A Connectionist Perspective on Laterality in Visual Attention

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February 23, 2005

Abstract

This paper contains a comprehensive review of attention with a significant emphasis on lateralization of function. Connectivity and computation associated with the human visual system is described in detail, and the existing body of psychophysical, neurophysiological and computational studies relating to attention is summarized. This provides the foundation for the later chapters which describe the nature of communication between hemispheres, and the relative efficiency with which each hemisphere handles different attentive and visuospatial tasks. Finally, we outline some possible directions for future research on these matters.

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Chapter 1

Introduction

Approximately 500 million years ago, a hostile period of tectonic activity gave rise to volcanic eruption, gross changes in the morphology of the environment, and overwhelming shifts in global climate. This planted the seed for an evolutionary period termed the Cambrian explosion that saw the emergence of segmented bodies and limbs, as well as, the inception of the ancestors of all animals that fly, swim, crawl, and walk. So one might say that around this time, left and right came to be, in a egocentric sense. In the half billion years since then, many animals including primates have evolved a bilateral anatomy roughly including two arms, legs, eyes, ears, and brain halves. The basis for the emergence of two physically separated cerebral hemispheres remains a mystery, with scientific efforts in explaining this episode not reaching far beyond accounts that are purely speculative. It seems likely that the emergence of pairs of limbs and organs derives from an evolutionary advantage associated with symmetry and bilaterally.

The concern of the following document is not in understanding general evolutionary mechanisms for the emergence of laterality but rather in understanding how laterality impacts on attention and visuospatial processing in primates. Understanding such mechanisms in this more limited domain should offer some principles that generalize to other domains of laterality research, although, this interest is very much secondary to the understanding of issues of laterality in visual attention and visual processing. Key questions that emerge in this context are as follows:

1. How do the two hemispheres communicate to ensure a unitary focus of attention with regard to visual processing, and how does attention proceed when such communication is severed?

2. Given that primates have two eyes, how does attention impact on the processing of the input stream received at the retinae, and in particular, what is the relationship between the two eyes with regard to attentional selection?

3. In what frame of reference does attentional modulation occur with respect to the frame of reference of each retinal image?

4. Do there exist asymmetries in terms of visual field, or hemisphere regarding the processing of visual information? If so, what computational advantages might such asymmetries afford in visuospatial processing?

5. Do there exist asymmetries in regard to how attention is allocated, and may such asymmetries be explained in terms of i. More general visuospatial asymmetries, or ii. Underlying computational principles?

6. In the case that asymmetries exist in visual processing, it is unlikely that such an arrangement is accidental or offers no evolutionary advantage. Bearing this idea in mind, are there computational principles or conditions in connectionist modeling under which such asymmetries might emerge?

7. What advantages or disadvantages do laterality and bilaterality afford from a computational perspective?

8. With regard to the preceding six points, what insight is gained with regard to advantages that might bear some utility in the context of human and machine vision and attention?

It should be made clear that the analysis and discussion appearing in this work exists at the level of connectionist modeling, and as such, description of mechanisms of human visuospatial processing and attention is at the level of connectivity between, and computational function of units involved. With the preceding discussion in mind, the structure of the document is as follows:

Chapter 2 contains a functional level description of the primate visual system. The intention of this section is to provide a very basic but necessary background for those readers unfamiliar with human vision. The background in this section includes a high level description of primate visual processing including issues of connectivity, and the computational role and organization of various visual areas in the brain.

Chapter 3 provides an overview of the current literature concerning the computational modeling of attention. Included is a variety of the more influential models of visual attention proposed in the past fifty years. Also included is a very general overview of the neurophysiology of attentional processing. Particular emphasis is placed on one computational model of attention, called the Selective Tuning Model[228] which directly addresses a number of issues that are also highlighted in this chapter as issues that attention should address beyond the complexity problem[226].

Chapter 4 provides an overview of communication and competition between hemispheres. The focus of this chapter is the connectivity between homologous regions in each hemisphere, and the relationship between such connections and visual space. The role of such communication in coordinating the focus of attention is also described.

Chapter 5 describes asymmetries observed in visual processing in the primate visual system. The focus of the chapter is on differences between the two hemispheres in processing visual input, and the impact that such differences have on the ability to navigate and act in a particular environment. Some speculation is included concerning the reasons that such asymmetries may have emerged in the context of visual processing.

Chapter 6 describes a number of hemispheric asymmetries tied specifically to experiments involving visual attention. It is unclear whether such asymmetries are attention specific or a result of more general asymmetries. The intention is to review the current literature concerning hemispheric differences and spatial non-uniformities in visual attention. Particular emphasis is placed on a number of visual search experiments in which attentional asymmetries are especially apparent.

Chapter 7 outlines the small body of connectionist and computational models that exist, surrounding the issues described in chapters 3 to 6. It is emphasized that the current understanding of phenomena observed in visual and spatial processing pertaining to laterality leaves much to be desired.

Chapter 8 highlights some areas that might benefit from analysis at the levels of computation, implementation, and simulation. Particular emphasis is placed on the idea that asymmetries are most likely related to underlying processing advantages that are inherent in the asymmetric bilateral processing architecture assumed by the brain. This last consideration hints at a possibly fruitful avenue for research to follow.

Chapter 2

From Two Eyes to Two Hemispheres: Visual Computation and Connectivity

An important consideration in modeling computational aspects of vision, is that of understanding the connectivity between visual areas and how computation is organized within the visual hierarchy. It is with this consideration in mind that the neural hardware and computation underlying human vision is outlined in this chapter.

2.1 The Eyes

The eyes provide the optics for sensing ones surroundings based on scene radiance, and are the primary source of input to the visual system. Light is projected by the lens onto the retina of each eye. Stimulation of rods and cones gives rise to activation of horizontal cells found in the outer plexiform layer, amacrine cells, bipolar cells, and finally, parasol and midget ganglion cells which in turn project to layers of the lateral geniculate nucleus (LGN). Rods are characterized by high sensitivity across a broad spectral range, and are found exclusively outside the fovea. In contrast, cones exhibit lower sensitivity across a narrow spectral band, and are highly concentrated in the foveal region of each eye with decreasing concentration with increasing distance peripherally. Further, cones exhibit three types of spectral tuning with peaks at wavelengths of 450nm (S-cones), 535nm (M-cones), and 565nm (L-cones). S-cones constitute on the order of 10% of the total number of cones, and the remaining cones (M and L cones) tend to be present in roughly equal proportions. Bipolar cells receive input from only cones or only rods. The various types of bipolar cells and their response properties are described in more detail in [17]. Ultimately, ganglion cells provide the output to higher visual areas where computation based on primitive types of information carried by ganglion cells occurs. Ganglion cells may be classified as midget or parasol ganglion cells.

Midget ganglion cells are sometimes referred to as colour-opponent cells. All midget ganglion cells project to parvocellular layers of the LGN. On the order of 90% of ganglion cells fall into this category. The response of midget ganglion cells is derived entirely from the responses of cones, and exhibits various combinations of green-centre red-surround, or blue-centre, yellow-surround with different combinations of on or off preference corresponding to each of the centre and surround.

Parasol ganglion cells are sometimes called achromatic ganglion cells because they do not exhibit a preference for a particular wavelength of light. All parasol cells project to magnocellular layers of the LGN. Receptive fields corresponding to parasol ganglion cells are significantly larger than those of midget ganglion cells and are sensitive to low luminance levels. Cells tend to exhibit on-centre off-surround or off-centre on-surround receptive fields. Inputs to parasol cells typically derive from either only rods, or from a variety of types of cones so that little spectral sensitivity is observed. Parasol ganglion cells have larger axons than midget ganglion cells and as such conduct nerve impulses more rapidly. Parasol ganglion cells are characterized by a greater sensitivity to temporal frequency but weaker spatial frequency tuning as compared with midget ganglion cells.

Horizontal cells form inhibitory synapses on bipolar cells. The role of horizontal cells is in facilitating lateral inhibition between activated photoreceptors so that bipolar cells exhibit increased sensitivity to discontinuities in photoreceptor activity.

A more recently discovered addition to the ganglion cell types are the bistratified ganglion cells that project to the interlaminar or koniocellular layers of the LGN. Bistratified ganglion cells exhibit response properties closer to parasol than to midget cells including high contrast gain, variable spatial resolution, and large cell size.[81] Bistratified cells also appear to be unique in their spectral selectivity, characterized by blue-on receptive fields.

Axons from ganglion cells project to the optic chiasma and from there, on to the LGN. At the chiasma, inputs from a given eye are divided so that half of the axons from each eye project to the ipsilateral LGN, and half to the contralateral LGN. The result of this configuration is that the left hemisphere represents all space to the right of the vertical meridian from both eyes and the right hemisphere, everything to the left of the vertical meridian. A schematic of this arrangement is shown in figure 2.1.

2.2 Lateral Geniculate Nucleus

The majority of axons in the two optic tracts project to the lateral geniculate nucleus (LGN). The LGN consists of six distinct layers comprised of relay cells[169]. Axons of relay cells project from the LGN to the primary visual cortex. It is important to note that as with many brain structures, the LGN may be discussed in terms of two symmetric halves. For a given half (left or right LGN), the ipsilateral optic nerve fibres project to layers 2,3 and 5 while contralateral optic nerve fibres project

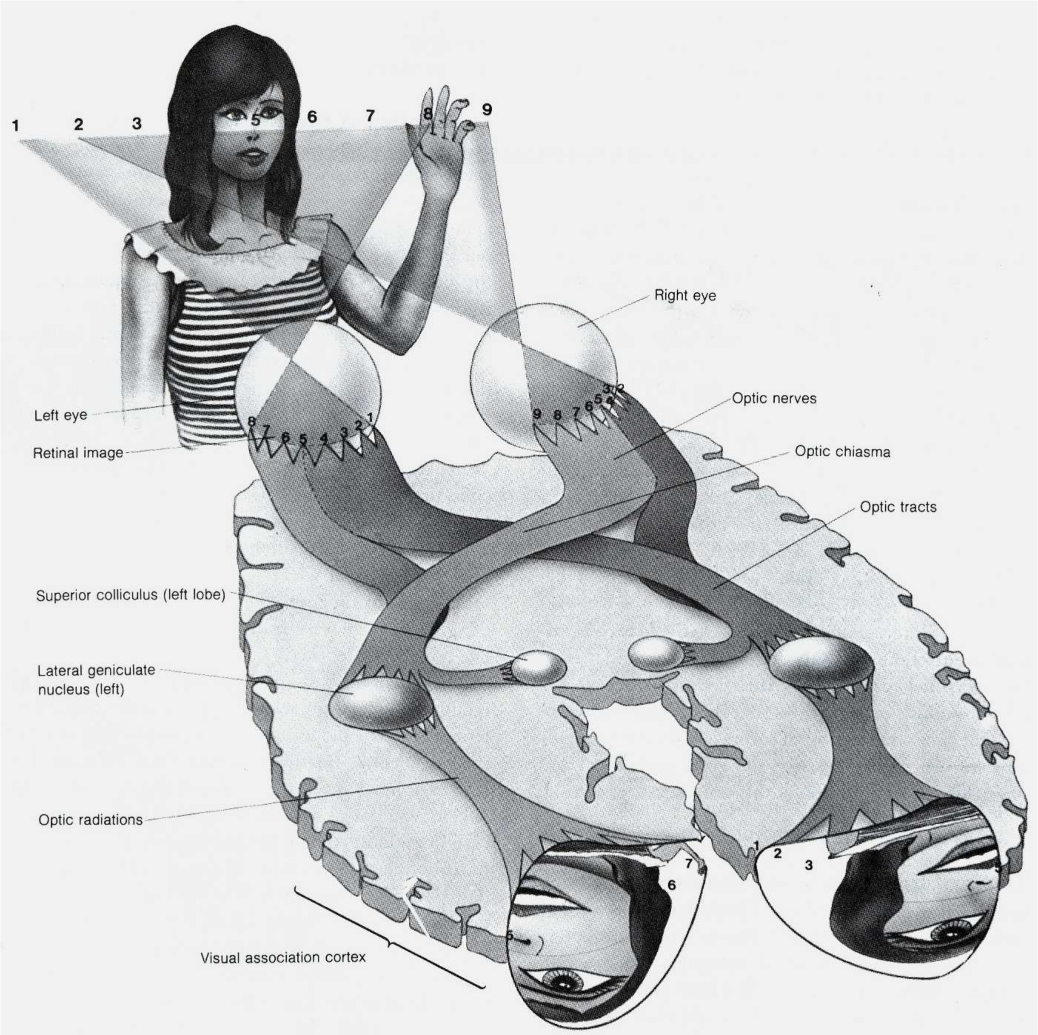

Figure 2.1: Projection of a scene on to the retinal image of each eye and the resulting topographic representation in V1. From [69].

to layers 1,4, and 6. Layers 1 and 2 of the LGN are known as the magnocellular layers and are characterized by larger receptive field size, achromatic signals, high contrast sensitivity, low spatial resolution and fast transfer rate. Layers 3,4,5 and 6 are known as the parvocellular layers and are characterized by smaller receptive field size, sensitivity to color information, low contrast sensitivity and high spatial resolution with a slower transfer rate. The right LGN consists of inputs entirely from the left visual field and the converse for the left LGN. Each of the magnocellular and parvocellular layers then consist of alternating representations of left and right eye input corresponding to a single visual hemifield and relay such information to the primary visual cortex. All LGN cells exhibit concentric receptive fields similar to those of ganglion cells. Magnocellular layers project to layer 4cα of the primary visual cortex and parvocellular layer project primarily to layer 4cβ with some to 4A. This is depicted in figure 2.3. There also exists a significant population of more recently discovered LGN layers known as the koniocellular or interlaminar layers. The properties of the koniocellular pathway remain relatively unknown in comparison to M and P pathways. The koniocellular layers project to the upper layers of the primary visual cortex that are rich in cytochrome oxidase which tend to correspond to V1 blobs[82, 81]. Though little is known about the functional role of the k-pathway, it appears to have an important role in color vision.[81].

2.3 Primary Visual Cortex

The primary visual cortex, receives the majority of output from the LGN and is responsible for characterizing a great deal of low-level image properties. V1 is organized as an array of hypercolumns that are on the order of 1mm by 1mm in size. All of the neurons within a hypercolumn correspond to the same localized area of the visual field. A schematic of this organization is depicted in figure 2.2. The organization of V1 is retinotopic, so that adjacent hypercolumns correspond to adjacent areas of the retinal image. In the fovea, the high concentration of photoreceptors gives rise to a detailed representation of foveal stimuli, with the number of hypercolumns involved in processing foveal content similar to the number for processing the rest of the visual field. Within each half of a hypercolumn, neurons respond primarily to stimulus in either the left or right eye. Such columns are termed ocular dominance columns. Within each ocular dominance column, neurons are arranged according to a smooth, regular configuration, with cells responding best to structure at a particular angular and radial frequency. Neurons exhibiting a similar tuning for structure orientation and spatial frequency tend to appear adjacent in this organization. There also appear to be neurons the respond best to a particular degree of motion disparity, or binocular disparity in the primary visual cortex. Cells tuned to such features are disjoint with little evidence of neurons tuned to motion in depth at the level of V1[13].

V1 consists of six layers. All input from the LGN is received at layer 4c and the majority of neuron responses at this level are monocular. Shifting to higher or lower layers, neurons that respond to input in either eye are found. Layers 5 and 6 of V1 project to the superior colliculus and back to the LGN and output from layers 1 to 3 projects to higher visual areas. Hypercolumns consist of a central blob region in each ocular dominance column surrounded by interblob regions. Neurons in blob regions have concentric receptive fields and typically respond to red-green and blue-yellow opponency. Note that in the case of complex cells, receptive fields are not clearly divided into inhibitory and excitatory zones so that luminance is integrated in a nonlinear fashion. Colored blob regions respond to only the one eye corresponding to the ocular dominance column in which they lie. Neurons that respond to stimulus in either eye tend to respond best to the same spatial frequency and orientation but may differ in preferred phase or may exhibit a slightly shifted receptive field centre.

2.4 Higher Visual Areas

As one ascends the visual pathway beyond V1, computation gradually diverges into ventral and dorsal streams[128]. The ventral stream includes (in order) areas V2, V3, V4, and the inferotemporal area. The dorsal stream includes areas V2, V3, MT, MST and parietal areas. The ventral stream derives primarily from parvocellular pathways and the dorsal stream from magnocellular pathways. The ventral pathway characterizes such information as shape, color, and disparity whereas the dorsal pathway deals primarily with location, motion, and disparity information. The following offers a brief outline of the computation and organization among these higher areas. Issues of connectivity are dealt with in the section that follows and are depicted in figure 2.6.

V2

The macaque V2, sometimes called the secondary visual cortex receives 90% of its input from V1. V2 is not organized into ocular dominance columns but does exhibit a striped configuration when stained with cytochrome oxidase, with stripes running parallel to the border between V1 and V2. There are three distinct types of stripes known as thick stripes, thin stripes and interstripes which lie between each pair of thick and thin stripes. The width of all three stripes together is approximately 1mm and there is on the order of 12 of each type of stripe in V2. In human V2, stripes are less distinct, instead appearing as a disordered set of jumbled patches, however the general logical arrangement seems to be the same. Livingstone and Hubel [127] have demonstrated that layer 4B in V1 projects to thick stripes of V2, layer 2 and 3 blobs

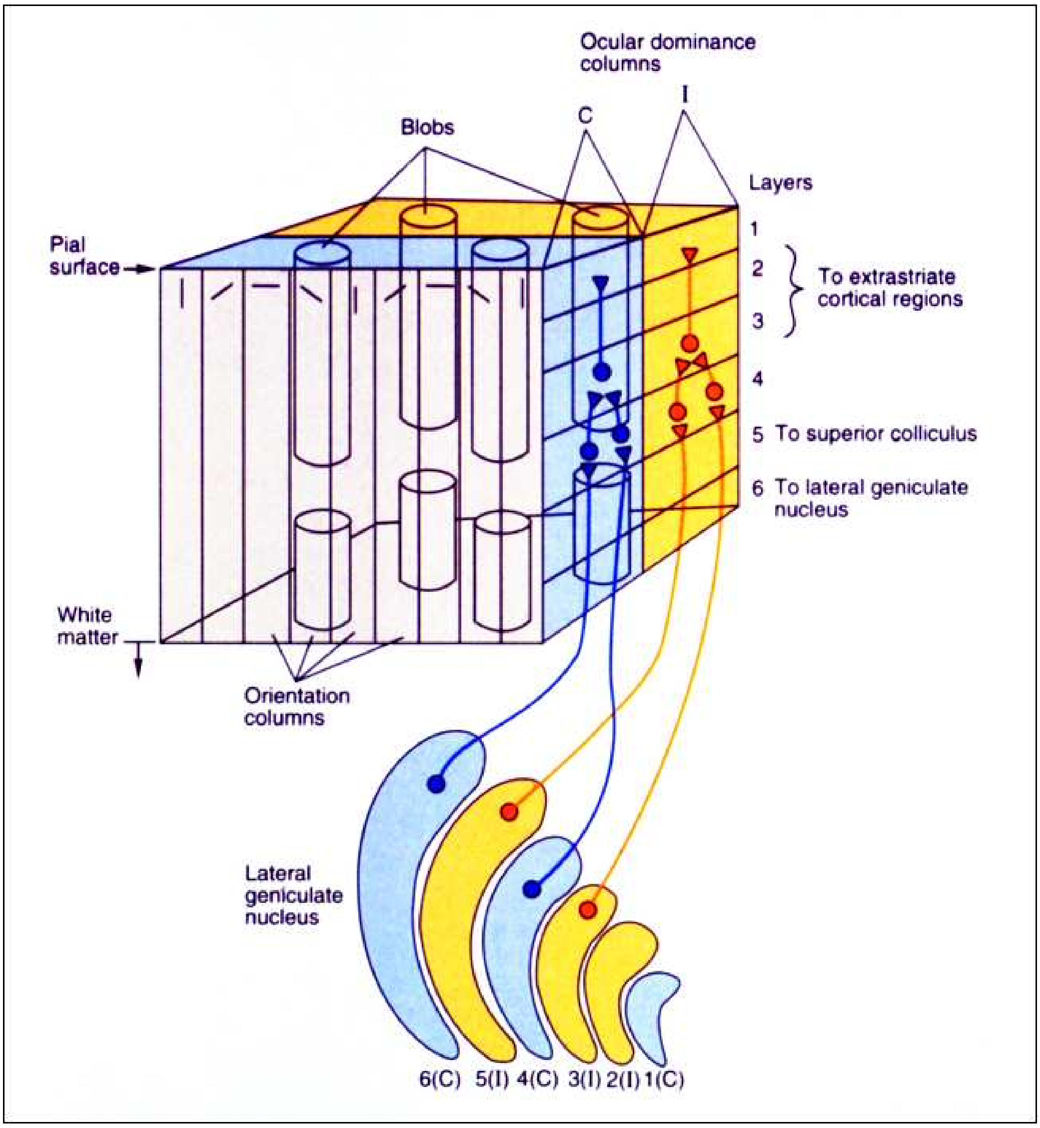

Figure 2.2: Connectivity between LGN and V1 and columnar organization of V1. (From [98])

project to thin stripes, and interblobs project to interstripes. It has been argued [128] that this division offers evidence of four functional pathways: thick stripes in V2 seem to be specialized for binocular depth perception, thin stripes for color perception and interstripes for form perception. Further, their is a direct pathway from layer 4B of V1 to MT that might facilitate motion processing[127]. Division into these four distinct pathways is by no means absolute since within any given stripe, there do appear to be patches selectively tuned for color, orientation, or disparity. V2 receptive field sizes are larger than those of V1 neurons.

V3

V3 is a smaller visual area that lies along the dorsal border of V2. V3 receives input from V2 and layer 4B of V1. V3 projects primarily to V4 and V5 and to a lesser extent to MST and parietal areas[134]. V3 receptive fields are larger than those found in V2. Most cells in V3 are orientation selective with on the order of 50% also showing a preference for direction of motion. V3 cells exhibit a greater preference for low spatial and high temporal frequencies than those found in V2[71]. Most recent estimates indicate that on the order of 50% of cells in V3 are color selective[71]. About 50% of V3 cells seem to respond to binocular disparity with joint tuning to disparity and orientation forming the basis for the columnar organization of V3. Such an ordering of computational units has been suggested as a means of facilitating extraction of orientation disparities and disparity gradients[252]. V3 seems to represent only 30 degrees of contralateral visual space. V3 lies adjacent to a smaller area called V3A which contains a distinct representation of lower and upper hemifields. The V3-V3A border corresponds to the vertical retinal meridian with calossal connections to the corresponding region in the opposing hemisphere.

V4

V4 is the first area that lies solely in the ventral pathway. V4 receives the majority of its input from V1, but also 50% of the output of V2 and some input from V3[154], and LGN[214]. In V4, only the central 35 degrees of the contralateral hemifield is represented and the topographic organization of processing elements is rather disordered. V4 is characterized by large receptive field size, and specialization for shape, colour and pattern disparity. Unlike earlier areas, cells tend to respond better to features such as angles and contours than simple edges. It appears that V4 performs rudimentary shape processing which is then used among higher areas of the ventral pathway. This is apparent in the severe deficit in form discrimination that results from V4 lesions[83, 204]. In humans, an area analogous to V4 is found among lingual and fusiform gyri. In humans, lesions within V4 have been shown to cause achromatopsia which results in a perception of the world in grays[254].

MT and MST

MT is the first area that lies only in the dorsal "where" pathway. MT input ultimately derives from magnocellular layers of the LGN, and corresponding layers of V1, V2 and to a lesser extent V3. The dorsal pathway is characterized by a specialization for processing low spatial, high temporal frequency stimulus, including fast flicker and motion, and coarse stereo disparity information. The function of the dorsal pathway is thought to entail the analysis of spatial location and motion processing. In humans, the homologue to MT is called V5. MT contains a complete topographical representation of contralateral space. Receptive field sizes in MT are on the order of 10 times those found in V1. Cells in MT appear to respond to motion, first and second spatial derivatives of motion[248, 225], and various patterns of optical flow including circular and radial patterns[147]. Motion tuned cells in MT also seem to respond to particular degrees of disparity or motion in depth[138].

IT

Following V4 along the ventral pathway is the inferior temporal cortex (IT). IT receives the majority of its input from V4. There is some grouping of IT cells on the basis of properties to which they are tuned but the organization is non-retinotopic with no apparent logical relationship between position of receptive field in space and position of neurons in IT. IT consists of two main areas known as TEO and TE that each project to parietal areas and also to certain areas of the frontal lobes(TEO primarily to parietal and TE to frontal)[241]. IT cells seem to respond best to certain combinations of shape, color and texture[215]. Further, IT neurons seem to respond to shape defined by luminance contrast, motion, texture, and binocular disparity[201]. IT neurons also seem to respond to recently memorized complex patterns[143]. IT appears to be the last purely visual region along the ventral pathway.

Parietal Areas

The parietal lobes are divided into a large number of areas each having a high level of connectivity with many other visual areas including early areas such as V1 and higher areas along the ventral pathway including IT. This section describes some of the more important parietal areas for visual function including superior temporal areas (caudal superior temporal cortex and rostral superior temporal cortex), ventral, lateral, medial and anterior intraparietal areas (VIP,LIP, MIP, AIP respectively), and superior and inferior parietal lobes. Lateral, medial, and anterior intraparietal areas lie in the posterior parietal cortex which also includes superior and inferior parietal lobes.

The medial superior temporal cortex (MST or V5A) receives the majority of its input from V5 and lies in the caudal superior temporal area. Receptive fields in MST are even larger than those found in MT. MST cells tend to respond best to global patterns of optical flow including translation, rotation, expansion, contraction and rotation in depth[199]. MST cells also respond to particular combinations of motion and disparity[58].

The rostral superior temporal area receives input from dorsal and ventral streams and has been suggested as playing a role in object recognition[100] and encoding form induced by motion[231]. Karnath and colleagues[100] have demonstrated that rostral superior temporal lesions in the right hemisphere may give rise to attentional deficits or neglect in the contralateral (left) hemifield.

VIP is specialized for coding certain aspects of optical flow and receives input from MT and MST[6]. VIP neurons have been implicated in coding rotation in depth[202] and direction of impact[30]. In general, the response of neurons in VIP seem to be similar to those found in MST.

AIP seems to respond to combinations of visual stimuli and tactile tasks such as grasping or manipulation of objects[151]. AIP also seems to encode more involved combinations of of complex stimuli such as orientation in three dimensions defined by stereo disparity, or texture gradients[211]. AIP receives its input from LIP and projects to the premotor cortex.

MIP and LIP receive inputs from a variety of brain areas including somatosensory, and vestibular inputs, as well as visual inputs from MT, MST and to a lesser extent, V3A. LIP has been implicated in shifts in attention and MIP in changing one's response to a particular stimulus[196]. LIP cells have also been tied to cueing of eye movements prior to their execution[212]. In more general terms, LIP seems to be involved in attentive behaviour, as well as execution of eye and hand movements via connections to the frontal lobes[3]. Some LIP and MIP neurons have been demonstrated as coding information in a head-centred frame of reference[198].

Areas 7a and 7b lie in the inferior parietal lobe. 7a neurons have been implicated in coding particular types of flow including rotation in three-dimensional space[197] and body-centric object position[212].

Frontal Lobes

Ventral and dorsal streams converge onto the frontal lobes, but project to different areas, and as such, cells tend to be tied to computation that one would expect from *one* of these pathways. That said, there are also neurons that appear to respond to combinations of "what" and "where" stimuli[182]. In the context of vision, frontal lobes seem to relate to tasks involving memory and visually guided movement[194, 68] although their role is not yet entirely clear.

2.5 Computation Requiring Two Eyes

A general property of bilateral species, is that many of the functional organs and basic components of such animals come in pairs. That is, generally, such animals have two arms, two legs, two ears, and two eyes. In the context of vision then, it may be worth considering what two eyes afford with regard to observing and navigating about one's surroundings. It is with this consideration in mind that the physiological mechanisms underlying binocular vision are described. It should be stated that the primary ambition of this document is that of understanding laterality and interhemispheric communication, and not the mechanisms underlying binocular vision. That said, a significant byproduct of laterality in the context of vision, is information gained from having two separate and similar views of one's surroundings.

2.5.1 Physiology of Disparity Detection

Although computation pertaining to stereo vision is not the focus of this document, it is nevertheless worth considering the connectivity underlying such computation in light of the fact that the presence of two eyes introduces additional constraints on how attentional processing may be resolved within and between hemispheres. Having two slightly different views of a scene allows the ability to perceive depth based on disparity between matching features within the two different views. The problem of matching corresponding features from the two views is called the correspondence problem, and primate visual systems show a remarkable ability for solving this task. The most vivid demonstration of this ability comes from studies involving random dot stereograms, originally conducted by Julesz[97]. In this setup, subjects were presented with two separate patterns of random dots, with a section of the random dot pattern shifted in one of the images. This gives rise to a distinct sense of depth even though no such depth cues exist in either of the individual views. A good understanding of the mechanisms underlying disparity detection in V1 has been achieved in recent years.

The primary visual cortex is the first site at which single neurons may be activated by stimulus in either eye. In a number of early studies[171, 8], V1 neurons were demonstrated to encode the relationship between the image in each eye through sweeping bar stimuli. Neurons respond to a particular feature, such as an oriented edge, and maximally to a particular disparity[8].

Disparity detectors are observed along both dorsal and ventral pathways with cells responding to local disparity in early areas such as V1, V2, and V3[236], disparity gradients in V2 and V3[1], 3D shapes in V4 and IT[239], motion in depth in MT[42], and shape defined by depth in IT.

Ohzawa and Freeman have carried out a number of studies observing response properties of neurons tuned to binocular disparity (see [163] for a review). On the basis of such studies, Ohzawa et al. have proposed a model for disparity selectivity which assumes simple cells with responses generating by summing the output of two monocular Gabor responses with the output rectified. Simple cells are grouped in pairs with the output of such pairs having an inhibitory response on their counterpart. Complex cell responses are then given by the sum of two such inhibitory pairs in quadrature[162].

2.6 Overview and Connectivity

It may be instructive at this point to provide an overview of the connectivity and computation involved between and among visual areas. Figure 2.6 serves this purpose. Input is received by way of light impinging on the photoreceptors at the level of the retinae. Responses project to the 4 parvo and 2 magnocellular layers of the LGN and in turn are relayed to layer 4c of V1. A number of cells compute basic local image properties within ocular dominance columns which are relayed to higher areas along dorsal and ventral pathways.

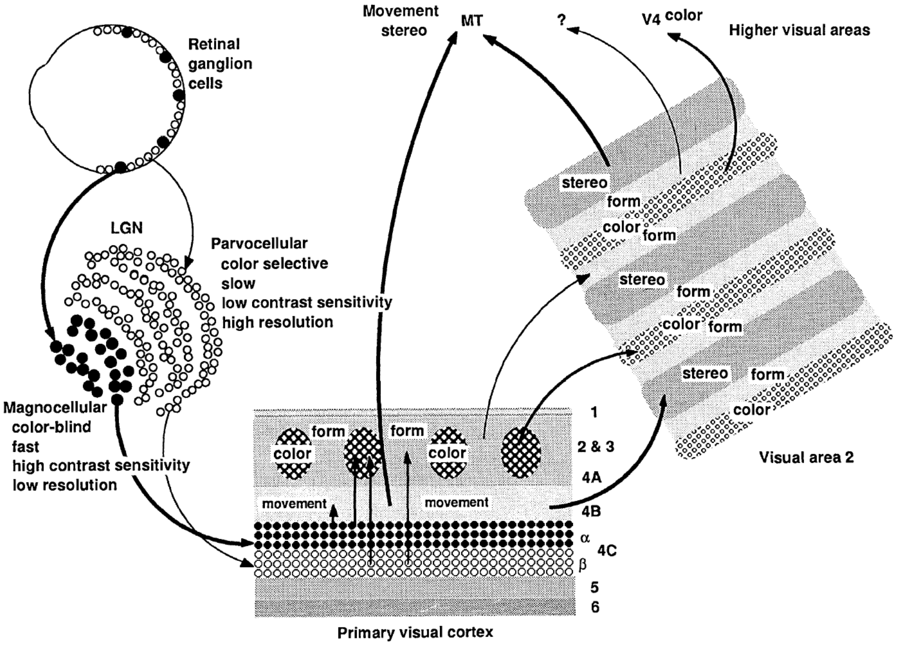

Figure 2.3: A depiction of the visual system from the eye, to early pathways, to higher visual areas. (From [128])

Chapter 3

Computational Modeling of Attention

Despite the perception that we ”see everything around us”, there is significant disparity between the amount of visual information that is received at the retinae, and the proportion of this visual information that reaches later processing or impacts on conscious awareness. Attention is crucial in determining visual experience. The spirit of attention is perhaps best captured by William James[95]:

> Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others.

Attention provides a mechanism for selection of particular aspects of a scene for subsequent processing while eliminating interference from competing visual events. A common misperception is that attention and ocular fixation are one and the same phenomenon. Attention focuses processing on a selected region of the visual field that needn’t coincide with the centre of fixation. This is perhaps exemplified by the perceived ability to 'look out of the corner of ones eye'. In the following sections, these issues are touched on in more detail with the hope that the reader will attain a greater appreciation of what exactly attention entails, and what attention bestows with regard to our ability to interpret and act upon visual stimuli. This chapter affords an overview of the current understanding of visual attention with consideration to neurobiology, the role of attention in computer vision, and with an emphasis on computational modeling of attention.

3.1 The Need for Attention

A question that frequently arises with regards to attention, particularly in the context of computer vision, is that of *why* attention is a necessary component of such a system. Computer vision systems are frequently developed with the intention of operating in real time but often fall short of this mark at the time of their inception (and not infrequently long after this time). It is not unusual to read statements such as "the algorithm should allow for real time performance given future hardware developments", or "this algorithm may operate in real-time given massively parallel computing hardware". Attention is typically thought of as a means of focusing processing on some subset of the incoming stimuli thus reducing the computational load. On the basis of this view, the importance of attention is sometimes downplayed with regards to its role in computer vision since, as some authors state, advances in hardware will eventually overcome such limitations. The intention of this section is to motivate *why* this is an invalid assumption, since the issue at hand is greater in scope than simply reducing computational running times. One of the primary goals of attention, unrelated to complexity, concerns interference between signals generated by unrelated image events and selecting between possible outcomes. In a feedforward network, crossover between signals and blurring may result in a response at the output level that is highly confused. This issue is elaborated on in the following discussion. Tsotsos examined the problem of visual search as derived from first principles[226] within a well defined framework including images, a model base of objects and events, and an objective function that affords a metric of closeness between an image subset and an element of the model base. On the basis of this formulation, it may be shown that visual search in the general case (i.e. when no explicit target is given) is NP-complete. One conclusion that emerges on the basis of this analysis and other complexity arguments [229, 22, 4, 155], is that the computational complexity of vision demands a pyramidal processing architecture. Such an architecture is observed in the primate brain on the basis of increasing receptive field size and the observed connectivity between neurons as one ascends the visual pathway[166]. Pyramidal processing may greatly reduce the computation required to accomplish a particular task by reducing the size of instances to be processed. Tsotsos et al. outline four major issues that arise in a pyramid processing architecture, all of which result in corruption of information as input flows from the earliest to later layers[228]. The four cases are depicted in figure 3.1. The pyramid depicted in the top left (Fig. 3.1a) demonstrates the context effect. The response of any given unit at the top of the pyramid results from input from a very large portion of the input image. As such, the response of a given unit at the top of the pyramid may result from a variety of different objects or events in the image. On the basis of this observation, it is clear that the response at the output layer with regards to a particular event depends significantly on the context of that event. The top right pyramid (Fig. 3.1b) demonstrates the blurring effect. A small localized event in the input layer eventually impacts on the response of a large number of neurons at the output layer. This may result in issues in localizing the source of the response at the output layer, as a localized event may

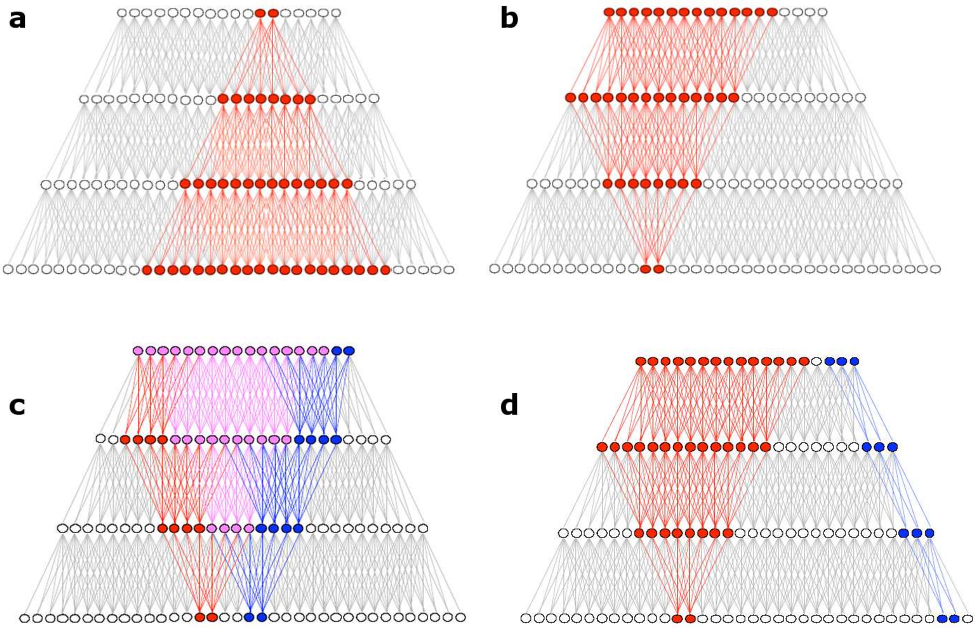

Figure 3.1: Four major issues in pyramid information flow: a. The context effect, b. The blurring effect, c. The cross-talk effect, d. The boundary-effect. Adapted from [227].

be represented by a large portion of the highest layer. The pyramid on the bottom left (Fig. 3.1c) displays the cross-talk effect. Cross-talk refers to the overlap of two image events in the pyramid which results in interference between signals in higher layers of the pyramid. Finally, the pyramid on the bottom right (Fig. 3.1d) displays the boundary effect. Units at the outer edges connect to fewer units in higher layers of the pyramid. As a result, a significantly stronger response may result from the same stimulus centered in the visual field relative to near the boundaries. Means of overcoming this difficulty are discussed in detail in [40].

At this point, the rationale of the preceding discussion may not yet be apparent. The motive for addressing such issues is that an appropriate attentional mechanism may overcome the aforementioned issues inherent in pyramid processing. In particular, the Selective Tuning Model[228] was designed with these issues in mind. Deactivation of appropriate connections in the network allows each of the aforesaid issues to be overcome. The exact mechanism by which such issues are handled becomes evident in the description of the Selective Tuning Model presented in section 3.4.

3.2 Attention in the Human Brain

The neurobiology of attention has been a controversial subject for decades with much of our understanding coming from behavioral studies often drawing ambiguous or conflicting conclusions. That said, recent advances in imaging technology (fMRI in particular) have given rise to a slew of imaging studies affording a more definite picture of the neuroanatomy and processes involved in attention. The following discussion offers a picture of the current understanding of the effects of top-down biasing on neural activity and in particular, some thoughts on where signals that initiate top-down bias originate.

3.2.1 Top-down Bias in the Visual Cortex

A key property of attention is the top-down modulation of visually evoked activity. Such modulation is believed to facilitate bias for a particular location of the visual field, or a particular stimulus property[45]. Modulation is thought to come in one of the following three forms: response enhancement, information filtering, and increase of response sensitivity[103].

There is evidence in favor of two distinct types of response enhancement resulting from top-down bias. The first of these types comes in the form of a presumed multiplicative enhancement of cell response brought about by top-down attentional bias.

Such enhancement has been detected in virtually every area of the primate visual system including LGN[161], V1[148], V2[148, 129], V4[75, 213, 148, 32, 129, 139], MT[225, 224], and the lateral intraparietal area (LIP)[23, 31]. Top-down attentional bias then seems to impact on neural activity in virtually every area of the visual cortex and even down to the level of a single cell[146]. It has been demonstrated that bias may act in favor of location in the visual field[44], or particular stimulus properties such as luminance and color[149], line orientation[75, 140], and direction of motion[63]. There also exists some evidence that biasing for location occurs at a faster rate than bias for stimulus type[87, 235]. Explanations for this observation range from a hierarchical model of attention wherein selection of stimulus attributes requires prior selection of location[87], to parallel channels mediating each of space and attribute modulation with the spatial channel faster[45].

Modulation of cell responses also seems to come in the form of an increase of baseline activity in the absence of any visual stimulus. Increase in baseline firing rates of 30-40% have been observed in response to covert deployment of attention in areas V1[102], V2 and V4[129], and LIP[31].

In a scene containing multiple competing stimuli, suppressive interaction between cells responding to competing stimulus may exhibit mutually suppressive interaction[187, 105, 104]. There is evidence that top-down attention may result in modulation of suppressive interaction. Spatially directed attention to a stimulus in the receptive field of a particular neuron may eliminate suppressive activity of non-attended stimulus falling in the same receptive field[187]. Attentional effects tend to be less pronounced when competing stimului falls outside of the receptive field of the neuron in question.

3.2.2 Where are Attentional Signals Generated?

Although the effects of attention may be seen in all areas of the visual cortex, there is evidence that top-down bias signals are generated outside the visual cortex and transmitted via feedback connections to the visual cortex. In particular, current evidence seems to favor selection achieved by way of competitive interaction in the visual cortex with bias signals originating within parietal and frontal cortices[103].

Unilateral lesions in a variety of brain areas give rise to unilateral neglect of the visual field contralateral to the lesion[14, 78, 181]. Cases range from mild, where patients have difficulties directing attention to competing stimuli in the affected visual hemifield, to severe resulting in a total lack of awareness of anything in the affected hemifield. Areas in which lesions result in the described effects include the parietal lobe[233], parts of the frontal lobe[77, 41], the anterior cingulate[96], the basal ganglia[41], and the pulvinar[240]. It has been hypothesized that such areas form a network for directing attention to visual areas[141, 173]. In the case of patients exhibiting neglect, it has been shown that bottom-up computation in the affected hemifield proceeds as normal and may have an impact on behaviour[50, 72, 137, 49, 51] further reinforcing the importance of the previously mentioned areas in top-down modulation.

Imaging studies have further reinforced some conclusions drawn from lesion studies while casting doubt on others. fMRI studies have suggested that activity in frontal and parietal areas seems to correspond to attentional operations, and not merely the attentional modulation of visual responses[184].

One phenomenon that remains poorly understood is a particular asymmetry that is observed in neglect cases. Right sided parietal lesions result in hemispatial neglect much more frequently and with greater severity than is the case with left side parietal lesions[232]. Based on the observed asymmetry, it has been suggested that the right hemisphere directs attention to stimuli in both hemifields while the left hemisphere directs attention in the right hemifield[141]. A variety of fMRI studies have explored this asymmetry with some reporting a significantly stronger activation of the right parietal lobe[37, 160, 234] and others reporting symmetric activation of parietal lobes[65, 104] with some observing such symmetric interaction regardless of the visual field in which stimulus is presented[104].

3.3 Selected Computational Models of Attention

There exists an abundance of "theories" of attention ranging in specificity from very general conceptual descriptions to highly detailed computational mechanisms. This section is intended to serve as a review of computational models of attention that are much better classified as belonging to the latter of these categories. The discussion that follows is intended to serve as a historical review of biologically plausible computational models of attention, or, neurobiological models of attention that include concepts that might impact on the computational modeling of attention. Any models that are purely computational, purely descriptive, purely speculative, or only propose small variations on existing models, are excluded. Following this review, Tsotsos Selective Tuning Model [226] is described in some detail as the Selective Tuning Model will form the basis for the modeling of bilateral attention and interhemispheric interaction that is expected to result from the ideas present in this document.

Early Ideas

Perhaps the earliest mention of attention that borders on modeling of attention comes in the form of Broadbent's theory of early selection[21]. Early selection posits that rudimentary visual processing occurs preattentively and that focused attention is then required to facilitate higher visual processes such as object recognition. Shortly after this time Deutsch and Deutsch proposed an opposing view known as late selection[46] that requires preattentive processing of the entire scene to a high-level with attention selecting a subset of this highly processed information. Since this time, a number of more detailed accounts of attention have been suggested mostly in agreement with ideas of early selection.

Adaptive Resonance Theory (Grossberg, 1976)

Adaptive Resonance Theory (ART) [74] falls under the classification of a model of attention based on its original concern for human cognitive information processing and filtering. Grossberg developed a theory of information processing based on a number of principles derived from experiments involving cognitive development, reinforcement learning and attentional blocking. Central ideas of ART with respect to attention are as follows: i. The magnitude of the response of a cell may be modulated by top-down priming. ii. Sufficiently large bottom up activation drives a cell. iii. A cell becomes active if it receives sufficient top-down and bottom-up activation. iv. top-down attentional modulation should exist in all cortical areas that learn. The basis for such rules revolves around the general principle of guarding stored memories against transient changes while maintaining plasticity in learning. ART has since evolved into a series of real-time neural network models for pattern recognition, unsupervised learning and classification([125], [52]). ART provides an interesting early account of the utility of attentive behavior in learning. Grossberg's description satisfies its ambitions in explaining the aforementioned tradeoff in learning behavior and outlines specific circuitry that accounts for the dynamics of attentive behavior in early visual areas. The chief contribution to the attention literature, is the idea of modulation of signals in the domain of sensory coding.

Feature Integration Theory (Treisman and Gelade, 1980)

Treisman and Gelade's Feature Integration Theory (FIT) [223], inspired by experimental work pertaining to visual search, proved to be a very influential early view of selective visual attention. FIT proposes that visual information is represented in a number of topographically organized feature maps. For example, a particular feature map might correspond to a topographic representation of local edge strength, or "blueness" over the image in question. Attention is then deployed on the basis of shifting an attentional spotlight over a "master map" constructed on the basis of information transfer from the various feature maps. In their proposed model, only information that falls under the attentional spotlight is said to reach the level of conscious awareness. The mechanism for information transfer between feature maps and the master map in the general case is not described with any specificity. A number of key predictions arise from FIT: First, visual search for a unique element is constant with regard to display size and number of distractors since activity in an appropriate feature map can guide the attentional spotlight directly to the unique element. Secondly, search for an element that is only unique on the basis of a conjunction of features increases linearly as a function of the number of distracting elements. This second effect is explained in the context of their model by the observation that no single feature map can directly shift the attentional spotlight and as such, a serial visit of each of the distracting elements is required. Ideas inherent in feature integration theory have had a profound influence on many models of attention that have been proposed in the quarter century since its inception. In particular, models that include a saliency map as a means of guiding attention typically share many attributes with FIT. When introduced, FIT provided a convincing computational explanation for trends observed in slopes derived from visual search experiments. That said, more recent psychophysical results suggest that search tasks are perhaps not simply divisible into two distinct search paradigms.

Correlation Theory (von der Malsburg, 1981)

von der Malsburg's Correlation Theory of Brain Function[237] marks the first reference to the binding problem in a computational context. Correlation Theory is motivated by the necessity of responses of cells corresponding to different parts or properties of a single object to be integrated to arrive at a single unified percept of the object. von der Malsburg proposes that this task is accomplished by way of synaptic modulation in which cells switch between conducting and non-conducting states. Such modulation is governed by correlation in the temporal structure of cellular signals. Correlation in the timing of cell responses, signals that such responses correspond to a single object. This paradigm allows connections corresponding to irrelevant stimulus responses to be deactivated momentarily to reduce interference between different memory traces affording an increase in memory capacity. Correlation theory is important from the perspective of its introduction of the binding problem to the attention literature, and satisfies its aim of highlighting the importance of, and describing a mechanism for, allowing active cells to express relationships amongst themselves

Koch and Ullman (1985)

In 1985, Koch and Ullman introduced a model of selective attention[115] based on a number of ideas inherent in Treisman's proposal[223]. Koch and Ullman suggested that, as was the case in Treisman's approach, attention is directed on the basis of a master feature map (called a saliency map by Koch and Ullman) derived from a variety of elementary feature maps. Feature maps are assumed to be computed in parallel over the entire image, and afford a topographical representation of image content with regard to a particular elementary feature (e.g. color, edge orientation, movement direction, etc.). Koch and Ullman's model is characterized by a second step wherein the early topographic representation (saliency map) is projected into a more central non topographic representation which contains properties of only the selected location. Items are chosen for the central representation on the basis of a winner-take-all network. Winning locations are successively inhibited so that attention continually shifts to the next most conspicuous position. It is worth noting that no single cell modulation occurs in the context of this model. Koch and Ullman suggest that the model might be implemented in "neural hardware" with a saliency map located in the striate cortex (V1) or lateral geniculate nucleus (LGN). Although the model of Koch and Ullman provides a more complete description of attention than some of the earlier models discussed, that focus on more specific concepts, it relies on a number of assumptions that one might question. Perhaps the biggest confound, is the inability to put into effect modulation at the level of a single cell. This is a consideration that is fundamentally important in any computational model of attention. Also, one might express concern with the claim that their exists a single unique topographical salience map in the brain that guides the focus of attention, since there is no significant evidence in favor of this hypothesis.

The Shifter Circuit Model (Anderson and Van Essen, 1987)

Anderson and Van Essen's Shifter Circuit Model [4] is based on an infrastructure in which a set of control neurons dynamically modify synaptic strength of intracortical neurons. The result is that information from within a windowed region of V1 is selectively routed to higher cortical areas. In neurobiological terms, Anderson and Van

Essen suggest that control neurons might reside in the pulvinar, with intracortical connection strength modified by way of multiplicative interactions on the dendrites. As was the case in many of the aforementioned models, Shifter Circuits rely on a master/saliency map which drives the responses of the control neurons. The representation of global saliency is suggested to be represented in the superior colliculus or, the parietal cortex. In addition to the contentious assumption of a single localized representation of salience, the suggestion that the routing of information relies on a simple switching mechanism among early visual areas is highly questionable, and further, fails to explain attentional modulation observed in extrastriate areas.

Sandon (1989)

The model of attention proposed by Sandon[200], marks the first complete implementation of a computational model of attention. The aim of Sandon's proposal is the selective routing of information to an object recognition processing step. An image processed by their model is first represented at three spatial scales. Scaled images are passed through a number of attention modules, which select features to be attended. The finest scale image is passed through the two attention modules, the intermediate scale image is passed through one attention module, and the coarsest scale image is not processed by any attention module. A scale arbitrator determines which of the three resulting streams is to be processed by the object recognition processor. The attention module consists of a hierarchical multi-scale network, in which features are computed in parallel, feature maps are transformed into feature contrast maps, and finally winner-take-all selection as described in Koch and Ullman's approach determines attended features. Given the criteria for models included in this review, one might question the inclusion of Sandon's model. The inclusion is based solely on the fact that Sandon's effort marks the first complete implementation of an attention model. That said, it offers little from a theoretical perspective in the context of attention, and lacks plausibility from the perspective of neurobiology.

Guided Search (Wolfe, 1989)

Wolfe and colleagues propose a computational model for visual search [247], that emphasizes a distinction between preattentive massively parallel computation of feature information, and a secondary stage that performs more complex operations over a selected portion of the visual field. An activation map is generated on the basis of a weighted sum of feature maps computed in parallel. Feature maps are also adjusted on the basis of top-down demands. That is, top-down task demands may bias processing of specific categorical attributes (e.g. bias for vertical lines). The activation map is transformed into a saccade map through convolution with an averaging operator. The peak of the saccade map then determines the next saccade position. Guided search is very similar to Koch and Ullmans model with the slight distinction that Wolfe stresses thinking of attention as a limited capacity resource that is distributed in order of strength in the activation map. As such, guided search suffers from the same difficulties attributed to the model of Koch and Ullman.

MORSEL (Mozer, 1991)

Mozer proposes a connectionist model of object perception that includes an attentional mechanism that limits input to a network (BLIRNET) responsible for building location invariant representations of letters and words[150]. Attention is directed on the basis of an attentional map produced by bottom up input from a number of primitive feature maps, and top-down task bias (e.g. a temporal ordering imposed by higher levels of cognition when reading). Primitive feature information is gated to BLIRNET by associating a probability with transmitted input based on the attentional map. From the perspective of attention theory, the sole distinction between MORSEL and its predecessors, is that a lower probability of transmission takes the place of inhibition. Some of the benefits of MORSEL have been its use in demonstrating the effects of deficits such as virtual lesions on attention. This last consideration is elaborated on in chapter 7.

VISIT (Ahmad, 1991)

Ahmed proposes a model for covert visual attention that predicts specific roles for a number of cortical areas[2]. The design proposed by Ahmed includes the following components: i. A set of basic feature maps assumed to correspond to the representation of the visual world on the retina, and in early areas of the brain including LGN, V1 and V2. ii. A gating system mediated by the pulvinar, which produces gated feature maps within higher visual areas such as MT, IT and V4 based on responses of early visual areas. iii. Bottom-up feature maps derived from early visual areas and represented in the superior colliculus. iv. A control center located in the posterior parietal cortex that controls access to working memory. The complexity of Ahmed's proposal is linear in the number of image pixels, and is successful in modeling aspects of visual search and spatial relationships. The primary contribution of VISIT to the literature might be considered the explicit inclusion of various areas of the brain, and specific predictions surrounding the role of such areas in attention.

Olshausen et al. (1993)

Olshausen and colleagues suggest an attentional model[164] based on an implementation of Anderson and Van Essen's shifter circuit model[4]. The intention of the model is to form representations of input stimulus that are invariant with regard to position, orientation, and scale at the output layer. Inputs from the retinal reference frame are selected based on modulation of synaptic weights in the network to route the desired input coordinates to an object centred reference frame. Such modification of synapic weights is achieved by control neurons originating in the pulvinar. Selection is based on Koch and Ullmans WTA mechanism[115]. Although the model achieves its aim of producing a position and scale invariant representation, the means of doing so is not biologically plausible.

Niebur, Koch, et al. (1993)

Niebur et al. [159] and Niebur and Koch[158], propose a model for the neuronal implementation of selective visual attention that is based on correlation in the temporal structure of a group of neurons. V1 neurons respond with a stimulus dependent mean firing rate according to a Poisson distributed spike train. Spike-trains of neurons within the receptive field of the focus of attention are distributed according to a time-dependent Poisson process while those outside the focus of attention respond with no correlation between action potentials. Temporal correlations in spike trains are detected by V4 inhibitory integrate-and-fire neurons that act as coincidence detectors inhibiting the response of unattended stimuli. Attentional effects on the temporal structure of firing rates affect cells in all visual areas. In contrast, attentional effects on neuron mean firing rates are limited to neurons in V4 and higher visual areas. Selection of attended regions is achieved by way of Koch and Ullman's attentional mechanism[115]. The model of Niebur et al. provides a plausible means of achieving synchronization, but only predicts modulation in V4 and later areas.

The Biased Competition Model (Desimone and Duncan, 1995)

Desimone and Duncan propose a Biased Competition model[45] wherein mutually suppressive interaction between competing stimuli facilitates selection. The model includes top-down bias for spatial location or feature type on the basis of a model of working memory. Strength of interactions is a function of the proximity of competing stimuli. Their initial proposal was largely descriptive but an updated account establishes a more detailed picture of biased competition in the context of a neural model. Reynolds, Chelazzi and Desimone[187] describe a number of single cell recording experiments focusing on areas V2 and V4 of the visual cortex. They demonstrate that when two stimuli fall in a single receptive field, the neuron may be biased to elicit a response similar to that resulting from each one of the stimuli presented alone, through the influence of attention. The neural circuit describing such interaction consists of an output neuron, relying on two input neurons having both excitatory and inhibitory influences on the output. It is demonstrated that the equilibrium response is proportional to the relative contributions of the excitatory input and inhibitory input to the output neuron. A distinction between the mechanism described by Desimone and Duncan is the presence of both excitatory and inhibitory connections from the input neurons to the output neuron.

VAM (Schneider, 1995)

Following von der Malsberg's correlation theory [237], Schneider proposed a model based on attentional selection for object recognition and space based motor action called VAM [205]. The main distinction between the two proposals is that in VAM, computation is divided into distinct "what" and "where" pathways. Low level features are represented at the level of the primary visual cortex, such as colour and contrast information. The "what" pathway encompasses V4, the inferior temporal cortex, and the superior temporal sulcus in VAM. Shape primitives and object templates are represented among these regions. The ”where” pathway is characterized by parietal areas that represent locations involved in various actions such as grasping or saccade execution. VAM includes an inhibition of return mechanism to avoid revisiting recently visited areas of space. The division of VAM into two distinct ”what” and ”where” pathways offers little with regard to advancing the understanding of attentive behavior, and this distinction is inherent in Ahmed’s VISIT. The division into streams for recognition and motor-action perhaps offers a more useful division from a control-systems perspective.

SCAN (Postma et al., 1997)

The Signal Channeling Attentional Network (SCAN) proposed by Postma et al.[175] consists of a scalable neural network model, intended to simulate attentional scanning. SCAN consists of a hierarchy of gating networks that select an output pattern from the input image (by way of a bottom-up WTA process) that best matches an expectation pattern. The primary contribution of SCAN might be considered the description of a network architecture capable of explicitly routing information based on expectation.

Itti and Koch (1998)

Itti and Koch [94] extend the earlier work of Koch and Ullman [115] with an updated implementation including a number of minor modifications. The steps involved in the newer proposal are as follows: i. 42 feature maps affording topographic representations of orientation, intensity and color information are produced from the input image. This stage involves linear filtering at 6 spatial scales followed by convolution with a centre-surround kernel and a normalization operator. Feature maps are combined across scale to produce a single conspicuity map corresponding to each of intensity, color and orientation information. A linear sum of the resulting conspicuity maps give rise to a saliency map which, combined with a WTA network and inhibition facilitates successive shifts in attention based on the topographical saliency map. The model of Itti and Koch might be viewed as a description of the model of Koch and Ullman expressed at a more specific level of abstraction. The basic properties remain the same, with specific details of the feature maps fleshed out in an implemented model. As such, the concerns expressed in regard to the Koch and Ullman model also apply to the Itti and Koch model.

Cave (1999)

Cave's feature gate model[24] is based on a hierarchical structure whereby elements at each level compete for selection for the next level. Responses at a given level are gated so that as one ascends the hierarchy, the proportion of the visual field represented is reduced. Inhibition takes place at a number of levels to prevent interference with competing stimuli. Selection of open-gate elements is made on the basis of local differences in a winner-take-all network with top-down biases impacting on selection. Bias in Cave's model is achieved within the gating of stimuli, so that no modulation of the signals at the input takes place, only selective routing. Further, the proposed mechanism only allows for gating from discrete non-overlapping regions. The mechanisms included in Cave's model lack neurobiological analogues, and as such the model is not predictive of the behavior of attentional mechanisms in the primate brain.

Deco and Zihl (2001)

Deco and Zihl propose a model that includes a number of modules each consisting of populations of neurons[43]. The model exhibits parallel computation across the entire visual field with a serial focal mode by nature of the dynamics of of the system. That is, neither saliency maps nor a focal search mode are explicitly included but emerge as a result of intrinsic properties of the system. The model consists of a number of feature maps produced on the basis of sensory input and top-down influences. Each feature map is associated with an inhibitory pool that mediates inhibition among competing elements. A high-level map used to guide the focus of attention is derived from the aforementioned feature maps. One element of the Deco and Zihl model that distinguishes it from others is the idea that attention serves to control the spatial resolution at which processing occurs. Whether there exists a neurobiological analogue of this operation is questionable. Deco and Zihl have also considered the effects of lesioning the model with reference to studies of unilateral neglect.

3.4 The Selective Tuning Model

This section describes key details involved in Tsotsos' Selective Tuning Model[228]. In the most detailed account of Selective Tuning, Tsotsos and colleagues outline a number of problems that arise in the context of pyramid computation (described in section 3.1). Many design choices in the Selective Tuning Model are formed on the basis of overcoming such limitations. The following describes details of the model with commentary on how various components overcome issues of complexity and problems inherent in pyramid processing. Selective Tuning simultaneously handles the issues of spatial selection of relevant stimulus *and* features. Spatial selection is accomplished by way of inhibition of appropriate connections in the network. Feature selection is accomplished through bias units which allow inhibition of responses to irrelevant features. The Selective Tuning Model is characterized by a multi-scale pyramid architecture with feedforward and feedback connections between units of each layer. A high level schematic of the model is depicted in figure 3.2. Details concerning

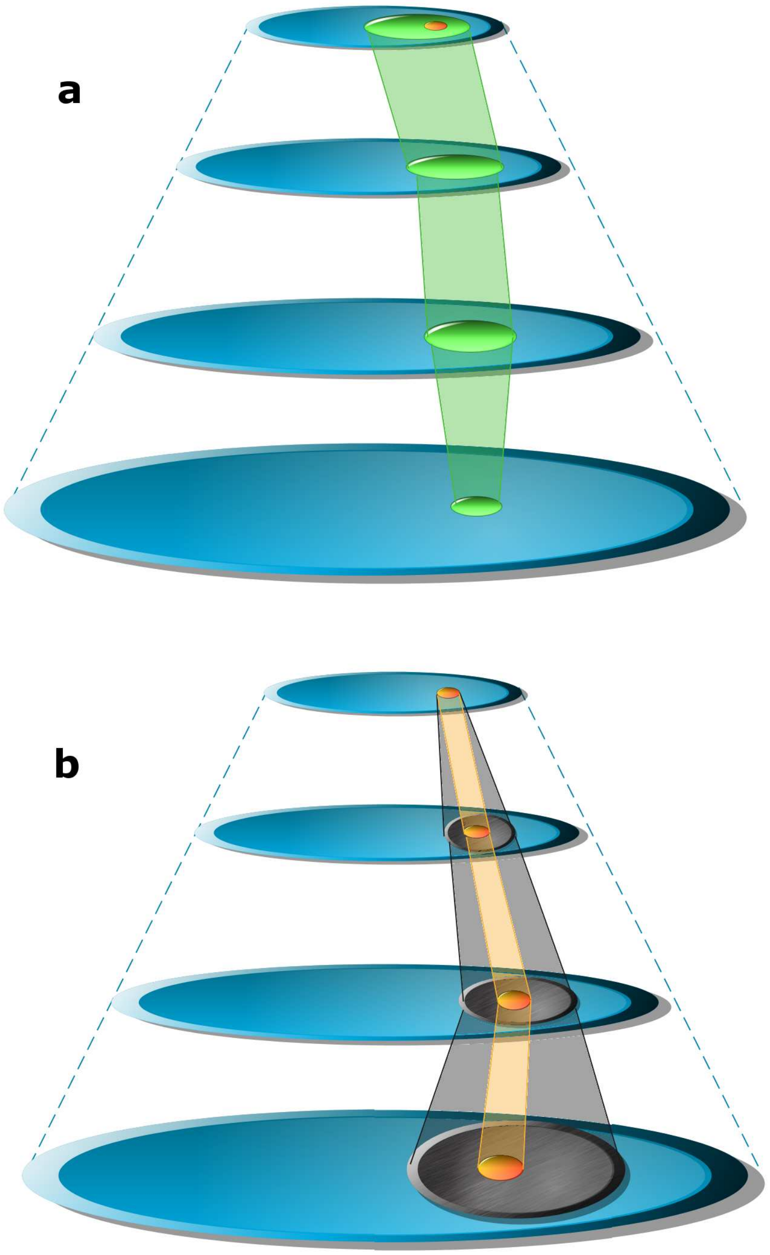

Figure 3.2: A high-level schematic of the selective tuning model. a. Bottom up feedforward computation. Stimulus at the input level (green) causes a spread in activity in successively higher layers. Winner selected at the highest layer is shown by the orange oval. b. Top-down WTA selection. WTA selection happens in a top-down-manner with the winning unit at each level indicated by the orange region. A suppressive annulus around the attended item caused by inhibition of connections is depicted by the greyed region.

the connectivity between adjacent layers are displayed in figure 3.3. Variables shown in figure 3.3 are as follows (Also refer to [228] for a more detailed description):

- $\hat{I}_{l,k}$: interpretive unit in layer l and assembly k
- $\hat{G}_l, k, j$: jth gating unit in the WTA network in layer l, assembly k which links $\hat{I}_{l,k}$ to $\hat{I}_{l-1,j}$
- $\hat{g}_{l,k}$: gating control unit for the WTA over inputs to $\hat{I}_{l,k}$
- $\hat{b}_{l,k}$: bias unit for $\hat{I}_{l,k}$
- $q_{l.j.i}$: weight corresponding to $\hat{I}_{l-1,i}$ in computing $\hat{I}_{l,j}$
- $n_{l,x}$: scale normalization factor
- $M_{l,k}$: set of gating units corresponding to $\hat{I}_{l,k}$
- $U_{l+1,k}$: set of gating units in layer l+1 connected to $\hat{g}_{l,k}$
- $B_{l+1,k}$: set of bias units in layer l+1 connected to $\hat{b}_{l,k}$

Selection is accomplished through two traversals of the pyramid. First, the responses of interpretive units are computed from the lowest level to the highest level of the pyramid in a feedforward manner. Next, WTA competition takes place between all units at the highest layer to select a single winning unit. In subsequent layers, units in layer l that connect to the winning unit in layer l+1 compete for selection. This ultimately leads to selection of a localized response in the input layer. Figure 3.4 depicts a series of stages in the selection process. Note that interference between competing elements is eliminated by way of selection. Bias is handled through a connected network of bias units that impact on the response of interpretive units they are tied to in a multiplicative manner. Bias units may be used to modify the response of interpretive units to a particular stimulus type, such as blue items. Bias values less than one might be assigned to the response of non-blue units to bias selection in favor of blue pixels. Bias values are entered at the top level of the pyramid and propagate downwards through inter-layer connections between bias units. The value a bias unit at layer l is given by the minimum of all bias values of units at layer

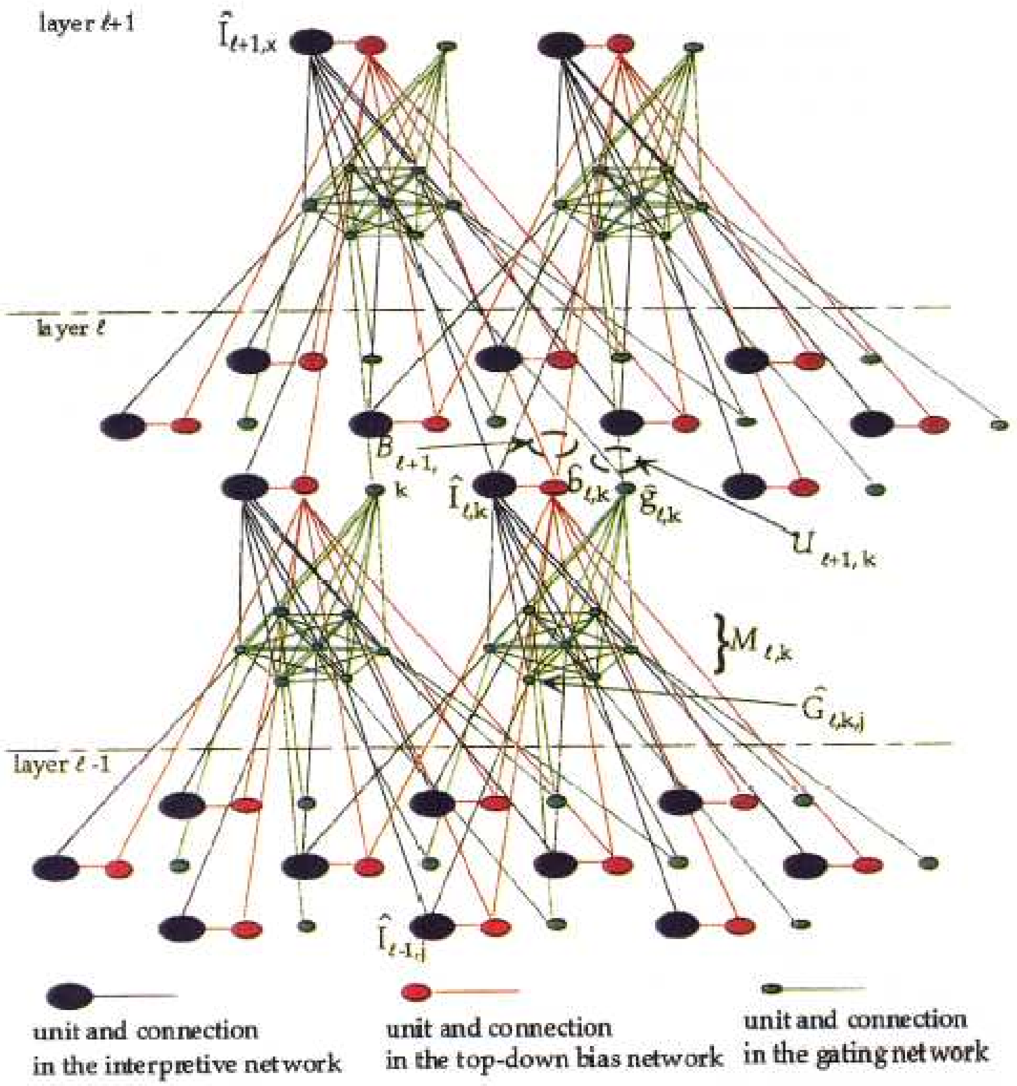

Figure 3.3: A detailed depiction of connectivity between units and layers in the Selective Tuning model. (From [228]).

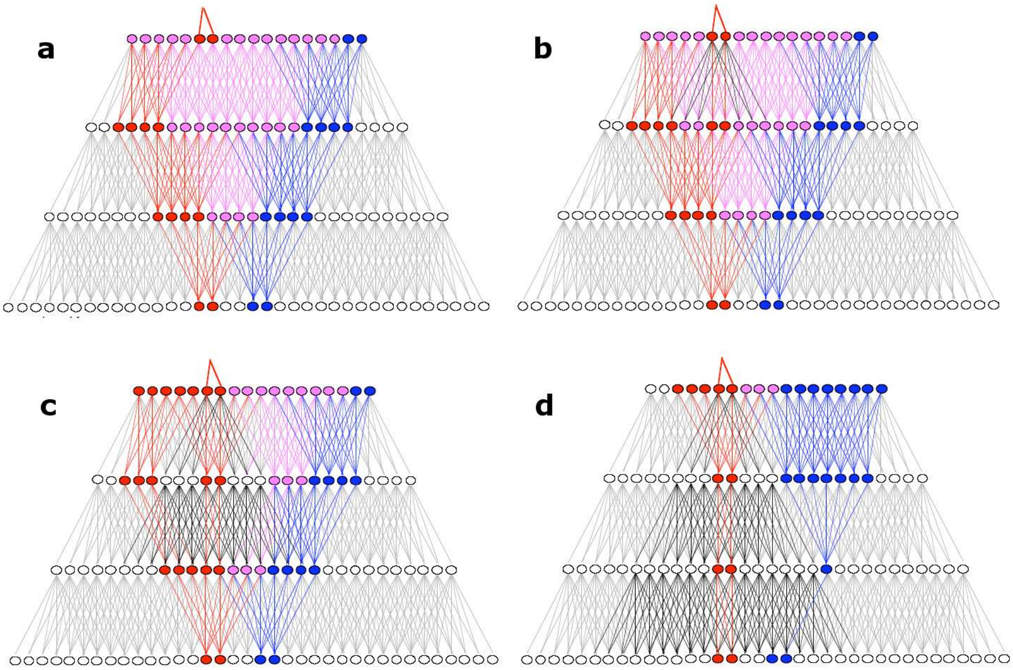

Figure 3.4: A series of stages in top-down winner take all selection. Note that attentional selection eliminates interference between the competing elements. a. Two winning units are selected at the highest level, no attentional effects are yet exhibited. b-d. Connections to winning units at layer (4,3,2 respectively) are inhibited and winners are selected at layer (3,2,1 respectively). (Adapted from [227]).

l+1 to which the layer l unit is connected. The WTA process employed in Selective Tuning differs from that of Koch and Ullman [115] in a number of aspects. The effect of unit i in the WTA network on unit j is quantified by the following expression:

$$y = \begin{cases} q_{l,k,i}G^{t-1}_{l,k,i} - q_{l,k,j}G^{t-1}_{l,k,j}, & \text{if } 0 < \theta < q_{l,k,i}G^{t-1}_{l,k,i} - q_{l,k,j}G^{t-1}_{l,k,j} \\ 0, & \text{otherwise.} \end{cases} \tag{3.1}$$

with $\theta = \frac{Z}{2^{\gamma}+1}$, γ a parameter that controls the convergence rate of the WTA network (converges within γ iterations) and $G^{t_0}_{l,k,j} = b_{l-1}n_{l-1}I_{l-1,j}$. A more detailed version of the preceding description concerning the WTA scheme may be found in [228].

3.5 Visual Search

One experimental paradigm that has proved particularly useful for studying visual attention, is the task of visual search. Subjects are typically required to localize a stimulus element with particular characteristics among a number of distracting elements, with a response of some kind to indicate when the element is found, or in some cases, whether no stimulus element with the desired characteristics is present. The timing of such decisions has provided insights concerning the attentional mechanisms underlying visual processing, since performance differences may be telling in terms of the ability to narrow down processing to some subset of the visual stimulus presented.

Visual search tasks are typically conducted under conditions in which the target item is present 50% of the time. The number of distracting elements (called the set size) is varied, and reaction time to indicate that the target has been located, or, whether no such target is present is measured and may be observed as a function of set size. Slopes and intercepts of reaction time versus set size are then used to infer the role of attention in searching among the stimulus elements. There are of course many variations of the setup described including searching for one of several target items, or, setups in which accuracy is measured in lieu of reaction time.

In demonstrating why reaction time is a useful measure in studying attention, it may be instructive to provide a few examples of extreme cases that demonstrate the utility of such results. Consider first the task of searching for a red item among green distractors. The trend observed in this task, is near zero slope in the number distracting elements, which suggests a search achieved by processing the entire visual field in parallel[153]. In contrast, the task of searching for 2 among 5's exhibits a slope that is linear in the number of distractors with a cost of 20-30ms per item[246] with twice as much time required for target absent than target present trials on average. The obvious conclusion that emerges from the trends observed under such conditions is that search requires a serial search in which elements are visited one at a time. For a number of years, following Treisman's Feature Integration Theory[223], search tasks were described in terms of a strict dichotomy of serial versus parallel searches. Since this time, it has emerged that visual search tasks fall in a continuum of slopes ranging from near zero to greater than 30 ms per distractor[246].

Drawing inferences from reaction time slopes is a practice that should be carried out with some caution. This is a view that is advocated particularly strongly by Townsend[220, 221, 222]. Wolfe notes that various limited capacity parallel models give rise to patterns that appear to correspond to serial searches. Further, serial search in which processing time associated with each item is sufficiently low might be misclassified as parallel searches[246]. The most important fact to put forth is that data drawn from visual search studies do not support a strict dichotomy between parallel and serial searches. Visual search slopes from different tasks range from shallow to steep. Although this does not preclude the possibility of parallel and serial processes acting together, it is important that visual search tasks not be grouped into parallel or serial categories. Feature searches may be made to exhibit linear slopes by narrowing the feature contrast between target and distractors. Wolfe proposes that search tasks may be more practically described using terms such as efficient or inefficient, owing to the obvious differences that do appear between tasks in which targets pop-out, versus those that do clearly require visiting a number of elements in series. Searches that are very efficient tend to be supported by a set of basic elements that may be computed in parallel including color, orientation, spatial frequency, curvature, motion, form, and depth.

Chapter 4

Interhemispheric Communication: Mechanisms and Models

Although our actions are governed by computation performed by two physically separated hemispheres, there is no visible effect of this physical division in everyday activities. The coordination of function between cerebral hemispheres is seamlessly knit via 100,000,000 fibres running between the two hemispheres. To put this number into perspective, communication of all of the visual information from each eye is handled by a mere 1,000,000 fibres[47]. Despite the obvious importance of this communication channel, the function of interhemispheric transfer remains relatively poorly understood in many domains. This chapter serves to convey the current understanding with regards to normal interhemispheric transfer of visual information, with a focus on visual attention.

4.1 The Corpus Callosum and Hemispheric Communication

The corpus callosum is the largest fibre tract in the brain and connects the two cerebral hemispheres, with an estimated 56 million axons in the rhesus monkey[122].

The connectivity of the hemispheres and properties of such connections might be best described by a number of general principles:

1. Axons may project to either excitatory or inhibitory neurons[33].
2. Each area in a given hemisphere is strongly connected to the corresponding area in the opposite hemisphere and weakly connected to a number of noncorresponding areas.
3. Each area is connected to a characteristic set of areas in the opposing hemisphere. This normally includes connections between areas that are normally connected intrahemispherically or share a particular function. Connections are almost always reciprocal[208].
4. Callosal connections are not evenly distributed. For example, in the visual cortex, connections are typically found between visual areas in the region corresponding to the vertical midline only. This same principle holds for other cortical areas as well[106].
5. The corpus callosum serves to integrate or to lateralize activity of the hemispheres. The structure of callosal connections may be telling in terms of discerning asymmetries as well as the role of various connections[20].
6. Callosal operations may be roughly divided into three categories: Mapping, weighting, and synchronization. Mapping refers to a spatial transformation from a cell of origin to a terminal bouton to which the axon projects[207]. Weighting refers to the fact that individual axons do not contribute an equal number of terminal boutons to the layers and columns to which they project. As such, an inherent weighting scheme is introduced[90]. Synchronization involves

the temporal transformation of signals among callosal axons. Parallel branches of callosal axons seem to have an important role in synchronizing computation between hemispheres[90, 92].

With regard to the development of cortical connections that facilitate interhemispheric interaction in the context of integrating visual information, it appears that this functionality only emerges when children reach on the order of 24 months in age[126]. Liegeois and Schonen carried out a study in which infants aged either 20, 24, or 26 months were presented with a pair of stimuli either unilaterally in the left or right hemifield, or bilaterally, straddling the midline. Subjects were required to maintain a central fixation, and determine whether the two stimuli were either a. aligned horizontally, or b. the shape of the stimuli match. Subjects in all of the age categories were able to perform the task adequately for unilateral presentation, but generally, only those in the 24 and 26 month groups were able to perform the task under the condition of bilateral presentation.

Although the corpus callosum is responsible for much of the connectivity between hemispheres, it should be noted that there do exist other connections between the hemispheres called commissures (The corpus callosum is also a commissure). The anterior commissure connects the anterior temporal lobes and olfactory structures between the two hemispheres. The hippocampal commissure connects the hippocampus in the two cerebral hemispheres. Connectivity among visual areas is established through the corpus callosum. As visual function is the primary focus of this document, specific connectivity of visual areas is described in the section that follows. For connectivity pertaining to other areas one may refer to [93].

4.1.1 Callosal Connectivity and the Visual Cortex

An important consideration with regard to the problem at hand, lies in the specific connectivity between visual areas in the two hemispheres. Observing connectivity among these regions should afford some insight concerning the role of callosal connections.

As discussed in chapter 2, inputs at the level of the eyes ultimately project to the visual cortex in such a way that each hemisphere represents contralateral visual space (as determined by the vertical meridian) at the level of the primary visual cortex. As a general principle, within visual cortical areas it appears that the corpus callosum serves to link the representation of the midline in the two hemispheres at several levels. That is, in V1 for example, parts of V1 that represent the horizontal midline in the left hemisphere are connected to regions of V1 that represent the horizontal midline in the right hemisphere[243]. Among peripheral areas, there are no such connections.

With regard to higher visual areas, on first examination, the distribution of fibres appears to be somewhat irregular. Connectivity via callosal fibres may be observed through staining and sectioning the brain. The distribution of callosal fibres in extrastriate areas is such that callosal connections lie at the borders between visual areas and correspond as is the case with V1, to the representation of the vertical midline[253].

In principle, one may find the result of connectivity at multiple levels to be somewhat counterintuitive since a connection between the two visual cortices at one level only would presumably be sufficient to coordinate function. Zeki notes that it is not surprising that connections exist at each level since the computation associated with each area is vastly different and as such, separate connections are required to coordinate various functions[255]. The perceived increase in disorder among callosal connections that appears to emerge as one ascends the visual hierarchy may be explained by relating this observation to the topography of the various areas. V1 and V2 each include precise topographic maps of visual space and as such the callosal connections among these regions appears as a narrow strip of connections corresponding to the vertical meridian. Among higher areas the connected region becomes broader and more diffuse corresponding to the relatively disordered nature of these areas. It seems then that the callosal topography is directly related to retinal topography within a visual area according to the very specific condition that vertical midline representations are linked.

4.1.2 Observations concerning corpus callosum size and hemispheric asymmetry

One might expect that greater brain asymmetries might be accompanied by a larger corpus callosum, presumed to aid in the greater degree of communication required to coordinate activities of the hemispheres. It is in fact the opposite trend that is observed: The size of the corpus callosum is inversely proportional to the degree of asymmetry between hemispheres[48]. This has interesting repercussions from a computational perspective. One might hypothesize that reduced communication between functional areas leads to the evolution of specialization in the form of asymmetries that reduce the need for such communication. As such, only the output of such a functional group would need to be transmitted since each hemisphere is not involved in the computation performed by the other. From a slightly different perspective, having a fast channel between hemispheres that perform mutually redundant computation might give rise to the sparing of such functionality in one hemisphere in favor of further specialization in a different domain. Such an evolutionary process would serve to reduce the redundancy of computation carried out in the two cerebral hemispheres. As a general principle, there are many areas in which a minimum redundancy representation appears to be in place (See [165] for a discussion of this in the context of early visual areas.). It is worth bearing the preceding ideas in mind in developing a computational theory of bilateral communication and asymmetry since such considerations may hint at some of the more fundamental principles by which the brain is organized.

4.2 Attentional Competition and Interaction between Hemispheres

The issue of communication between hemispheres in the context of attention is central to the subject matter of this document. Although the two hemispheres appear to have significant symmetries and the ability to act independently, attention appears to be directed unifocally. That is, there must exist some mechanism by which the attentional activities of the two hemispheres are coordinated to ensure a unitary attentional focus. Some recent studies lend support to the idea that attention involves competitive interaction between hemispheres to arrive at a consensus on the focus of attention. Hilgetag and colleagues carried out a number of experiments in which an attention task was carried out with virtual lesions induced by transcranial magnetic stimulation (TMS)[86, 85]. Subjects were presented with stimuli that appeared either unilaterally in the left or right visual field, or bilaterally in both visual fields. A key press was required to indicate which of the three cases had appeared. TMS was applied in a repetitive paradigm for 10 minutes on either the left or right parietal lobe prior to stimulus presentation. The findings were as follows: TMS significantly improved response time to targets ipsilateral to the lesion site, and severely impaired attention to the contralateral lesion site. TMS also severely impaired correct responses to bilateral trials with an extinction-like effect exhibited (response misreported as ipsilateral to lesion site only). The results seem to suggest that attention is mediated by a processing hierarchy that involves competition between the two hemispheres. Suppression of the response to contralateral stimuli improves the response time to ipsilateral stimuli and biases the response to ipsilateral stimuli in the case of bilateral presentation. One trend worth noting is that the ipsilateral enhancement is significantly greater (in % correct) than the contralateral decrement in performance. Hilgetag et al. suggest that this effect might be explained by a translation or rotation of attentional space to the ipsilateral side. Such a rotated attentional space has been previously reported[101] but may be attributed to the nature of competitive interaction between hemispheres described in [84]. Although the pattern of effects for the two hemispheres was identical, the magnitude of effects was more pronounced for right parietal TMS. This might be explained by apparent asymmetries observed in attentional processing performed by the two hemispheres which are discussed in the chapter that follows. Overall the results of Hilgetag and colleagues suggest that spatial attention is based on competitive interhemispheric interaction in the context of a topographic neural representation of visual space[85]. A natural consequence of such a structure, that is observed in the experiments, is the disinhibition of structures in the hemisphere ipsilateral to the lesion resulting from impairment of the contralesional hemisphere.

Much of the current knowledge concerning competitive interaction between hemispheres comes from pathological cases. In particular, the severing of the corpus callosum disrupting communication between hemispheres and to a lesser extent, unilateral lesions causing within hemisphere effects have been particularly telling domains for research involving hemispheric communication. Outside of these pathologies, there is virtually no way of observing the interaction between the cerebral hemispheres. The sections that follow outline literature pertaining to attentional effects observed in split brain patients, particularly, insights gained from such studies. Attentional competition between hemispheres is further discussed in the following chapter in the context of asymmetries observed in attention and visual search in the context of lesion and split-brain studies. It should be stressed that the sections that follow focus on cases in which no such asymmetries are observed, and as such may shed more light on the underlying competitive attentional network than issues of functional organization or laterality.

4.2.1 Visual Computation and the Split-Brain

An intuitive means of observing the role of communication between hemispheres might involve observing the effects of preventing such communication from occurring. This type of observation is in fact possible by virtue of a medical procedure that is performed in humans to deal with intractable multifocal epilepsy, which involves the complete sectioning of the corpus callosum[185]. Clearly this affords an extraordinary opportunity for studying the function of communication between hemispheres as well as issues of laterality. Within animals, the procedure is sometimes performed along with a split of the optic chiasm to restrict visual input from one hemifield to one hemisphere. The discussion that follows serves to outline a variety of phenomena that are observed following severing of the callosum and the implications that such results have concerning the role of callosal communication in visual processing and attention.

Much of the early work observing visual function in split-brain patients was pioneered by Roger Sperry. Sperry introduced the visual half-field technique wherein a stimulus is presented to either the left or right visual field of a split-brain patient, with one eye patched so that processing was lateralized to one hemisphere [152]. Such studies afforded a much improved understanding of lateralization of function for which Sperry won a Nobel prize in medicine in 1981.

One simple result that emerges from split-brain studies concerns the representation of the vertical meridian. It has been determined that an area two degrees wide centered at the vertical midline, is represented in both hemifields[124]. This observation is difficult to demonstrate in normal subjects due to the difficulty in showing that this representation arises from direct inputs to one hemisphere or the other, and not callosal transfer. Signals projecting to each hemisphere from the ipsilateral hemiretinae appear to be somewhat degraded which may suggest that the functional role of this overlap is limited.

With regards to visual abilities, it appears that function is duplicated within each hemisphere for basic perceptual processes. Split-brain patients have an inability to integrate information presented in opposing hemifields. This is demonstrated by the spectacular failure observed in visual matching tasks. Subjects are able to identify the stimulus present in each hemifield individually but are no better than chance in determining whether such stimului match[36]. Failure to integrate information in this manner extends to other sensory modalities and all forms of visual information[70]. One exception to this observation is that some experiments seem to suggest an apparent transfer of very crude spatial information. The mechanism by which this transfer is accomplished remains unknown[88].

Some interesting insights concerning visual attention also emerge from studies involving split-brain patients. Some accounts suggest that each hemisphere seems to rely on central attentional resources rather than deploying attention independent of each other. One study that favors this hypothesis is that of Kutas et al.[119] who measured event-related potentials associated with simultaneous target detection in the two visual hemifields. The ERP responses during the task were shown to not be elicited independently in the two hemispheres. The conclusion from this finding was that in both split-brain and normal subjects, the attentional system appears to be unifocal. Holtzman and colleagues employed a Posner-like task to demonstrate that either hemisphere is capable of directing attention to a point in either visual hemifield[89]. This conclusion was drawn from the observation that a spatial cue to direct attention to a certain position in the visual field was used regardless of the hemifield in which the cue was presented.

Further efforts have been carried out for the purpose of investigating hemispheric differences. These differences are discussed in some detail in the chapter that follows.

4.2.2 Subcortical interaction

An important consideration with regards to hemispheric transfer in studying the human visual system, is that of whether any transfer of visual information remains following severing of the corpus callosum and anterior commissures. There does appear to be limited transfer of certain visual information following commissurotomy mediated by subcortical structures. The first study that exemplified this point was that of Holtzman and colleagues[88] who demonstrated that crude spatial information may be transferred in some circumstances following total commissurotomy. Subjects were presented with a pair of 2x2 grids, one in each hemifield, and a cue to one of the grid corners in one hemifield. The subjects were then required to fixate on the corresponding corner in the opposite hemifield. This task was performed above chance. The same result was not found when the task was repeated with symbol types providing the cue. Cronin-Golomb and colleagues[39] carried out an experiment in which subjects were presented with three pictures in one visual field and one picture in the other. Subjects were required to indicate whether there was a conceptual relationship between any of the three images in the one hemifield and the one image in the other. Split-brain patients performed well on this task with no significant hemifield effect. Sergent demonstrated that subjects were unable to determine a match between numbers in opposite hemifields, but were able to state if the two were both even, both odd, or different[35]. Kingstone and Gazzaniga demonstrated that when drawing, patients were able to combine information between stimuli presented to opposite hemispheres, although this was attributed to dual hemispheric control of the hands[108]. Some of the aforementioned studies have been suggested as suffering from certain methodological problems but it is undeniable that there does exist some transfer of visual information at a subcortical level.

Chapter 5

Hemispheric Asymmetries in Visuospatial Processing

A pairing of anatomical elements and organs is presumably a favorable design in facilitating survival in the natural environment. The human brain consists of two physically divided halves, similar in shape, and similar in the ability to process incoming patterns of stimuli. The coordination of activities in the two distinct cerebral hemispheres was described in some detail in chapter 4. In this chapter, the primary concern is the *differences* that exist between hemispheres in visual processing. Understanding functional differences may afford some idea of the computational advantages that arise from cerebral asymmetry and may ultimately provide some indication for why a physical division between hemispheres emerged. It is expected that asymmetries in visual processing play an important role in the analysis of visual information. As such, understanding the underlying computational reasons for asymmetric processing should further the understanding of the manner in which visual processing is organized in the brain. There is also a high likelihood that principles that emerge from the analysis of visual patterns assumed by the brain may have significant utility in the context of machine vision. In this light, a best case scenario would be to establish a single fundamental dichotomy which adequately describes the functional role of the cerebral hemispheres in visual processing. It is with these considerations in mind that the current literature describing cerebral asymmetries in visual processing is reviewed.

5.1 Hemispheric Asymmetry in Spatial Frequency Processing

Early studies on the nature of visual processing in the two hemispheres tended to converge on the idea that the left hemisphere was primarily involved in analytic processing, and the right in holistic processing[18]. There is something rather unsatisfying about this dichotomy, namely, it is entirely descriptive and not tied to any quantitative or measurable entity. The processing of the whole vs. the parts of an object or event, is a phenomenon that seems intrinsically linked to the more concrete measure of spatial frequency. In practice, one would expect information concerning the parts of an object to be better represented by the high spatial frequency range, and more general whole properties such as form to be carried by the low spatial frequency range. It is with this consideration in mind that asymmetries in visual field and hemifield processing of spatial frequency content are described.

Early studies on hemispheric differences in visual processing focused on contrast detection thresholds[15, 183, 67, 113, 170]. For the most part, such studies revealed little in terms of asymmetry in contrast differences, and also in spatial frequency processing. It is important to note that all of the abovementioned studies involved detection tasks, for threshold or suprathreshold stimuli. Since this time, studies have been carried out involving discrimination tasks for visual stimuli carrying different spatial frequency content[16, 114] and under such conditions, differences in performance as a function of visual field consistently arise. The general finding is that the right visual field tends to exhibit an advantage for discriminating between high spatial frequencies, and the left visual field for the processing of low spatial frequencies[157]. Since this time, a variety of different paradigms have been employed to examine hemispheric differences in spatial frequency processing. These are briefly summarized in the following list:

- Identification: Kitterle and colleagues carried out a study in which subjects were required to identify the spatial frequency of a sinusoidal grating presented in one of the visual fields[111]. They found no visual field differences for low spatial frequency stimuli, and an increasing advantage of right visual field presentation for high spatial frequency stimuli. Percentage correct and response time both exhibited this trend.

- Judging Orientation: Tei and Owens[216] carried out a study in which subjects were required to make same-different judgements concerning orientation of an adapting grating versus a briefly presented test grating for a single spatial frequency of 4 cycles per degree (cpd) and observed a right visual field advantage for the task. Previc[178], Kitterle and Kaye[113], and Fendrich and Gazzaniga[62] each carried out similar studies with a range of spatial frequencies to examine the effect of spatial frequency. In each of these studies, no significant effect of visual field versus accuracy was observed.

- Compound Stimuli: Kitterle and colleagues examined hemispheric differences in processing local versus global levels of hierarchical figures consisting of a global oriented bar made up of smaller oriented bars of the same or of a different orientation[110]. Subjects were required to perform two tasks. In the first, observers were required to indicate the orientation of bars at a pre-designated level. This yielded a faster and more accurate response for low spatial frequencies and with a left visual field advantage. The effect of interference from the stimuli presented at the irrelevant level was larger for the ignore global in the left visual field, and only significant in the right visual field for the ignore local condition. In the second task, subjects were required to specify whether a particular orientation was present at either the global or local level. In this task, response time when the target orientation was present at the global level was faster for the left visual field and the converse for the local level.

- Relative Frequency: Christman, Kitterle and Hellige performed a study in which subjects were required to identify which of two different compound gratings was presented. In the first condition, the compound gratings consisted of 0.5 cpd and 1.0 cpd components, and 0.5 cpd, 1.0 cpd, and 2.0 cpd components respectively. In the second condition, the gratings consisted of 4.0 and 8.0 cpd components, and 2.0, 4.0 and 8.0 cpd components respectively. Under condition one the gratings differ only by the addition of a higher spatial frequency component and in the second case only in the addition of a lower spatial frequency component (2.0 cpd in each case). There was a RVF advantage observed in condition one and a LVF advantage in condition two. This finding relates to that of Kitterle and colleagues who reported a RVF advantage for harmonic frequency components and a LVF advantage for fundamental frequency[112]. The importance lies in the fact that relative frequency appears to be relevant.

- Task Related Factors: In another study[112], subjects were required to make two types of judgements with 1.0 and 3.0 cpd square and sine wave gratings presented. Judgements were made concerning whether the stimuli were wide or narrow, and whether the stimuli were fuzzy of sharp. In the first condition, there was a significant LVF advantage and in the second task, a RVF advantage. The difference is proposed to arise from having to selectively process lower versus higher frequency components of the stimulus.

- Phase: Two studies observing phase judgements as a function of visual field have been carried out each employing low frequency stimuli[67, 186]. The finding in each case was a LVF advantage for discriminating between phases. It is unclear whether this reflects a difference in spatial frequency processing or a phase judgement *per se* owing to the limited scope of the studies.
- Low Pass and Band Pass Filtered Stimuli: One technique that has been applied with the hope of determining whether hemispheric specialization results from higher-level processing, versus low-level processing such as simple spatial frequency differences, involves the filtering of different ranges of spatial frequency content from the stimulus under consideration and observing the effects of such an operation. Such studies typically involve either blurring or high-pass filtering of stimuli. The results of such efforts are varied but generally exhibit trends similar to those resulting from the presentation of simple sinusoidal stimuli. Sergent carried out a study in which subjects were required to make judgements on face stimuli in a task that normally exhibits a RVF advantage. Following the removal of low spatial frequency content, subjects exhibited a LVF advantage[210]. Whitman and Keegan performed a similar study with the removal of high spatial frequency content revealing a RVF advantage[242]. In other form discrimination tasks (primarily involving letters), studies revealed a greater impairment on RVF performance following blurring[142, 27]. In a study involving bandpass filtering of stimuli centered at five different spatial

frequencies, a significant effect was shown for the left visual field for high spatial frequency ranges and right visual field for low spatial frequency ranges[170].

It is clear that there appears to be some fundamental difference in the ability to process high versus low spatial frequency content as a function of hemisphere. Tasks involving discrimination, identification, and comparison present especially strong differences between hemispheres in processing spatial frequency content. The variability between results drawn from the various studies is quite telling in itself. The picture is a complex one involving low level early visual processes and higher level interactions. That said, in studies involving simple sinusoidal stimuli, there is an undeniable visual field/ frequency interaction when spatial frequency is the only factor that is varied. It is important to bear the consideration of fundamental asymmetries in visuospatial processing in theorizing on issues related to vision. In establishing a theory of hemispheric asymmetry in attentional processing, the importance of asymmetry in spatial frequency processing is certain to be an important consideration in getting at the underlying computational issues in the deployment of attention.

5.2 Global versus Local Processing

Differences in hemispheric processing are frequently discussed in terms of global versus local processing. The conception of this terminology and ideology ultimately derives from a 1977 study carried out by Navon[156]. In this experiment, hierarchically organized figures (e.g. an H made up of small T's) were presented and subjects were required to indicate the letter at a predefined level. His two main findings were that global structure interferes with local structure to a greater extent than the converse, and response to global stimuli is faster. This has since been coined as the global precedence effect. At the time, these differences were attributed to differences in the rates at which low versus high spatial frequency signals travel. The relationship between hemispheric asymmetry and spatial frequency required for analysis of global versus local form[11] was also made around this time. In a task requiring patients with unilateral left or right hemisphere damage (typically parietal of frontal) to arrange a particular combination of red and white blocks into a particular form, there was a clear difference between the type of errors resulting from left versus right hemisphere damage[99]. Specifically, patients with left hemisphere damage tended to arrange the elements in the right form while making mistakes on individual elements. Conversely, right hemisphere patients tended to have all of the correct elements with some errors in the global form. The findings of such block studies have been reinforced by more recent studies requiring patients with unilateral brain damage to draw a copy of a figure[190]. Left hemisphere patients performed very well in reproducing the global form of the figure but had difficulties in drawing local elements, generally neglecting them entirely. The converse was true for right hemisphere patients with local elements reproduced with high accuracy, but not arranged in the appropriate configuration. In a more recent imaging study[133], subjects were required to respond to either local or global levels of hierarchical stimuli while cerebral blood flow was observed via fMRI. Greater activation of the right posterior occipital cortex was observed in global processing and of the left anterior cingulate cortex for local processing regardless of the visual field in which stimuli were presented[133]. The implication of each of the aforementioned studies is that there appears to be a specialization for the representation of global form or low spatial frequency content in the right hemisphere and local form or high spatial frequency content in the left hemisphere. It is important to stress that global versus local process might be thought of as a reformulation of spatial frequency processing and should not necessarily be discussed as a different and isolated phenomenon.

5.3 Categorical versus Coordinate Processing

Another slightly different dichotomy in which visual processes are discussed, is that of categorical versus coordinate processing. The hemispheres are thought to differ in their abilities to localize stimuli in space and to make judgements concerning relationships between stimuli. The categorical versus coordinate distinction was initially proposed by Kosslyn et al.[116] and suggests that the right hemisphere is more adept at encoding spatial relationships with the left hemisphere superior in categorical judgements. Experiments examining this distinction typically involve some modification on a task originally proposed by Hellige and Michimata[80]. In this experiment, a stimulus involving a line, and a dot above or below the line, is flashed in either the left or right visual field. Subjects are required to judge whether the dot appears near or far from the line in the first task, and above or below the dot in the second task. The near-far task typically exhibits a right visual field advantage, with the converse found in the case of the above/below judgement. More recent tests have repeated this type of experiment with the selective filtering of high spatial frequency content from the stimulus. The outcome of such an operation involves a significant effect of increased reaction time and reduced accuracy on the categorical task and no effect on the coordinate task. It has been suggested that this result might arise from the blurring resulting in attenuation of processing along the parvocellular pathway which might be more critical in categorical judgements. To further test this idea, experiments have been designed with the aim of causing similar effects along magnocellular pathways. Perception of stroboscopic motion and metacontrast masking are significantly weaker when the background on which stimulus is presented is red as compared to green[19]. This result has been interpreted as a demonstration that transient or magnocellular visual channels are attenuated more by red than green backgrounds.

Of note, is that there exists a subpopulation of magnocellular neurons characterized by a red-dominant surround receptive fields[127]. In further support of this idea, tonic suppression of magnocellular cell responses has been detected in response to the presentation of red light[127, 61]. Cowin and Hellige have taken advantage of this finding in order to investigate the relationship between categorical versus coordinate processing, and magno and parvo pathways[38]. Their stimulus consisted of two dots presented above or below a line with the spacing between dots varied. Subjects were required to indicate either whether the dots were above or below the line, or whether the line could fit between the dots. The task was performed with black line and dots on a green background or a red background. For the coordinate task, the response time was significantly increased for the red relative to green background. No such effect was observed for the categorical task reinforcing the relationship of observed asymmetries to differential reliance on magnocellular or parvocellular pathways. Roth and colleagues also conducted the same study with bandpass filtering in a high or low frequency range in place of the change of background color. High-pass filtering resulted in a significant increase in time to respond to the coordinate task. The task versus hemisphere conditions were not reported in relating performance to attenuation in magnocellular or parvocellular pathways. Christman and colleagues[26] performed a similar task and found visual field advantages for black on white stimuli but not green on red. This suggests that the two hemispheres differ in their efficiency in processing the different types of information (HSF vs. LSF) and perhaps a difference in the visual information available to, or computational mechanisms associated with each hemisphere. In 1994, Laeng and colleagues examined the problem in the context of patients with unilateral lesions[121]. Patients with left hemisphere damage made mistakes more frequently on categorical tasks, and right hemisphere patients on the coordinate tasks. Such a demonstration has also been made for dynamic input with judgements made concerning the growth of a dot in the visual display[26]. Subjects were required to indicate whether the dot was grown quickly vs. slowly or to indicate the actual growth rate. The coordinate task exhibited a LVF advantage and the categorical task, no significant effect.

It is clear that there are differences in the ability of each hemisphere to perform particular types of tasks. Presumably such tasks differ in the information required to make judgements on such tasks, ultimately tied to the spatial frequency of test stimuli. The distinction between coordinate and categorical judgements is somewhat unsatisfying since often it is not clear to what degree a particular visuospatial task falls into one of these categories. The preceding experiments do however offer some particular insight with regard to the matter at hand. In particular, they reinforce the perceived importance that specialization for processing different spatial frequency bands may have in higher level tasks. Secondly, it appears that the differences are not attributed to differential access to magnocellular versus parvocellular streams within each hemisphere, but rather differences in how each hemisphere processes such information. Given the apparent specialization the two hemispheres exhibit in regard to spatial frequency processing, it is worth deliberating on the manner in which coordination is achieved between the hemispheres. This mechanism however, remains poorly understood, but it is clear that callosal connections are necessary to combine information carried by different spatial frequency bands. This consideration is made clear in studies involving split-brain patients described in the chapters that follow.

5.4 Upper/Lower Visual Field Asymmetries

While lateralized effects in visual processing are abundant in the literature, there are relatively few studies examining asymmetries across the horizontal meridian. Previc carried out a series of experiments that indicated an upper-lower visual field asymmetry analogous to the right-left asymmetry with the upper visual field exhibiting asymmetries similar to those observed in the right visual field, and lower visual field asymmetries analogous to those of the left visual field[179]. Such a finding begs the question of whether asymmetries are attributed to a physical division of hemispheres *per se*, or some other factor. An explanation may come from the fact that upper and lower visual fields project preferentially to ventral and dorsal pathways respectively[251]. Upper-lower visual field asymmetries seem to be as significant and prevalent as lateral asymmetries with upper-lower differences observed in reaction time[168], spatial frequency processing[132, 110, 157], and visual search[54, 250]. Christman and Niebauer suggest that the similarities between left-right and upper-lower visual fields are not purely coincidental, but rather correspond to functional divisions determined by horizontal and vertical meridians[26]. An important consideration concerning this question, is the functional role that such asymmetries play. Humans navigate the world with an upright posture, which might give rise to differential specialization of upper-lower visual fields on the basis of different task demands. As for left-right visual fields, speculating upon the specialization that emerges in this domain is more difficult. Other suggestions that have been made with regard to explaining the lateral asymmetries observed, include effects of head-tilt with a rightward tilt preference[73], and neonatal reaching bias, although these possibilities have been challenged[179]. A more plausible explanation which was alluded to in section 5.3, concerns a differential role of magno and parvo pathways in the two hemispheres. Although there is no obvious anatomical asymmetry in the projection of these pathways, it has been suggested[114] that hemispheres differ in how output from early visual areas are weighted within higher visual areas. Another avenue worth considering, is the role of handedness in visual field laterality. One might expect that certain kinds of processing are more important in the visual field corresponding to the dominant hand. It appears that visual field asymmetries do not vary appreciably between left and right handed subjects. That said, in left handers, asymmetries tend to be less pronounced[79].

5.5 Hemispheric Asymmetry in Temporal Frequency Processing

An issue that receives rather little attention in comparison to lateralization in the processing of spatial frequency, is that of laterality in temporal frequency processing. There is relatively little in the literature on this matter. In an early study, Sergent showed a LVF advantage for face categorization, which shifted to a RVF advantage when exposure time was increased beyond 200ms[209]. The interaction between temporal and spatial frequency in the processing of visual stimuli evidently arises from the different spatiotemporal tuning of M and P cells. Kosslyn and colleagues have proposed that the contrast sensitivity peak occurs at low spatial frequencies for right hemisphere processing and high spatial frequencies for left hemisphere processing[118]. The functional difference between the two curves is proposed to arise from a differential contribution from the magno and parvo pathways which would account for temporal differences as well. Livingstone makes this connection more explicitly in stating that such a situation might result from a greater tendency for magnocellular ganglion cells to project to the right hemisphere[118]. There is however, no documented evidence of such an asymmetry in the neurophysiology literature. A more recent study has demonstrated that the ability to detect flicker that is out of phase with the rest of the display depends critically on the right parietal cortex, as lesions in this area severely impair the ability to make this distinction[10]. It has also been shown that unilateral damage at this level severely impairs high order motion processing[9]. These tasks each critically rely on the processing of high temporal frequency information, and lend support to the observation that the hemispheres differ in their ability to process temporal frequency content, with a preference for high temporal frequency content in the right hemisphere and low temporal frequency content in the left hemisphere.

5.6 Anatomical Lateral Asymmetries in the Visual Cortex

Despite marked hemispheric differences between a variety of anatomical structures, there are virtually no reports of significant and consistent lateral asymmetries among visual structures. It has been proposed that some of the aforementioned asymmetries might be explained by a preferential projection to one or the other hemisphere of magnocellular or parvocellular pathways. There is however, no evidence that such an asymmetry exists. One recent effort that may illuminate some of the causal factors of visuospatial asymmetries comes from a study documenting the average size of magnocellular cell bodies in the primary visual cortex of the left or right hemisphere among dyslexic and normal subjects. Jenner, Rosen, and Galaburda report that the average size of cells with magnocellular inputs is larger in the left hemisphere than in the right hemisphere of normal subjects[5]. Interestingly, no such asymmetry is observed in dyslexic patients. In non-dyslexic brains, such asymmetries were observed in layers IVB, IVcα, IVcβ, and V of the primary visual cortex.

Chapter 6

Lateral Asymmetries in Attention

Perhaps even more instructive than observing normal and symmetric function in visual processing and attention, are asymmetries observed under such conditions. In the context of visual attention experiments, the spatial location of target and distractors are typically not recorded, or dismissed as having little impact on trends observed in visual and attentional processing. In practice, the positions of target and distractors have been shown to be very relevant with many spatial non-uniformities observed in attentional processing. Such asymmetries may be important in elucidating the underlying computational advantages that such asymmetries present. In this spirit, asymmetries in attentive and spatial frequency processing are described in the sections that follow.

6.1 General Asymmetries in Orienting Attention

A variety of asymmetries have been noted in regards to the characteristics that each hemisphere exhibits in the cueing and orienting of attention. The picture is by no means clear, and many conflicting accounts are found in the literature. That said, current findings seem to suggest the following hemispheric differences:

- The two hemispheres appear to differ in the impact of cueing on the top-down control of attention.
- The right hemisphere appears to have a role in orienting attention to both hemifields with the left hemisphere only having an impact on deployment of attention to the right visual field.
- The right hemisphere exhibits a greater cost to invalid cues than the left hemisphere.
- There are some phenomena observed in split brain patients that suggest competition for a common subcortical center that interacts with both cerebral hemispheres, though the nature of this interaction may differ between the two hemispheres.

The following discussion centers around evidence for these high-level differences between the hemispheres. The above list is produced with the intention of highlighting key hemispheric differences that may impact on the computational modeling of bilateral attention. Much of the current knowledge concerning hemispheric asymmetries in attention derives from studies involving visual search tasks. As such, section 6.2 has been devoted to reviewing relevant visual search studies that impact on hemispheric asymmetries in attention. The current discussion is restricted to simple cueing and detection tasks which introduce some trends reinforced by findings from visual search paradigms.

In one of the earlier studies on hemspheric asymmetries in attention, Mangun and colleagues [136] carried out a series of experiments involving split-brain patients. Subjects performed the same task as that in the classic experiment of Posner[174]. In Posner's experiment, a central directional cue predicts the location of a subsequent target. In the case of a valid cue, average reaction time is reduced and invalid cues result in increased reaction time relative to the no cue condition. In the Mangun et al. experiment, for a set of 10 control subjects, similar trends were observed for valid versus invalid cues in both hemifields with a greater cost of invalid cue in the right visual field. In the case of 3 split-brain patients, no cue effect for either valid or invalid cues was observed in the right visual field. In contrast, an advantage of valid cue and a very large cost of invalid cue was observed for LVF suggesting a special role of the right hemisphere in orienting attention.

Proverbio et al. carried out a similar experiment without cueing while varying the distance of the stimulus to be detected from the fixation point and found a trend similar to that of Mangun et al: Response time was slowest for the leftmost target and fastest for the rightmost target. This same result was replicated by Berlucchi and colleagues[12]. This set of results is consistent with observations concerning neglect that results from parietal damage. Neglect is typically far more severe following right parietal damage. It has been suggested that this phenomenon, and the findings of Mangun et al., and Proverbio may be explained by a stronger rightward bias of the left hemisphere, than leftward bias of the right hemisphere in attentional control resulting in the observed left to right preference, and the rightward asymmetry in neglect.

Berlucchi, Mangun and Gazzaniga have followed up Mangun's studies to further test the observed trend[12], with tasks performed by patients with lateralized parietal damage. Subjects were required to indicate whether a flash of light appeared in the LVF, RVF, or bilaterally. The two patients each having right parietal damage exhibited left-visual field extinction for bilateral presentation, misreporting 47% and 74% respectively, of bilateral trials. As in the previous cases, a significant rightward advantage was observed. Paradoxically, response times were fastest for bilateral trials regardless of the response given. The suggestion made by the authors is that the motor response, and percept of the stimuli may be dissociated in this particular task. An important result to consider in the modeling of attention, is perhaps the similarity of effects observed in split-brain versus parietal lesion patients. The similarity of such effects might eliminate or suggest certain possibilities for the structure of the competitive network underlying the deployment of attention.

Pollman and Morillo carried out a series of lateralized cueing studies coupled with fMRI measurements[172]. Signal increases in left and right cortices were greatest when both cue and target occurred in the contralateral hemifield and least for ipsilateral cue and target. However, in all invalid trials, right hemisphere activation was similar regardless of the cued hemifield. In contrast, left hemisphere activation was high for right visual field cues and low for left visual field cues. The implication is that right visual field cues impact on the activation in both hemifields whereas the effect of left visual field cues is lateralized to the right hemisphere. This account is consistent with the reaction time studies outlined.

The two hemispheres also appear to differ in the effect of flanking distractors in attending to a target stimulus. Reaction times are faster for single targets in the left hemifield and shorter for single targets surrounded by distracting flankers in the right hemifield[25].

The most parsimonious interpretation of these studies is that the attentional differences result from differences in the visual space for which each hemisphere performs visual processing, or allocates attention to. It is worth mentioning that such differences seem to be possibly tied to the various asymmetries in spatial frequency processing observed.

6.2 Asymmetries in Visual Search

Visual search has served as a useful tool for observing attentional behavior for some time. More recently, visual search tasks have been studied with a particular focus on differences between hemifield of presentation, offering some idea of underlying attentional asymmetries between hemispheres. Although comparatively little work has been conducted in this area relative to visual search in general, some trends do appear to be emerging from these studies.

One of the earliest studies involving specifically hemifield asymmetries was carried out by Luck and colleagues in 1989[130, 131]. The study involved a visual search task carried out by split brain patients, with stimuli presented to one of the two visual hemifields, or split between the two hemifields. Their finding was that in cases where the stimuli were split between visual fields, search time was twice as fast. No such effect was observed in normal subjects. The conclusion was drawn that each disconnected hemisphere was performing an independent visual search on its corresponding hemifield. Since this time, a number of studies have provided a more detailed picture of visual search in split brain patients. Recent efforts are discussed and the findings of Luck and colleagues are touched on in light of more recent discoveries.

An important issue to consider, is whether there exists a hemispheric advantage for visual search as a function of spatial frequency on the basis of results discussed in the previous chapter. Enns and Kingstone have conducted a number of experiments looking specifically at this relationship[59]. For a review of many of their studies refer to [60]. Enns and Kingstone carried out a number of reaction-time experiments in which subjects were required to indicate as quickly as possible whether a particular target was present or absent from the display, and indicate the visual field of the target by pressing one of two keys in the case that the target was present. The number of distractors in the display was varied. Targets were selected so that one task required the use of more localized visual information, and a second task, more global information. Enns and Kingstone did observe a significant advantage of left visual field on the global search task, and right visual field on the local search task.

Experiments were then repeated with a number of split-brain patients as subjects, with the expectation that the observed asymmetries would be even more pronounced. Surprisingly, no visual field asymmetries were observed in reaction time. Experiments were repeated with an emphasis on response accuracy, and the only visual field effect was steeper search slopes for low-discriminability local and global targets in the left hemisphere. The suggestion made by Enns and Kingstone was that this might be considered evidence of greater efficiency in visual search by the left hemisphere, and not a global versus local effect. This is a rather confusing result in light of the fact that identification tasks give rise to such obvious hemifield asymmetries. One possibility proposed by Enns and Kingstone is that each hemisphere might draw on a common system involved in spatial attention.

The possibility that attention requires that the two hemispheres draw on some shared resource seems to strongly conflict with the early results of Luck et al. Some further details are required to resolve this conflict. Luck et al. carried out a study involving stimulus sizes of 2, 4, or 8 elements. In an earlier study Pashler demonstrated that the 2 to 1 slope for absent versus present trials is observed only in cases in which the number of elements was greater than 8[167]. Enns notes that this may indicate that the observed hemispheric independence may only hold for so-called preattentive processes, given the limitations of the stimulus set. To test this idea, Enns and Kingstone repeated the experiments of Luck and colleagues with display sizes ranging from 2 to 24 elements, presented either unilaterally in one visual field or bilaterally.

The foremost finding of this experiment was that visual field of the target had a much stronger influence when stimuli were presented bilaterally versus unilaterally. In the unilateral displays, search times for left or right visual field did not differ significantly (12ms vs. 10ms per item). In the case of the bilateral displays, RVF targets still required on the order of 10ms per item. In contrast, LVF targets required roughly 6ms per item for 2-8 stimulus elements and 14 ms per item for larger displays. The data suggests that the two hemispheres may differ in the mechanisms involved in visual search, but perhaps only when competition is required. The same task was carried out by a split-brain patient, and no visual field advantage was observed for either the unilateral or bilateral presentations, suggesting callosal involvement in the competitive effect. Of note, is the fact that split-brain patients exhibited search slopes that were much larger in unilateral than bilateral displays.

Experiments were repeated, measuring accuracy on a brief display rather than response time for both normal subjects and the split-brain patient. On unilateral displays, the decrease in accuracy for added distractors showed no effect of visual field. In contrast, the bilateral presentation revealed differences related to visual field. For RVF, accuracy decreased by 0.1% per item for the first 8 items and on average 2.3% after this. The left visual field exhibited a cost of roughly 2.1% over the entire range of distractors. In the case of the split-brain observer, accuracy was greater for RVF stimuli in both unilateral and bilateral presentations.

The preceding results seem to suggest the possibility that the hemispheres are competing for resources, and that there exists an asymmetry in how those resources are allocated to the two hemispheres. It may be worth trying to summarize the preceding results into a set of general conclusions that might prove useful in formulating a theory of bilateral control of attention:

- Competition is observed between hemispheres and is only evident when callosal connections are intact.
- For bilateral displays, the right hemisphere tends to search more efficiently than the left compared to unilateral displays. No bias is observed in unilateral displays.
- Disconnecting the hemispheres eliminates the hemispheric competition that gives rise to this effect.
- Callosotomy appears to reveal a subcortical competition involving the two hemispheres apparent in the search times of unilateral versus bilateral presentation of stimuli, and accuracy is greater for unilateral displays.
- There appears to be a left hemisphere advantage observed in split brain patients in visual search for unilateral or bilateral presentation.
- The overt competition between hemispheres observed among split-brain patients seems to rely on the failure of interhemispheric competition at the cortical level.

With regard to some of the abovementioned observations, it may be instructive to speculate on some possible explanations for these unusual results. Puzzling is the fact that a hemispheric advantage is only observed in the case that stimuli are divided between hemispheres. A possible explanation might be that there is an inherent bias to scan from left to right. This explanation however leaves much of the data unexplained. Enns and Kingstone bring to light a very important consideration regarding these findings[60]. The hemispheric competition/bias that was observed among the various search tasks, was only present in the case that targets were distinguished on the basis of a conjunction of features. A number of theories are considered on the basis of such an observation[60]: One possibility that has been suggested is that the brain allows a particular conjunction of features, corresponding to a particular location or object to enter consciousness at any given time[29, 28]. In the case of a split brain, separate conjunctions might be made simultaneously in the separated hemispheres. A second possibility is that attention involves distinct functional units, cortical and subcortical for attentional processing. Subcortical regions, notably the superior colliculi seem to have an important role in executing covert shifts of attention[120] whereas the temporal lobes have been suggested as having a central role in feature integration[120].

Another dichotomy that might be drawn to explain the observed asymmetries is that of exogenous versus endogenous control. Previous accounts have suggested this dichotomy as a possible explanation for the observed asymmetries[130, 131, 107] with the left hemisphere having a key role in voluntary deployment of attention and the right hemisphere preferred in bottom up processing. Absence of this effect in split brain patients further reinforces the idea of cortical competition for endogenous control of attention. The importance of the left hemisphere in the voluntary control of attention appears to be sufficiently strong that it was once claimed that the left hemisphere is exclusively involved in guided search[107]. This finding has since been retooled as an indication of a dominance of the left hemisphere in the endogenous control of attention. With regard to the split-brain observer, left hemisphere search was more efficient, and the cost of distributing stimuli between hemifields was overwhelming suggesting competition for subcortical resources that typically is resolved in part by cortical competition.

6.3 Attention in Global versus Local Processing

There appears to be a functional relationship between top-down attentional processes and the dichotomy based on global versus local processing described in chapter 5. Proverbio et al. carried out a study in which subjects were required to discriminate between gratings while reaction time was measured[180]. Subjects were instructed to respond only to a particular hemifield and one of three spatial frequencies. Response times for the 1.5 cpd gratings showed a significant right visual field advantage and the 6cpd gratings a significant left visual field advantage. This is perhaps not an attentional effect per se, but a result of each hemifield having a different aptitude for processing particular spatial frequency bands. That said, there do seem to be instances in which lateralized activation corresponding to the processing of global versus local activity are clearly attentional.

Yamaguchi, Yamagata, and Kobayashi carried out a study in which event related potentials were measured under conditions in which subjects were cued to attend to either the global or local level of Navon style hierarchical figures[249]. A cue stimulus was presented indicating a global, local, or neutral trial, followed by the test stimulus. Subjects performed a go/no-go task which required the press of a button to indicate if the target letter (H or S) appeared at the cued level. On neutral trials, subjects had to indicate whether the target letter was present at either level. The ERP responses to cue stimuli demonstrated greater activation in right-temporal parietal regions following global cues and left posterior temporal regions following local cues. It is important to note that such activation occurred shortly after cueing but well before onset of the test stimulus. An important implication of this finding is that hemispheric asymmetry in activation arose from top-down cueing and not the bottom up processing of stimuli. This finding agrees with neuropsychological evidence of a local processing deficit resulting from lesions in the left superior temporal gyrus and global processing from the analogous right hemisphere region and also the right inferior parietal lobe[189, 123].

Fink et al. carried out an fMRI study involving attentional cueing tied to hierarchical stimuli[64]. Navon style letters were presented, with two different global and local size pairs. Sizes were selected so that global form in the smaller stimuli was the same size as the local form in the larger stimuli. This was done in an effort to dissociate findings concerning differences in spatial frequency processing, and attentional cueing. The foremost finding of the study was increased activation in the right lingual gyrus associated with global orienting, and in the left inferior occipital cortex for locally oriented attention. This effect was independent of the size of the compound stimuli. This further reinforces the role of cueing in the observed asymmetry. A very similar study was carried out in which stimuli were presented either in left or right peripheral hemifields rather than at the central fixation[133]. Under such conditions, a global cue resulted in increased activation of right posterior occipital cortex, and local processing the left posterior occipital cortex. Local cues also gave rise to increased activation in the right anterior cingulate which the authors suggested may reflect suppressive activity corresponding to global stimuli. Such asymmetric activation has also been reported in earlier studies in which conclusions were less lucid[66, 117].

6.3.1 The Global Precedence Effect

The original global-local study carried out by Navon, revealed an asymmetry with regard to the processing of global versus local form[156]. In particular, reaction times to identify global targets tend to be much faster than those to respond to local targets. Further, the degree to which global form interferes with incompatible local form (different letters), is much greater than the converse. A number of explanations have been proposed for the observed phenomenon which range from proposals that dorsal and ventral pathways might preferentially carry the two types of information with a faster transfer time along the dorsal pathway[238], to attentional effects such as the suggestion that more time is required to narrow the attentional window[191]. The mechanisms responsible for global precedence remain unknown, and as such, it is a phenomenon that should be considered in postulating upon the computational machinery involved in attention.

6.3.2 The Level Repetition Effect

Another effect that is observed in the context of global versus local attention is called the level repetition effect. When responding to a target (a letter for example), response time is faster when the target appears at the same hierarchical level as the previous target. Unlike global precedence, this effect is symmetric for global and local stimuli. A suggestion that has been made to explain the observed effect is that target-level information remains from one trial to the next in the form of weights associated with various spatial frequency channels[188]. Clearly this gives rise to an intrinsic level specific priming effect. Priming effects become stronger for repeated presentation at the same level, reinforcing this idea[244].

6.4 Binocular Rivalry and Attentional Effects

Recently, attention has been demonstrated as having some influence on the relative contribution of signals captured at the retina of each eye to higher level processes or conscious awareness[144, 192].

In an fMRI study, Lumer, Friston, and Rees demonstrated that activity in the frontoparietal cortex, an area often associated with attentional activity, was specifically tied to perceptual alternation in binocular rivalry[53].

Ooi and He have shown that voluntary attention can reduce the likelihood of a dominant image being suppressed under conditions of binocular rivalry in a psychophysical paradigm[218]. Further, it was demonstrated that if the stimulus presented to one of the eyes contains a pop-out cue, it is much more likely to become dominant. These results suggest bottom-up and top-down influences on ocular dominance in binocular rivalry.

Wilson, Krupa, and Wilkinson describe a model that accounts for a phenomenon in which lateral inhibitory interactions give rise to perceptual alternations in periodic dot patterns[91]. The similarity of such an effect to bincular rivalry is made explicit, hinting at the possibility of an attentional influence on perceptual alternations observed in binocular rivalry.

Meng and Tong observe the ability to voluntarily control perceptual alternation in the context of binocular rivalry and ambiguous figures[135]. It is shown that the rate of Necker cube reversal is more easily controlled, than that of simple rivalrous binocular stimuli. They conclude that binocular rivalry involves a more automatic form of competition than that of the Necker cube reversal. This conflict is perhaps resolved in considering the findings of Nguyen, Freeman, and Alais[230] who determined that binocular rivalry suppression appears to deepen along the visual pathways. This hints at the possibility that signals among higher extrastriate areas are more readily modulated by attentional feedback.

Mitchell and colleagues[144] carried out a study in which subjects were presented with a pair of overlapping transparent surfaces, with attention cued to one of the two surfaces. Upon removing one of the surfaces from each eye giving rise to binocular rivalry, subjects reported seeing only the surface to which attention was directed. The implication is that attention and rivalry rely on a common mechanism for routing information to higher levels of processing.

Chapter 7

Connectionist Models of Lateralization in Vision and Attention

Much of the discussion in the previous chapters takes place in its original context at a level of abstraction well above that of a connectionist model. This chapter outlines the few attempts at exploring some of the ideas existent in the previous chapters at the level of computational or connectionist modeling. It is expected that analyzing the phenomena discussed in earlier chapters in this more specific context might afford some insight concerning the potential computational advantages or roots of the asymmetries observed in visual and attentive processing.

7.1 Categorical versus Coordinate Processing and Receptive Field Size

Much of the early work involving neural modeling in the context of visual field asymmetries comes from Kosslyn and colleagues[7, 118]. In a first effort, Kosslyn et al.

carried out simulations in which a neural network model was put to the task of determining whether a dot was above or below a bar in a given test image (categorical task) as well as whether the dot was within 4 units of the bar (coordinate task). Each task is performed simultaneously by the network using separate sets of output units. Two distinct types of networks are applied to the task so that either all hidden units connect to all output units, or, hidden units are separated into two groups and connect exclusively to output units corresponding to one of the two judgements. Input/output mappings were established using the backward error propagation algorithm of Rumelhart, Hinton, and Williams[195]. Their findings were that the split network model is advantageous in performing both tasks relative to the unsplit model. The authors conclude that the division offers an advantage since distinct types of information are required to perform the two tasks. Kosslyn et al. also carried out a simulation on the two tasks while varying the receptive field size used in making judgements. The result was greater performance on the coordinate task for larger overlapping receptive fields, and for the categorical task for smaller non-overlapping receptive fields. Cook et al. criticized this model because the absolute position of the dot in input stimuli was correlated to the position of the bar in the stimuli used[34]. This confound was rectified in a more recent effort[7] verifying the original findings. A similar paradigm was employed for encoding shape information[117] with receptive field sizes varied. Larger receptive fields were advantageous in encoding identity of shapes, and smaller receptive fields in assigning shapes to categories. This finding seems to reinforce the varying utility of different spatial frequencies in categorical versus coordinate tasks. It is perhaps worth commenting, that the findings of Kosslyn et al. relating to advantages of a split/unsplit network are perhaps not pertinent in the domain of neural processing, since it is unlikely that coordinate or categorical judgements are achieved by two entirely disparate neural processes.

7.2 Connectionist Modeling of Unilateral Visual Neglect

There exist a number of implemented connectionist models of unilateral neglect. Such models typically focus on the task of line bisection, which has offered a variety of detailed quantitative data concerning unilateral neglect. The line bisection task requires a subject to judge the center point of a horizontal line. In neglect patients, the judgement is typically displaced to the ipsilesional side[203]. In the context of neural modeling, an input line is mapped to an output line that reflects the judgement of position and length of the input line from which the centre point might be inferred. The network is trained to reproduce the input line at the output layer. Effects of lesioning may be also be observed in this context by introducing virtual lesions in the network. The method of introducing ”damage” varies and is noted in cases where this has been considered.

In chapter 3, the basic structure of the MORSEL model was described with a focus on the attentional mechanism involved. Mozer, Halligan, and Marshall also considered the effects of lesioning in the model by introducing a rightward bias in the attentional mechanism, which resulted in errors in line bisection judgements and neglect of the leftmost components of input stimuli.

Kinsbourne describes an account of neglect as a result of damage to one of the contralaterally oriented attentional gradients in each hemisphere[109]. Pouget and Sejnowski have outlined a neural basis for the contralateral attentional gradients Kinsbourne originally described[177]. The description of Pouget and Sejnowski include parietal neurons that respond most strongly to stimulus at the center of their receptive fields, response modulation based on eye position, and the receptive field centers fit along a contralateral gradient. Pouget and Driver have provided a detailed justification for such a gradient in the parietal cortex[176]. The model of Pouget and Sejnowski was lesioned by removing right parietal neurons, and demonstrated neglect like behavior in line bisection and cancellation tasks.

Monaghan and Shillcock implemented a model based on the idea of attentional gradients which involves a hidden layer divided between left and right parietal neurons distributed according to the attentional gradients described in [177]. Lesions of the right hemisphere resulted in a rightward bias for longer lines and a small leftward bias for short lines in agreement with psychophysical data.

A different account of the asymmetries observed in neglect, which has had influence on connectionist models is that of Heilman and Van Den Abell[76]. Their proposal involves a global distribution of attention by the right hemisphere, a local distribution of attention by the left hemisphere, and with the right hemisphere attending to both hemifields and the left hemisphere to the right hemifield. Anderson has proposed a computational model of this account with the right hemisphere distributing attention over the whole visual field, peaking in the middle, and the left hemisphere attending to a narrower window peaking slightly to the right of the center. Lesioning of such a model also gives rise to phenomena in agreement with clinical accounts of neglect.

Monaghan and Shillcock carried out a number of experiments with neural network simulations on the task of line bisection[145]. The neural model involves the mapping of a one dimensional input line onto a one dimensional output representation of the line. The single hidden layer consists of half fine coding narrow receptive fields, and half coarse coding large receptive fields. Virtual lesions were introduced by reducing the activity from all of the input units to all hidden units of one type (large or small RF). Errors in determining the centre of the line under lesion conditions were found to be consistent with clinical data from patients with unilateral neglect.

7.3 Yund's Extension of Guided Search

There exists one previous attempt at modeling visual search asymmetries within a connectionist paradigm. Efron and Yund [55] propose an extension of Wolfe's Guided Search Model[245], that includes spatial non-uniformities in the bottom-up stage of processing. Efron and Yund's proposal is inspired by a variety of visual search experiments carried out in their lab, which characterize target detectability as a function of location in the visual field. Experiments include a number of vertical, horizontal, and colored targets each among a number of distractors. Search efficiency was measured as a function of position in the visual field, and a right visual field advantage was observed with a right to left gradient of superiority[57, 56].

The model of Efron and Yund, is described at the level of a theoretical model, and lacks certain details that would be required at an implementation level. Their proposal entails Wolfe's Guided Search model[245], with the difference that feature responses include parameters based on position in the visual field. The details of including such parametric variations in feature response are left at a descriptive level, and not stated explicitly. That said, the authors do provide some general guidelines regarding the spatial non-uniformities that such parameters should characterize as follows:

1. The decrease in photoreceptor density with increasing distance from the fovea.
2. Radial organization: Movement detection and resolution of gratings is best when motion or orientation is aligned with a meridian passing through the fovea, and worst when orthogonal to such a meridian[193, 217, 206, 219].
3. Hemispheric processing differences, such as those described in the previous two chapters.

4. Possible differences in lateral interaction between stimuli and distractors, although there is evidence that lateral interactions have no effect on the shape of the detectability gradient.

Efron and Yund's model does not offer any simulation results concerning asymmetries observed in visual search, but does highlight a number of important general spatial non-uniformities that might contribute to the performance asymmetries observed. Understanding the nature of such asymmetries might afford some insight concerning the underlying computational advantages that such asymmetries may afford in visual processing.

Chapter 8

Discussion

The preceding chapters outline a variety of interesting and intriguing phenomena that continue to defy explanation given the current outlook concerning spatial non-uniformities in vision. The literature is rife with psychophysical results that outline unexpected asymmetries in visual and attentive processing, but shed little light on the underlying source of such non-uniformities. The result of this, is that the current understanding of these phenomena exists in a domain that lends itself ideally to connectionist modeling. The current situation is such that much is known concerning the overall dynamics of the system that produces the observed asymmetries, and much is known concerning the individual computational units involved. What is lacking, is an understanding of how such units interact to produce the observed dynamics. As such, it is apparent that much headway may be made in considering lateral asymmetry in the visual domain at the level of description of connectivity between the neural units involved. This chapter aims to highlight some specific issues that one might expect will shed light on the foundations of visual asymmetries when cast in the context of a connectionist model.

It remains unclear whether the two hemispheres are capable of focusing attention independent of each other, both in the case that the cerebral hemispheres are connected via the corpus callosum, or in the case that this pathway is severed. The relatively small number of studies observing this issue have drawn conflicting conclusions, with differences apparently resulting from varying numbers of distractors in visual search experiments on this matter, and differences in the distribution of elements between the two visual hemifields. This issue is related to the more fundamental issue of how attention is coordinated between hemispheres in the normal brain to ensure a unitary attentional focus. Each of these issues remains unresolved and requires careful consideration of the range of results that have emerged from psychophysical efforts as well as consideration of the potential role of subcortical structures in explaining the observed results. A careful and comprehensive look at existing efforts pertaining to this matter should allow stronger conclusions to be drawn concerning interhemispheric coordination in attention.

Perhaps the most fundamental visual phenomenon associated with the bilateral design of primates, is that visual information arrives via a pair of sensory organs. The frame of reference associated with attentional modulation has become a topic of discussion in recent years with arguments typically advocating modulation in either a world, retinotopic, or object-based reference frame. What is entirely absent from this discussion, is the fact that the sensing frame of reference consists of two distinct retinotopic representations. This consideration begs an number of questions such as: *What is the relationship between the two eyes from the perspective of attentional modulation?* And *What happens when the input from the two eyes doesn't match?* Recent studies seem to indicate that attentional behavior is paramount in eliminating interference between signals received by the two eyes under conditions of binocular rivalry. Investigation of the relationship between the two eyes with regards to attentional modulation may be useful in understanding the the mechanisms underlying the dynamics of rivalrous perception, and coordinate systems associated with attentional modulation.

The asymmetries that manifest in visual search, cueing, and discrimination experiments lack explanation, particularly from the perspective of the cause of such asymmetries. This is an area that as alluded to at the beginning of this chapter may benefit from analysis within a modeling context. There is a wide range of effects that should be taken into consideration in formulating a connectionist explanation of these results as follows:

- Reaction time and accuracy differences in detection tasks considering target position in the visual field.
- The apparent advantage of the left hemisphere in employing top-down modulation to guide visual search.
- The greater cost of invalid cues associated with processing in the right hemisphere.
- Asymmetries in activation observed in ERP, PET and fMRI patterns associated with left or right visual field stimulus presentation or cueing.
- Differences in the effects of flanking distractors in left or right visual field.
- Apparent independent search within each hemisphere in split-brain patients among few distractors, and the dissolution of this effect for increased numbers of distractors.
- The lack of visual hemifield advantage in visual search carried out by split-brain patients.
- The apparent importance of the right parietal cortex in processing high-temporal frequency stimuli.

- Asymmetries in the global/local form of drawings in patients with left or right parietal damage, or in split-brain patients drawing with either the left or right hand.

- The very different manifestations of hemineglect that arise from right and left hemisphere damage.

- The global precedence effect.

- The relationship of the observed asymmetries to exogenous versus endogenous activity in the deployment of attention.

In formulating a neural model, one might achieve a comprehensive explanation of the aforementioned asymmetries, explicating many of the described phenomena in an single architecture that does pose any serious conflict with those observations that elude explanation in the same framework.

It is quite peculiar that such palpable asymmetries exist, since it is in no way apparent that they afford any advantages from the perspective of acting and perceiving in our natural environment. Cast in the domain of a neural framework, one may explicitly consider advantages that the existent asymmetric configuration produces appealing to principles such as energy minimization, learning strategies, and advantages pertaining to statistical regularities in the patterns encountered by the visual system. Such analysis might be conducted in a more general context relating visual asymmetries to more general hemispheric asymmetries. One might also consider specific advantages that an asymmetric configuration allows in the context of visual orienting from the perspective of shifting attention between different scales of a scene, and minimizing interference from computational units that carry information irrelevant to task demands (e.g. fast motion analysis presumably relies primarily on high-temporal low-spatial frequency information).

As a whole, the current understanding surrounding spatial non-uniformities in attention and visual perception leaves much to be desired. The preceding discussion offers a variety of research areas that require considerable further investigation, in order that that the mechanisms responsible for the observed asymmetries may be fully understood. Further, it appears that a connectionist perspective on these phenomena may be instrumental in elucidating the causes, effects, and advantages of non-uniformities in attentive and visual processing.

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