattern of neglect. A patient with lesion involving inferior temporal lobes tended to neglect the upper part of space. In the experiment, he bisected vertical lines below their midpoint and ignored the upper portions of visual stimuli (Shelton, Bowers, & Heilman, 1990). In addition, this patient also had attentional neglect in another spatial dimension. He seemed to have neglect for far portions of space because he consistently bisected radial lines too close to his body. After finding the far space neglect in this patient, the researchers tested a neglect patient in another study (Mennemeier et al., 1992). This patient was found to have a significant tendency to bisect radial lines too far away from her body, an indication of neglect of near space. In both these patients, neural representation of space in the vertical dimension was linked to representation of space in the near-far dimension. One patient with bilateral inferior tempero-occipital lesion neglected both the upper half and far region of space, while the other patient with bilateral parietal lobe lesion neglected both the lower and near part of space. This may indicate that visual attention about different regions of the 3-D space is mediated by distinct brain structures. Some times neglect shows the dissociation of extrapersonal space and personal space. Guariglia and Antonucci (1992) described a patient who was attentive to all aspects of his surroundings and used objects to perform activities on both sides of space (e.g., serving tea or dealing cards). Yet, this patient exhibited neglect for personal space because when objects such as razors and combs had to be used on his own body, he ignored the left side of his body.

2.3 Attentional influence on LGN

In a neuroimaging study, O'Connor et al. (2002) found that selective spatial attention modulated neuronal activity in LGN in several ways: it enhances neural responses of relevant brain areas to attended stimuli; it attenuates those for ignored stimuli; and increases baseline activity in the absence of visual stimulation. Consistent with this role of LGN, Schneider and Kastner (2009) found that neural activity in magnocellular layers of LGN are more strongly enhanced by sustained attention than the parvocellular layers. When two different images are presented to the two eyes simultaneously, the images compete to become consciously perceived by the brain. Alternatively, each image is visible for a few seconds as the other is suppressed. This kind of binocular rivalry is most likely to be processed in V1 or at a higher level of visual system because information from the two eyes is segregated before V1. With high-resolution fMRI, some groups of researchers found that the neural processing of binocular rivalry is not merely the function of cortical areas where cells with binocular receptive fields were found, but rather happens as early as in the LGN layers. For example, Haynes et al. (2005) found that neural activity in LGN cells was reduced during binocular rivalry when the observer did not attend to the stimulus presented at the eye preferred by these cells. Wunderlich et al. (2005) also showed that neural activity in the LGN increased when a high contrast stimuli was perceived and decreased when a low contrast stimuli was perceived. In addition, neural activity in the LGN can be elevated by visual imaginary in human in the absence of external visual input (Chen et al., 1998).

For neuronal characteristics in controlling information transmission, it was shown that the response mode of LGN cells can switch between “tonic” and “burst” modes. Although both of the response modes transmit approximately equal levels of information, the quality of the information differs between modes. Burst firing shows nonlinear distortions in transmitting information. In contrast, tonic firing affords good linear relay in transmitting information to the cortex, thereby supports a more faithful reconstruction of the visual world. The switch between the two response modes is not controlled by retinal input, but rather by local inhibitory inputs affected by neural feedbacks from cortex (Sherman, 2001; Sherman & Guillery, 2002). These types of neural activity changes makes LGN an ideal place to actively control the information flow according to attentional requests from higher levels of perceptual and cognitive systems.

Taken together, converging evidence suggests that the function of LGN goes far beyond simply relay visual information, and instead plays a more active role in visual perception. Chapter 4 provides behavioural evidence suggesting that the strength of information transmission in LGN can be modulated when viewing distance changes.

3. Neural representations for Near and Far space

3.1 Different brain regions involved for interaction with 3-D space

The idea that human observers use different brain systems to deal with different part of the 3-dimentional (3-D) space was first inspired by the observations of the behaviour in brain damaged patients. Brain (1941) examined the visual behaviour of several patients wounded during the Second World War. Two patients had difficulty on localizing objects at grasping distance in the visual field contralateral to the damaged hemisphere, whereas one patient showed attentional deficit at walking distance but not in space near the body. By single-cell recording, Pettigrew and Dreher (1987) observed that separate visual subsystems were differentially activated when cats were attending to different regions of 3-D space. Specifically, the cortical areas receiving inputs from Y-type ganglion cells responded to transient visual information in space closer than fixation, whereas the cortical areas receiving inputs from W-type ganglion cells responded to sustained visual information in space at greater distance, farther than fixation. By creating lesions in the brains of monkeys, Rizzolatti and colleagues observed different kinds of attentional neglect. Following lesion in premotor area 6, monkeys showed contralateral neglect within space close to the head rather than for more distant space, but vice versa following lesion in area 8. Moreover, the attentional neglect relating to the extrapersonal space (beyond arm's reach) was observed after lesion in frontal eye field (Rizzolatti et al., 1983).

3.2. Models for division of 3-D space

Several models of how the 3-D world can be partitioned for differential neural processing have been proposed by researchers from behavioural or neuropsychological perspectives. Previc (1990) put forth a neuropsychological model to divide the visual space into two major 3-D realms: a peripersonal space (within arm's reach) that is important in visually guided reaching and manipulation, and an extrapersonal space (beyond the arm's reach) that is important for visual search and object recognition. Based on neuropsychological evidence, Previc (1990) proposed that visual interactions within peripersonal space are mediated primarily by the dorsal cortical visual stream whereas interactions within extrapersonal visual space are processed mainly by ventral cortical visual stream.

Based on evidence from animal lesion studies, Rizzolatti and colleagues proposed a model with three regions of 3-D space: a personal space for oral and tactile interactions, a peripersonal space for reaching, grasping and manipulating objects, and lastly, a far space which is beyond arm's reach (Rizzolatti & Camarda, 1987; Rizzolatti, Gentilucci, & Matelli, 1985). They suggested that parietal area 7b and postarcuate frontal area 6 were involved in processing personal space, parietal area 7a and 7b and frontal area 6 and 8 were involved in processing peripersonal space, whereas frontal area 8 and parietal area 7a were important for processing information in far space.

Based on human visual observation of the world and the behaviour of some brain damaged patients, Grusser (1983) proposed a four-region division of 3-D space: grasping space, near-distance action space, far-distance action space, and visual background. By analyzing how human observers use various depth information in the 3-D space, another three-region model of the 3-D space was proposed by Cutting and Vishton (1995): a personal space within 2 m, an action space that extended to 30 m, and a vista space for even further distances.

The most complicated model, however, was proposed by Previc (1998) who suggested a four-zone division of 3-D space: visual grasping and manipulation are performed in a peripersonal space which is less than 1 m; visual search, object recognition are performed in focal extrapersonal space; navigation, scene memory and target orientation in the action extrapersonal space and finally, spatial orientation, postural control and locomotion in the ambient extrapersonal space.

3.3. Ecological perspective for 3-D visual space

The division of 3-D space relating to various neural processes was also proposed based on ecological benefits about how animals use information in different regions of the space in order to better interact with the world. As Previc (1990) suggested, information from the peripersonal space is mainly used by primates to reach for, grasp and manipulate objects manually. There is little need to recognize and memorize objects in space within arm's reach because they have already been recognized before being brought into peripersonal space. Visual inputs from peripersonal space are typically optically degraded, because the image of the hand that is used to reach for and later grasp an object is highly blurred by rapid motion. Hence, the information processing for peripersonal space is specialized for global form, depth, and motion. These functions are more likely to be carried out by the magno-dorsal pathway of the visual system.

Information in the focal extrapersonal space is mainly used to search for and recognize objects, faces, and other relevant visual targets. Therefore, visual processing for focal extrapersonal space demands high visual acuity to resolve the details of visual targets and is thus consequently reliant on the process of central visual field which provides the highest resolution for object recognition. Moreover, visual memory is important for interactions with the larger world, for example, deciding which object or face is proper to attend to. These functions are more likely to be carried out by the parvo-ventral pathway of the visual system.

In addition to the idea proposed in his 1990 paper, Previc (1998) divided the extrapersonal space into two more regions. One is action extrapersonal space that is large and covers 360° surround the body. Information from this space is used to orient and navigate in relationship to objects and places in external space. Hence, information processing for the action extrapersonal space is closely linked to the remembrance of specific places or events, but without a need for detailed motion, depth, or form perception. These functions are more likely to be carried out by the medial temporal lobe. Another region is ambient extrapersonal space in which information comes from the entire expanse of the visual world with the emphasis of peripheral visual field. This information processing is to help our bodies keep proper orientation in gravitational or earth-fixed space, and to achieve effective postural control during locomotion.

3.4. Neuroanatomy of visual system for near space

Although researchers have suggested many models to reflect our interactions with 3-D space, one common part of these models is to divide the neural representation of 3-D space into peripersonal (near) and extrapersonal (far) space, which is also widely supported by behavioural evidence and neural anatomical features.

As suggested by Previc (1990) and many other researchers, the major visual pathway processing information in near space is the classical dorsal stream. This system runs from layer 4B of striate cortex (V1), which receives inputs from magnocellular layers of LGN, to the thick cytochrome oxidase stripes of area V2; some projections also run directly into area V3 and MT. The final terminations of this system include the middle superior temporal (MST) area, area 7a, and the ventral intraparietal (VIP) area. Continuing the neural features of the cells in magnocellular pathway, cells in dorsal stream are transiently activated and specialized for global motion analysis and global stereopsis but not for form and color analysis (Maunsell & Newsome, 1987). Cells in later dorsal stream have receptive fields typically covering the central 60º which is much larger than that in the ventral stream. Neurons in superior temporal sulcus (STS) respond in association with pursuit eye movement (Komatsu & Wurtz, 1988; Lynch, et al., 1977). Cells in area MT respond to reaching movements especially when the reaching is visually guided and intended to obtain biological reinforcement (Maunsell & Van Essen, 1987).

In the dorsal stream, the posterior parietal lobe plays a crucial role in peripersonal operation because of its integration of somatosensory information, vestibular information and visual information. Areas such as 7a, 7b, ventral intraparietal area (VIP) and anterior intraparietal area (AIP) are involved in reaching, grasping, smooth eye movements (Colby et al., 1993; Hyvarinen & Poranen, 1974, Jeannerod et al., 1995; Lynch et al., 1977; Mountcastle et al., 1975; Rizzolatti et al., 1985; Sakata et al., 1985). Lesions to the inferior portion of the posterior parietal lobe produce deficits in visually guided reaching, pursuit tracking, gaze shifting to peripheral targets, motion judgment, and global perception (Hyvarinen, 1982; Stein, 1989; Wasserstein et al., 1987). However, the ability to travel through the visual environment and to remember various topographical features of the visual environment appears less impaired following damage to the inferior parietal lobe (Brain, 1941; Barrash et al., 1996; Habib & Sirigu, 1987).

Another major region that is heavily involved in visual operation for near space is frontal area 6 in premotor cortex. Neurons in the inferior region are most responsive to stimuli near the animal, and most spatial receptive fields are body centered (Fogassi et al., 1992, 1996; Graziano, Yap, & Gross, 1994). It has been shown that two portions of Area 6 are particularly involved in visual-manual coordination. These are: F4 which is primarily involved in proximal arm movements (Fogassi et al., 1996), and F5, which is most involved in grasping movements (Jeannerod et al., 1995). These regions are primarily connected with parietal areas AIP, 5, and 7b. Lesions to the F4 and F5 portions of Area 6 produce a bimodal (tactile and visual) neglect of the area immediately surrounding the monkey and the degraded contralateral reaching movements as well as oral grasping movement (Rizzolatti et al., 1983).

3.5. The neuroanatomy of visual system for far space

As suggested by Previc (1990) and many other researchers, the focal extrapersonal (far) space is heavily processed in ventral visual stream. The ventral cortical visual stream receives input from layer 4A and layer 4Cβ of the striate cortex, which are targets of the parvocellular pathway. Neurons in these layers project to the cytochrome-oxidase-stained blob and interblob regions of V1 and to the thinly striped and interstriped regions of V2, and then into V4, which is heavily involved in the processing of form and color. There is also a magnocellular input, via the V1 blob and V2 thinly striped cytochrome-oxidase regions, into area V4 (Ferrera, Nealey, & Maunsell, 1994).

The inferior temporal visual region (involving area 20 and 21) has long been recognized as important to object recognition (Ungerleider & Mishkin, 1982). This region receives neural inputs from posterior visual regions (such as V4) that are highly involved in visual search and scanning, visual attention, and visual feature analysis. In contrast, neurons in the inferior temporal visual region appear to be more specialized for object perception and memory (Miyashita, 1993; Tanaka, 1996). Neurons in the inferotemporal region have receptive fields that almost always include the fovea to about 20º of the visual field. Lesions in these regions produce deficits for colour, object and facial recognition (Damasio, 1985). Generally, these deficits are not associated with reaching deficits and locomotion problems that are typically produced by dorsal posterior cortical damage (Levine et al., 1985). In humans, Shelton et al. (1990) reported on a patient with bilateral inferior temporal lesions who showed an upper-field attentional neglect. Another patient reported on by Adair et al. (1995) with lesions on occipital-temporal lobe showed also upper-field neglect. Both of these patients showed neglect for far space tested by radial line bisection task.

Another important cortical region involved in visual interaction with extrapersonal (far) space is the arcuate region of the frontal lobe. By creating lesions on monkey cortex, Rizzolatti et al. (1983) found that the arcuate region (areas 8a and 45) was related with attentional neglect for far space. The arcuate region that contains the frontal eye fields is better connected with occipital-temporal and posterior inferotemporal cortices than with the anterior temporal cortex (Goldman-Rakic, 1987), therefore is greatly involved in oculomotor-driven visual search as opposed to visual memory functions. The ventral arcuate region, which contains the small-saccade eye-movement region, is heavily connected with the inferotemporal cortex (Schall et al., 1995; Stanton et al., 1995).

The lateral intraparietal (LIP) area of the posterior parietal cortex is also heavily involved in the visual processing of objects in far space. Area LIP is highly connected with both the ventral arcuate cortex and the inferior and ventromedial portions of occipital-temporal cortex (Stanton et al., 1995), as well as with superior colliculus. Area LIP neurons are highly activated by central fixation and are believed to provide information about current and intended eye position to structures that process visual information from the environment (Andersen, 1995). Duhamel, Colby, and Goldberg (1992) suggested that LIP neurons create a new retinotopic coordinate system based on the intended eye position.

The superior colliculus is also believed to contribute to the visual processing for far space (Rizzolatti et al., 1985; Rizzolatti & Camarda, 1987). Extensively involved in visual search and scanning operations (Bender & Butter, 1987), the superior colliculus neurons have receptive fields biased towards the upper visual field (Previc, 1990). Lesions on the superior colliculus produced upper-field neglect in rodents (Foreman, 1983; Marshall, 1978). The colliculus receives important direct or indirect projections from several upward-biased structures, including the frontal eye fields, LIP, and the caudate nucleus (Andersen et al., 1992; Hikosaka, 1991).

3.6. Behavioural difference for near and far visual processing

The idea that different regions of 3-D visual space are mediated by different neural systems was proposed very early based on evidence from animal single cell recordings, animal brain lesions and brain damaged patients. However, the concept that information in near and far space is processed by different part of human brain has been tested by empirical research only two decades ago. Using a radial line bisection task, Shelton et al. (1990) showed that patients with bilateral temporo-occipital lesions marked the estimated mid-point of a line closer to the body. By contrast, an estimated mid-point significant away from the body was observed in patients with bilateral parieto-occipital cortex lesions (Mennemeier et al., 1992). However, the convincing dissociation of the visual representations for near and far space should be testified by visual tasks separately performed in near and far spaces. Using horizontal line bisection task, Halligan and Marshall (1991) observed that a patient with lesions in right posterior parietal cortex showed severe left visuo-spatial neglect in peripersonal space, but not so in extrapersonal space. In contrast, Vuilleumier et al. (1998) reported on a patient with a right temporal hematoma showed severe left neglect when performing a series of visual tasks in far space but not in near space. Thus, the suggested double dissociation of the neural representations for near and far space was observed in different brain damaged patients. The neurological implication is that, if the processing of visual information from near or far space is selectively impaired without disruption to another visual space, different visual mechanisms or pathways should be responsible for different viewing distances. Intuitively, one should expect that neurologically intact observer would also perform differently when viewing in near versus far space given that the assumed neural subsystems mediating near and far visual spaces exhibits distinct processing functions and neuronal characteristics. In addition, patients with visual neglect usually suffer from wide areas of brain damage, which makes it difficult to pinpoint the specific neural subsystems involved. It would be more convincing to dissociate the near and far visual representation based on behavioural differences produced by neurologically intact brains.

In addition to the neurological patients, some behavioural differences regarding near and far visual spaces were observed in healthy human observers when using the visual tasks based on the phenomenon of “pseudoneglect” (Bowers & Heilman, 1980). Because of the attentional asymmetry between the left and right hemisphere, healthy participants normally have a tendency to mark their estimated mid-points of lines to the left of the true mid-point. By testing right-handed normal subjects, McCourt and Garlinghouse (2000) observed a significant leftward bias when bisecting lines in all conditions, with stimuli presented at near and far, upper and lower visual fields. But this pseudoneglect was greater for lines presented at a 45 cm viewing distance than it was for lines presented at a distance of 90 cm. Using a similar task, Varnava et al. (2002) showed a leftward bias in near space but rightward bias in far space, although the latter was less severe. However, this influence of viewing distance on the attentional bias was observed only when the left-to-right scanning strategy was employed. Interestingly, the effect of viewing distance is not only related with the scanning direction, but also relies on tools used in doing the line bisection task. Longo and Lourenco (2006) asked healthy students to bisect lines with either laser pointers or sticks. A left to right shift in bias with increasing distance was observed when subjects responded with laser pointers, whereas no effect of distance when using sticks. The authors explained that coding the stimuli in near space may activate right parietal visual mechanisms for directed attention and results in leftward bias of attention, whereas the presentation of stimuli in far space does not. However, when a stick is used, near space sensations are strongly activated in both near and far viewing conditions and a constant leftward bias is observed. Although the authors tried to explain the pseudoneglect phenomenon with the relationship between dorsal/ventral processing and near/far space, the behavioural results could not serve as evidence of differential near/far visual representations because the explanation was based on the assumption that stimuli in near space would activate the dorsal visual mechanisms more than that in far space.

In addition to tasks testing spatial neglect, some other studies showed difference in reaction time in detecting visual target presented in peripersonal space versus extrapersonal space. In detecting a small flash in various viewing distances, Downing and Pinker (1985) found that targets were detected more rapidly in near space than in far space. Gawryszewski et al. (1987) also found that without vergence eye movements, human observers respond faster to visual stimuli presented closer than the focused point of attention as opposed to that when stimuli were father away. For shifting attention across the 3-D space, Couyoumdjian et al. (2003) found an enhanced performance (10 ms faster) when shifting attention toward to observer than away from the observer. Using a covert visual orienting task, Losier and Klein (2004) found that the cuing effect on orienting attention was greater for targets in the lower visual field of peripersonal space as compared to extrapersonal space.

Other studies had pointed to differences in cognitive performances between viewing objects in small and near versus large and far visual fields. Bakdash, Augustyn, and Proffitt (2006) trained their subjects to learn target locations of unseen landmarks on either a large display (72” at 17.33’ away) or a small monitor (25” at 6’ away) which both subtended to the same angle, and tested them in a virtual reality environment with a large (far) visual field. They found that training with larger (farther) visual displays decreased the subjects’ absolute angular pointing error compared to the small display. By matching the visual angle in the small and large screen, Tan et al. (2003) showed that individuals perform better in a spatial orientation task done on the large screen, although no difference was found between doing reading comprehension tasks in larger and small screen. Moreover, in another study with similar large and small screen paradigm, Tan et al. (2004) showed that people were more effective at performing 3-D virtual navigation tasks involving path integration on large displays. For sex difference in performing object location memory task, Saucier et al. (2007) observed a female advantage in peripersonal space but a male advantage in extrapersonal space.

Taken together, various lines of research suggest that the human brain processes visual information in near and far space differently. However, the neural mechanism underlying these behavioural differences regarding near and far viewing remains unclear. The current thesis developed various visual perception tasks to test healthy human observers’ visual behaviour in near and far viewing conditions. The behavioural differences in perceiving visual information in near and far space would provide insight on how the brain works in perceiving the complex 3-dimensional world.

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Chapter 2

FOREWORD

The brain processes visual information based on the retinal image of the 3D environment. It is tempting to assume that as long as visual information on the retina (e.g., retinal eccentricity and image size, luminance, contrast etc) is the same, the visual percept will be the same regardless of how far the objects that produce these images are located. However, some recent evidence from studies involving single cell recording, brain lesions, and brain damages suggest that there could be differential neural mechanisms for visual processing of objects presented in near (peripersonal, within arm's reach) and far (extrapersonal, beyond arm's reach) space. Although this assumption was also supported by neuroimaging data, as of yet, no convincing behavioural evidence from healthy human observers has been reported.

Traditionally, the dissociation of visual representation of near and far spaces is measured by a line bisection task or its modified versions in human observers. Researchers have found that the attentional bias to one side of visual space, either in brain damaged patients or in healthy human observers, could be influenced by viewing distance. However, the extent of spatial bias only reflects cortical asymmetry between the left and right hemispheres, which lend less support to the neurologically observed visual subsystems, e.g. dorsal and ventral cortical streams, for specialization in mediating the near and far visual space.

Chapter 2 sought to investigate whether healthy human observers perceive near and far visual space in different ways. Instead of the traditional line bisection task, I employed visual detection task and visual identification tasks that potentially reflect the features of basic visual perception processes in the brain. Most previous studies have used two types of target objects or visual displays for near and far viewing conditions; thereby retinal information may differ a lot in the two viewing conditions due to unmatched luminance and contrast of the visual stimuli. The experiments reported here used two projectors to provide large and small images in two viewing conditions, with the two images being carefully adjusted so that stimuli were always matched for size (subtended angle), contrast and luminance across near and far viewing conditions.

If different visual performance regarding near and far viewing was observed in healthy human observers, that would not only provide evidence for the dissociation of the neural representations for the near and far spaces, but also indicate that the brain can actively modulate the information processing depending on the ecological demands of the information usage.

Differential visual processing for equivalent retinal information from near versus far space

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Abstract

Converging evidence from animal neurophysiology and human clinical studies has suggested that visual information arising from near versus far space may be mediated predominantly by different visual subsystems in the human brain. In five experiments, healthy observers either detected or identified brief peripheral targets presented in near (peripersonal) versus far (extrapersonal) space. Apparent size (subtended visual angle) and luminance were equated to provide equivalent retinal information across near and far viewing conditions. Peripheral detection accuracy declined more rapidly with increasing target eccentricity in far viewing versus near viewing conditions. Peripheral identification accuracy under similar conditions showed no such dissociation of near versus far processing with eccentricity. These data suggest that retinal information from near versus far space may be preferentially processed by substantially different neural substrates, with active modulation of the relative contributions of involved magnocellular-dorsal and parvocellular-ventral visual pathways, depending on various potential ecological uses of the retinal information.

Keywords

Peripersonal/extrapersonal space, detection, identification, eccentricity, dissociation, visual pathways

1. Introduction

Does the human brain process the same retinal information differently for objects in near versus far space? Based on neurophysiological and neuropsychological evidence from single cell recordings, brain lesions, and clinical studies, there is considerable evidence that visual information for near space (peripersonal, within arm's reach) and far space (extrapersonal, beyond arm's reach) may be mediated by substantially different neural substrates in visual cortex (Cutting & Vishton, 1995; Grusser, 1983; Halligan & Marshall, 1991; Mountcastle, 1976; Pettigrew & Dreher, 1987; Previc, 1990, 1998; Rizzolatti, Gentilucci, & Matelli, 1985; Rizzolatti, Matelli, & Pavesi, 1983). In a series of studies most pertinent to the typical human case, Weiss and colleagues (Weiss et al., 2000; Weiss, Marshall, Zilles & Fink, 2003) showed that healthy human brains preferentially employ dorsal visuomotor processing areas when attending to and acting in near space, with greater ventral visuoperceptual processing observed with visual tasks in far space. From these and related findings above, it is possible that healthy human observers may process the same visual information quite differently when it is presented in near versus far space, considering the distinct functional characteristics of visual cortical areas seen to be preferentially active when working in near versus far space.

A degree of support for this general idea comes from studies of hemispheric attentional asymmetries in both clinical and normal populations. In human patients with spatial hemineglect due to brain injury, classical attentional asymmetry findings have been observed to vary as a function of attending to near versus far space (Butler et al., 2004; Halligan & Marshall, 1991; Mennemeier, Wertman, & Heilman, 1992; Shelton, Bowers, & Heilman, 1990; Vuilleumier et al., 1998). More recently, similar behavioural distinctions have been observed with asymmetric attentional biases in healthy adults (a phenomenon known as pseudoneglect), with these normal attentional biases also varying as a function of near versus far viewing distance (Garza et al., 2008; Heber et al., 2010; Longo & Lourenco, 2006; McCourt & Garlinghouse, 2000; Varnava et al., 2002).

While encouraging, these near/far effects on hemispheric bias are not easily interpretable with respect to the neurological dissociations in processing of near versus far space reported by Weiss and colleagues (2000, 2003). The present study sought to discover a functional dissociation for visual processing in near versus far space, using more fundamental visual tasks—namely spatial detection and object identification. We conducted a series of five experiments, incorporating either simple detection/localization or object identification tasks, in a range of single- and dual-task situations. In all experiments, visual displays were manipulated so that stimuli were always matched for size (subtended angle), contrast and luminance across near and far viewing conditions. With retinal information thus matched between near and far viewing conditions, we sought to observe behavioural dissociations of typical visual performance measures across processing in near versus far space.

2. Experiment 1. Central identification + peripheral detection

A divided attention task was employed to encourage participants to focus on the center of a visual display while detecting a peripheral target. Participants' task was to identify a letter presented briefly at the center of a display, and to detect the location of a white spot flashing simultaneously on the periphery, positioned randomly around the center at various eccentricities and directions. This visual dual task was performed in blocks of near and far viewing distance conditions alternatively.

2.1. Method

2.1.1. Participants

Ten (3 male, 7 female) undergraduate students taking introductory psychology course at McMaster University participated in Experiment 1 for a course credit. All had normal or corrected to normal vision and ranged in age from 17 to 20 years (mean 18.80, SD ±1.03).

2.1.2. Apparatus, stimuli and procedure

The central target was a white letter (0.68 º × 1.08 º, 18.04 cd/m^2) on a green patch (1.32º × 1.32 º, 3.80 cd/m^2), briefly presented on the center of the screen. It was chosen randomly from the letter set: E, F, H, and L. The peripheral target was a filled white circle (1.20º diameter, 18.58 cd/m^2) that could appear at one of 32 positions around the center, on a grey background (4.25 cd/m^2). The 32 peripheral positions were arranged into eight evenly spaced radial spokes; each spoke contained four locations at eccentricities of 5º, 10º, 15º, and 20º from the center. At the beginning of each trial, a filled light green circle (4.00º diameter, 3.53 cd/m^2) was presented at the center and 32 unfilled white circles (1.50º diameter, 18.58 cd/m^2) were presented at all of the possible positions where the peripheral target might appear (Fig. 1a). Upon hearing a brief auditory cue, participants fixated on the central green circle; 1.2 sec later, the central fixation and peripheral place holders disappeared, and the central and peripheral targets were presented simultaneously on screen (Fig. 1b) for a brief duration previously determined for that block of trials. After the brief display of the two targets, a box (4.10 º × 4.10º) with light blue random texture (64×64 pixels in blue-green and white, 4.11 cd/m^2 on average) masked the central position; meanwhile 32 checkerboard masks (1.52 º × 1.52 º, 19.32 cd/m^2 at white, 1.96 cd/m^2 at black) covered all of the possible peripheral target positions. Eight radial arms textured with light blue random dots (elongated 64×64 pixels in blue-green and white, 6.14 cd/m^2 on average) were also presented to cover the eight possible peripheral directions behind the checkerboard masks, serving as additional masks to reduce the ceiling effect on peripheral performance at inner eccentricities. For a trial response, the mouse cursor and four central letters were presented 1.5 sec later after the appearance of the masks. The participant used the mouse to select one out of the 4 letters to report the central target identity, and to select one out of the eight radial arms to indicate the direction of the peripheral target (Fig. 1c).

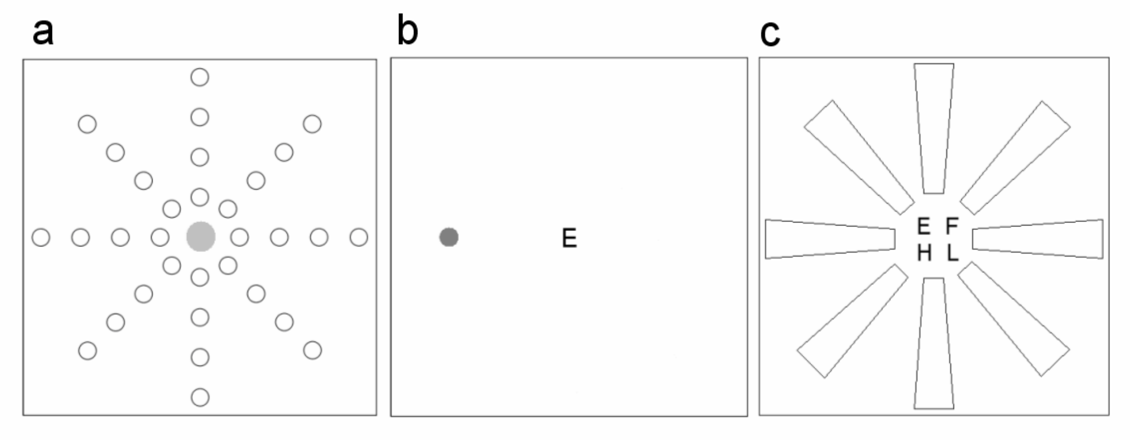

Figure 1. Schematic graphs of Central identification + peripheral detection task in Experiment 1. (a) Central focus and the peripheral place holders. (b) Central target and the peripheral target. (c) Choices for the central target and the peripheral directions.

The same visual task was performed under two viewing conditions. In the near condition, a 40.9 cm × 32.5 cm visual image was projected from the back of a white screen. A chin rest was used to maintain a 39 cm viewing distance. In the far condition, the same screen was positioned further away to show a 140 cm × 112 cm image from another projector. The subject sitting on a chair would also move back to a pre-marked position and kept a viewing distance of 133 cm. As a result, the visual image would cover the same retinal angle in both the near and far conditions. The two projectors (both DLA SX-21, JVC Inc.) were connected to a computer with an NVIDIA Quadro FX 3400 video adapter, receiving identical video signals from the computer, with one projector dedicated to presenting near stimuli, and the other to far stimuli. The projectors were physically aligned with one on top of the other, and matched for projection geometry and luminance calibrated through a photometer at two luminance levels (white and 50% grey).

Participants completed four to six practice blocks (the number determined by the experimenter), followed by eight experimental blocks. Each block contained 16 trials. There was a 1 to 3 minute break between blocks. The near versus far viewing condition alternated every block, with the starting condition counterbalanced across participants. Across the experiment, the same set of target stimuli were used for both near and far conditions, with trial order randomized separately within near and far conditions. Practice blocks were used to familiarize participants with the task, and also to titrate the stimulus presentation duration to equate relative performance levels across participants and avoid floor and ceiling performance effects in individual participants. Practice blocks began with a target duration of 374 ms. Target duration was decreased across subsequent practice blocks, to achieve peripheral target accuracy of approximately 50% to 60%. Target durations (34-85 ms) were determined for each participant individually, and were kept constant across all experimental blocks once determined in the practice blocks. The entire experimental session lasted approximately 50 minutes. The same procedure was used for all the subsequent experiments.

2.2. Results and discussion

For this and subsequent dual task experiments, central letter identification performance was at ceiling regardless of peripheral target eccentricity, in both near and far viewing conditions. For brevity and clarity, we concentrate our analysis and discussion on peripheral visual performance. Mean peripheral target detection accuracy data (correctly indicating in which of eight radial arms a peripheral dot stimulus appeared) are shown in Figure 2a. For this and subsequent experiments, data were assessed by a 4 (eccentricity) by 2 (viewing distance) repeated measures ANOVA. Peripheral detection accuracy declined with increasing eccentricity, $F(3, 27) = 22.864$, $p < 0.001$, $\eta^2=0.718$. A main effect of viewing distance was also observed, $F(1,9) = 6.878$, $p = 0.028$, $\eta^2=0.433$, with participants better able to detect peripheral targets in the near condition compared to the far condition, despite equivalent retinal size and luminance of all stimuli. This near/far difference varied systematically with eccentricity, with peripheral target detection accuracy declining rapidly in the far condition, compared to a milder decline with eccentricity in the near condition, supported by the interaction of eccentricity and viewing distance, $F(3, 27) = 11.355$, $p < 0.001$, $\eta^2 = 0.558$.

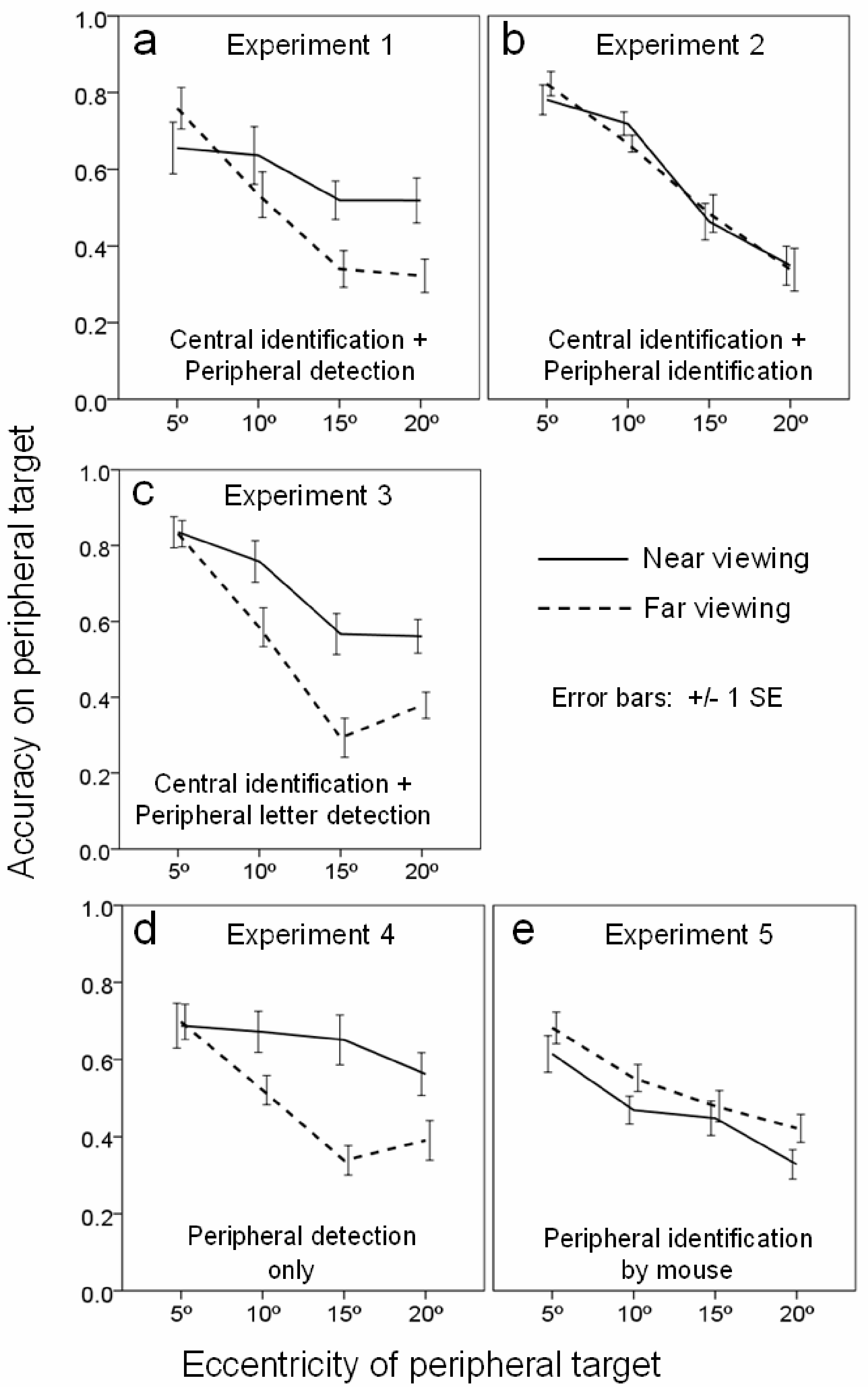

Fig. 2. Visual accuracy on peripheral targets as a function of eccentricity tested by 5 perceptual tasks in near (solid lines) and far (dotted lines) viewing conditions.

3. Experiment 2. Central identification + peripheral identification

3.1. Method

3.1.1. Participants

Twelve (2 male, 10 female) undergraduate students taking introductory psychology course at McMaster University participated in Experiment 2 for course credit. All had normal or corrected to normal vision and ranged in age from 18 to 22 years (mean 18.83, SD ±1.34).

3.1.2. Stimuli

Experiment 2 repeated most of the elements of Experiment 1, with the substitution of letter identification instead of simple dot detection as the peripheral task, still as a dual task with the same central letter identification task. All the possible positions for the targets and masks were the same as in Experiment 1, but there were no placeholder circles indicating the possible peripheral locations before the presentation of the peripheral target letter. The peripheral target was a white letter presented on one of the 32 peripheral positions. Following initial pilot testing to establish ranges of ceiling and floor effects for peripheral letter identification at different eccentricities, the size of peripheral letter stimuli and corresponding masks were scaled by factors of 1, 1.28, 1.56, and 1.84 at 5º, 10º, 15º and 20º eccentricities respectively, in comparison to the size of the central letter and masks in Experiment 1, but with each maintaining the same luminance. For each trial, the central letter and the peripheral letter were randomly chosen from a set of 17 letters (all letters excluding W, G, I, M, Q, U, Y, F, and O in order to reduce the variation in identification difficulty). The procedure for each trial was similar to that in Experiment 1. Participants reported the central and peripheral letters by typing the two letters on a computer keyboard in order (central then peripheral) following each trial. To avoid confusion between positions of central and close peripheral targets, 32 light brown dots were displayed on all the possible positions of the peripheral target at the responding phase.

3.2. Results and discussion

Mean peripheral letter identification accuracy data are shown in Fig. 2b. As expected, a strong main effect of eccentricity was observed, $F(3, 33) = 47.732$, $p < 0.001$, $\eta^2 = 0.813$, even with peripheral targets scaled progressively larger with eccentricity. There was no main effect of the viewing distance $F(1, 11) = 0.001$, and no interaction between peripheral target eccentricity and viewing distance $F(3, 33) = 0.669$.

The absence of any influence of near versus far viewing condition in Experiment 2 is markedly different from the results seen in Experiment 1. In comparing the two experiments, it is possible that different processes may be involved when simple detection of peripheral stimuli is required (as in Experiment 1). The need to identify a peripheral stimulus may recruit additional common processes in both near and far viewing conditions, obscuring the behavioural differences seen in Experiment 1. To rule out the possibility that the different patterns of performance between Experiment 1 and Experiment 2 was due to the effect of different luminance, size, shape or spatial frequency in stimuli, (e.g. dot versus letter for peripheral target), Experiment 3 asked participants to simply detect the appearance (not identify) the peripheral letter stimuli used in Experiment 2, in a similar dual task experiment.

4. Experiment 3. Central identification + peripheral letter detection

4.1. Method

4.1.1. Participants

Ten (1 male, 9 female) undergraduate students taking introductory psychology course at McMaster University participated in Experiment 3 for course credit. All had normal or corrected to normal vision and ranged in age from 18 to 22 years (mean 19.60, SD ±1.57).

4.1.2. Stimuli

Stimuli included a central letter plus a size-scaled peripheral letter. As in Experiment 1, participants also used the computer mouse to indicate the identity of the central letter, and then indicate in which of the eight radial arms the peripheral letter was presented, regardless of its identity. Central and peripheral masks and the 8 radial arms indicating the potential stimulus positions were used as in Experiment 1. Different from Experiment 1 and 2, the peripheral masks in this experiment were solid green boxes. We chose not to use the checkerboard masks used in the earlier two experiments to reduce the requirement for pattern discrimination between test stimulus and its mask. Sizes of peripheral target letters, placeholders and masks were scaled by a factor of 0.91, 1.21, 1.51 and 1.81 relative to the central target at 5º, 10º, 15º and 20º eccentricities respectively, but maintained the same luminance, in order to avoid ceiling or floor effects at different eccentricities. The central target was always one of the four letters E, F, T and L. The peripheral target was always one of the four letters K, N, H and Z.

4.2. Results and discussion

Mean peripheral letter detection accuracy data are shown in Fig. 2c. The expected main effect of eccentricity was significant, $F(3, 27) = 21.627$, $p < 0.001$, $\eta^2 = 0.706$. There was a main effect of viewing distance $F(1, 9) = 23.710$, $p < 0.001$, $\eta^2 = 0.725$, and a significant interaction of eccentricity and viewing distance, $F(3, 27) = 6.598$, $p = 0.002$, $\eta^2 = 0.423$. Peripheral detection accuracy decreased rapidly over greater eccentricities in the far viewing condition, but decreased much less dramatically in the near viewing condition. These results for peripheral letter detection replicate those for peripheral dot detection in Experiment 1, and are a sharp contrast to the lack of any near/far differences with peripheral letter identification in Experiment 2.

Experiment 1, 2, and 3 showed that peripheral detection (but not identification) of retinally equivalent visual stimuli may involve substantially different processes for visual presentations in near and far space. However it is not clear whether this conclusion can be generalized beyond the tasks of divided attention used in these experiments, we thus conducted two additional experiments to test this phenomenon outside of a dual task paradigm. Experiment 4 sought to replicate and generalize the near/far differences in peripheral dot detection seen in Experiment 1, but without any central task, where participants' primary and only goal is to detect the peripheral target.

5. Experiment 4. Peripheral detection only

5.1. Method

5.1.1. Participants

Ten (5 male, 5 female) undergraduate students taking introductory psychology course at McMaster University participated in Experiment 4 for course credit. All had normal or corrected to normal vision and ranged in age from 18 to 26 years (mean 19.33, SD ±2.27).

5.1.2. Stimuli

This task was modified from Experiment 1 by removing the central target. Without the central focus, there were 32 white circles indicating the possible positions before the appearance of the peripheral target, a white dot. Participants were asked to indicate in which of eight radial arms a peripheral target was presented, by clicking with a computer mouse following stimulus and mask presentation. The size of the peripheral targets, masks and placeholders were scaled by factors of 0.96, 1.08, 1.20 and 1.32 at 5º, 10º, 15º and 20º eccentricities respectively, with luminance kept constant. A filled light green circle (4.00º, 4.82 cd/m^2) appeared centrally 1.5 sec after mask presentation to signal participants to indicate their response with the mouse cursor.

5.2. Results and discussion

Mean peripheral dot detection accuracy data are shown in Fig. 2d. The expected main effect of eccentricity was observed, $F(3, 27) = 12.101$, $p < 0.001$, $\eta^2 = 0.573$. As in Experiments 1 and 3, there was a main effect of viewing distance, $F(1, 9) = 15.059$, $p = 0.004$, $\eta^2 = 0.626$, and a significant eccentricity by viewing distance interaction, $F(3, 27) = 10.491$, $p < 0.001$, $\eta^2 = 0.538$. Single-task peripheral detection accuracy declined rapidly with greater eccentricities in the far viewing condition, with the near viewing condition showing a much slower decline with increasing eccentricity.

Experiments 1, 2 and 3 used a form of dual task, in which observers had to divide their attention between central and peripheral requirements. Using a single task with only a peripheral target, Experiment 4 replicated the differential behavioural performance in near versus far space seen in Experiments 1 and 3, for detecting a briefly displayed and retinally equivalent peripheral target. This makes it unlikely that the observed processing differences for near versus far visual detection are a result of having to divide attention across tasks or between central and peripheral targets, and suggests that these near versus far differences more likely reflect a general phenomenon of differential perceptual processing of retinally equivalent visual stimuli in near versus far space.

6. Experiment 5. Peripheral identification by mouse

Similar to Experiment 4, in Experiment 5 we also used a task focusing only peripheral processing. Moreover, previous research has suggested that the presence of motor action may be important for differences in behavior relating to visual processing of near versus far space (Pizzamiglio et al., 1989). It is possible that the absence of near versus far processing differences in Experiment 2 was due to using a keyboard to make letter choice responses, instead of using a mouse to identify the response presented in the visual field. This visual guidance of action in mouse-based responding was used in our Experiments 1, 3 and 4, where we have observed differential near versus far effects. To rule out the potential effect of visually guided action on near versus far task performance, Experiment 5 asked participants to identify a peripheral target letter (as in Experiment 2), but this time to select a response on screen using a computer mouse, with only a single peripheral stimulus and task.

6.1. Methods

6.1.1. Participants

Twelve (3 male, 9 female) undergraduate students taking introductory psychology course at McMaster University participated in Experiment 5 for course credit. All had normal or corrected to normal vision and ranged in age from 19 to 24 years (mean 21.42, SD ±1.78).

6.1.2. Stimuli and Procedure

There was no central target. The peripheral target and the masks were the same as that in Experiment 3, but the participants were asked to indicate the identity of the peripheral target letter by pointing and clicking with a mouse. Different from Experiment 3, after the masks were presented, a set of 4 possible letters were presented at the position where the peripheral target had appeared 1.2 sec ago, waiting for the participant's response.

6.2. Results and discussion

Mean peripheral letter identification accuracy data are shown in Fig. 2e. An expected main effect of eccentricity was observed, $F(3, 33) = 30.395$, $p < 0.001$, $\eta^2 = 0.734$. Peripheral identification accuracy was better in the far viewing condition compared to near viewing, $F(1, 11) = 7.38$, $p = 0.020$, $\eta^2 = 0.402$, across all eccentricities. This was opposite to participants' performance in peripheral detection in Experiment 4, where observers performed better in detecting peripheral stimuli in near viewing conditions compared to far viewing. The interaction of eccentricity and viewing distance was not significant, *F*(3, 33) = 0.430, indicating that participants' accuracy in identifying peripheral target letters changed in the same way across eccentricities in the visual field for visual stimuli in both near and far space. The comparable slopes of accuracy performance for near and far conditions over visual field eccentricities replicates the peripheral identification findings from Experiment 2, although participants here used the mouse to make relevant visual-manual responses within the visual display, instead of typed keyboard responses. From these data, differences in visual processing for equivalent stimuli in near versus far space do not seem to be due to response mode differences. These findings are consistent with the neuroimaging result that separable neural representations primarily engaged in processing near versus far space were not modulated by the motor or perceptual demands of the task (Weiss, et al., 2003).

7. General Discussion

By testing healthy human observers, the present study demonstrated a behavioural difference in detecting briefly displayed and retinally equivalent visual stimuli in near (peripersonal) versus far (extrapersonal) space. In three experiments that required participants to localize a briefly presented peripheral target, performance declined with increasing target eccentricity at a steeper rate for stimuli in far space compared to near space (see Fig. 2a, c, d). We note that accuracy was not simply better in one condition over the other — a difference that could be the result of unmatched luminance of visual stimuli in near versus far conditions, or of participants' preference for a near or far viewing distance. In contrast, when participants had to identify (instead of just detect) comparable peripheral targets, slopes of identification accuracy over target eccentricity were the same for near and far conditions (see Fig. 2b, e).

Differences in peripheral detection accuracy slopes over eccentricity for retinally equivalent stimuli in near versus far space (Experiments 1, 3 and 4) suggest that the same retinal information was processed differently when perceived to be in near versus far space, and may represent distinct neural processes or mechanisms contributing differentially for near versus far visual information. One such possibility is the anatomical and functional distinctions between dorsal and ventral visual processing streams (Mishkin & Ungerleider, 1982; Goodale & Milner, 1992). Previc (1990, 1998) has proposed that there are ecological advantages of near space being mediated predominantly by dorsal stream, and far space by ventral stream, an idea for which he cites both neuropsychological and neurophysiological evidence. Consistent with these ideas, in our present data the steep slope of detection accuracy across eccentricities in far space may reflect neuronal features of the ventral (predominantly parvocellular) system; the milder change of detection accuracy across eccentricities in near space may reflect emphasized visual processing in the dorsal (predominantly magnocellular) stream. This explanation is supported by the fact that the density of parvocellular ganglion cells (projecting mainly to ventral stream) declines much more rapidly from the fovea to the surrounding peripheral regions of the retina compared to that of the magnocellular ganglion cells (projecting mainly to dorsal stream) (Dacey

& Petersen, 1992; Tychsen, 1992).

In contrast to this near versus far processing dissociation for target detection, target identification performance showed equivalent accuracy functions across eccentricities for retinally equivalent stimuli in near and far space (Experiments 2 and 5). These data suggest that when performing stimulus identification, retinal information was processed in a similar manner for equivalent stimuli in both near and far space. Considering the separation of dorsal/ventral processes above, we suggest that target identification may require stimuli in both near and far space to be processed via ventral stream in order to extract detailed object information (e.g., Mishkin, Ungerleider & Macko, 1983), leading to similar identification performance in both near and far conditions.

Previously, behavioral findings suggesting dissociations between the neural representations of near and far visual space have been mainly provided through studies of brain-damaged patients (Ackroyd et al., 2002; Berti & Frassinetti, 2000; Halligan & Marshall, 1991; Keller et al., 2005). Although lesion studies can be used to infer whether specific brain areas are important for certain behavioral functions, they do not readily reveal the underlying mechanisms through which these processes occur. The present study suggests that the brain can actively modulate information processing in different visual pathways with the same retinal image, relative to stimuli appearing in near versus far space. This is consistent with previous neuroimaging results showing enhanced neural activity in dorsal or ventral streams corresponding to stimuli at near versus far viewing distances (Weiss et al., 2000, 2003). Such neural modulation may have ecological benefits — enhanced dorsal processing for near space would make information easier to integrate with the visual motor system and facilitate grasping or manipulating object within peripersonal space; enhanced ventral processing of far space would enhance visual identification of more distant objects, where coordination of interactive motor action is not relevant (Previc 1990, 1998).

In contrast to previous studies that measured human observers' left/right attentional bias, the present study employed some basic visual perception tasks to reveal visual differences in near versus far viewing conditions. The different performances in near versus far viewing in Experiment 1, 3, and 4 suggested that simple visual detection of the appearance of a briefly presented target could be processed by neural mechanisms in both ventral and dorsal cortical streams, with their contributions varying according to viewing distance. The indicated dorsal stream involvement of simple perception in the lack of on-line motor action is inconsistent with the perception-action model (Goodale & Milner, 1992; Milner & Goodale, 1995) which assumes that the ventral stream is specialized in visual perception processing whereas the dorsal stream works only for visual guidance of action. Based on new evidence incompatible with the perception-action model, recent studies (Glover, 2002; 2004; Glover & Dixon, 2001a; 2001b; 2001c; 2002a; 2002b; Glover et al., 2004) have suggested a planning-control model. According to this model, the traditional dorsal stream may be divided into two systems: The inferior parietal lobe (IPL) is specialized for planning actions whereas the superior parietal lobe (SPL) is specialized in on-line control of action. Consistent with this planning-control model, our data may indicate that the simple visual perception for targets in near space can be processed in IPL (part of the dorsal stream) so that the visual information would be easily used for planning of motor action but not necessarily for the on-line control of action.

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Chapter 3

FOREWORD

Experiments in Chapter 2 employed some visual tasks other than the traditional line bisection task to measure visual performance in near and far viewing. The observed different patterns of visual performance in visual detection task regarding near and far viewing may reflect the neuronal characteristics of the visual pathways that were differentially involved in processing information arising from near and far spaces. The relevant neuronal feature is that the density of the ganglion cells declines more steeply from the fovea to the periphery of the retina in the parvocellular pathway as compared to the magnocellular pathway. The experimental results of Chapter 2 suggested that the neural processing may be switched between the parvo-ventral and magno-dorsal pathways according to viewing distance. To further investigate how the human visual system processes visual information arising from near and far space, experiments in Chapter 3 were designed to utilize another neuronal feature to dissociate the neural processing between magnocellular and parvocellular pathways. Specifically, achromatic information can be processed in both parvocellular and magnocellular pathways while chromatic information can only be processed in the parvocellular pathway. If as suggested in Chapter 2, that the change of viewing distance would lead to a change of contribution for information processing between ventral and dorsal streams, differences in visual performance regarding near and far viewing should be observed when perceiving stimuli in isoluminant colour.

Differential Detection of Visual Targets Presented in Near and Far Space and its Dependence on the Chromatic Properties of the Targets

Abstract

Healthy human observers were asked to detect a spot briefly presented at the peripheral visual field in near and far viewing conditions, with matched luminance and visual angle for the visual display in the two conditions. The visual accuracy was higher in near viewing than far viewing when detecting an achromatic white spot in either high or low contrast. However, participants showed much lower detection accuracy in near viewing compared to far viewing when the visual target was an isoluminant green spot. Receiving equivalent retinal information, the remarkably different visual ability in detecting isolumiant target presented at near versus far space suggests that a neurologically intact brain can actively modulate the neural efficiency for visual detection processing in the parvo-ventral pathway according to viewing distance.

1. Introduction

Do human observers perceive the visual information arising from near and far space differently? Based on evidence from single cell recordings, brain lesions, and clinical studies, researchers have suggested that there are differential visual representations for near (peripersonal, within arm’s reach) and far (extrapersonal, beyond arm’s reach) space in the human visual system (Cutting & Vishton, 1995; Grusser, 1983; Mountcastle, 1976; Halligan & Marshall, 1991; Pettigrew & Dreher, 1987; Previc, 1990, 1998; Rizzolatti, Gentilucci, & Matelli, 1985; Rizzolatti, Matelli, & Pavesi, 1983). Consistent with this view, brain imaging data showed elevated neural activity in dorsal or ventral stream of visual cortex when healthy human observers performed visual tasks in near viewing or far viewing conditions respectively (Weiss et al., 2000, 2003). Previc (1990) suggested that there is ecological advantage for visually guided action in peripersonal (near) space and visual recognition in extrapersonal (far) space if the dorsal (with rich connections to motor areas) and ventral (solely vision) cortical streams are specialized in processing visual information from near and far space respectively. However, little behavioural evidence supporting this functional dichotomy has been found in healthy human observers given that the neural functions differ so much between the ventral and dorsal cortical streams. Regarding near and far viewing, some behavioural distinctions have been observed with asymmetric attentional biases in healthy adults (a phenomenon known as pseudoneglect), with the normal leftward attentional biases varying as a function of near versus far viewing distance (Garza et al., 2008; Heber et al., 2010; Longo & Lourenco, 2006; McCourt & Garlinghouse, 2000; Varnava et al., 2002). However, these near/far effects on hemispheric bias are not easily interpretable with respect to the dorsal/ventral dissociations in processing information from near versus far space reported by Weiss and colleagues (2000, 2003), because the measured behavioural performance could not reflect the specific neural features in dorsal and ventral streams.

A recent study in our lab showed a better performance for near viewing compared with far viewing in visual detection tasks but not in visual identification tasks (see Chapter 2). In the present study, in order to explore the possible dorsal/ventral involvement in such a near/far effect, we examined the detection performance further by manipulating the luminance and chromatic properties of the target. This is because the dorsal stream mainly receives input from the magnocellular pathway which is only sensitive to luminance contrast and ventral stream mainly receives input from the parvocellular pathway which is sensitive to both chromatic and luminance contrast (Livingstone & Hubel, 1988). Visual display was presented in near or far viewing distance with matched visual angle and luminance to ensure equivalent retinal information was received by observers in two viewing conditions.

2. Methods

2.1. Participants

Thirty six undergraduate students taking introductory psychology course at McMaster University participated in our three experiments for course credit. All had normal or corrected to normal vision and the passed the Ishihara color test.

Twelve (5 male, 7 female) students participated in Experiment 1 with their age ranging between 17 to 37 years (a mean of 20.58 ± 5.42 SD).

Twelve (9 male, 3 female) students participated in Experiment 2 with their age ranging between 18 to 25 years (a mean of 18.92 ± 2.02 SD).

Twelve (5 male, 7 female) students participated in Experiment 3 with their age ranging between 18 to 23 years (a mean of 19.17 ± 1.70 SD).

2.2. Apparatus

The same visual task was performed under 2 viewing conditions in a dimly lit room. In the near viewing condition, a 40.9 cm × 32.5 cm visual image was projected from the back of a white screen. A chin rest was used to maintain a 39 cm viewing distance. In the far condition, the screen was moved to a further place in order to make a 140 cm × 112 cm image from another projector. The subject sitting on a chair would also move back to a pre-marked position and kept a 1.33 m viewing distance from the screen. As a result, the visual image subtended the same retinal angle in both the near and far viewing conditions.

Two DLA SX-21 projectors (JVC Inc.) were connected to a computer with a NVIDIA Quadro FX 3400 video adapter. Receiving identical video signals from the computer, each of the projectors, one on top of the other, could cast the same image to a mobile screen, but in small or large size at near or far distance respectively. To ensure the retina of the observer received equivalent visual stimuli in both the near and far viewing conditions, the smaller image in near viewing condition and the larger image in far viewing condition were adjusted to same luminance at corresponding points on the screen. This was done by adjusting the brightness and the contrast of the two projectors to make both the white portion and grey portion of a test image to be constant luminance across near and far viewing conditions, measured by a photometer. This obtained parameter setting would be used in all three experiments.

2.3. Stimuli and procedure

Experiment 1: Detection of the white spot

The visual target was a white spot (9.5 cd/m^2) that could appear at one of the 32 positions on a grey background (2.8 cd/m^2). The 32 positions were arranged into eight evenly spaced radial spokes, and each spoke contained four locations at the eccentricity of 5º, 10º, 15º, and 20º from the center. Before the onset of the visual target, upon a brief tone, 32 unfilled white circles (9.5 cd/m^2) served as place holders were presented for 1200 ms at all the possible positions where the peripheral target might appear (Figure 1a). At the time when the 32 place holders disappeared, a white spot was presented at one of the 32 locations for a brief duration determined by experimenter for the block of trials (Figure 1b). After the brief display of the target, 32 checkerboard masks (17.6 cd/m^2 at white, 1.2 cd/m^2 at black) covered all the possible positions where the white spot might had appeared. Eight radial arms textured with random pixels（elongated 64×64 pixels in grey and white, average 4.1 cd/m^2）also presented on the back of the checkerboard masks, marking the 8 possible directions the visual target had appeared (Figure 1c). To avoid the visual confusion between the target and the mouse cursor, the mouse cursor would appear from hiding 1.2 seconds after the onset of masks, indicated by the appearance of a filled circle (3.6º in diameter, textured with random grey pixels 2.4 cd/m^2 in average) in the center of the visual field. Then participants would move the mouse cursor onto one of the eight arms and click to report the location of the target, regardless of eccentricity. The target was scaled to the size of 1.4º, 1.7º, 2.0º, and 2.3º in visual angle when appearing at the eccentricity of 5º, 10º, 15º, and 20º from the center in order to avoid the ceiling and floor effect of visual performance at the inner and outer eccentricities. The diameters of the 32 place holders were 1.2 times of that of the white spot at the corresponding eccentricity. The width and height of the 32 masks were 1.13 times the diameter of the place holders at the same locations.

To avoid the imbalanced influence of the practice effect or fatigue on the visual performance tested in near and far viewing conditions, the experimenter would always switch to the other condition, either near or far, for the next block. This was done by moving the screen and switching the projectors during the break between two blocks, in both the practice session and the experimental session. Therefore the experimental session was interlaced by 4 blocks of near condition and 4 blocks of far condition alternatively, with starting condition counterbalanced across participants. The same set of data determining the target position for every trial were used in both the near and far conditions, but the order of the trials was randomized independently for the two conditions.

The practice session was started with a block at the target duration of 374 ms. Then, in the following blocks the target duration was reduced by the experimenter in order to let the participant perform at 50 to 70 percent correct within the block. The optimal target duration was determined in 4 to 6 practice blocks, which was then used as the target duration for this participant in the following 8 experimental blocks for both near and far viewing conditions. The entire experiment lasted about 50 minutes.

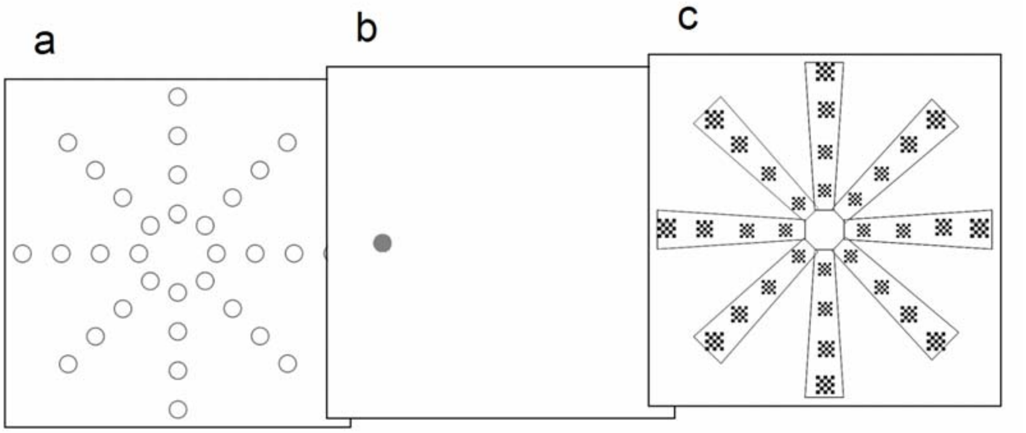

Figure 1. Schematic graphs of Detection for white spot task in Experiment 1. (a) Place holders. (b) Target. (c) Masks and selections for response.

Experiment 2: Detection of the green spot

The task was modified from Experiment 1 by changing the white spot and the 32 unfilled white circles (place holders) into isoluminant green, i.e. equal luminance with the grey background. The target was scaled to the size of 1.4º, 1.8º, 2.1º, and 2.5º in visual angle when appearing at the eccentricity of 5º, 10º, 15º, and 20º from the center.

The scaling factor for increasing the size of peripheral target at each outer eccentricity was larger than that of Experiment 1 because participants' performance would be much worse for detecting the isoluminant target at the outer eccentricity than for the inner eccentricity provided the same scaling factor was used.

The isoluminant green was determined for each participant before the practice session. A flicker patch alternated between green and the background grey at 15 Hz. Subjects adjusted the brightness of the green until the perceived flicker was minimized. The optimal brightness of green was used for the isoluminant target in the practice and experimental session. All the other visual stimuli and procedures were the same as in Experiment 1.

Experiment 3: Detection of the grey spot

The task was modified from Experiment 1 by changing the white spot and the 32 unfilled circles, i.e. place holders, into low luminance grey (3.2 cd/m^2). All the other visual stimuli and procedures were the same as in Experiment 1.

3. Results

Experiment 1: Detection for white spot

For this and the subsequent experiments, visual accuracy indicated by percent correct were assessed by a 4 (eccentricity) × 2 (viewing distance) repeated measures ANOVA. There was no main effect of eccentricity (F (3,33)= 0.793, p=0.507), indicating participants' detection accuracy was similar at inner and outer eccentricities after the target was scaled progressively larger with the increase of eccentricity. A main effect of viewing distance (*F*(1,11)= 5.327, *p*=0.041, η=0.326) indicated that participants' overall performance was moderately better in the near viewing condition than in the far viewing condition (Figure 2a). On average for the 4 eccentricities, the difference of the accuracy between near and far conditions was 0.363 times their standard deviation. No eccentricity by viewing distance interaction was observed (*F* (3, 33) =0.646).

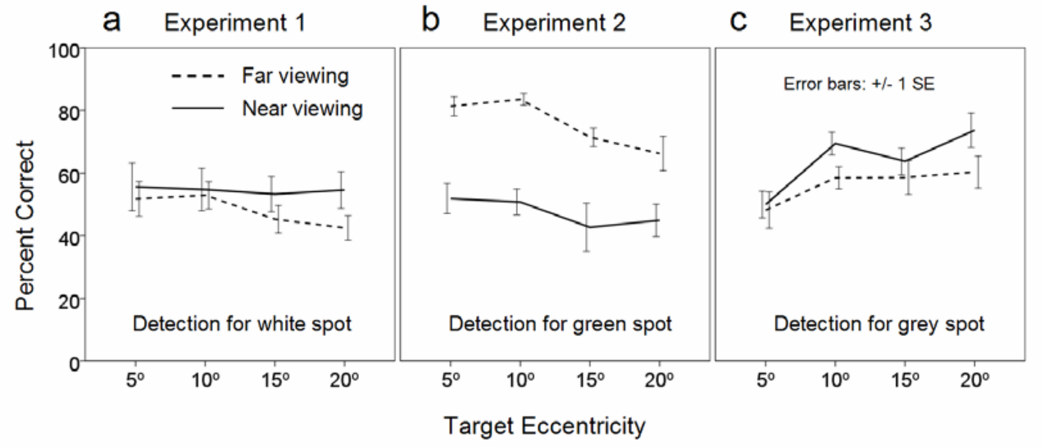

Figure 2. Visual accuracy as a function of target eccentricity in detection a peripheral spot in near (solid lines) and far (dashed lines) viewing conditions. Error bars indicate standard error of the mean.

Experiment 2: Detection for green spot

In detecting the isoluminant visual target, participants' performance was poorer in near viewing condition than in far viewing condition (*F* (1, 11) = 47.122, *p* < 0.001, η=0.811). On average for the 4 eccentricities, the difference of the visual accuracy between two viewing distance conditions was 1.324 times their standard deviation, which was much larger than that in Experiment 1 (0.363). The average target duration (112 ms) in Experiment 2 was also much longer than that in Experiment 1 (57 ms) ($t(11)=7.38$, $p<0.01$). Several participants needed greater number of practice blocks for near conditions than for far conditions in order to make the performance in experimental blocks not diverge to ceiling and floor in two viewing conditions when using the same target duration. Note that the near/far difference was reversed when participants were asked to detect a green spot in Experiment 2 instead of a white spot in Experiment 1, indicating that the visual ability to detect chromatic change was worse in near viewing than in far whereas better in near viewing than in far when detecting luminance change (Figure 2a, b). A main effect of eccentricity ($F\ (3,33)= 4.556$, $p=0.009$, $\eta=0.293$) indicated the visual accuracy was worse at outer eccentricity compared with that at inner eccentricity, although the scaling ratio for target size across eccentricities was larger in Experiment 2 than in Experiment 1. There was no eccentricity by viewing distance interaction ($F(3,33) =0.811$) (Figure 2b).

Experiment 3: Detection for grey spot

When the luminance-contrast between the target and the background was small, the average target duration as 98 ms, which was much longer than that in Experiment 1 ($t(11)=7.726$, $p<0.001$), but marginally shorter than that in Experiment 2 ($t(11)=2.081$, $p=0.049$). Similar as the results in Experiment 1, visual accuracy was moderately higher in near viewing condition than in far viewing condition (*F* (1, 11) = 5.742, *p* = 0.035, η = 0.343) (Figure 2c). On average for the 4 eccentricities, the difference of the visual accuracy between two conditions was 0.413 times their standard deviation, which was similar to that in Experiment 1 (0.363) but much smaller than that in Experiment 2 (1.432). There was no eccentricity by viewing distance interaction (*F*(3,33)=1.092). A main effect of eccentricity (*F* (3,33)= 6.250, *p*=0.002, η=0.362) indicated the performance was better when detecting target at outer eccentricities than that at inner eccentricities, although the same scaling factor for changing target size across eccentricities was used as that in Experiment 1 which did not show effect of eccentricity.

4. Discussion

By testing healthy human observers in a simple visual perception task, the present study demonstrated a clear near/far difference in detecting a briefly presented stimulus. Moreover, the difference in near/far visual performance can be dramatically reversed depending on the stimulus properties, most likely due to the sensitivity to different stimulus attributes by dorsal and ventral streams.

According to the hypothesis proposed by Previc (1990), the ventral and dorsal cortical streams are mainly involved in processing of far and near visual space respectively. While the dorsal stream mainly receives input from magnocellular pathway which is only sensitive for luminance-defined stimuli, the ventral stream normally receives inputs predominantly from parvocellular pathway which is sensitive for both luminance-defined and chromatically defined stimuli. Therefore when an achromatic luminance-defined stimulus is presented, the processing of near target could be either comparable to that of the far target or could even be enhanced. In contrast, according to Previc's near/far model, because only the parvocellular pathway but not the magnocellular pathway provides information about chromatic stimuli, when an isoluminant chromatic target is presented, the processing of near targets should be greatly impaired compared to that for far targets.

The results of our three experiments are consistent with the predictions based on this dorsal/ventral hypothesis. Experiment 1 showed a slight but statistically significant enhancement of performance for near targets compared to that of the far targets. In contrast, results of Experiment 2 showed a dramatic reversal of this pattern of performance: a much greater impairment of performance for near targets compared to that of the far targets.

Results found in Experiment 2 using isoluminant targets offer important behavioural evidence for the underlying neural mechanisms for near/far processing. It is well known that the information of an isoluminant green target is primarily transmitted through the parvocellular pathway and subsequently processed in the ventral stream of visual cortex (Livingstone & Hubel, 1988). When experiencing the equivalent retinal information, the parvo-ventral pathway of the visual system receives the same amount of visual inputs although in near and far viewing conditions. As a result of neural processing, the behavoural difference in near viewing versus far viewing would indicate the change of visual processing in the parvocellular pathway or/and in the ventral stream of visual cortex when the viewing condition changes. Therefore, the much worse performance in detecting an isoluminant target in Experiment 2 in near viewing compared to far viewing indicated the information processing in parvo-ventral pathway was greatly reduced in near viewing than in far viewing. In other words, in analyzing the equivalent retinal information for visual detection task, the visual processing in parvo-ventral pathway was much more effective when the visual target is presented in far space compared to near space, indicated by the much higher visual accuracy in far viewing. Experiments 1 and 3 revealed important baseline performance. Although we observed statistical significant difference between near and far conditions, because luminance information of the visual target can be transmitted through both parvocellular and magnocellular pathways and processed in both dorsal and ventral streams, conclusive conclusion about the neural mechanisms from those experiments alone can not be generated.

It is important to point out that the near/far difference in visual performance found here could not be due to the unmatched visual angle, luminance or contrasts or participants' viewing preference for visual stimuli presented at near or far space, because Experiment 1 and 2 showed the opposite near/far difference. One might wonder that the extremely poor performance for near viewing in detecting isoluminant green target in Experiment 2 could be due to the inadequate visual information received by the eye, suggested by the required longer presentation duration for isoluminant target. In Experiment 3, participants were asked to detect a low contrast achromatic target, a task which was harder than that in Experiment 1 and also required longer presentation durations. Because the result of Experiment 3 was still quite similar to that of Experiment 1, we believe that the huge visual difference regarding near and far viewing found in Experiment 2 was not due to reduced information inputs or general task difficulty.

In conclusion, in contrast to previous findings for selective impairment in visual representations of the 3D space in neurological patients (Butler et al., 2004; Halligan & Marshall, 1991; Mennemeier, Wertman, & Heilman, 1992; Vuilleumier et al., 1998), the present study reports novel findings in healthy human observers demonstrating remarkable differences in visual processing of near and far space using simple visual detection tasks. Our data suggest that a neurologically intact brain can actively reduce or enhance the processing efficiency in parvo-ventral pathway of the visual system according to viewing distance.

Intuitively, in a scenario in which the retinal information from the near and far targets is equivalent, visual information from either near or far should be processed equally. However, we have demonstrated that visual information arising from near and far space is processed differently. It has been well established that some visual neurons are selective for certain stimulus attributes (e.g., orientation, direction etc.). Given the near/far visual behaviour observed in the present study, how information about the viewing distance can modulate the different involvement of neural pathways in perceiving near and far spaces would be an interesting topic to explore in the future.

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Chapter 4

FOREWORD

Although the results in Chapter 2 and Chapter 3 provide the behavioural evidence supporting the view that visual information about near and far visual spaces is preferentially processed in different neural subsystems, it is still unclear at which level of visual processing the supposed neural modulation takes place when the viewing distance changes. As indicated by data in Chapter 2 and Chapter 3, the viewing-distance related neural modulation could occur at the subcortical stage of visual processing, i.e., in the parvocellular and magnocellular pathways, or at the dorsal and ventral visual cortex.

One of the distinct functional differences between parvocellular and magnocellular pathways is the ability to process information in chromatic contrast. Most cells in the parvocellular pathway are sensitive to chromatic information while cells in the magnocellular pathway are color blind and respond only to achromatic contrast. Therefore, to dissociate the neural processing between the two visual pathways, the stimuli in the experiments of Chapter 4 were presented in either isoluminant green or in achromatic white. The different visual performance in perceiving the chromatic-contrast or luminance-contrast stimuli would provide evidence about the distinct visual mechanisms for processing information arising from near and far spaces, and more importantly, at which stage of the visual processing the viewing distance related neural modulation occurs.

Seeing differently in near and far: gating information in parvocellular and magnocellular pathways

Abstract

The notion that human visual processing for near (peripersonal) and far (extrapersonal) spaces is specialized in dorsal and ventral streams has been supported by visual behaviours of brain damaged patients and neuroimaging results of healthy human observers. We tested this hypothesis with a series of visual perception tasks, in which visual stimuli were presented in near or far space, with matched visual angle and luminance. Healthy human observers were asked to identify a letter briefly presented on peripheral visual field. In 4 experiments, the visual target, mask, or precue was presented in either achromatic white or isoluminant green in order to be differently processed in parvocellular and magnocellular pathways. Different patterns of near/far impact on visual accuracy across target eccentricities suggest that the change of viewing distance will lead to a modulation of information transmission in magnocellular and parvocellular pathways, and eventually result in different information processing in cortical visual subsystems. The behavioural data reported here suggest that LGN serves as a gatekeeper to regulate and redistribute visual information for later cortical analysis.

Key words: Near/far viewing, isoluminance, identification, magnocellular, parvocellular, LGN.

1. Introduction

Based on evidence from animal single cell recording, animal brain lesion, and human brain damage studies, researchers have suggested that visual information arising from near (*peripersonal,* within arm's reach) and far (*extrapersonal,* beyond arm's reach) space is processed predominantly by distinct neural structures in the human visual system (Cutting & Vishton, 1995; Grusser, 1983; Halligan & Marshall, 1991; Mountcastle, 1976; Pettigrew & Dreher, 1987; Previc, 1990, 1998; Rizzolatti, Gentilucci, & Matelli, 1985; Rizzolatti, Matelli, & Pavesi, 1983; but see Cowey, Small, & Ellis, 1994, 1999). Moreover, based on the observed lesion areas or neural activations in the brain relative to different visual performance in near or far viewing distances, it is tempting to assume that the encoding of near and far spaces are predominantly mediated by dorsal and ventral visual streams respectively (Butler et al., 2004; Halligan & Marshall, 1991; Mennemeier, Wertman, & Heilman, 1992; Previc, 1990, 1998; Vuilleumier et al., 1998; Weiss et al., 2000, 2003). If so, we should expect that healthy human observers rely more on dorsal stream when looking at near space, whereas rely more on ventral stream when looking at far space. Hereafter we refer this neural mechanism as the *Ventral/Dorsal* hypothesis.

In recent years, behavioural distinctions have been observed for asymmetric attentional biases in healthy adults (a phenomenon known as pseudoneglect), with normal attentional biases to the left of visual field also varying as a function of near versus far viewing distance (Garza et al., 2008; Heber et al., 2010; McCourt & Garlinghouse, 2000; Varnava et al., 2002; but see Thomas & Elias, 2010). Using basic visual perception tasks that are more directly related to the neuronal characteristics of different visual pathways, previous work in our lab (See Chapter 2) showed that visual detection ability was better and declined less with the increase of eccentricity in near viewing than in far viewing. In addition, another study in our lab also showed that when detecting an isoluminant green target, participants' performance was much poorer in near viewing condition compared to far viewing condition. However, the detection performance was moderately better in near viewing than in far viewing condition when the visual target was in achromatic white with high contrast or low contrast against the background (See Chapter 3). This different ability in detecting isoluminant targets influenced by near and far viewing distance suggested that the information processing in parvo-ventral pathway was greatly decreased when viewing distance changed from far to near. Although in accordance with the *Ventral/Dorsal* hypothesis which assumes a cortical modulation of information processing, such behavioural evidence and some previous neuropsychological and neurophysiological evidence about near/far visual processing can also be explained by a *LGN* hypothesis assuming a subcortical modulation. That is, more visual information is transmitted by parvocellular pathway when viewing at far compared to near, and thus results in more information received by the ventral stream of visual cortex. Likewise, when viewing at near space, more visual information is transmitted via magnocellular pathway and consequently leads to increased input and greater neural activation in dorsal cortical stream. In other words, for healthy human observers, the neural modulation according to viewing distance can occur at ventral and dorsal cortical streams or occur at a subcortical level, i.e. in parvocellular and magnocellular pathways.

The aim of the present study is to investigate human visual perceptual behaviour regarding near and far viewing, and more importantly, to test whether the viewing-distance related processing modulation, as suggested by Chapter 2 and 3, takes place at the subcortical level (the *LGN* hypothesis), which is earlier than the cortical level (the *Ventral/Dorsal* hypothesis) suggested by previous neurophysiological and neuropsychological evidence (Butler et al., 2004; Halligan & Marshall, 1991; Mennemeier, Wertman, & Heilman, 1992; Previc, 1990, 1998; Vuilleumier et al., 1998; Weiss et al., 2000, 2003). One important feature of the subcortical visual system is that the parvocellullar pathway is sensitive to both chromatic and achromatic change whereas the magnocellular pathway is virtually colour blind, through which only achromatic information can be transmitted (Livingstone & Hubel, 1988). Therefore, to decouple the visual processing in magnocellular and parvocellular pathways relating to near and far viewing, the components of visual stimuli, i.e. target and mask, would be presented in either achromatic white or isoluminant green in different experiments.

Another neuronal characteristic useful for distinguishing the parvocellular and magnocellular contribution to visual processing is the density distribution of the LGN cells. By labeling retrogradely from striate cortex, the parvocellular to magnocellular ratios of the LGN cells were shown to decrease with the increasing retinal eccentricity from fovea to periphery (Azzopardi, Jones, & Cowey, 1999). Similarly, the density of ganglion cells decreased more steeply from the fovea to the periphery of the retina in parvocellular pathway compared to magnocellular pathway (Dacey & Petersen, 1992; Tychsen, 1992).

In order to determine whether the near/far viewing distance related neural modulation occurs at the subcortical level of visual processing, i.e. following the *LGN* hypothesis, we asked participants to identify a briefly presented letter in the peripheral visual field, a task argued to be primarily processed by ventral visual stream which receives afferent inputs from both parvocellular and magnocellular pathways (Ferrera, Nealey, & Maunsell, 1992, 1994; Livingstone & Hubel, 1988) (Figure 4.3). In various experiments, the visual target would be isoluminant green and masked by an isoluminant green-and-grey checkerboard or by a black-and-white checkerboard; therefore their visual information can be processed differently in magnocellular and parvocellular pathways. The ability in perceiving these visual stimuli would be measured in near and far viewing distances, with the visual image adjusted to subtend equal visual angle and luminance in the near and far viewing conditions. Resembling the different distributions of ganglion cell density in the two pathways, two different slopes for visual accuracy over target eccentricities in near versus far viewing would indicate the weight change of information transmission between parvocellular pathway and magnocellular pathway. If so, the *LGN* hypothesis would be supported indicating the near/far modulation of visual processing occurs before the ventral cortical processing.

2. Methods

2.1. Participants

Forty-eight undergraduate students taking introductory psychology course at McMaster University participated in our four experiments for course credit. All had normal or corrected to normal vision and passed the Ishihara color test.

Twelve (5 male, 7 female) students participated in Experiment 1, ranging between 18 to 22 years old (a mean of 19.33 ± 1.44 (SD) years).

Twelve (3 male, 9 female) students participated in Experiment 2, ranging between 18 to 39 years old (a mean of 20.42 ± 5.90 (SD) years).

Twelve (8 male 4, female) students participated in Experiment 3, ranging between 16 to 21 years old (a mean of 18.92 ± 1.56 (SD) years).

Twelve (7 male, 5 female) students participated in Experiment 4, ranging between 18 to 21 years old (a mean of 19.08 ± 1.00 (SD) years).

2.2. Apparatus

The same visual task was performed under 2 viewing conditions conducted in a dimly lit room. In the near viewing condition, a 40.9 cm × 32.5 cm visual image was projected from the back of a white screen. A chin rest was used to keep the 39 cm viewing distance. In the Far condition, the screen was moved further back in order to make a 140 cm × 112 cm image using another projector. The subject sitting on a chair would also move back to a pre-marked position and thus kept a 1.33 m viewing distance from the screen. As a result, the visual image would cover the same retinal angle in both near and far conditions.

Two DLA SX-21 projectors (JVC Inc.) were connected to a computer with a NVIDIA Quadro FX 3400 video adapter. Receiving identical video signals from the computer, each of the projectors, one on top of the other, could cast the same image to a mobile screen, but in small or large size at near or far distance respectively. To ensure the retina of the observer received equivalent visual stimuli in both the near and far viewing conditions, the smaller image in near viewing condition and the larger image in far viewing condition were adjusted to the same luminance at corresponding points on the screen. This was done by adjusting the brightness and the contrast of the two projectors to ensure both white portions and grey portions of the test image were at a constant luminance, as measured by a photometer, across near and far viewing conditions.

2.3. Stimuli and procedure

Experiment 1: Identification for white letter

The visual target was a white letter (11.6 cd/m^2) that could appear at one of 32 positions on a grey background (2.8 cd/m2). The 32 positions were arranged into eight evenly spaced radial spokes (45º apart), and each spoke contained four locations at the eccentricity of 5º, 10º, 15º, and 20º from the center. Before the appearance of the target, and upon a tone, a circle filled with random grey pixels (4.2º in diameter, 3.4 cd/m^2 in average) was presented for 1200 ms on the center of the visual field and served as central fixation (Figure 4.1a). 200 ms after the offset of the center fixation, a white letter, randomly selected from K, N, H and Z, was presented at one of the 32 possible locations for a duration determined by the experimenter for that block of trials (Figure 4.1b). Then a black-and-white checkerboard (15.2 cd/m^2 at white, 1.1 cd/m^2 at black) which served as mask was presented at the position where the target had appeared (Figure 4.1c). 1500 ms later, with the disappearance of the mask, 4 letters were presented around the target location (Figure 4.1d). Meanwhile the mouse cursor also appeared and participants could click on one of the four letters to indicate the perceived target. The size of the target letter was scaled to 1.3º, 1.6º, 2.0º, and 2.4º in height when appearing at eccentricities of 5º, 10º, 15º, and 20º from the center respectively. The width and height of checkerboard mask was also scaled to 1.3 times the height of target letter at correspondent eccentricity.

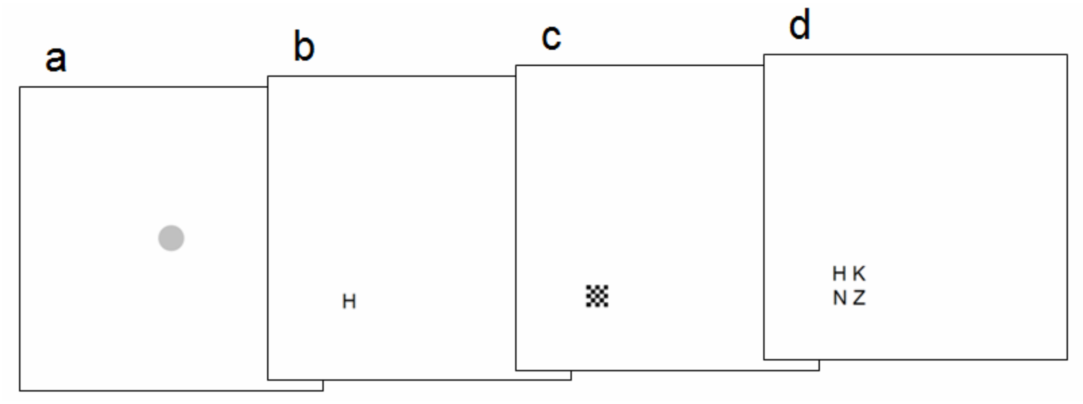

Figure 4.1. Schematic graphs of Identification for white letter task in Experiment 1. (a) Central fixation. (b) Target. (c) Mask. (d) Waiting for response.

Experiment 2: Identification for green letter with green mask

Experiment 2 was modified from Experiment 1 by changing the target letter from white into isoluminant green. The checkerboard mask was also made green-and-grey, with equal luminance of the grey background. The size of the letter was scaled to 1.3º, 1.7º, 2.2º, and 2.5º in height when appearing at the eccentricity of 5º, 10º, 15º, and 20º from the center respectively. The width and height of the mask was 1.3 times the height of the letter at the corresponding eccentricity.

Experiment 3: Identification for green letter with black-and-white mask

Experiment 3 shared the same features as Experiment 2. The checkerboard however reverted back to being black-and-white, as thus similar to the mask used in Experiment 1.

Experiment 4: Identification for green letter with white precue

Experiment 4 was modified from Experiment 2 by presenting a white annulus serving as a precue before the onset of the target. 200 ms after the offset of the center fixation, a white annulus (6.5 cd/m^2) appeared for 34 ms surrounding the position where the green letter would appear 102 ms later. All the other stimuli and procedures were the same as that in Experiment 2. The isoluminant green letter was scaled to the size of 1.4º, 1.5º, 1.7º, and 1.8º in height when appearing at the eccentricity of 5º, 10º, 15º, and 20º from the center respectively. The inner and outer rim of the white annulus was also scaled to the size of 2.8º~3.4º, 3.0º~3.7º, 3.3º~4.1º, and 3.6º~4.5º in diameter when appearing at the four eccentricities respectively.

2.4. General procedure

For Experiment 2, 3 and 4, the isoluminant green was determined for each participant before the practice session. A flicker patch alternated between green and the background grey at 15 Hz. Subjects adjusted the brightness of the green until the perceived flicker was minimized. The optimal brightness of green was used for the isoluminant stimuli (e.g. the isoluminant target or mask) in the practice and experimental session.

To avoid the imbalanced influence of the practice effect or fatigue on visual performance tested in near and far viewing conditions, the experimenter would always switch to the other condition, either near or far, for the next block. This was done by moving the screen and switching the projectors during the break between two blocks, in both the practice session and the experimental session. Therefore the experimental session was interlaced by 4 blocks of near condition and 4 blocks of far condition alternatively, with starting condition counterbalanced across participants. The same set of data determining the target position for every trial were used in both the near and far conditions, but the order of the trials was randomized independently for the two conditions.

The practice session began with a block at the target duration of 374 ms. Then, in the following blocks this target duration was reduced by the experimenter in order to allow participants to perform at 50 to 70 percent accuracy within the block. The optimal target duration was determined in 4 to 6 practice blocks, which was used as the target duration in the following 8 experimental blocks. The entire experiment lasted about 50 minutes.

3. Results and discussion

Experiment 1: Identification for white letter

Participants were asked to identify a briefly presented white letter. The visual accuracy indicated by percent correct was submitted to a 4 (eccentricity) × 2 (viewing distance) repeated measures ANOVA. Because the visual target was scaled progressively larger with the increase of eccentricity and at different scale factors for different experiments, the main effect of eccentricity on visual accuracy could not be compared between experiments. We thus will not report eccentricity effect in this and in subsequent experiments. There was a main effect of viewing distance on visual accuracy ($F(1,11) = 7.774$, $p=0.018$, $\eta=0.414$), indicating participants' identification performances were moderately better in far viewing than that in near viewing. There was no eccentricity by viewing-distance interaction ($F(3,33)=0.768$, $p=0.520$) (Figure 4.2a). On average for the 4 eccentricities, the difference of the visual accuracy between two conditions was 0.369 times their standard deviation. The average duration of the visual target applied to each participant was 41.08 ms. As all the four experiments in the present study displayed visual stimuli with the same equipment setting for matched luminance and visual angle in two viewing distance conditions, the performance in identifying a white letter in Experiment 1 serves as a baseline for the visual identification performance in the experimental paradigm, and would be compared with the results in Experiment 2, 3 and 4 which employed isoluminant green letter as target.

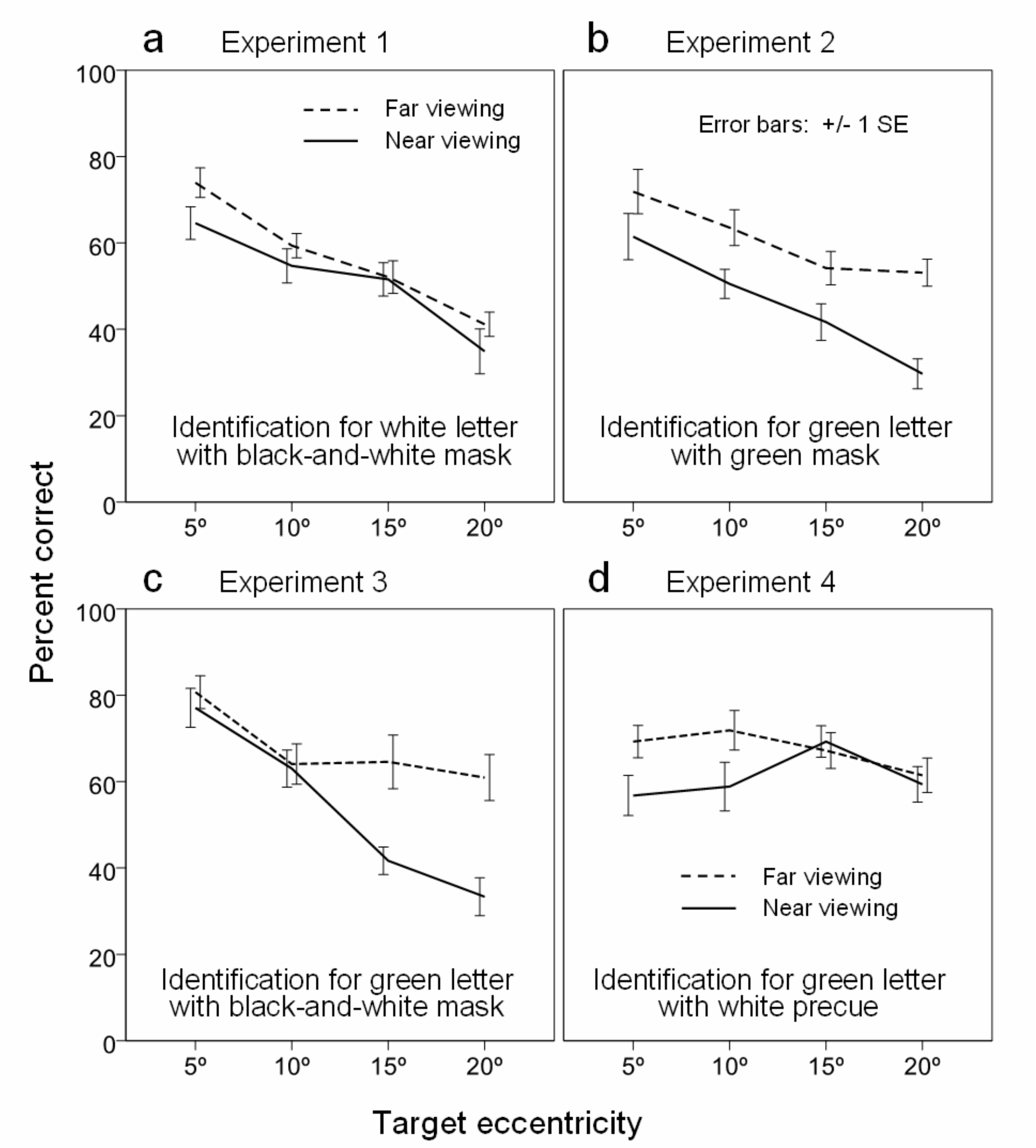

Figure 4.2. Visual accuracy as a function of target eccentricity tested by 4 visual identification tasks in near (solid lines) and far (dashed lines) viewing distance conditions. Error bars indicate standard error of the mean.

Experiment 2: Identification for green letter with green mask

The visual task was modified from Experiment 1 by making the target and the mask into green colour but in equivalent luminance with the grey background. A 4 (eccentricity) × 2 (viewing distance) repeated measures ANOVA revealed a main effect of viewing distance ($F(1,11)=18.023$, $p = 0.001$, $\eta=0.621$) on visual accuracy, but no effect of eccentricity by viewing distance interaction ($F(3,33)=1.89$, $p= 0.15$). The average duration of the visual target was 328.66 ms, which is much longer than that in Experiment 1 ($t(11)=15.786$, $p<0.001$), suggesting that the isoluminant information is much more difficultly processed in visual system compared with high-luminance-contrast stimuli. On average for the 4 eccentricities, the difference of the visual accuracy between two conditions was 0.855 times their standard deviation, which was much higher than that in Experiment 1 (0.363). In contrast to the performance dealing with white target and mask in Experiment 1, participants showed even poorer visual ability in identifying isoluminant green target in near space compared with in far space (Figure 4.2b). Since the visual task was to identify letters in isoluminant color, the information analysis is little likely to be processed in magnocellular pathway and dorsal stream due to their poor color sensitivity and worse spatial resolution (Livingstone and Hubel, 1988). The different visual performance for near and far viewing observed here suggests that information processing was reduced either in parvocellular pathway or in ventral stream when viewing distance changed from far to near (Figure 4.3). The visual behaviour in Experiment 2 will be compared with that in Experiment 3 and 4 in order to determine whether the near/far related neural modulation takes place in parvocellular and magnocellular pathways as stated in the *LGN* hypothesis.

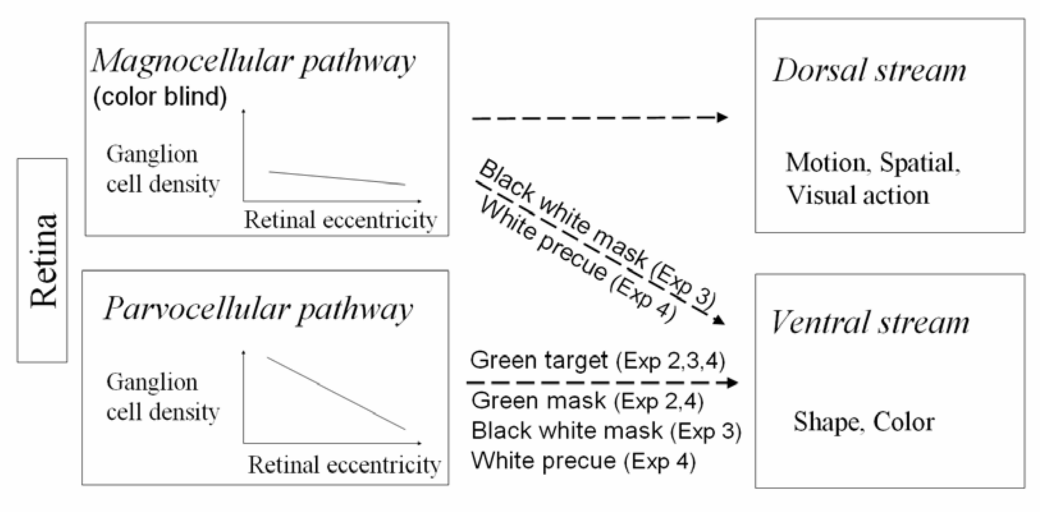

Figure 4.3. Schematic diagram for simplified information transmission from retina to cortical visual streams in Experiment 2, 3, and 4. Visual identification for isoluminant target is processed in the ventral cortical stream, which receives afferent inputs from both the parvocellular and magnocellullar pathways. However, the parvocellular pathway provides both chromatic and achromatic information while the magnocellular pathway provides only achromatic information to the ventral stream. Note that the density of the ganglion cells declined much more steeply with the increase of retinal eccentricity in parvocellular pathway as compared to that in magnocellular pathway (adapted from Azzopardi, Jones, & Cowey, 1999).

Experiment 3: Identification for green letter with black-and-white mask

Experiment 3 used isoluminant targets as in Experiment 2 but a black-and-white mask as in Experiment 1. In other words, Experiment 3 was modified from Experiment 2 by changing the mask from isoluminant green-and-grey checkerboard into a black-and-white checkerboard, or modified from Experiment 1 by changing the target from a white letter into an isoluminant green letter. Similar to Experiment 2, a main effect of viewing distance ($F(1,11)=24.898$, $p < 0.001$, $\eta=0.694$) on identification accuracy indicated that overall performance was better in far condition compared to that in near condition. The average target duration was 354 ms, slightly longer than that in Experiment 2 but not significant ($t(11)=0.975$, $p=0.34$), although greater masking effect would be produced by the more salient contrast information of black-and-white checkerboard as compared to that of the isoluminant green-and-grey checkerboard used in Experiment 2. A significant interaction between the viewing distance and eccentricity ($F(3,33)=6.939$, $p=0.001$, $\eta=0.387$) suggests that viewing distance has a different impact on identification accuracy at inner and outer eccentricities (Figure 4.2c), a pattern that differs from the parallel change of visual accuracy across eccentricities regarding near and far viewing in Experiment 2 (Figure 4.2b).

The visual stimuli in Experiment 2 and 3 differed only in the colour of the mask. The information of isoluminant green mask in Experiment 2 can be transmitted only through parvocellular pathway, whereas the visual information about the black-and-white mask in Experiment 3 can be transmitted through both parvocellular and magnocellular pathways (Figure 4.3). This could be the reason that visual accuracy across eccentricities in Experiment 3 showed two different slopes for near and far viewing (Figure 4.2c), in contrast to the parallel slopes shown in Experiment 2 (Figure 4.2b). Note that the density of ganglion cells also changes in a different slope across retinal eccentricities in magnocellular pathway as compared with that in parvocellular pathway (Figure 4.3). Since the ventral stream responsible for letter identification analysis receives inputs from both parvocellular and magnocellular layers of LGN (Ferrera, Nealey, & Maunsell, 1992, 1994; Mishkin, Ungerleider, & Macko, 1983), it is possible that when viewing distance changed from far to near in Experiment 3, the ventral stream received achromatic mask information more from magnocellular pathway and less from parvocellular pathway thereby resulted in two different slopes in Figure 4.2c. If so, it would support the *LGN* hypothesis rather than the *Ventral/Dorsal* hypothesis. However, it is also possible that the different influence on identification performance produced by isoluminant mask versus achromatic mask was the result that participants' attention was easily attracted by the strong luminance contrast of the black-and-white mask and led to better ability in identifying green target at outer eccentricities, which could easily be ignored when the mask was in isoluminant green. To rule out this possibility and to reveal the neural modulation in parvocellular and magnocellular pathways, Experiment 4 presented a white precue to explicitly direct participants' attention to the target location.

Experiment 4: Identification for green letter with white precue

The visual identification task was modified from Experiment 2 by briefly presenting a white annulus at the position where the green letter would appear 102 ms later, serving as a precue to attract participant's attention to the location before the onset of the target. The average target duration was 306 ms, significantly shorter than that in Experiment 3 (*t*(11)=2.415, *p*=0.031), indicating the precue effect was quite different from the masking effect. Compared with that in Experiment 2, the target duration was shorter in Experiment 4 but not significant ($t(11)=1.201$, $p=0.251$), although spatial attention was facilitated by the precue. Similar to Experiment 2 and 3, there was a main effect of viewing distance on visual accuracy ($F(1,11)= 14.026$, $p= 0.003$, $\eta=0.560$), indicating that identification accuracy was better when visual stimuli were presented at far space as compared to near space. There was also an eccentricity by viewing distance interaction ($F(3,33)= 3.135$, $p= 0.038$, $\eta=0.222$). However, this disproportional influence of viewing distance upon visual accuracy at various target eccentricities was in the opposite pattern to that in Experiment 3 (Figure 4.2c, d). Specifically, comparing performance between near viewing and far viewing, the identification ability declined more steeply with the increase of target eccentricity in near viewing in Experiment 3, more steeply in far viewing in Expeirment 4, where in the similar rate in Experiment 2. The reversed pattern of viewing distance by eccentricity interaction in Experiment 3 versus Experiment 4 suggests that the attention effect of white precue is different from the masking effect of the black-and-white checkerboard, therefore it is unlikely that the unevenly distributed near/far effect across eccentricities in Experiment 3 (Figure 4.2c) was due to the attentional attractiveness of the luminance-salient mask. Note that because the target was scaled progressively larger with the increasing eccentricity in the experimental display, the visual performance was not worse at outer eccentricities compared with that at inner eccentricities (Figure 4.2d) as it normally is.

Moreover, the results in Experiment 4 could also support the LGN hypothesis:

Compared with Experiment 2, the additional information of white precue in Experiment 4 can be transmitted through both the parvocellular and magnocellular pathway and facilitates visual identification processes. For the visual accuracy across eccentricities in Experiment 4, the different slope in near condition compared to far condition (Figure 4.2d) resembles the distinct density distributions of ganglion cells across retinal eccentricity in the two pathways (Figure 4.3), suggesting that the ventral stream receives more precue information from magnocellular pathway and less from parvocellular pathway in near condition.

4. General discussion

In order to reveal the different visual processing for near and far space and to determine whether the viewing distance related neural modulation originates at the subcortical level, i.e., in the parvocellular and magnocellular pathways, participants were asked to identify a briefly presented letter in four experiments. In contrast to Experiment 1 with achromatic stimuli, Experiment 2 showed that performance was much poorer at every eccentricity when identifying isoluminant green letter masked by isoluminant green-and-grey checkerboard in near condition compared to that in far condition. Consistent with both the *Ventral/Dorsal* hypothesis and *LGN* hypothesis, this parallel change of visual accuracy across eccentricities in two viewing distance conditions could be the result of decreased visual processing in ventral stream or reduced neural efficiency in parvocellular pathway when viewing in near condition, since the magnocellular pathway is colour blind and provides virtually no isoluminant information to ventral stream (Figure 4.3).

However, when using a black-and-white checkerboard instead of isoluminant green-and-grey checkerboard as mask, Experiment 3 did not show parallel performance for visual accuracy across target eccentricities in two viewing conditions; instead, the slope was steeper in the near viewing condition compared to that in the far viewing condition (Figure 4.2c), indicated by the significant viewing distance by eccentricity interaction effect. Note that ganglion cells in parvocellular and magnocellular pathways also have different slopes for the density distribution across retinal eccentricities (Figure 4.3). In Experiment 3, participants were asked to identify briefly presented isoluminant green letters. Performing this kind of object perception task requires the neural analysis of visual patterns, which was mediated in ventral stream of visual cortex (Ungerleider & Mishkin, 1982). Since area V4, a critical intermediate stage in the ventral stream for shape processing (Van Essen & Gallant, 1994), receives visual information from both parvocellular and magnocellular pathways (Ferrera, Nealey, & Maunsell, 1992, 1994), the performance change in visual identification task relative to near and far viewing might reflect the processing change in the two subcortical pathways.

The result of Experiment 3 could be explained by the *LGN* hypothesis, which assumes that a change from far to near viewing distance would result in reduced information transmission in the parvocellular pathway and increased information transmission in the magnocellular pathway. In Experiment 3, the visual information about the achromatic mask could be transmitted through both parvocellular and magnocellular pathways. As a result, when viewing distance changed from far to near, the ventral stream would receive achromatic mask information more from magnocellular pathway and less from parvocellular pathway. Consequently, the transmitted mask information at various eccentricities should show different slopes in near viewing compared to far viewing, similar as the different slopes for the density of ganglion cells across retinal eccentricities in magnocellular and parvocellular pathways (Figure 4.3). On the other hand, the information about the isoluminant green target could be transmitted through only parvocellular pathway but not magnocellular pathway. As a result, when viewing distance changed from far to near, the ventral stream would receive less isoluminant target information from the parvocellular pathway but still no target information from the magnocellular pathway. Therefore, without reflecting the different slope of ganglion cell density across eccentricities in the magnocellular pathway, isoluminant target information received by the ventral stream decreased in a parallel way over eccentricities in near viewing compared to far viewing. Taken together, when the evenly reduced isoluminant target information was disturbed by the luminance mask information which changed disproportionally across eccentricities, the visual identification ability based on the neural analysis of these two components of input information would also change disproportionally across eccentricities when viewing distance switched from far to near. This consequently resulted in two different slopes for visual accuracy at various eccentricities (Figure 4.2c).

However, the data in Experiment 3 are difficult to be explained by the

Ventral/Dorsal hypothesis. This is because if we assume that the near/far impact on modulation of neural processing takes place in ventral and dorsal cortical streams but not in parvocellular and magnocellular pathways, the input information received by the ventral stream coming from the parvocellular and magnocellular pathways would not be altered by the viewing distance (Figure 4.3). If so, the reduced neural processing in ventral stream in near condition should result in poorer identification performance for all the retinal eccentricities. In other words, the assumption that no near/far impact on the neural processing in parvocellular and magnocellular pathways would result in two parallel performance changes over eccentricities relating to near and far viewing when using the black-and-white mask in identifying isoluminant target, and would not reflect the neuronal features of the parvocellular and magnocellular pathways, i.e. the different patterns of ganglion cell density distribution. This prediction based on the *Ventral/Dorsal* hypothesis is not consistent with the significant viewing distance by eccentricity interaction effect observed in Experiment 3 (Figure 4.2c).

Although the result of Experiment 3 can be plausibly explained by the *LGN* hypothesis, it is also possible that the unevenly changed visual performance across eccentricities results from the different ability to orient attention to the target location in near versus far viewing condition, because the high-luminance-contrast mask in Experiment 3 was easier to be detected compared to the isoluminant green mask in Experiment 2, indicated by the slightly shorter target duration. Experiment 4 addressed this question by adding a precue to indicate the location where the isoluminant green target would appear. Compared with the luminance mask used in Experiment 3, the white annulus precue had more power to attract observers' attention to the target location and had less masking effect on identifying the green target presented 102 ms later, since the luminance change caused by the onset of precue was located surrounding the target position and did not overlap. If the unevenly distributed near/far effect at various eccentricities in Experiment 3 was due to attention effect induced by the high-luminance-contrast mask, Experiment 4 should show the near/far effect in a similar or even more extreme pattern. However, the opposite fashion of eccentricity by viewing distance interaction was observed in Experiment 4 when a white precue was used (Figure 4.2c,d). Therefore, the result of Experiment 4 ruled out the attention explanation for the result in Experiment 3.

Moreover, the reversed pattern of near/far effect affected by white precue in Experiment 4 versus luminance mask in Experiment 3 is also consistent with the *LGN* hypothesis, which assumes the information transmission in parvocellular and magnocellular pathways would be altered by the change of viewing distance. Both being transmitted through the parvocellular and magnocellular pathways, the luminance information for precue was actually helpful for the visual identification of the green letter whereas the luminance information for mask was more likely to disturb this perception process. Therefore the two kinds of luminance information should have different impacts on the perceptual ability when the information transmission in parvocellular and magnocellular pathways changed corresponding to viewing distance change. In Experiment 4, when viewing distance changed from near to far, the information about the white precue feeding the ventral stream would be increased in parvocellular pathway while decreased in magnocellular pathway, therefore would reflect more parvocellular feature than magnocellular feature. Consequently, facilitated by this precue information, visual accuracy would increase at inner eccentricity while decrease at outer eccentricity when viewing distance changed from near to far (Figure 4.2d), similar as the slope change of ganglion cell distribution from the magnocellular pathway to the parvocellular pathway (Figure 4.3). In Experiment 3, the information about the black-and-white mask feeding the ventral stream would also reflect more parvocellular feature than magnocellular feature when viewing distance changed from near to far. However, at any target eccentricity, increased mask information would result in decreased letter identification ability. Consequently, visual accuracy would actually decrease at inner eccentricity while increase at outer eccentricity (Figure 4.2c), a pattern opposite to the slope change of the ganglion cell distribution from the magnocellular pathway to the parvocellular pathway (Figure 4.3).

The results of Experiment 4 can also be explained by the *LGN* hypothesis. In Experiment 4, when viewing distance changed from far to near, the information transmission for the luminance precue was reduced in parvocellular pathway whereas increased in magnocellular pathway. As a result, the ventral cortical stream received precue information representing more magnocellular features whereas less parvocellular features in near viewing as opposed to far viewing (Figure 4.3). As the density of the ganglion cells in magnocellular pathway does not decline as steeply as that in parvocellular pathway with the increase of eccentricity (Azzopardi, Jones, & Cowey, 1999; Dacey & Petersen, 1992; Tychsen, 1992), the precue information across eccentricities received by the ventral stream should have a different slope when the viewing distance switched from far to near, similar as the slope change for the density of ganglion cells over eccentricities from the parvocellular pathway to the magnocellular pathway (Figure 4.3). On the other hand, the isoluminant target and mask information could be transmitted only in parvocellular pathway, thereby would decline at the same rate across eccentricities when viewing distance changed from far to near. Taken together, with the disproportional change of the white precue information and the parallel change of the isoluminant green target and mask information, afferent information received by ventral stream should have a different slope across eccentricities when viewing distance changed from far to near. This consequently would result in a steeper decline of visual accuracy with the increase of target eccentricity in far viewing as compared to near viewing, exactly as we observed in Experiment 4 (Figure 4.2d). Without the help from the information of white precue, Experiment 2 did not show the eccentricity by viewing distance interaction, even using the same isoluminant target and mask (Figure 4.2b).

On the other hand, it is difficult to explain the result of Experiment 4 with the *Ventral/Dorsal* hypothesis when assuming that information transmission in parvocellular and magnocellular pathways would not be affected by the change of viewing distance. If this is the case, the precue information received by ventral cortical stream from magnocellular and parvocellular pathways would not be altered by the change of viewing distance. As a result, even if the ventral cortical stream would reduce the processing efficiency when viewing distance changed from far to near, the identification accuracy at inner and outer eccentricities would be similarly affected, without reflecting the change of neuronal characteristics of magnocellular and parvocellular pathways (i.e., the different slopes of ganglion cell density over eccentricities in two pathways). But such kind of parallel performance across eccentricities was not observed in Experiment 4.

Taken together, the behavioural data in the present study suggest that the change of viewing distance results in altered information transmission in parvocellular and magnocellular pathways. Thus, the neural modulation of visual processing in responding to near or far viewing occurs at subcortical level. Because the neurons in the parvocellular and magnocellular pathways project predominantly to the ventral and dorsal cortical streams respectively, the viewing distance related neural modulation in subcortical pathways should result in altered afferent input and thereby different strength of visual processing in the two cortical streams. This is consistent with the previously observed viewing-distance related neural activity changes in dorsal and ventral cortical streams (Weiss et al., 2000; Weiss, Marshall, Zilles & Fink, 2003); therefore the *LGN* hypothesis supported by our data does not contradict with other neuropsychological evidence suggesting that the near and far visual spaces are differentially mediated by dorsal and ventral visual streams (Butler et al., 2004; Halligan & Marshall, 1991; Mennemeier, Wertman, & Heilman, 1992; Shelton, Bowers, & Heilman, 1990; Vuilleumier et al., 1998). In addition, although the results in the present study suggest a subcortical modulation of visual processing, they do not rule out the possibility that the information processing in ventral and dorsal visual cortical streams can also be influenced by factors other than the LGN modulation regarding near and far viewing.

It has long been known that the anatomical feedback connections in LGN outnumber the feed-forward connections (Montero, 1991). But the ecological role of this feedback system is still not well understood, although it potentially allows LGN to modulate the information transmission according to the demands of higher levels of neural processing. The results of the present study suggest that a neurologically intact human brain can actively increase or decrease information transmission in parvocellular and magnocellular pathways according to viewing distance. This implies that the LGN serves as a gatekeeper to regulate the flow of information and thus optimize the working load of later neural processing in different visual conditions, to meet the ecological demand of the information usage. The neuronal activation change of LGN in responding to different attentional demands has been reported recently by some neural imaging studies. For example, it has been shown that visual spatial attention could enhance neural activity in LGN for attended stimuli (McAlonan et al., 2008; O'Connor et al., 2002; Schneider & Kastner, 2009); performing the binocular rivalry task is related to the modulation of neural activity in LGN (Haynes et al., 2005; Wunderlich et al., 2005). In addition to the previous neuropsychological evidence, the data in the present study provide behavioural evidence to support the view that the function of LGN goes far beyond simply relaying visual information.

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Chapter 5

General discussion

5.1 Dissociation of visual representations for near and far space

The human brain processes visual information based on the retinal image of the three dimensional environment. It is tempting to assume that as long as the visual image about the 3-D world projected to the retina is the same (e.g., the same image size, retinal eccentricity, luminance, contrast etc.); the visual processing for that information will be the same regardless of how far the objects that produce these images are located from the eye. However, the result of experiments in chapter 2 showed two types of visual behaviour regarding near and far viewing. In visual detection task, visual accuracy declined steeply with the increase in target eccentricity in far viewing conditions as compared to performance in near viewing conditions. Thus, healthy human observers exhibited two fashions of visual behaviour when viewing at far space or at near space, even though the retina experienced equivalent visual information in the two viewing distance conditions. Furthermore, this pattern of visual behaviour was not observed when healthy human observers identified a briefly presented letter on the peripheral visual field, although in the same near/far experimental paradigm. All five experiments in Chapter 2 were conducted in near and far viewing conditions with visual stimuli being adjusted to the same visual angle and luminance in order to let participants receive equivalent retinal information in the two viewing conditions. Thus, the similar visual identification performance across viewing distances indicates that the same visual mechanism was primarily involved in both near and far viewing conditions. In contrast, the different patterns of visual behaviour in detecting a peripherally presented target in near versus far viewing conditions suggest that at least two distinct visual mechanisms were involved in the visual processing, and their relative contributions for visual detection analysis can be changed according to viewing distance.

The data in Chapter 2 provide behavioural evidence supporting the notion that near and far visual spaces are predominantly processed in different neural subsystems (Previc, 1990, 1998). Previously, this notion was suggested based on evidence from studies involving animal single cell recording, animal brain lesion, and brain damaged patients (Cutting & Vishton, 1995; Grusser, 1983; Mountcastle, 1976; Pettigrew & Dreher, 1987; Previc, 1990, 1998; Rizzolatti, Gentilucci, & Matelli, 1985; Rizzolatti, Matelli, & Pavesi, 1983; Halligan & Marshall, 1991). Although two later neuroimaging studies (Weiss et al., 2000, 2003) confirmed that in healthy human observers, the neural activity in dorsal and ventral visual streams could be increased or decreased when viewing in near or far distances, the lack of behavioural difference between near and far viewing conditions in those two studies left it unclear about whether the changed neural activity reflected the assumed visual processing for analyzing the target information or was the result of processing some other aspects of visual information relating to near or far viewing distance. For example, the different neural activity in various parts of the brain could be relative to different processing for accommodation or convergence in adapting the visual depth.

The behavioural evidence from brain damaged patients is also not convincing enough to suggest the specification of ventral and dorsal cortical stream for processing visual information arising from near and far space. For example, a very influential paper from Nature (Halligan & Marshall, 1991) reported a patient with a unilateral damage on right posterior parietal lobe and provided the first reported evidence for the dissociation between near and far visual representations with respect to visual neglect along the horizontal dimension. This patient showed a severe left visuo-spatial neglect when performing line-bisection task in peripersonal space but not in extrapersonal space. However, this result could not be replicated in a later study testing more patients. Using the same experimental procedures as did by Halligan and Marshall (1991), Cowey, Small, and Ellis (1994) actually reported the opposite pattern of spatial neglect regarding near and far viewing. All of their five patients displaced their attempted bisections to the right of the true center in both near and far space, with greater error in far space than in near. In a subsequent study, Cowey, Small, and Ellis (1999) also failed to find any patient whose neglect was more prominent in near space. On the contrary, 5 of their 13 patients showed a greater neglect in far space. Although Brain (1941) made the first suggestion that external space should be divided into “grasping distance” and “walking distance”, the described lesion areas in the brain are not consistent with the brain areas specific for processing near and far space suggested by later neuroimaging studies (Weiss et al., 2000, 2003). The lesion reported in Case 2 of the Brain (1941) study was on the upper part of the parietal lobe and related to the “inability to localize distant objects”; whereas the lesion in Case 3 involved the posterior part of the right temporal lobe, and was related to the deficit for visual-motor operation in peripersonal space.

Other evidence supporting differential visual representation for near and far space comes from animal single cell studies. Pettigrew and Dreher (1987) reported that separate visual streams in cat were differentially tuned for different regions of 3-D space. Specifically, (a) the cat Y-cell system, which is most comparable to the magnocellular system of the primate, processes transient information in near space (by disparity technique); (b) the cat X-cell system, which is more comparable to the parvocellular system of the primate, processes sustained information in the plane of fixation; and (c) the cat W-cell system, for which no clear primate analogue exists, processes relatively slow angular information presented at divergent disparities and at great distances. However, this study did not test neural activity when animals viewed at near or far distances; instead, the receptive field responding to binocular retinal disparity was measured for various brain areas. With the Risley biprism technique, divergent or uncrossed retinal disparities were presented to cats. The neural response to this artificial depth cue may not reflect the neural processing for near and far space in the natural environment.

Some animal lesion studies had shown the dissociation of brain representations for near and far spaces. However, the lesions were not in the dorsal or ventral cortex as revealed by neuroimaging studies in relating to near or far viewing (Weiss et al., 2000, 2003). For example, Rizzolatti et al. (1983) made lesions in the premotor area and frontal areas of the monkey brains and observed attentional deficits in near space or far space respectively.

By measuring the attentional bias of healthy human observers, some studies also claim that their data supported the dissociation of neural representation of near and far space (Heber et al., 2010). However, the visual tasks to test the difference in pseudoneglect relied on the asymmetrical emphasis of visual attention in the left and right hemispheres of the normal human brain. Therefore, the behavioural difference regarding near versus far viewing in line bisection task or its modifications could not easily be explained as an indication of differential involvement of neural structures, i.e. dorsal and ventral cortical streams suggested by neuroimaging studies (Weiss et al., 2000, 2003).

Although the evidence from various lines of research mentioned above do not support one another well, many researchers still believe that different parts of human brain are specialized for mediating near and far visual space. In addition to previous neurophysiological and neuropsychological evidence, the behavioural data reported in Chapter 2 support the notion that the near and far visual spaces are preferentially mediated by two distinct neural subsystems. Because the patterns of visual accuracy in detecting a white spot across target eccentricities in near and far viewing conditions resemble the patterns of density distribution of ganglion cells in magnocellular and parvocellular pathways respectively, it is likely that neural processing for the visual information in near and far spaces is differentially specialized in magno-dorsal pathway and parvo-ventral pathway respectively.

This behavioural dissociation for the near and far visual space was further demonstrated by experiments in Chapter 3. In Experiment 2 of Chapter 3, healthy human observers showed extremely poor visual ability in detecting an isoluminant green spot in near viewing conditions as compared to that in far viewing conditions. In contrast, in Experiment 1, participants showed better performance in detecting a white spot in near viewing condition as compared to that in far viewing condition. Because the information of the isoluminant green spot can be processed in parvocellular pathway but not in magnocellular pathway, and is mainly processed in ventral cortical steam, the results from Experiment 2 suggest that information processing in parvocellular pathway or in ventral cortical stream was greatly reduced in near viewing than in far viewing condition. The opposite pattern of performance regarding near and far viewing in Experiment 1 when detecting a white spot ruled out the possibility that the huge near/far difference in Experiment 2 was due to the unmatched luminance or contrast of the stimuli in near and far conditions or due to participants' preference for near or far viewing.

5.2. The LGN modulation of neural processing for near and far viewing

Previous neurophysiological and neuropsychological evidence (Butler et al., 2004; Halligan & Marshall, 1991; Mennemeier, Wertman, & Heilman, 1992; Previc, 1990, 1998; Vuilleumier et al., 1998; Weiss et al., 2000, 2003) suggested that the dorsal and ventral cortical streams most likely mediate the visual representation for near and far spaces. Let's call it as the *Ventral/Dorsal* hypothesis, assuming the modulation of information processing originated in the ventral and dorsal cortical streams but not in earlier stages of visual processing. Because the pattern of visual detection performance in near and far viewing observed in Chapter 2 resembles the density distribution of ganglion cells in magnocellular and parvocellular pathways, it is possible that the change of viewing distance could result in the modulation of information transmission in magnocellular and parvocellular pathways. Let’s call this neural mechanism as the *LGN* hypothesis, assuming the modulation of information processing originated in the subcortical stage, i.e., in the parvocellular and magnocellular pathways. As a relay station from retina to V1, the lateral geniculate nucleus (LGN) receives much more feedback information from visual cortex than feed-forward information from retina (Montero, 1991); thereby LGN is the best candidate to modulate information transmission in magnocellular and parvocellular pathways depending on the processing demands from the visual cortex. Since the dorsal stream of visual cortex receives inputs predominantly from magnocellular pathway and the ventral stream receives inputs mainly from parvocellular pathway, the visual behaviour predicted by the *Ventral/Dorsal* hypothesis can also be the result of the neural mechanisms described by the *LGN* hypothesis; however, not vice versa. Thus, the different visual ability regarding near and far viewing distances reported in Chapter 2 and Chapter 3 can be explained by both the *LGN* hypothesis and the *Ventral/Dorsal* hypothesis.

Although some of the previous neurophysiological and neuropsychological evidence for processing visual information in near and far spaces (Butler et al., 2004;

Halligan & Marshall, 1991; Mennemeier, Wertman, & Heilman, 1992; Shelton, Bowers, & Heilman, 1990; Vuilleumier et al., 1998; Weiss et al., 2000; Weiss, Marshall, Zilles & Fink, 2003) is consistent with the Ventral/Dorsal hypothesis, data in Chapter 2 and Chapter 3 indicate the neural mechanism described by the LGN hypothesis, even though can not reject the Ventral/Dorsal hypothesis. Sought to determine at which level, i.e. LGN or visual cortex, the neural modulation of information processing takes place in the human visual system, experiments in Chapter 4 manipulated the color for various components of the stimuli in order to be differentially processed by parvocellular and magnocellular pathways.

Simple visual detection task is not suitable for distinguishing the two hypotheses because the neural analysis of the brief appearance of a spot can be processed in both ventral and dorsal streams which receive inputs mainly from parvocellular and magnocellular pathways respectively. We cannot determine whether the performance change with regard to near and far viewing was the result of the processing change in ventral and dorsal streams or was the consequence of the altered information transmission in parvocellular and magnocellular pathways. Therefore, Chapter 4 employed the visual identification task in which the neural analysis of visual pattern is mainly processed in ventral stream but not in dorsal stream (Livingstone & Hubel, 1988). Because the ventral stream receives neural inputs from both the parvocellular and the magnocellular pathways (Ferrera, Nealey, & Maunsell, 1992, 1994), the pattern of performance in visual identification task may reflect the neural processing change in parvocellular and magnocellular pathways.

The *LGN* hypothesis is consistent with the results of the experiments in Chapter 4 in many ways. Chapter 4 includes four visual identification experiments: White target with black-and-white mask in Experiment 1, isoluminant green target with isoluminant green mask in Experiment 2, isoluminant green target with black-and-white mask in Experiment 3, isoluminant green target with isoluminant green mask and a white precue in Experiment 4. Presenting the target and mask in the same chromatic category, Experiment 1 (both achromatic target and mask) and Experiment 2 (both isoluminant green target and mask) showed two parallel performance for identification accuracy across eccentricity in near viewing and far viewing conditions (Figure 4.2a,b). In Experiment 2, visual information about the isoluminant target and mask can only be processed in parvocellular pathway but not in magnocellular pathway. According to the *LGN* hypothesis, when viewing distance changed from far to near, information transmission is increased in magnocellular pathway while decrease in parvocellular pathway. Consequently, without the contribution of the magnocellular pathway, the isoluminant information in the parvocellular pathway was reduced at every retinal eccentricity when the viewing distance changed from far to near and thereby resulted in parallel behavioural change for accuracy across eccentricities. In Experiment 1, the information transmission about the white target and the white mask was similarly affected when the emphasis of visual processing switched from parvocellular to magnocellular pathway, thereby the similar change of the two parts of information about the target and the mask could cancel each other. Thus the performance in Experiment 1 and 2 did not reflect the different slopes of the density of the ganglion cells across retinal eccentricities in magnocellular pathway and the parvocellular pathway (Azzopardi, Jones, & Cowey, 1999; Dacey & Petersen, 1992; Tychsen, 1992).

In Chapter 4, the visual performance in identifying a briefly presented letter was quite different between Experiment 1 and Experiment 3. There was a significant viewing distance by target eccentricity interaction in Experiment 3 but not in Experiment 1 (Figure 4.2a,c). For visual stimuli, the only difference between the two experiments was the colour of the target. Participants identified a white letter in Experiment 1 but an isoluminant green letter in Experiment 3. The visual information about the white target can be transmitted by both the parvocellular and magnocellular pathways, while visual information about the isoluminant green target can be transmitted only by parvocellular pathway but not by magnocellular pathway. In light of the *LGN* hypothesis, in Experiment 1, when viewing distance changed from far to near, the emphasis of neural processing switched from parvocellular pathway to magnocellular pathway. However, the information transmission for the white target and the black-and-white mask would be similarly affected by the change of viewing distance. Thus, the similar change of the target information and mask information would cancel each other and result in two parallel performance in visual accuracy across eccentricities regarding near and far viewing (Figure 4.2a). In Experiment 3, however, the change of target information and mask information cannot cancel each other when viewing distance changed from far to near, because the information about the isoluminant green target can be transmitted only by parvocellular pathway while the information about the black-and-white mask can be transmitted by both the parvocellular and magnocellular pathways (Figure 5.1). Thus, a two-slope performance for visual accuracy across eccentricities regarding near and far viewing were observed in Experiment 3 (Figure 4.2c). These two different slopes of performance resemble the different density distributions of the ganglion cells across retinal eccentricities in parvocellular and magnocellular pathways (Figure 5.1).

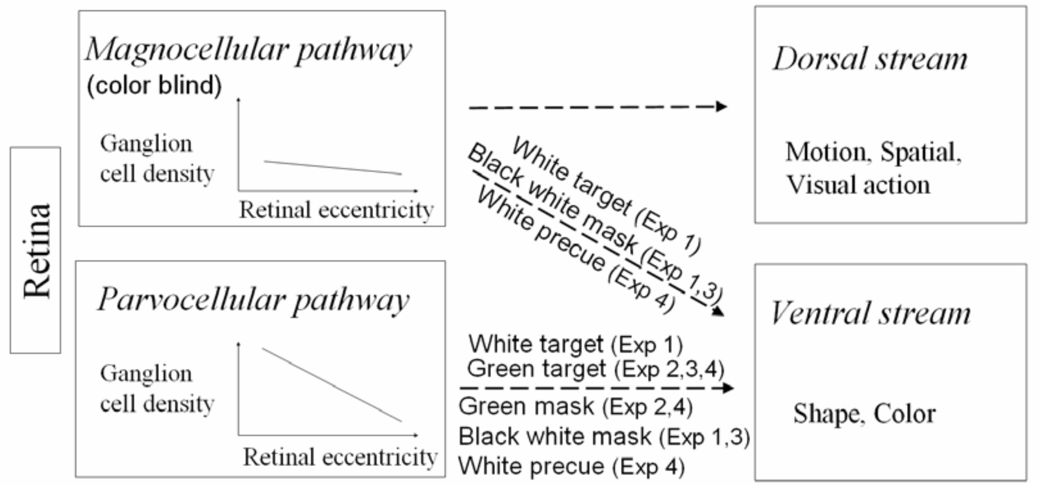

Figure 5.1. Schematic diagram for simplified information transmission from retina to ventral cortical stream in 4 experiments of Chapter 4. Note that the density of the ganglion cells declined much steeply with the increase of retinal eccentricity in parvocellular pathway compared with that in magnocellular pathway.

Similarly, the different visual performance between Experiment 2 and Experiment 3 is also consistent with the *LGN* hypothesis. The viewing distance by target eccentricity interaction was observed in Experiment 3 but not in Experiment 2 (Figure 4.2b,c). Both of the two experiments used the same isoluminant green letter as visual target. However, Experiment 2 used isoluminant green-and-grey checkerboard as mask while Experiment 3 used black-and-white checkerboard as mask. In Experiment 2, both the isoluminant target information and the isoluminant mask information can be transmitted only in parvocellular pathway. In light of the *LGN* hypothesis, when viewing distance changed from far to near, the reduced information transmission in parvocellular pathway would result in the declining visual performance at all the retinal eccentricities and consequently two parallel slopes as shown in Figure 4.2b. In Experiment 3, however, the transmission of the target information and mask information in the two pathways was unbalanced. The information about the isoluminant target can be transmitted only by parvocellular pathway while the information about the black-and-white mask can be transmitted by both the parvocellular pathway and magnocellular pathways. In light of the *LGN* hypothesis, when viewing distance changed from far to near, information transmission would be reduced in parvocellular pathway while increased in magnocellular pathway. Therefore, the mask information received by the ventral cortical stream would reflect more magnocellular feature in near viewing condition whereas reflect more parvocellular feature in far viewing condition (Figure 5.1). This is what we observed in Experiment 3. The different slopes of the visual accuracy across target eccentricities (Figure 4.2c) resemble the different pattern of density distribution of the ganglion cells across retinal eccentricities in parvocellular and magnocellular pathways (Figure 5.1).

Experiment 4 used the same isoluminant target and mask as that in Experiment 2.

However, before the appearance of the target, a white precue was presented to direct participants' attention to the target location. Again, the transmission of the target information and the precue information in the two visual pathways is unbalanced. The information about the isoluminant target and isoluminant mask can be transmitted through only parvocellular pathway while the information about the white precue can be transmitted through both the parvocellular pathway and magnocellular pathways. Visual performance also showed a viewing distance by target eccentricity interaction in Experiment 4 (Figure 4.2d), but in the opposite pattern as compared to that in Experiment 3 (Figure 4.2c). Similar to visual information about the black-and-white mask in Experiment 3, the information about the white precue can be transmitted in both parvocellular and magnocellular pathways. However, the mask information in Experiment 3 would more likely disturb visual identification of the isoluminant letter whereas the white precue information in Experiment 4 would more likely facilitate the orientation of attention and thereby should be helpful for visual identification process. This different influence on the identification performance by the precue and the mask resulted in the two opposite patterns of visual performance, i.e., the visual accuracy was lower at outer eccentricity in Experiment 3 (Figure 4.2c) whereas lower at inner eccentricity in Experiment 4 (Figure 4.2d) in near viewing condition as compared with that in far viewing condition. Participants' visual performance in Experiment 4 also remarkably differed from that in Experiment 2. There are two different slopes for the visual accuracy across eccentricity regarding near and far viewing conditions in Experiment 4 (Figure 4.2d) whereas the performance across eccentricity regarding near and far viewing conditions is parallel in Experiment 2 (Figure 4.2b). Consistent with the LGN hypothesis, the different behavioural patterns regarding near and far viewing in Experiment 4 (Figure 4.2d) resemble the difference in ganglion cells' density distribution across retinal eccentricities between the parvocellular and magnocellular pathways (Figure 5.1).

Note that when the two components of visual stimuli were in two different chromatic categories, i.e. luminance versus isoluminance, Experiment 3 and Experiment 4 showed performance in two different slopes for visual accuracy across eccentricities regarding near and far viewing (Figure 4.2c,d). Contrariwise, when all the stimuli were in the same color, either luminance-contrast or isoluminance-contrast, parallel slopes regarding near and far viewing were observed in Experiment 1 and Experiment 2 (Figure 4.2a,b). The visual performance in the four visual identification tasks in Chapter 4 is consistent with the *LGN* hypothesis but not with the Ventral/Dorsal hypothesis. As stated in the *LGN* hypothesis, changed viewing distance would result in the modulation of information transmission in parvocellular and magnocellular pathways. Because the density of ganglion cells in the two visual pathways declined in different rate with the increase in retinal eccentricity, the visual inputs received by the ventral cortical stream would be affected in different ways when the processing emphasis switched from parvocellular pathway to magnocellular pathway. The two different slopes for the visual accuracy across eccentricities regarding near and far viewing distances resemble the two patterns of ganglion cell density change across retinal eccentricities in magnocellular and parvocellular pathways. This kind of two-pattern change was observed in Experiment 3 and Experiment 4 (Figure 4.2c,d), in which the information of isoluminant visual target can be processed only in parvocellular pathway while the information of luminance-contrast mask or precue can be processed by both parvocellular and magnocellular pathways. On the other hand, the visual behaviour observed in Experiment 3 and 4 cannot be explained by the Ventral/Dorsal hypothesis. If as stated in *Ventral/Dorsal* hypothesis, the change of viewing distance would affect the information processing in ventral and dorsal cortical stream; however, without altering the information transmission in parvocellular and magnocellular pathways, the performance in Experiment 3 and 4 should not show different slopes across target eccentricities regarding near and far viewing. Instead, the parallel performance across eccentricities should be observed, similar as that in Experiment 2, in which the transmission of isoluminant information was not switched from parvocellular pathway to magnocellular pathway when viewing distance changed from far to near.

The data in Chapter 4 provide the first behavioural evidence suggesting that information transmission in parvocellular and magnocellular pathway can be modulated depending on the viewing distance. Most likely, this neural modulation in visual pathways takes place in LGN, which is the first stage in the visual system where cortical top-down feedback signals could affect visual processing. In primates, the retinal information received by LGN constitutes only 10% of its overall afferent input. However, 30% of LGN input is comprised by the corticothalamic feedback projections from V1, while another 30% from the thalamic reticular nucleus (TRN), which receives not only inputs from the LGN and V1, but also from several extrastriate areas and the pulvinar (Sherman & Guillery, 2002). It has been shown that cooling of V1 leads to decreases of contrast-gain in LGN neurons, which suggests that contrast gain in the LGN is controlled by cortical mechanisms (Przybyszewski et al., 2000). In recent years, some neuropsychological studies have provided evidence that the human LGN plays a role in perception and cognition far beyond that of a relay nucleus.

O'Connor et al. (2002) presented high- or low-contrast checkerboard stimuli to the left or right hemifield and asked participants to perform either an easy attention task or a hard attention task at fixation. Subjects were instructed to direct attention to the checkerboard stimulus and to detect its luminance changes in some conditions while not in other conditions. The fMRI results showed that neural activity in LGN was enhanced in the attended condition relative to that in the unattended condition. Moreover, the neural activity in LGN evoked by the high- and low-contrast stimuli decreased significantly when performing the hard attention task at fixation as compared with the easy task condition. When an expectation period was inserted between the occurrence of the cue and the onset of the stimulus on peripheral visual field, fMRI signals in LGN increased significantly at this expectation period as compared with the preceding blank period. Thus, the changed neural activity relating to task performance suggests that selective attention can modulate neural activity in LGN in various ways; it enhances neural responses to attended stimuli, attenuates the neural processing for ignored stimuli, and also increases the baseline activity even in the absence of visual stimulation. These effects of attention on the modulation of neural activation in LGN were similar to those obtained in visual cortical areas (Kastner et al., 1998).

Wunderlich, Schneider, and Kastner (2005) measured the neural activity in LGN during binocular rivalry task. A high-contrast green horizontal grating was presented to one eye meanwhile a low-contrast red vertical grating was presented to the other eye. The fMRI signals in LGN increased when participants reported perceiving the high-contrast grating, and decreased when they reported perceiving the low-contrast grating. The neural activity pattern relating the percept of high-contrast and low-contrast grating was found to be similar in the LGN and V1 neurons, and its magnitude were correlated with the duration of the subjects' perceptual experience during binocular rivalry. The authors suggested that LGN could be a possible site at which the invisible stimulus is suppressed during binocular rivalry and therefore serves as an early gatekeeper of visual awareness. Using a high-resolution fMRI, Haynes, Deichmann, and Rees (2005) measured the neural activity for population of cells in LGN layers biasing for either left or right eye. In a similar binocular rivalry paradigm, a clearer neural modulation between different functional groups of neurons in LGN layers was observed. The activity was enhanced in group of neurons with a preference for left-eye when left-eye stimulus became perceptually dominant, so were the right-eye preference neurons when right-eye stimulus was perceived. This neuropsychological result indicates a neural strategy similar as that suggested by the behavioural findings in Chapter 4. That is, the information transmission in different neural groups in LGN can be modulated according to the perceptual demand of the higher level visual processing.

If as suggested in Chapter 4 that viewing in near or far space could result in the modulation of information transmission in LGN, then there should be corresponding neural activity changes in LGN relating to near and far viewing. However, previous neuroimaging studies (Weiss et al., 2000, 2003) only observed the increased neural activation in dorsal and ventral cortical streams relative to near and far viewing. It is possible that spatial resolution was too low in their brain-mapping techniques which cannot distinguish the change of neural activity between layers of LGN. Actually, one early study using single cell recording has indirectly suggested the role of LGN for the differential visual processing of near and far space. Pettigrew and Dreher (1987) reported that separate visual streams in cats were differentially tuned for different regions of 3-D space. They recorded the neural activity in cortical areas 17, 18, and 19 when presenting visual images at different binocular disparities. Because these cortical areas receive parallel but largely segregated inputs from three types of ganglion cells, the authors concluded that: the cat Y-cell system, which is most comparable to the magnocellular system of the primate, processes transient information in near space; the cat X-cell system, which is more comparable to the parvocellular system of the primate, processes sustained information in the plane of fixation; and the cat W-cell system, for which no clear primate analogue exists, processes relatively slow angular information presented at divergent disparities and at great distances. However, no study has directly measured the neural activity in layers of LGN for near and far viewing.

5.3. Potential Limitations

Although the dissociation of visual representations for near and far space had been proposed by many researchers for a long time, behavioural evidence in healthy human observers is rare. In Chapter 2, all three experiments involving visual detection tasks showed remarkable different performance when participants were tested in near versus far viewing conditions. However, this behavioral difference regarding near and far viewing may be only revealed in some restricted experimental conditions. For example, using the similar visual detection task, Experiment 1 in Chapter 3 did not yield a significant viewing distance by target eccentricity interaction effect on visual accuracy. There are two possible reasons that might account for this incongruity.

First, the overall luminance of the visual display differed between the experiments in Chapter 2 and Chapter 3. After data collection for experiments in Chapter 2, the lamp of one projector stopped working and was replaced. Because the new lamp was brighter than the old one, the brightness and the contrast of the two projectors were adjusted into new parameters in order to get equivalent luminance and contrast at corresponding angular eccentricities in near versus far viewing conditions. As a result, the luminance of the visual display was lower in experiments in Chapter 3 (e.g., 2.80 cd/m^2 at the grey background) as compared to that in Chapter 2 (e.g., 4.25 cd/m^2 at the grey background). It is possible that in the low luminance visual environment in Experiment 1 of Chapter 3, the visual system relied heavily on magnocellular pathway rather than parvocellular pathway in processing visual information, since the cells in the magnocellular pathway are much more sensitive for low-luminance achromatic stimuli than that in parvocellular pathway (for reviews see Kaplan et al., 1990; Valberg & Lee, 1992). It is possible that the overemphasis of information processing on one pathway may diminish the behavioural difference relating to the change of viewing distance, which requires the switch of relative contribution between the two pathways.

Second, the experiments in Chapter 2 used coloured textures for visual stimuli (Figure 5.2) whereas only achromatic textures were used in Experiment 1 of Chapter 3. In Chapter 2, all the eight radial arms indicating the eight target directions were textured in coloured random dots (elongated 64×64 pixels in blue-green and white, 6.14 cd/m^2 on average); the central fixation and central mask were also in green. It is possible that the presence of coloured stimuli made the parvocellular pathway properly activated as compared with the less activated state in the achromatic stimuli condition. As a result, the parvocellular pathway and magnocellular pathway had comparable contribution in transmitting visual information to the cortical areas. Consequently, behavioural difference was observed when the processing emphasis changed between the two pathways according to the viewing distance. Another possibility is that participants' eyes may have been more comfortable in the nearly one hour visual test when being presented with green and blue textures rather than the always black-and-white textures. This was also the consideration when designing the experiments in Chapter 2. When participants' eyes were tired for being exposed to the achromatic stimuli in Experiment 1 of Chapter 3, the ability to adapt to the viewing distance by accommodation and convergence may have decreased and thereby might have also diminished the near/far effect on visual behaviour. Supporting this explanation, it has been reported that colour is helpful for binocular depth perception (den Ouden, van Ee, & de Haan, 2005) and for detecting transparency targets in complex 2D displays (Kingdom & Kasrai, 2006).

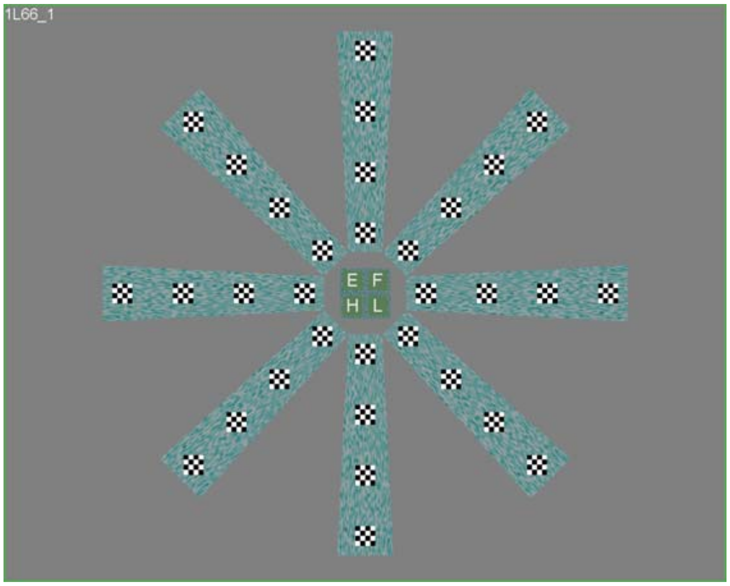

Figure 5.2. Visual display for response phase in Experiment 1 of Chapter 2.

In Chapter 2, all the three experiments involving the visual detection of a briefly presented white spot showed different visual performance regarding near and far viewing. In these visual tasks, participants clicked on one of the eight radial arms to indicate the location where the target had appeared. Thus, the result of the supposed visual detection tasks could also reflect participants' ability to spatially locate an object. This may lead to other explanations about the observed difference in performance regarding near and far viewing, because in the traditional view, the dorsal visual stream mediates the spatial localization of an object (Ungerleider & Mishkin, 1982). However, there are three reasons that suggest the observed near-far effect was unlikely due to the different spatial abilities in identifying or memorizing the spatial direction of the visual target regarding near and far viewing distance. First, an earlier study (Anderson & Yamagishi, 2000) showed that targets at the eccentricity of 10 º could be localized at the accuracy of less than 1.5 º, which is much smaller than the 7 º difference for nearby target positions in our experiments. As such, localization errors were less likely to be reflected in the behavioural results in our experiments. Second, by presenting stimuli favored by either magnocellular (dorsal) or parvocellular (ventral) system, the behavioural results in Anderson and Yamagishi (2000) study indicated that the two visual pathways process visual localization task at similar accuracy. Third, if we measured the visual accuracy by including the two directions adjacent to the correct one, making the selection of the target direction from 1-out-of-8 to 3-out-of-8, or from 45 º to 135º polar angle for tolerance limits which is much higher than the localization threshold; the similar two-slope accuracy across eccentricities for near and far viewing conditions was still obtained.

In Chapter 4, different patterns of visual performance regarding near and far viewing conditions suggested that the neural modulation of information processing takes place earlier than the ventral and dorsal streams as assumed by previous studies (Butler et al., 2004; Halligan & Marshall, 1991; Mennemeier, Wertman, & Heilman, 1992; Previc, 1990, 1998; Vuilleumier et al., 1998; Weiss et al., 2000, 2003). The LGN is a strong candidate to carry out this kind of gain modulation without changing the corresponding neurons' response selectivity. This is because the LGN receives rich feedback connections from layer 6 of V1, and this feedback information can influence the firing pattern (burst or tonic) of LGN cells (Sherman, 2001) and also influences how their discharge might synchronize when activated by the same stimuli (Sillito, et al., 1994; Worgotter, et al., 1998). However, it is also possible that the indicated near/far modulation of information processing tasks place in V1. While segregated, the magnocellular and parvocellular cells project to layer 4Cα and layer 4Cβ of V1 respectively. Similar to the LGN, neurons in layer 4 of V1 also receive more feedback synaptic input from layer 6 of V1 than the feed-forward input from LGN (Ahmed et al., 1994). Although the influence of feedback information on neural response in layer 4 of V1 is less studied compared to that of LGN cells, the information processing in layer 4 of V1 is also likely to be modulated according to the change of viewing distance as suggested by the behavioural results in Chapter 4. Further research is needed to understand the neural mechanisms relative to near and far viewing.

5.4. Conclusion

The present thesis employed some novel behavioural tasks and methods to examine the visual processing for information arising from near and far spaces. Healthy human observers were shown to have different performance in perceiving visual information in near versus far spaces, although equivalent retinal information was provided by matching the visual angle and luminance of the stimuli in the near and far viewing conditions. The behavioural evidence reported here indicates that the information from near and far visual spaces is preferentially processed by distinct neural mechanisms in the neurologically intact brain. It had been assumed by previous researchers that the dorsal and ventral cortical streams are specialized in processing visual information from near and far spaces respectively. However, data presented here suggest that this neural regulation mechanism occurs at an earlier stage of visual processing. That is, the information transmission in parvocellular and magnocellular pathways was modulated according to the viewing distance. This is the first behavioural evidence indicating that the LGN serves as a gatekeeper to modulate and redistribute visual information for later cortical analysis, according to the ecological demands for the use of visual information arising from near or far space.

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