DESCRIPTION OF THE NEURAL PROCESSING OF VISUAL INFORMATION

By Bruce Hilliard

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Appendix 1: Description of the Key Neural Processes used for Managing Visual Information

1.1.   Overview

1.1.1.   The Intent of this Appendix

The objective of this appendix is to outline the key elements of the visual systems, which are utilised for top-down and bottom-up processing.   Additional implications related to this physiology, and the psychophysical consequences, are described in Chapters 3, and 6 within Volume 1 of this thesis.

1.1.2.   Overview of the Visual System Elements

According to Grill-Spector & Malach (2004, p. 649) 'visual perception is achieved via a gradual stage wise process in which information is first represented in a localized and simple form and, through a sequence of processes, is transformed into more abstract, holistic, and even multimodal representations'.   Additionally, within this processing model there are specialised neural pathways 'that process information about different aspects of the visual scene' (Grill-Spector & Malach, 2004, p. 650).   The visual system is therefore 'much more complicated than the notion of taking a picture' (Fulton, 2003b, p. 33).

It is important to note that, as specified by Schutz, Braun, and Gegenfurtner (2011, p. 1), the scientific community are yet to reach a 'satisfactory consensus' on all of the processes that are utilised to manage visual stimuli within the human brain.   However, there is enough research available on this topic to create a suitable working model for utilisation within the experimental framework applied in this thesis.

Figure 1.1 provides a simplified overview of the key elements of this process[1] and illustrates how this links to the top-down and bottom-up processes discussed in Chapter 2 of the thesis.

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1.   This model was developed by the author, through amalgamation and rationalisation of information provided by Fulton (2008); Underwood (2005); Sekuler (1977); Garrett (2003); Feldman (2005); Graven & Browne (2008); Cao, Pokorny, Smith & Zele (2008); Mohand-Said et al (2001); Calvo, Nummenmaa & Hyönä (2008); Bargmann (2012); Doré-Mazars, Pouget & Beauvillain (2004); Crick & Koch (1998); Pins & ffytche (2003); Wurtz, McAlonan, Cavanaugh & Berman (2011); Muggleton, Juan, Cowey & Walsh (2003); Lisberger (2010); Sprague (1972); Schutz et al. (2011); Silvanto, Lavie & Walsh (2006) and Tatler, Hayhoe, Land & Ballard (2011).
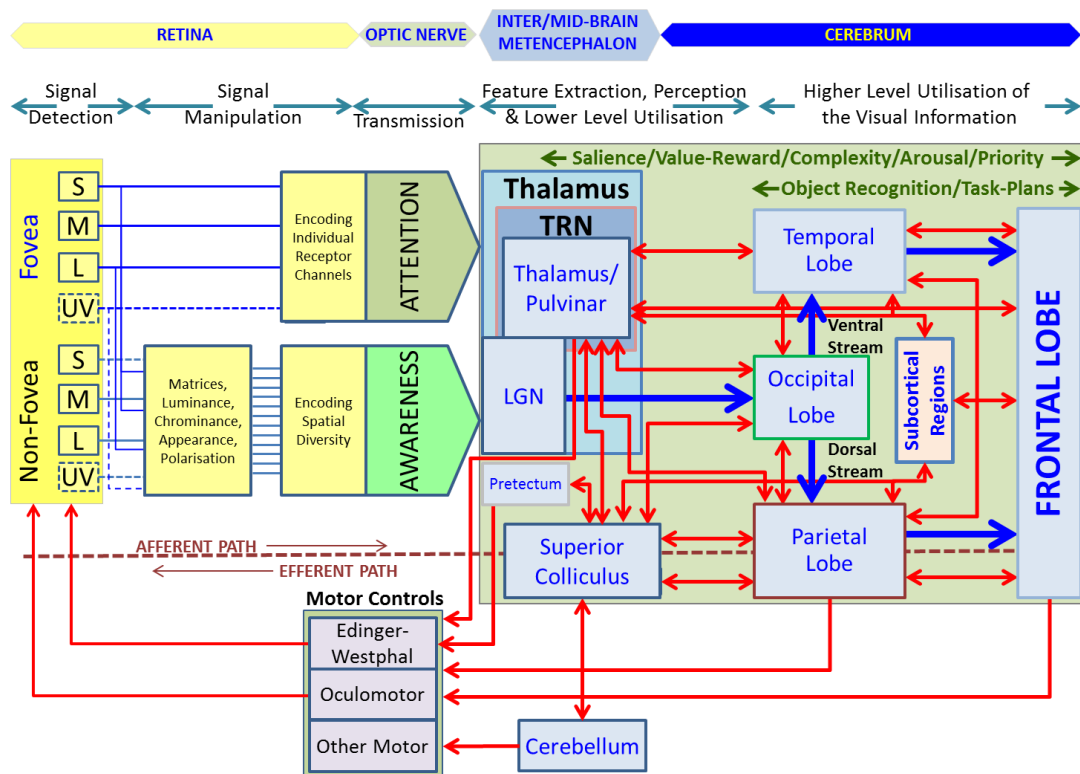
Figure 1.1:   Overview of the Visual Processing System

This model is separated horizontally into specific regions of the human visual system, as shown in the top line of the diagram.   At the top left is the eye *(and specifically the retina)*, which is utilised for detection and initial manipulation of the visual stimuli. Signals produced within the retina are then transferred to the processing areas within the brain, through the optic nerves.   Functional areas within the 'Interbrain' *(Diencephalon)* and 'Midbrain' *(Mesencephalon)* then process these signals, and provide some fundamental interpretation and management of the visual information.   In particular, the regions within the thalamus, which are known as the Lateral Geniculate Nuclei (LGN), Thalamic Reticular Nucleus (TRN), and Pulvinar; and other regions within that vicinity, which are known as the Pretectum, and the Superior Colliculus (SC) play important roles in feature extraction, primary perception, and low level utilisation of the visual information received through the eyes.

From these interbrain and midbrain elements, signals are then passed to various parts of the:

• **Cerebrum**[2].   Visual signals are transmitted to a range of different regions within the human brain.   The most important of these appear to be within the Occipital Lobes (OL), Parietal Lobes (PL), Temporal Lobes (TL), and Frontal Lobes (FL). The heavy blue arrows within Figure 1.1 illustrate the primary pathways connecting the OL, PL, TL and FL.

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2.   The cerebrum *(or neo cortex)* consists of two cerebral hemispheres (Fulton, 2011), which are delineated into the lobes illustrated in Figure 1.2 and Figure 1.3.

- *Subcortical Regions.* Whilst processing the visual stimuli through the cerebrum, a range of subcortical areas are also utilised.

- *Efferent Systems*. The preceding elements fit into a grouping known as afferent systems, because they carry sensory information inward from the sensing organ *(e.g. the eyes)* to the brain for processing (Fulton, 2011). However, these also feed into sensory loops, which are known as efferent systems. Efferent systems are directed away from the central processing systems to an effector, to cause some relevant action *(e.g. moving the eyes to a new location through oculomotor[3] systems)* (Fulton, 2011). These efferent systems are shown within Figure 1.1 below the brown dotted line.

Additionally the red connectors within Figure 1.1 illustrate some of the key feed-forward and feed-back connections that are utilised for processing the visual information.

The approximate location of these key physiological elements, and others that will be discussed in this thesis, are shown in Figure 1.2 and Figure 1.3[4].
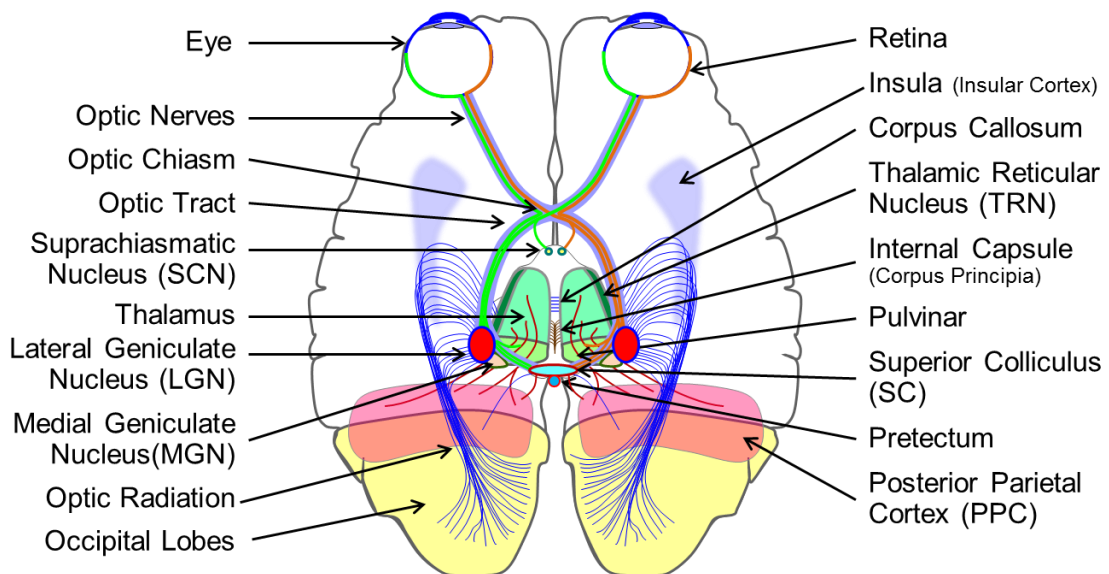
Figure 1.2:   Top view of the key physiology of the visual processing system

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3. Oculomotor systems support the conscious or autonomous movement of the eyes (Sekuler, 1977). These movements are discussed in more detail later in Section 1.6 of this appendix.

4. The physiology diagrams *(which were developed by the author)*, apply information listed in the sources at Footnote 1 and other references listed within this appendix. Some aspects of the physiology in these diagrams have been simplified, to facilitate their illustration.
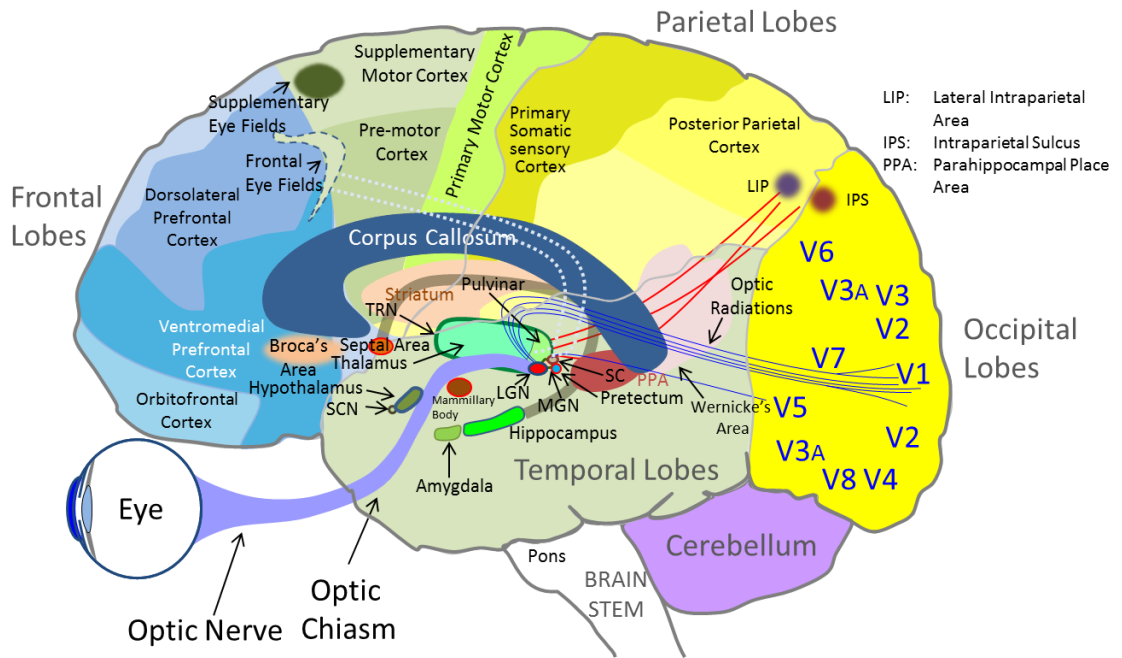
Figure 1.3:   Side view of the key physiology of the visual processing system

Each of these physiological elements, and the part they play in perception, is explained in the following sections.   For the purpose of brevity, this thesis only discusses the elements of the physiology that are most pertinent to the research questions.   However, to put each of these elements into context, the next section addresses the important general concepts of awareness and attention.

1.2.   *Awareness and Attention*

As illustrated within the preceding overview, human vision utilises multiple areas within the brain to implement processes that allow people to develop an understanding of their environment, and then use this information through the efferent systems.   For this thesis the visual processing channels have been delineated in terms of generating awareness and attention.
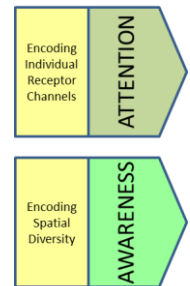
The relationship between these aspects is illustrated in Figure 1.4[5].
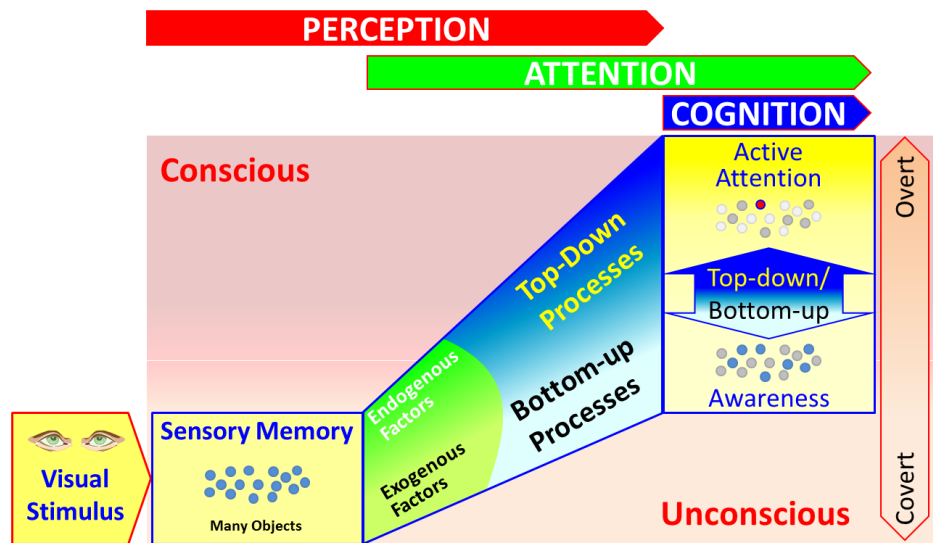
Figure 1.4: The relationship between perception, awareness, cognition, and attention

As illustrated within this diagram, perception, attention and cognition are interlinked, so they can process visual stimuli, and allow people to focus on the most important aspects within their environment. Each element within this diagram is discussed in the following subsections.

1.2.1. Perception

Perception is the process utilised to translate and begin the process of interpreting sensory information (Feldman, 2005; Garrett, 2003). Within the thesis, this term is applied to the primary *(lower-level)* aspects of perception, which process the visual stimuli to develop percepts[6], without generating awareness[7]. This differentiation is

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5. This model was developed by the author, by synthesising information provided in Lamme (2003); Irvine (2011); Jennings (2012); Carrasco (2011); Crick & Koch (1998); Crick & Koch (2003); Taylor (2011); Itti & Koch (2001); Suchow & Alvarez (2011); Neisser (2012); Badgaiyan (2012); Gallese (2007); Wallis & Bex (2011); Tatler & Land (2011); Ries (2007); Lamme & Roelfsema (2000); Smith, Cotton, Bruno & Moutsiana (2010); and Kanwisher & Wojciulik (2000). It is noteworthy that there are still numerous competing views within the scientific community on how visual attention and awareness work (Carrasco, Eckstein, Verghese, Boynton, & Treue, 2009; Jennings, 2012). However, this model aligns to commonly accepted principles applicable to the hypotheses being tested in this research.

6. A percept is a blended construct of visual stimuli, which allows the brain to handle congruent or incomplete information (Crick & Koch, 2003; Navarra, Alsius, Soto-Faraco, & Spence, 2010). This term aligns to Gibson's (1960, 1973, 1979) direct perception concept, which equates percepts to the 'physical variables of the stimulus' (Gibson, 1960, p. 695). However, the model used in this thesis diverges from the direct perception concept, by limiting percepts to lower level constructs, and treating higher level perceptual structures as 'representations' *(See Footnote 13)*. This approach reflects more recent investigations by researchers like Ullman (1980), Costall & Still (1989), Stoffregen

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designed to separate the lower level processes from visual cognition *(which is described in Section 1.2.3).* The key physiological elements utilised to achieve perception are covered in Section 1.3 of this appendix.

1.2.1.1. Receiving Visual Input

As illustrated in Figure 1.4, the process begins when the visual stimuli are received through the eyes. This visual information is then managed and assessed unconsciously and consciously[8], to generate attention and awareness, as described in the following sections.

1.2.1.2. Sensory Memory

Sensory memory initially relates to the very short retention[9] of stimuli within the sensory systems (Feldman, 2005). However, as the visual stimuli are processed through the perception system, they are then handled within a network of working memory elements. Working memory[10] 'refers to the temporary representation of information that was just experienced or just retrieved from long-term memory. These active representations are short-lived' (Curtis & D'esposito, 2003, p. 415), and typically last only for about 15 to 25 seconds (Feldman, 2005).
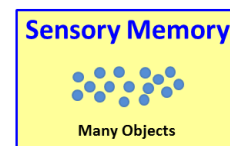
This level of awareness:

• is considered unconscious, which means that the viewer is not consciously aware of *(and cannot report on)* all of the visual stimuli collected through the eyes (Irvine, 2011); and

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& Bardy (2001), and Mira & Delgado (2009), whose concepts and theories have been better able to reflect the neural processes that are applied within the human brain.

7. See Section 1.2.3.1.3 for a definition of the term awareness. The delineation in terms of generating awareness was used to separate perception without awareness and perception with awareness, as defined by Merikle, Smilek, & Eastwood (2001). Additionally, this separation aligns to the physiological division at the visual cortex as detailed in Zeman (2004) and Tong (2003), and then link this to the visual cognition model detailed in Cavanagh (2011) and the awareness model developed by Dehaene, Changeux, Naccache, Sackur, & Sergent (2006).

8. See Section 1.2.3.1.2 for a definition of the terms unconscious and conscious.

9. The general duration of visual sensory memory is typically only around 250-300 milliseconds (ms), but it can also vary with age, getting shorter as the individual gets older (Walsh & Thompson, 1978).

10. For the purposes of this thesis the term Working Memory (WM) will be used, rather than Short Term Memory (STM), or visual Short Term Memory (vSTM) This approach conforms to the recognition that working memory is a more suitable term, noting that this type of memory is not so much a 'holding store' *(which better aligns to the STM or vSTM concepts)*, but 'the cognitive system's processing engine' (Sweller, 2002, p. 1502). See Section 1.4.4.2 for more information on working memory.

- may hold a large amount of visual stimuli, which cannot all be processed effectively (Jennings, 2012; Wallis & Bex, 2011), 'because there are severe limits on our capacity to process visual information' (Carrasco, 2011, p. 1486).

Because of this limitation in mental capacity, the attention processes are very important.

1.2.2.   Attention

'Attention is a selective process' (Carrasco, 2011, p. 1486), which is used 'to inform cognition or action' (Wu, 2011, p. 96), in response to particular aspects within the field of view[11].   For example, Lamme (2003) refers to visual attention as the method that is applied to implement faster and more detailed processing of certain stimuli.   Such attention can be applied consciously or unconsciously (Kanai, Tsuchiya, & Verstraten, 2006; Kramer, Irwin, Theeuwes, & Hanh, 1999).
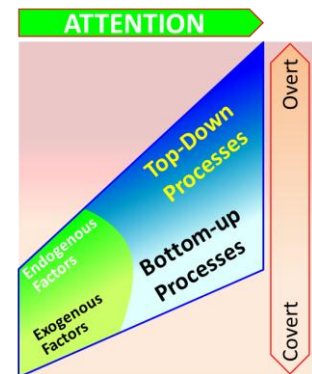
The application of conscious or unconscious attention is applied within a continuum, which is defined within the following categories:

- *Overt Attention.*   In overt attention the area of central vision, which is known as the fovea *(see Section 1.3.1.2)*, is moved consciously or unconsciously to the point of interest within the field of view (Wu, 2011).   These types of movements are known as saccades, or smooth pursuits *(see Section 1.6 of this appendix for an explanation of these eye movements)*, and they are important because they move the area of reference for the high definition visual areas within the retina, so the point of interest is visualised through the area of the eye that typically has the greatest visual acuity[12] (Rossi & Roorda, 2010).

- *Covert Attention.*   This type of attention is achieved without moving the eye, so the fovea does not necessarily focus on the point of interest (Wu, 2011).   Covert attention is therefore used to monitor the environment (Carrasco, 2011), and it can also trigger overt attention (Carrasco, et al., 2009; Kramer, et al., 1999; Peterson, Kramer, & Irwin, 2004).

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11.   The field of view refers to the angle over which visual information can be projected onto photoreceptor cells on the retina *(see Section 1.3.1.2.1)*.   This aspect is influenced by the structure of the retina, and the positioning of the eyes *(e.g. looking left or right, up or down)* (Fulton, 2005, 2009).   As a general guide, the horizontal coverage when looking straight ahead is illustrated in Figure 1.12 on Page 38.   There is also another conceptual variation to the term field of view.   This is referred to as the Functional Field of View (FFOV), which 'is defined as the range of the visual field around the fixation point where recognition is possible' (Nobata, Hakoda, & Ninose, 2009, p. 887).   The FFOV is also referred to in other papers as the Useful Field Of View (UFOV) *(e.g. Couperus (2009) and Richards, Bennett, & Sekuler (2006))*.   In this thesis the FFOV/UFOV concepts will be utilised and simply referred to as the field of view.

12.   The term visual acuity is used to define the clearness of the vision, and it is dependent on the sharpness of the retinal focus and the brain's ability to interpret the visual stimuli (Cline, Hofstetter, & Griffin, 1997).

The application of overt and covert attention is driven by exogenous factors *(environmental factors that induce visual stimuli)*, and endogenous factors *(factors that are internally driven within the brain of the observer)* (Chua, 2009; Jennings, 2012). Theeuwes (2004) identified that these exogenous and endogenous factors interact, to shape human attention and awareness.   As explained by Turatto & Galfano (2001), the processes utilised to manage these factors are known as:

- *Bottom-up processes.* Exogenous factors can draw attention covertly or overtly, to process the visual information through bottom-up processes (Chua, 2009). Bottom-up processes are typically identified as:

  ➢ unconscious (Breitmeyer, Ogmen, & Chen, 2004; Breitmeyer, Ro, Ogmen, & Todd, 2007; Ro, Singhal, Breitmeyer, & Garcia, 2009; Taylor, 2011; Wu, 2011; Zhaoping, 2008), or producing fleeting consciousness (Crick & Koch, 2003); and

  ➢ involuntary, in response to the visual stimuli (Fischer & Weber, 1998; Neo & Chua, 2006), so these bottom-up processes are assessed as being more mechanistic than top-down processes (Rusanen & Lappi, 2006).

- *Top-down processes.*   The endogenous factors are handled through top-down, goal-directed processes (Chua, 2009).   Top-down processes can be unconscious (Kanai, et al., 2006; Shipp, 2006), or conscious (Tapia & Breitmeyer, 2011), and are typically driven by the intent of the individual viewing the content (Inukai, Kumada, & Kawahara, 2010).

- These processes are described in more detail in Chapter 2 of this thesis, but it is important to note that these perceptive and cognitive activities interact with each other (Inukai, et al., 2010).   For example, as explained by Turatto & Galfano (2001) colour, which can be treated as an exogenous factor, can be handled through both bottom-up *(e.g. salience)* and top-down *(e.g. planned visual search)* processes.   Top-down and bottom-up processes should therefore not be seen as separate methods, but techniques which interact to shape attention (Inukai, et al., 2010; Sarter, Givens, & Bruno, 2001; Sawaki & Luck, 2010).   For instance, D. Wang, Kristjánsson, & Nakayama (2005) identified that efficient 'multiconjunction' processing was successfully achieved in situations where disassociated top-down and bottom-up processing models would have indicated that the visual search should have been inefficient.   It is therefore the interaction between these processes that is of particular import in terms of this thesis, and for this reason, top-down and bottom-up processes are illustrated in Figure 1.4 within an integrated continuum.

1.2.3.   *Visual Cognition*

Visual cognition (VC) is a 'central aspect of human cognition' (Sweller, 2002, p. 1501). The term visual cognition:

- relates to the integration and analysis of the information that was collected through the perception process, which is then utilised within higher level representations[13] (Logan, 1999);

- covers processes that occur on a subset of the visual stimuli *(e.g. percepts or representations)*, which were developed and selected using attention related processes (Cavanagh, 2011; Müller & Krummenacher, 2006); and

- incorporates neural systems that apply local inferential processes, to develop an understanding of what is seen in the environment (Cavanagh, 2011; Henderson & Hollingworth, 2003).

As illustrated in Figure 1.4 visual cognition is conducted consciously and unconsciously. These differentiators create a continuum of awareness, which is discussed in more detail in the following subsection. The physiological elements of the brain that are used to manage visual cognition within the continuum of awareness, are covered in Sections 1.3.5 *(particularly the extrastriate cortex)* and 1.4 of this appendix.
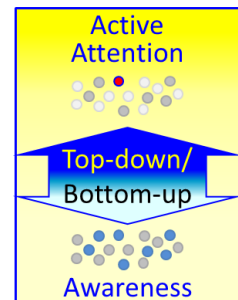
1.2.3.1. The Continuum of Awareness

Figure 1.5[14] illustrates the key levels, which define the continuum of awareness.

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13. Representations are higher level (Crick & Koch, 2003; Pugh et al., 2000) mental constructs (Wu, 2011), which are based on feature *(e.g. percept)* conjunctions and these can then be linked to previous knowledge (Becker & Horstmann, 2009; Lewis, Borst, & Kosslyn, 2011). Each representation is developed as required (Kristjánsson & Nakayama, 2003), and they are typically volatile, which means that they are forgotten quickly unless attention is focussed on them (Chua, 2009).

14. This model was developed by the author, by rationalising and coalescing information provided in: Jennings (2012); Bradley (1902); Dehaene, et al (2006); Wu (2011); Hassin, Bargh, Engell, & McCulloch (2009); Yates (1985); Bishop (2008); Merikle, et al., (2001); Kida, Wasaka, Nakata, Akatsuka, & Kakigi (2006); Rahnev, Huang, Lau (2012); Konstantinou, Bahrami, Rees, & Lavie (2010) and Lamme (2004).
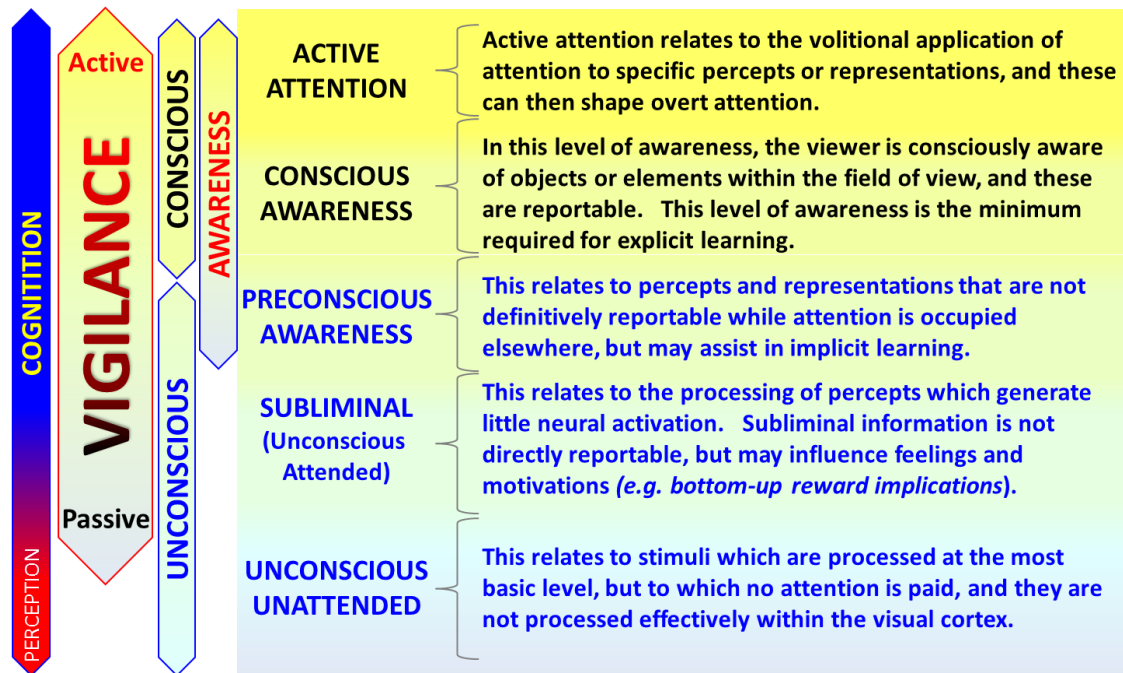
Figure 1.5: The continuum of awareness

The demarcation of perception and cognition is illustrated at the far left of this model. The next vertically aligned elements *(vigilance, conscious, unconscious, and awareness)*, which are shown towards the left of this diagram, are designed to broadly scope key drivers and thresholds.   The five levels of awareness utilised in this model are not illustrated with defined boundaries, because there is considerable debate about the differentiation between these levels.   For this reason, although the following subsections discuss them as defined elements, these should only be seen as tags, to characterise broad levels within the continuum.

1.2.3.1.1. Vigilance

The term vigilance relates to the concept of providing sustained attention (Maclean et al., 2009).   Vigilance is therefore used within this framework to bind the concepts of bottom-up and top-down attention processes, while separating this from the identified levels of consciousness[15].   This separation is applied in light of the research conducted by Koch & Tsuchiya (2012), which indicated that the neural processes that give rise to attention and consciousness are related, but different.   For example, bottom-up processes can lead directly to the development of consciousness, or top-down processes may generate or suppress consciousness (Van Boxtel, Tsuchiya, & Koch, 2010).   This concept is discussed in more detail in Section 1.2.3.2.

Therefore, a more effective framework is provided by assessing the level of engagement with the stimuli.   For instance, in terms of the model cited by Jennings (2012),

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15.   This approach is modelled on the framework utilised by Dehaene, et al (2006), which separates vigilance from consciousness, and then links this to activations within the brain's neural networks, as discussed in Section 1.2.3.2.

vigilance *(attention processes)* can be applied within a continuum, which is defined within the following range:

- at the top of the range the viewer is actively paying attention, and is likely to be applying top-down processes *(e.g. Task, Plans, Object Recognition, Value and Reward)*, which may suppress some bottom-up processes, as discussed in Chapter 2 of Volume 1 in this thesis; and

- at the bottom of the continuum the person is only passively attending to the stimuli, but may be applying both top-down and bottom-up processes.

The amount of active or passive vigilance applied to specific percepts or representations will then affect the level of consciousness and vice versa (Campbell & Macdonald, 2011).

1.2.3.1.2. Unconscious and Conscious Processes

The term unconscious refers 'to those mental processes of which the individual is not aware while they occur' (Borchert, 2006, p. 570). Although the individual may not be aware of these processes, they can play an important role in perception and cognition (Mayer & Merckelbach, 1999). These unconscious processes are also identified as being fast and automatic (Evans, 2008).
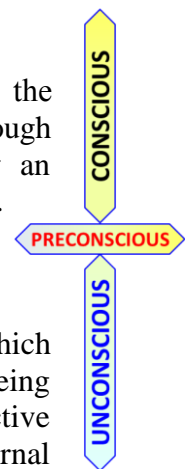
Consciousness can be classified as the level of neural activity, which generates 'awareness of the sensations, thoughts, and feelings being experienced at a given moment. Consciousness is our subjective understanding of both the environment around us and our private internal world' (Feldman, 2005, p. 148). These processes are typically identified as being slower, and more deliberate than unconscious methods (Evans, 2008).

Although they are shown in Figure 1.5 as being separate, there is significant evidence to support the 'notion that perceptual processing does not always achieve consciousness, despite the fact that at some level the mental representations of conscious and unconscious percepts, and presumably their neural correlates, are quantitatively similar.' (Milner & Goodale, 2008, p. 775). For this reason, this continuum of awareness includes a level known as preconsciousness, which relates to percepts and representations that are capable of entering the conscious state (Dehaene, et al., 2006) *(as discussed in Section 1.2.3.1.6).*

1.2.3.1.3. Awareness

Awareness is a continuous (Bugental, 1964), and subjective (Badgaiyan, 2012) mental state, which relates to the active processing of information, but it does not necessarily imply consciousness (Norman, 2002). For instance, significant elements of the cognitive processes are managed without conscious awareness being generated (Merikle, et al., 2001; Ro, et al., 2009). Therefore awareness is delineated as preconscious and conscious *(as described in Sections 1.2.3.1.6 and 1.2.3.1.7 respectively).*

Awareness is an important concept in terms of this thesis, because it is required as a minimum state to achieve visual cognition (Fulton, 2005), and learning will typically not take place without conscious or unconscious awareness (Norman, Price, Duff, & Mentzoni, 2007)[16].   As an example, conscious awareness is required to achieve explicit learning (Rose, Haider, & Büchel, 2010), while preconscious awareness can generate implicit learning[17] (Schnotz & Kurschner, 2007).   In turn, implicit and explicit learning can then shape active attention (Couperus, 2009).

1.2.3.1.4. Unconscious Unattended Level

UNCONSCIOUS UNATTENDED

The term unconscious unattended is used to identify the situation in which visual stimuli receive little or no attention.   This equates to the lowest level of what Mayer & Merckelbach (1999) refers to as the 'dumb' unconscious.   In practical terms, this level is delimited by the absence of significant stimulation within the visual cortex (Dehaene, et al., 2006), as discussed in Section 1.2.3.2.   This means that the stimuli may be processed within the early visual systems *(see Sections 1.3.1 to 1.3.5 of this appendix)*, but they are not consciously perceived or attended to, as a part of the visual cognition process.

1.2.3.1.5. Subliminal Level

SUBLIMINAL (Unconscious Attended)

The term subliminal 'refers to perception so subtle it cannot reach conscious awareness' (Baumeister & Vohs, 2007, p. 954).   For instance, visual stimuli of less than 10-15 milliseconds duration cannot be accessed consciously, but 'they can have brief and subtle effects on our feelings and thinking' (Baumeister & Vohs, 2007, p. 954). The type of attention applied to stimuli at this level of awareness is initially associated with bottom-up processing, but it can also be driven by top-down feedback (Dehaene, et al., 2006).   Although this information is handled unconsciously, subliminal activity can influence:

- impressions about the content, and the persuasiveness of the communication (Lakhani, 2008);

- emotional arousal (Krosnick, Betz, Jussim, & Lynn, 1992);

- task related behaviours (Lau & Passingham, 2007); and

- subconscious motivation (Hart & Albarracín, 2009; Pessiglione et al., 2007), which has direct implications for the application of reward and goal processes (Custers & Aarts, 2010), within the framework utilised in this thesis.

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16.   Note: E. Norman, Price, Duff, & Mentzoni (2007) refer to preconsciousness as 'fringe consciousness', which can be equated to preconscious awareness.

17.   'Implicit learning is defined as the ability to learn without conscious awareness' (Couperus, 2009, p. 342). As cited by Perruchet, Vinter, & Gallego (1997) processes related to implicit learning shape percepts and representations.   Shaping the percepts and representations in this way may then support contextual cueing *(e.g. allowing the visual information to be linked to the relevant task)*, which appears to be required for implicit learning to take place (Jiang & Chun, 2001).

For these reasons, subliminal advertising techniques have been used for many years (Rogers, 1992). However, as pointed out by Beato (2010), the powerful subliminal controls that were promised by marketers are not realistic. That being said, there is significant research, which indicates that subliminal information can create subtle influences on cognition (Custers & Aarts, 2010).

These influences appear to be created through cognitive priming[18] (Strahan, Spencer, & Zanna, 2002), in which the unconscious processing shapes percepts and representations of the information being received (Perruchet, et al., 1997). For example, Tsai, Wen-ko, & Liu (2007) identified that subliminal product placement in movies can influence impressions. However, this effect worked best when the viewers were already knowledgeable about the product's trade mark (Tsai, et al., 2007). These findings can be explained by the research published by Brooks et al. (2012), which infers that priming is most successful when it can be linked with memories accessed through the ventral stream processing[19].

1.2.3.1.6. Preconscious Awareness

PRECONSCIOUS AWARENESS

Preconscious awareness can be defined as a perceptual state in which the percepts, or representations, are capable of entering consciousness, but are not consciously perceived at that time (Dehaene, et al., 2006). A useful model for understanding this level of awareness is based on James' (2010) 'Ignore-ance' concept. Ignore-ance reflects the lack of conscious acknowledgement of specific information. In other words, the knowledge may be available within working memory, but the active level of attention paid to the percept or representation is insufficient to elevate the information into consciousness.

However, endogenous or exogenous factors can change this. For example, when a person looks at a picture like Figure 1.6, numerous percepts and representations will be handled at the preconscious level[20]. For example, the lack of other people, the colours, the harsh sterility, and the body language of the person in the picture may all be assessed as percepts or representations. Many of these percepts and representations would be handled at the preconscious level, but the aggregation of these various visual aspects can then create conscious feelings in the viewer.

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18. Priming is an unconscious process, which creates perceptual associations that facilitate cognition (Schacter, Dobbins, & Schnyer, 2004). For example, showing an arrow pointing to a particular location can prime the brain to look at a particular point in space even before the salient object appears (Becker & Horstmann, 2009). This priming can therefore enhance perception and shape attention (Kristjánsson & Nakayama, 2003).

19. See Section 1.2.3.2 for a diagram *(Figure 1.7)*, which illustrates how subliminal information is processed within the ventral stream. More detailed information on the ventral stream is provided in Section 1.4.1.

20. This scenario is based on the findings identified in the experimentation published by M.L. Smith (2012).

Figure 1.6:   An example picture for assessing preconscious awareness

If that person is then asked to explain why they have those feelings, without looking at the picture again, they would then discuss the different aspects of what they had seen. This appraisal would be achieved by elevating individual preconscious percepts into conscious awareness.

This move from preconsciousness to consciousness is important.   As mentioned earlier, implicit learning can be achieved through preconscious awareness (Jiang & Chun, 2001).   However, the duration of retention for implicitly learnt material tends be shorter than information gained through explicit learning (Scott, Minati, Dienes, Critchley, & Seth, 2011).   The effective presentation of material should therefore be aiming to support the viewer to elevate key information into conscious awareness.

1.2.3.1.7. Conscious Awareness

CONSCIOUS
AWARENESS

Conscious awareness (CA) is defined as the level at which an individual becomes conscious of a percept or representation.   In other words, this is the level of awareness at which a person can report on their perceptions (Dehaene, et al., 2006).

CA can comprise a mixture of memory, and the momentary awareness of the environment (Tulving, 2002).   This combination allows higher order processing *(visual cognition)* to be implemented within the framework of subjective experience (Lau & Rosenthal, 2011).

Additionally, conscious awareness is typically the minimum level needed to implement context relevant (Gawronski & Walther, 2012) volitional activities (Hassin, et al., 2009).

1.2.3.1.8. Active Attention

Active attention[21] refers to the volitional application of attentive processes to specific items within the visual field (Bradley, 1902).   In other words, this level of awareness reflects the situation in which mostly endogenous factors drive attention to focus on specific percepts or representations (Dayan, et al., 2000).   This type of active attention also typically triggers overt attentional shifts (Berman & Colby, 2009).   Such focus is important, because it helps to resolve competition between the percepts and representations being managed within working memory, so the brain can consciously focus on the most important visual aspects (Serences & Yantis, 2006).

1.2.3.2. *Changing the Levels of Awareness*

The attention processes *(as described in Section 1.2.2)* are the drivers which move elements of working memory through differing levels of awareness (Shin, Stolte, & Chong, 2009), so the information can be managed and manipulated (Baddeley, 2000). For instance the following scenarios explain how the level of awareness can change within the continuum, through combinations of bottom-up and top-down attentional drivers:

* ***Bottom-up can influence Top-down.***   Stimuli could initially be received and managed using bottom-up processes at the subliminal level.   If this stimulus is sufficiently strong, the percept or representation could then influence top-down cognition, even if the person is not initially aware of the visual information (Rahnev, et al., 2012).

* ***Bottom-up can drive Top-down.***   A new visual stimulus *(e.g. the appearance of a highly salient object)* can capture active attention immediately (Chua, 2009; Folk, Remington, & Wu, 2009).   In other words, if the bottom-up processing is sufficiently strong, it can immediately trigger active attention which applies top-down processing.

* ***Top-Down can Suppress Bottom-up***.   Alternatively, the viewer may be utilising active attention with top-down processing, to focus attention on a specific task. In these circumstances the bottom-up processing of other percepts is likely to be suppressed (Desimone, 2007; Kida, et al., 2006; Theeuwes & Chen, 2005), which means awareness of other items within the visual field is likely to remain at the unconscious or preconscious levels.

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21.   Many publications refer to this as 'selective attention' *(e.g. Ban, Lee, & Lee (2008); Dayan, Kakade, & Montague (2000) and Schupp et al. (2007))*.   Others, such as Wu (2011), refer to this as 'action awareness', which is contained within the awareness continuum.   Alternatively, Kida, et al. (2006) refer to active and passive attention.   It is this nomenclature, combined with the action awareness concept, which formed the core within the model that was applied in this thesis.   However, it also takes into account selective attention, and the 'focal awareness' model utilised by Merker (2007). Additionally, it allows this model to avoid the ambiguity generated by the implications of covert selective attention, which are described in papers such as Serences & Yantis (2006).

These changes in the level of awareness, and the neural activation through top-down and bottom-up processes, can be mapped to the brain's physiology as illustrated in Figure 1.7[22].
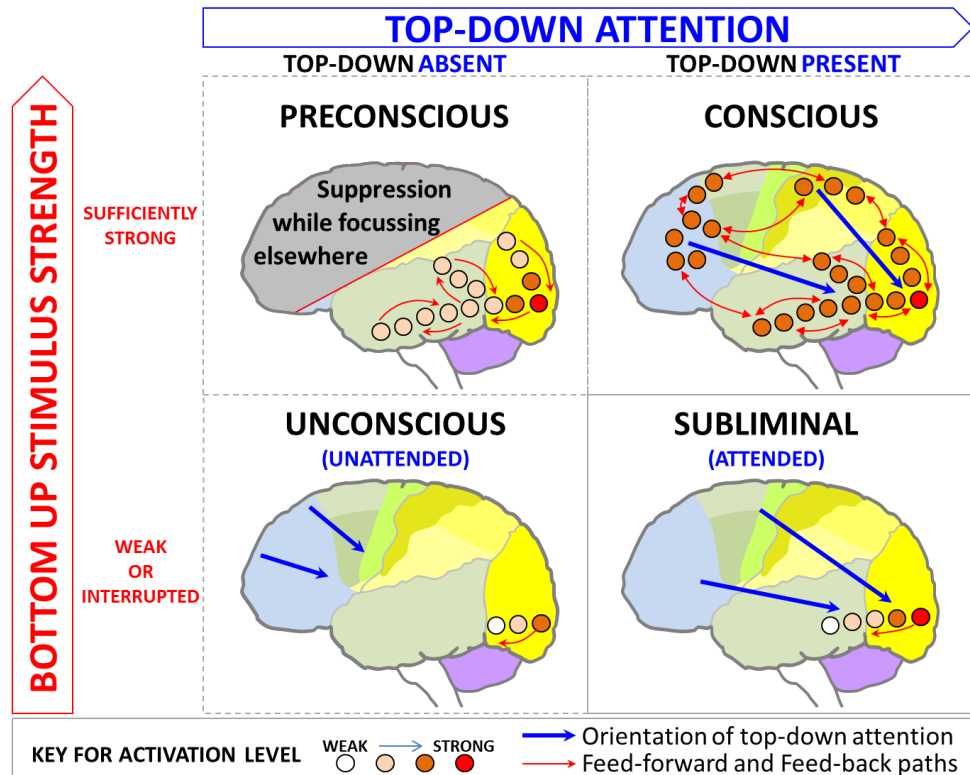
Figure 1.7:   Top-down and Bottom-up processes and the effect on awareness

As shown in this diagram, weak or interrupted bottom-up stimulus produces Unconscious Unattended or Subliminal levels of awareness.   As the strength of the bottom-up stimulus increases, preconscious awareness can be generated without the presence of top-down attention drivers.   Conscious levels of awareness are created when the bottom-up stimuli are sufficiently strong, and top-down processing is also applied.

The neural activations associated with each of these levels of awareness can be characterised as follows[23]:

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22.   This diagram is based on Figure 1 in Dehaene, et al. (2006, p. 206).   The orientation of the diagram has been amended to align with the bottom-up and top-down diagrammatic paradigm used in this appendix.   Additionally, the text has been removed from the diagram to minimise visual distractions, and these related issues are discussed below. Finally, a nomenclature change has been applied within the diagram.   Dehaene et al. (2006) uses the term 'Subliminal (unattended)'.   In Figure 1.7, this has been modified to better align with the awareness continuum model *(Figure 1.5)*, because some level of attention is required to achieve the subliminal effects referred to in other papers *(e.g. Hsieh, Colas, & Kanwisher (2011); Rahnev, et al. (2012))*.   Therefore, the term 'Unconscious (unattended)' has been used to replace Subliminal (unattended).

23.   This information is drawn from Dehaene, et al. (2006) unless specified otherwise.

- ***Unconscious Unattended.*** At this level of awareness there is very little activation within the visual cortex, and the stimulation is already very weak by the time it is being processed within the extrastriate areas *(see Section 1.3.5)*. In this situation, the stimuli typically decay quickly *(within about 1-2 seconds)*, so the percept cannot be recalled after that time.
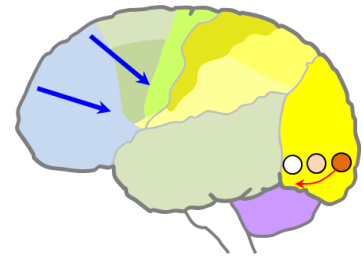
- ***Subliminal (Attended).*** In subliminal activation, the percepts are processed more extensively within the visual cortex, and begin to stimulate the ventral stream *(see Section 1.4.1)* for processing within the temporal lobe. However, the depth of processing is dependent on the strength of the stimuli, and the amount of bottom-up and top-down attention that are applied. This type of stimulation is short lived, and it is therefore impossible to report on the stimuli through conscious awareness. However, as discussed in Section 1.2.3.1.5, stimulation of this type can generate neural priming, which can create subconscious impressions, or higher levels of awareness.
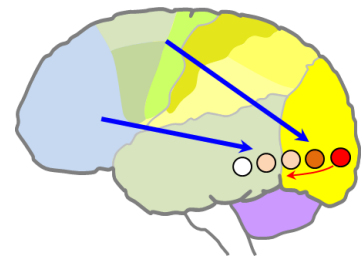
- ***Preconscious.*** When the bottom-up stimuli is sufficiently strong, the viewer can become preconsciously aware of the percept. In this state of awareness significant activation is achieved within the occipital lobe and the ventral stream. Additionally, feed-forward[24] and feed-back is implemented with the interbrain and midbrain regions *(see Sections 1.3.3 and 1.3.4)* to stimulate attentional control. However, activation of the streams that transfer the percepts and representations to the frontal lobes *(see Section 1.4.3)* for higher level cognition are suppressed, while attention is focussed elsewhere. This means that preconscious percepts can only be processed consciously once the brain changes the focus of attention, and this is normally achieved by applying top-down drivers. To assist in this transition, preconscious primers appear to feed forward very quickly through the dorsal stream *(see Sections 1.4.2)* to trigger the elevation of awareness for that percept (Bishop, 2008). If the triggered top-down drivers are sufficiently strong this will generate conscious awareness.
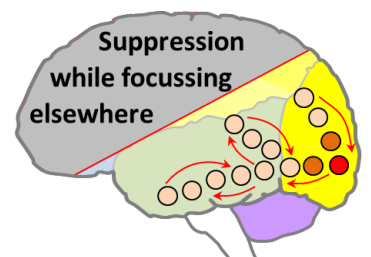
- ***Conscious.*** Once the percept is being handled consciously it is also processed through the dorsal stream and within the frontal lobes. In these situations, significant feed-back and feed-forward systems are implemented to shape the focus of attention. For example, an exogenous percept *(e.g. a highly salient object)* will be processed within the

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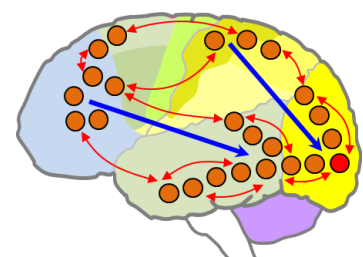
24. See Section 1.4.4 for a discussion of feed-forward and feed-back systems.

frontal lobe, which will provide feedback that shapes where the eye will look, so active attention can be focussed on the salient object (Kanwisher & Wojciulik, 2000; Lamme, 2003).

Each of the key elements of the physiology utilised to support the attentional processes, and these levels of awareness, are described in the following sections of this appendix.

1.3.   Perception System Elements

1.3.1.   The Eye

1.3.1.1.   General Description

In simplistic terms the eye acts as the camera through which visual information is captured.   The key elements of the eye covered in this paper, are those specified by Graven & Browne (2008).   They are the cornea, lens, iris, and retina. These elements of the physiology, and others that will be discussed later in this appendix, are illustrated in Figure 1.8.
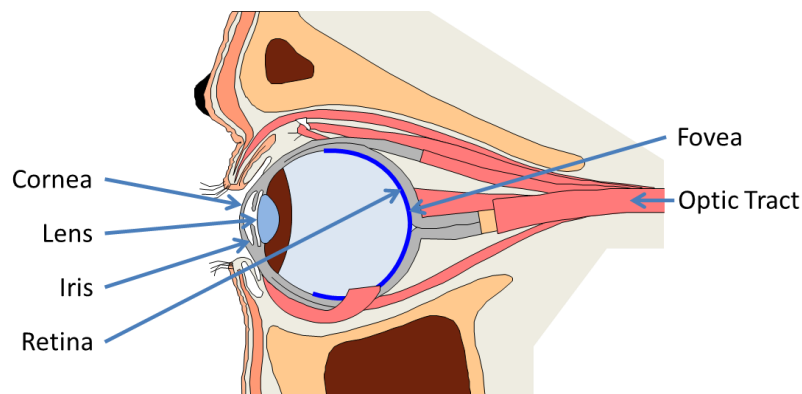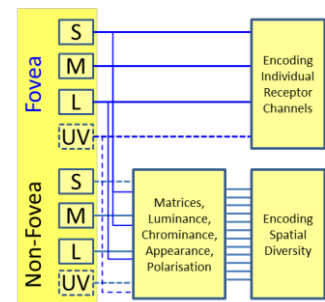
Figure 1.8:   Key aspects of the physiology within the eye

The first three of these physiological elements shape the way the light reaching the eye is controlled.   These elements are:

- ***The Cornea.***   The cornea is the opaque layer covering the lens, which allows light to enter the eye, and actually has more effect on focus than the lens itself (Fulton, 2003a, p. 14).

- ***The Iris.***   The iris is autonomously controlled to dilate or contract the size of the pupil through which light enters the eye.   It does this to balance two competing factors.   Firstly, a small pupil 'increases the range of distances at which objects are in focus.   With a wide-open pupil, the range is relatively small and details are harder to discern.' (Feldman, 2005, p. 106).   In other words, if the pupil is dilated, more light enters the eye, but it can be harder to focus. Alternatively, if too much light enters the eye, this can over-energise the photoreceptor cells within the retina, and reduce visual acuity (Fulton, 2003a).

- ***The Lens.*** Muscles around the lens change its shape *(through squeezing or stretching)* to modify the focus of the eye, and therefore the image reaching the retina (Sekuler, 1977).

- ***The Retina***. The retina covers most of the inside structure of the eye (Fulton, 2008), and it is 'made up of light-sensitive receptor cells, and the neural cells that are connected to them' (Garrett, 2003, p. 253). Because of the importance of the retina, it is discussed in more detail in the following section.

1.3.1.2. The Retina

The key element of the eye *(in terms of this thesis)* is the retina, because it 'carries out the first steps in the conversion of light into vision' (Neves & Lagnado, 1999, p. 674). There are five pertinent types of cell within the retina, and these are illustrated in Figure 1.9[25].
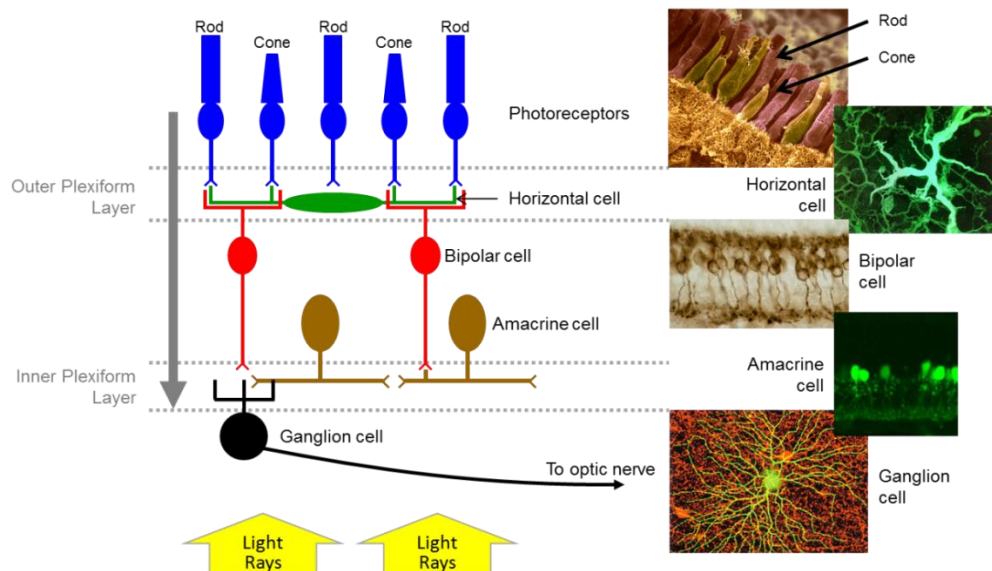
Figure 1.9: A simplified model of the cells within the Retina

These cells are described in the following subsections.

1.3.1.2.1. Photoreceptor Cells

Types of Cells

The human eye typically contains about six million cone cells and around 120

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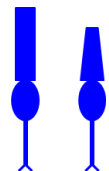
25. This basic diagram reflects information provided in Neves & Lagnado (1999) and Garrett (2003). Graphics used to illustrate the physiology have been sourced as follows:
Rods and Cones: http://www.sciencephoto.com/media/308896/enlarge;
Horizontal Cell:http://wellcometrust.wordpress.com/2011/10/25/wellcome-to-the-cell-matrix/; Bipolar Cell: http://bmcdb.wordpress.com/2012/05/10/;
Amacrine cell: http://viperlib.york.ac.uk/categories/75-retina;
Ganglion Cell: http://www.olympusfluoview.com/gallery/retinaganglionsmall.html.

million rod cells (Garrett, 2003).   These types of cell can be classified as follows:

- ***Cone Cells.***   As explained by Feldman (2005) the cone cells support high quality perception of colour, and work best in relatively bright light.   There are three main types of cone cell, which respond maximally to different wavelengths of light, as illustrated in Figure 1.10[26].   These photoreceptor cells are classified as follows, in accordance to the wavelengths of light that stimulate them (Hunt, 2004):

  - ➢ ***Short (S) Wave***.   The S cones respond best to so called 'cool'[27] colours, like purple *(light wavelengths of about 420-440 nanometres (nm))* or blues. This type is commonly described as being a 'Blue' cone.

  - ➢ ***Medium (M) Wave***.   The M cones are best stimulated by light of a yellowish-green colour (534-545 nm), and they are commonly described as 'Green' cones.

  - ➢ ***Long (L) Wave.***   L cones respond best to yellow/red light (564-580 nm)[28], and they are classified as 'Red' cones.
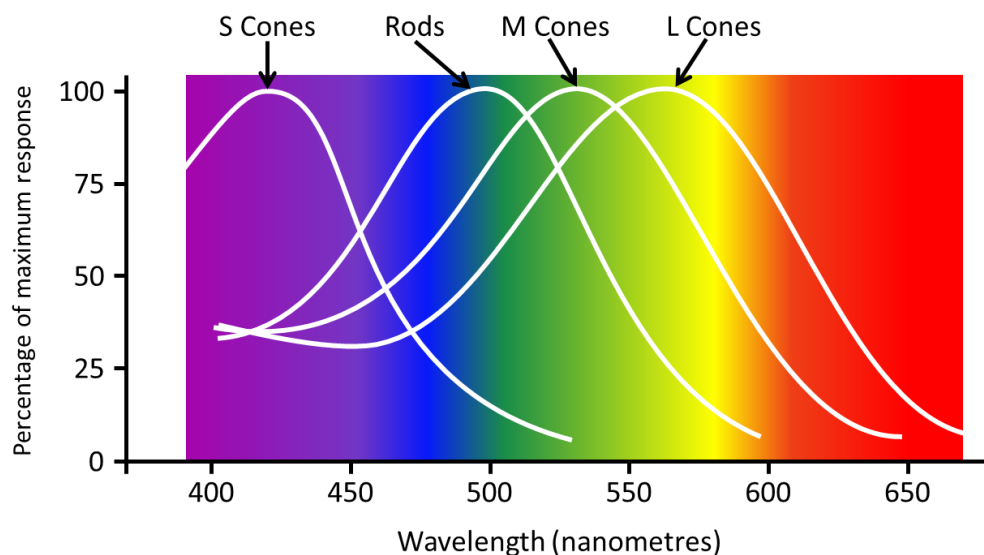
Figure 1.10:   Relative absorption of light for S, M, L Cones and Rods

26.   Developed from information provided in Bowmaker & Dartnall (1980) and Figure 9.11 in Garrett (2003, p. 262).

27.   See Section 3.4.1 in Volume 1 for a more detailed description of the concept of cool colours.

28.   Fulton (2003) also argues that human vision is tetrachromatic, which means that the photoreceptors are sensitive not only to the S, M, and L wavelength, which are typically considered as the visible spectrum, but also to ultraviolet and other shorter and longer wavelength regions of the wider spectrum.   However, this capability in humans is suppressed by the eye's lens and cornea.   Therefore, for the sake of this paper, the UV spectrum is included in Figure 1.1 for correctness, but the more widely used trichromatic vision model will be utilised, as the exclusion of UV does not directly affect the model, hypotheses, or findings.

- ***Rod Cells.*** The rod cells are much more sensitive to light, and therefore work better in lower luminance than cone cells (Mustafi, Engel, & Palczewski, 2009). However, they provide lower visual acuity, and are slower to respond to changes in light (Fulton, 2003a). These cells are most sensitive to bluish-green colours (498 nm) and are relatively insensitive to light wavelengths above 640 nm (red) (Brown & Wald, 1964).

The Influence of Luminance on the Retina

The photoreceptor cells are also stimulated in different ways by the level of luminance *(the intensity of the light)* reaching the retina (Fulton, 2008). Figure 1.11 gives an overview of the different luminance levels, and their effect on the various types of photoreceptor cells[29].
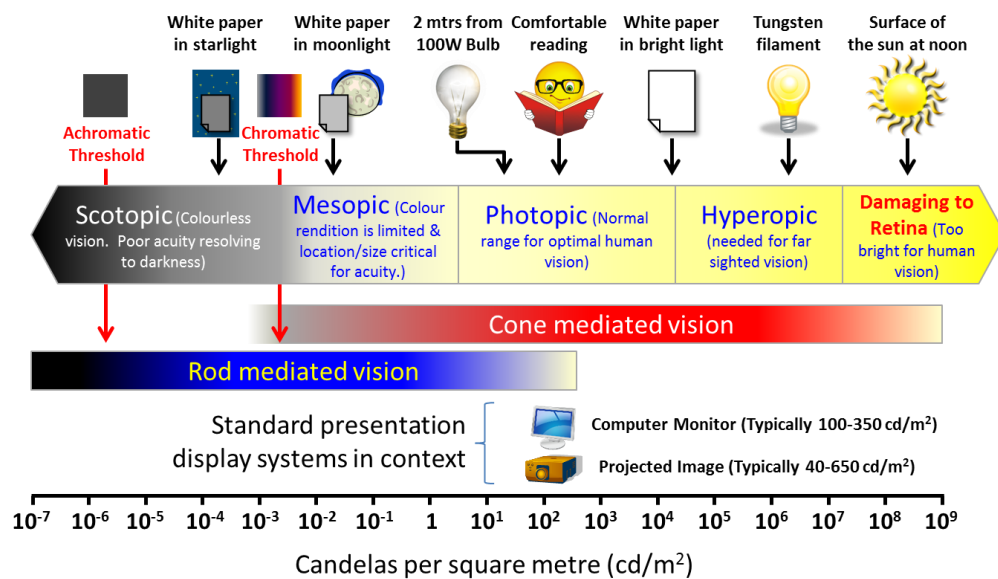
Figure 1.11:   Luminance Levels and Rod and Cone Mediation

This diagram uses a logarithmic scale, measured in candelas per square metre (cd/m^2). Zones related to the level of luminosity have been illustrated, which range from Scotopic *(no light to very low light vision)*, to Hyperopic *(high levels of luminosity needed for far sighted vision)*. In terms of this thesis, the key range relates to Photopic luminance *(similar to normal daylight vision)*. However, some aspects will also refer to the Mesopic range *(lower luminance, where colour rendition is limited and acuity is affected)*, due to the display mechanisms and techniques that are utilised to present some visual information *(e.g. using projectors or computer monitors to deliver PowerPoint® presentations)*. Some practical examples of each of these levels of luminance are provided in the top row of the diagram. Additionally, the range of luminance levels provided by most computer monitors and projectors are contextualised towards the bottom of the diagram.

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29.   This model was developed by the author from information provided in Fulton (2007, p. 168); Schubert (2006, p. 276); Fotios & Cheal (2011); Hayashi (2006); Shin, Yaguchi & Shoioiri (2004); Stojmenovik (2008) and Read (2012).

Figure 1.11 also illustrates how the luminance levels affect the different photoreceptors in the retina. As shown in this diagram, the cones are the critical mediator for vision through the Photopic range. However, as the luminance falls into the Mesopic range the cone cells become less effective, and colour constancy and general acuity generated by the cones becomes poorer. Once the luminance levels fall below the chromatic threshold the cones can no longer accurately generate visual input (Wilson, 1969).

Because the rod cells are more sensitive to light, they mediate vision from around the middle of the Photopic range, and remain activated down into the Scotopic levels of luminance. In people with normal vision, these cells can generate visual information down to the achromatic[30] threshold. Therefore, in the zone marked as comfortable reading within Figure 1.11, both the cones and rods are being stimulated to provide visual information. However, at this level of illumination, the cones tend to be much more important. As the level of luminance falls, the rods become more important to visualisation.

Cell Distribution

The rod and cone cells are not evenly distributed across the retina (Sekuler, 1977), and their general distribution is illustrated in Figure 1.12[31].

Figure 1.12: Distribution of Rod and Cone cells within the Retina

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30. The achromatic threshold reflects the smallest amount of luminance that can be detected by a dark adapted eye (which equates to about 10^{-6} cd/m^2). All colours therefore lose their hue as this level of luminance is approached (Bouman & Walraven, 1972).

31. Adapted from Figure 2 in Mustafi, et al. (2009, p. 292) and includes zone information provided in Kuchenbecker, Sahay, Tait, Neitz, & Neitz (2008), and Fulton (2011).

The grey zone reflects the optic disk, which is an 'area on the surface of the retina where the optic nerve[32] leaves the eye.' (Fulton, 2011, p. 44). Because there are no photoreceptor cells in this region, a blind spot is created at this point on the retina (Fulton, 2011). This diagram also demarcates the retina into three key zones, which are known as the fovea, parafovea, and peripheral regions. As shown in Figure 1.12, the fovea mostly comprises closely packed cone cells, which provide high quality colour vision. Outside the foveal region there are relatively few cone cells, in relation to the number of rod cells. Just as importantly, the density of the photoreceptor cells decreases markedly, further from the fovea.

Other key aspects related to the general distribution of these photoreceptor cells within the retina are illustrated in Figure 1.13[33].
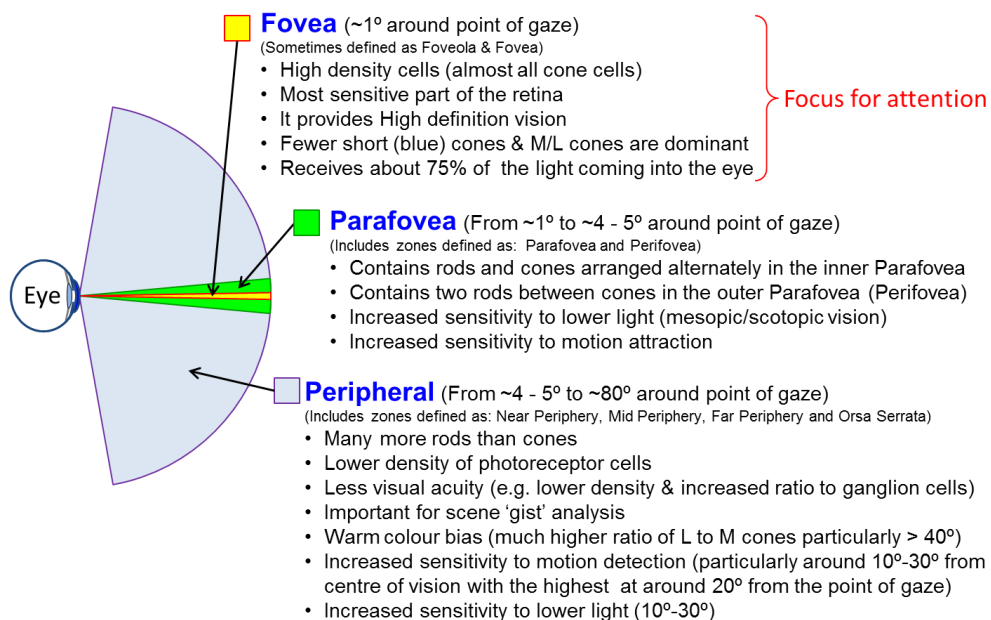
Figure 1.13: Additional key aspects related to the distribution of Photoreceptor cells

Within this general distribution, the different types of cone (S, M and L) and rod photoreceptor cells are distributed within a mosaic, which is not uniformly dispersed, and this is particularly true outside the fovea. This type of distribution can cause significant 'fluctuations in the colour appearance' (Roorda & Williams, 1999, pp. 521-522) within different parts of the visual field. These uneven mosaics of photoreceptor cells are also grouped into receptive fields, because of their linkage to individual, or groups of, ganglion cells.

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32. See Section 1.3.2 for information on the optic nerves.

33. This model was developed by the author from information provided in Fulton (2011); Kuchenbecker, Sahay, Tait, Neitz, & Neitz (2008); Hofer, Carroll, Neitz, Neitz, & Williams (2005); Larson & Loschky (2009); Sekuler (1977); Roorda & Williams (1999) and Garrett (2003).

Effects on Visual Acuity

Because of this distribution of rod and cone cells, and the way in which the receptive fields adaptively link to different ganglion cells *(see Section 1.3.1.2.2 below)*, the acuity within the visual field varies markedly. Figure 1.14 illustrates the reduction in visual resolution *(in terms of cycles per degree)* at varying eccentricities from the centre of gaze[34].
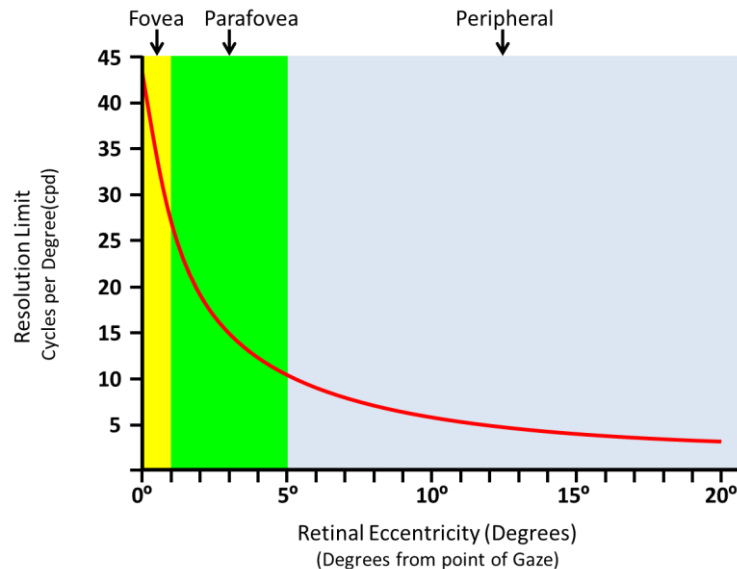
Figure 1.14:   Resolution of Visual Acuity in Terms of the Zones in the Retina

As illustrated in this graph, the visual resolution falls rapidly outside of the fovea, and is relatively poor within peripheral vision. The fovea and parafovea are therefore critical in developing high quality visual information. However, as pointed out by Larson & Loschky (2009), the peripheral vision also has an important role to play in developing scene awareness.

1.3.1.2.2. Horizontal Cells, Bipolar Cells and Amacrine Cells

The receptive fields are connected to the ganglion cells through the horizontal, bipolar and amacrine cells. However, rather than just providing a conduit between the photoreceptors and the ganglion, these intermediate cells provide a 'gain control' (Neves & Lagnado, 1999, p. 676) through autonomous adaptation. For example, in lower light, the receptive field for ganglions can increase due to chemical changes within horizontal and bipolar cells, which means that vision can be improved in lower light by creating more visual linkages within the receptive field for each ganglion, but this is also likely to provide less visual acuity (Roorda & Williams, 1999). Additionally the amacrine cells play a key role in signalling change, because they are optimised to adapt to moving stimuli (Neves & Lagnado, 1999).

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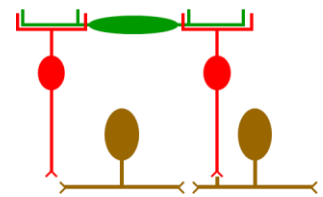
34.   This graphic has been adapted from Figure 2 in Larson & Loschky (2009, p. 2).

1.3.1.2.3. Ganglion Cells
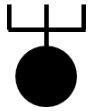
The ganglion cells receive the messages passed through from the photoreceptors and then channel these through the optic nerves.   Because of their configuration, and their use of an adaptive receptive field, the ganglion cells are typically stimulated by edges, and particularly high contrast edges and content (Neves & Lagnado, 1999).   Additionally, ganglion cells adapt over time, so their response to steady light typically decays as time passes[35].   This means that the ganglion will not send a new signal to the brain for processing unless the information within the receptive field changes significantly (Amthor, Tootle, & Gawne, 2005).

Colour perception is also achieved in some ganglion cells (Goldstein, 2002), by linking inputs from groups of colour opponent photoreceptor cells within the associated receptive field (Garrett, 2003; Murray, Parry, & Mckeefry, 2006).   For example, Figure 1.15 illustrates this colour opponent principle for cone cells[36].

| L | M | M | L | L/M | S | S | L/M |
| Cones | Cones | Cones | Cones | Cones | Cones | Cones | Cones |
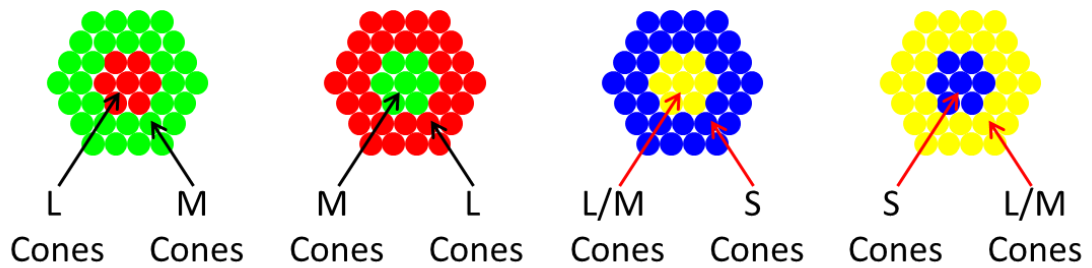
Figure 1.15:   Colour Opponent Groupings in Photoreceptor Cells

As shown in this diagram the L (Red) and M (Green) cones are typically linked in common receptor fields.   The S (Blue) cones are linked with yellow as the opponent colour.   This perception of yellow is created by linking L (Red) and M (Green) inputs within the ganglion, as illustrated in Figure 1.16[37].

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35.   Such changes appear to begin within as little as 125 milliseconds (ms), as the ganglion adjust to the mean luminance, so contrast can be detected more readily (Freeman, Graña, & Passaglia, 2010).   However, longer periods in stable lighting conditions help to set the mean rating widely across the retina, and this affect appears to become highly significant within about 3 seconds, in Photopic conditions (Freeman, et al., 2010).

36.   Adapted from Figure 9.12 in Garrett (2003, p. 263).

37.   This model was developed by the author, by merging information from Figure 9.10 in Garrett (2003, p. 261) and including information from Fulton (2009).
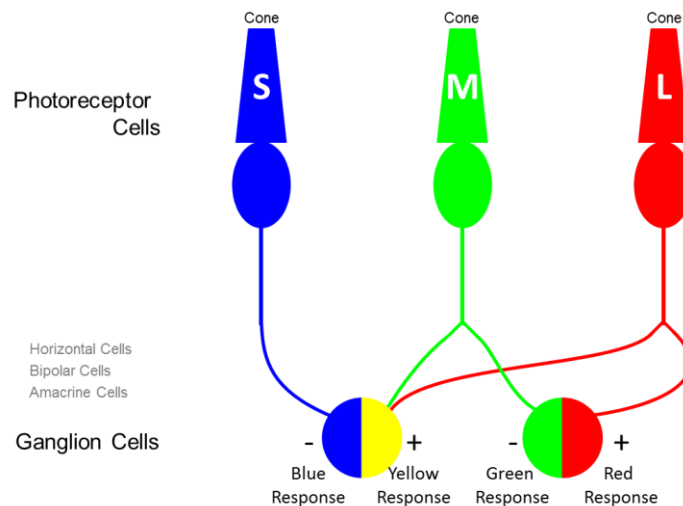
Figure 1.16:   Interconnection of Ganglion for Colour Development

Therefore, as illustrated in Figure 1.16, colour perception from the cone cells is created by merging inputs from different photoreceptors in the receptive field, to create three base colour groups (Red, Green, Blue), and the yellow colour group, which is based on merging input from Red (L) and Green (M) cone cells.   Rod cell inputs can also be combined with cone cell input (Neves & Lagnado, 1999), or can feed directly to specific ganglion cells (Stabell & Stabell, 1996).   Because of this approach within the receptive fields, many millions of colour combinations can be processed.   As an example, within the standard Red, Green, Blue (RGB) model utilised within most computer monitors, a total of 16,777,216 colour combinations can be created by mixing:

•   the three basic colours that align to the S (Blue), M (Green), and L (Red) cones, and the rods (Blue) sensitivities (Lee, Smith, Pokorny, & Kremers, 1997); and

•   different levels of luminance.

However, it appears that the normal human eye can only detect differentiation for around two million different colours (Marín-Franch & Foster, 2010).

1.3.2.   The Optic Nerves

OPTIC NERVE
Transmission
ATTENTION
AWARENESS

Visual stimulus information generated by the ganglion cells is transferred to the interbrain region through the optic nerves.   As illustrated in Figure 1.2, the information from the retina is bifurcated at the optic chiasm, so the left side of the brain conjoins the information from the temporal side *(the side away from the nose)* of the retina in the left eye, and the nasal region *(on the side of the nose)* from the right eye.   The right side of the brain then handles the nasal region of the left eye, and the temporal region of the right eye.   This physiology assists in the development of binocular vision[38] (Feldman, 2005; Sekuler, 1977), which supports stereopsis[39].

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38.   Binocular vision *(also sometimes called stereoscopic vision)* refers to the linkage of visual information obtained from both eyes (Fulton, 2011).

Several different models are utilised to explain the delineation of information passed through the optic nerves. For simplicity within this thesis, only one model will be utilised, and this relates to the provision of three pathways, which are described as parvocellular, magnocellular and koniocellular. As pointed out by Cheong, Tailby, Martin, Levitt, & Solomon (2011, p. 1) 'these parallel visual pathways not only carry different kinds of visual signals but also contribute differentially to brain circuits'. These pathways are broadly outlined in the following subsections.

1.3.2.1. Parvocellular

The parvocellular (PC) channel predominantly receives input from M (Green) and L (Red) cones in Photopic conditions (Shapley & Hawken, 2011). However, as the luminance is reduced *(and particularly within the Mesopic range)*, this channel also receives signals from the rods (Cao, et al., 2008). Key characteristics of this channel are as follows:

• it provides high levels of visual acuity (Cao, et al., 2008; Lee, et al., 1997) with small receptor fields being managed by this channel (Chica & Christie, 2009);

• it is highly receptive to chromatic *(colour)* changes and contrasts, particularly within the Red/Green (L/M) ranges (Martin, 2004);

• it is less sensitive than the magnocellular channel to changes in the levels of luminance within the Photopic range, (Peterson, Belopolsky, & Kramer, 2003; Skottun & Skoyles, 2006; Szmajda, Grunert, & Martin, 2008); and

• it is relatively slow to react to temporal changes within the visual field (Hong & Blake, 2009; Peterson, et al., 2003), so it is less able to support motion tracking, and even appears to have a moderating or inhibitory effect on motion tracking, in the other channels (Chica & Christie, 2009; Martin, 2004).

Because of these attributes, the parvocellular channel is thought to provide the high quality vision needed to support the viewer's attentional focus (Skottun & Skoyles, 2006). Additionally, the parvocellular pathway can be delineated further, in terms of the areas within the visual cortex *(in the occipital lobe)*, which this channel of information predominantly feeds (Allen, Smith, Lien, Kaut, & Canfield, 2009; Chica & Christie, 2009). These are known as the Blob and Interblob feeds, because of the physiology of the cells being stimulated within the visual cortex within the occipital lobes. The Blob feed supports higher quality spectral composition *(e.g. more sensitive to changes in colour and luminance)*, and the Interblob sub-channel is optimised to manage edges and orientations (Allen, et al., 2009).

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39. Stereopsis relates to the process of discerning depth or distance by merging the information generated through binocular vision (Lee & Bingham, 2010; Ponce & Born, 2008). For example, at shorter distances the determination of distance is achieved by assessing the parallax differences between the two eyes, whereas at longer distances apparent motion and perspective are utilised to assess range (Feldman, 2005; Fulton, 2011).

1.3.2.2. Magnocellular

In Photopic lighting conditions, the magnocellular channel also receives information from the M (Green) and L (Red) cone cells (Cao, et al., 2008)[40].   However, as the level of luminance falls into the Mesopic range, this channel also receives stimuli from the rods (Lee, et al., 1997).   Although this channel is receiving the information from the same types of photoreceptor cells as those used in the parvocellular pathway, it handles this stimuli very differently.   The magnocellular pathway can therefore be characterised as channelling visual information as follows:

- it's conductance of the visual information is much faster than the parvocellular pathway (Allen, et al., 2009);

- it is sensitive to motion (Lambert, Wells, & Kean, 2003; Peterson, et al., 2003) and this channel appears to contribute significantly to motion perception and tracking (Seno, Sunaga, & Ito, 2010);

- it provides relatively low levels of visual acuity, with moderately low spatial frequencies in relation to the parvocellular path (Schutz, et al., 2011), and relatively large receptor fields associated with this channel (Martin, 2004; Szmajda, et al., 2008), which means that it appears to be better adapted to managing form rather than detail (Breitmeyer, Koc, Ogmen, & Ziegler, 2008);

- this channel responds significantly to changes in luminance levels (Hong & Blake, 2009); and

- it is relatively insensitive to colour, but may be desensitised by long (L) wave (Red) colours (Seno, et al., 2010), which has implications that are discussed in Section 3.2.3 in Volume 1 of this thesis.

As this channel provides rapid response to changing stimuli, but lower quality vision, this channel has been predominantly linked to the provision of general awareness for objects, their context, and movement within the environment (Allen, et al., 2009).

1.3.2.3. Koniocellular

The koniocellular pathway is the least understood of the three (Madary, 2011). However, it appears that it receives information from the S (Blue) cones (Roy et al., 2009), and also from rod cells in lower light conditions *(e.g. Mesopic luminance range)* (Cao, et al., 2008).   The koniocellular channel appears to support the communication of the following information:

- it may be supporting the mediation and transmission of Blue/Yellow colour information (Lee, et al., 1997; Martin, 2004) to round out the four colour chrominance model illustrated in Figure 1.16, when conjoined with the Red/Green (L/M) light stimuli;

- this channel is also linked to the transfer of coherent motion information (Skottun & Skoyles, 2006);

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40. It is also possible that this pathway receives inputs from the S (Blue) cones, but the evidence in this respect is not conclusive (Martin, 2004).

- it appears to pass information through to key areas of the cortex faster than the other channels (Morand et al., 2000); and

- the acuity of information transferred within this channel is considered relatively low *(in relation to the content within the parvocellular pathway)*, because it mostly appears to transmit information from wide receptor fields within the retina (Szmajda, et al., 2008).

Therefore, the koniocellular pathway supports the rapid transfer of relatively low acuity information. It has therefore been postulated that the koniocellular information supports the implementation of divided attention[41], but experimentation has not proven this empirically (Maeda, Nagy, & Watamaniuk, 2009).

1.3.2.4. Synopsis

Table 1.1[42] provides a synopsis of the characteristics of the three channels.

Table 1.1: Characteristics of the pathways and the information they appear to conduct

Characteristics	Magnocellular (MC)	Parvocellular (PC)		Koniocellular (KC)
		Interblob	Blob	
Spatial frequency sensitivity *(Level of acuity)*	Low (This also displays characteristics of surround suppression)	Highest	High	Low
Sensitive to luminance variation	Yes (Responds better to low contrast stimuli and have relatively long latencies)	Less sensitive than Blob	Yes (within certain ranges)	Less sensitive than MC channel and has long latencies.
Sensitivity to hue variation	No (lacks colour selectivity)	Yes (but not as sensitive as Blob)	Yes (particularly colour contrast)	Yes (Particularly Blue/Yellow)
Sensitivity to movement	High	Low	Low	High
Conduction Rate (speed of processing)	Fast	Slower	Slower	Very fast

41. Divided attention refers to the ability to attend to multiple stimuli within one or more modality (Loose, Kaufmann, Auer, & Lange, 2003). For instance, this refers to situations in which a person can attend to aural and visual information at the same time, or pay attention to more than one object in the field of view (Mcmains & Somers, 2005).

42. This table was developed by the author, by consolidating information provided in Allen, et al. (2009, pp. 282, 291); Morand, et al. (2000); Skottun & Skoyles (2006); Hong & Blake (2009); Lambert, et al. (2003); Peterson, et al. (2003) ; Martin (2004); Lee, et al. (1997); Wiesel & Hubel (1966); Pammer & Lovegrove (2001); Roy, et al. (2009); Shipp (1995); Kandel, Schwartz & Jessell (2000); Briggs & Usrey (2011) and Saalmann & Kastner (2011).

Characteristics	Magnocellular (MC)	Parvocellular (PC)		Koniocellular (KC)
		Interblob	Blob	
Processing	Motion, form, depth and luminance	Colour, texture & patterns in fine detail	Brightness, hue, texture & shape information	Colour (B/Y) and motion

1.3.3. Interbrain Region

1.3.3.1. Thalamus

The thalamus acts as a pivotal driver and modulator for the neuronal transfer of information within the afferent and efferent systems (Sherman & Guillery, 2000). To achieve this objective it contains a group of interconnected nuclei, which support multi-modal interaction (Glimcher & Lau, 2005). For the purpose of this thesis only the key elements of the thalamus that relate directly to visual processing are discussed in the following subsections.

1.3.3.1.1. Lateral Geniculate Nuclei

The Lateral Geniculate Nuclei (LGN) are the primary relay nucleus for afferent visual signals (Wurtz, et al., 2011). However, as specified by Saalmann & Kastner (2011) the LGN are more than just a relay, and receive modulatory information from other areas of the brain, which they appear to use to moderate visual information processing *(which has ramifications for attention suppression)*.

The basic physiology of the LGN, the key areas to which they feed information, and the areas from which they appear to receive modulatory information, are illustrated in Figure 1.17[43].

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43. This graphic was developed by the author from information provided in Saalmann & Kastner (2011); Martin (2004); Graven & Browne (2008); Briggs & Usrey (2011) and Wurtz et al. (2011).
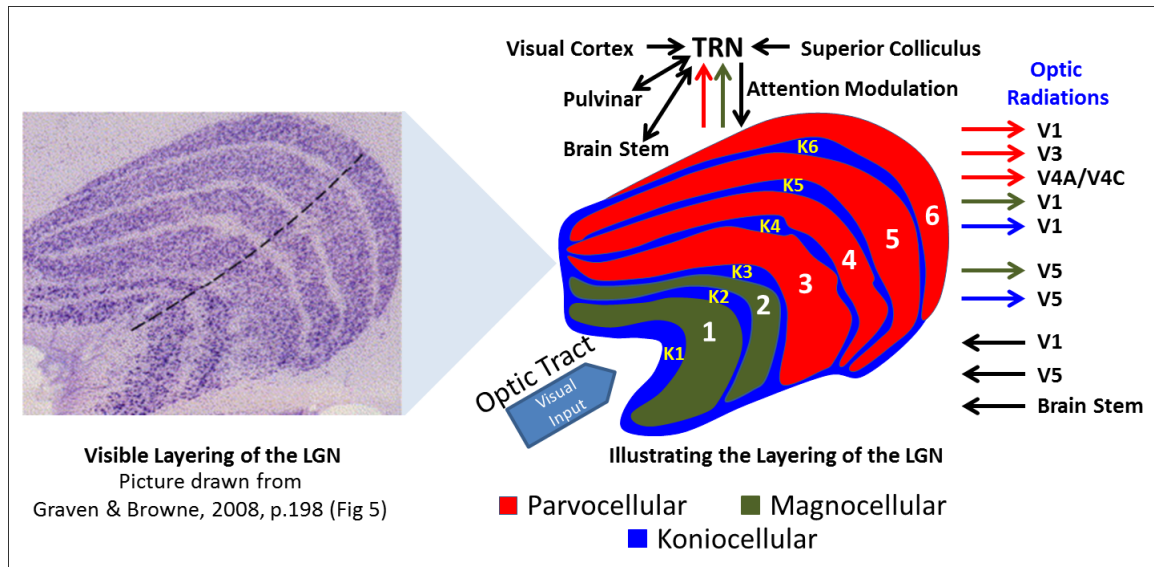
Figure 1.17:   Lateral Geniculate Nucleus

As shown in this diagram, there are six primary layers with six koniocellular layers interspersed between them.   The first two primary layers manage input from the magnocellular pathway.   One layer within the magnocellular region is allocated to the input from each eye.   The top four primary layers handle information from the parvocellular pathway, so it contains much more processing capacity than the magnocellular layers.

Visual stimuli information received from the optic nerves appears to be processed within these layers within a separated retinotopic[44] format (Rowland & Kentros, 2008; Saalmann & Kastner, 2011).   The LGN then appears to conduct spatial-frequency filtering *(rather than feature analysis)* on this visual feed (Allen, et al., 2009) prior to:

• forwarding the stimuli information to the visual cortex *(predominantly through the optic radiations)* (Fulton, 2003a; Saalmann & Kastner, 2011; Wurtz, et al., 2011); and

• providing visual feeds to the TRN and Pulvinar (Saalmann & Kastner, 2011) as a part of the visual moderation process, and to feed the efferent systems.

Just as importantly, there appears to be clear feed-back loops from the visual cortex *(e.g. V1 and V5)*, the TRN, and the brain stem *(pedunculopontine tegmentum and parabigeminal nuclei)* (Briggs & Usrey, 2011; Saalmann & Kastner, 2011).   This feedback is likely to modulate attention and perception, so the visual system can focus very early in the processing on important aspects within the environment (Saalmann & Kastner, 2011).   For example, Fulton (2003a) has postulated that this early processing is also critical for generating 'alarm' mode signals, within an efferent loop which draws the human eye to rapidly focus on important items within the visual field.

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44.   Retinotopic means that the information is organised topographically in a way that is directly relatable to the geometry of the retina's perception of object space (Fulton, 2011).

1.3.3.1.2. Thalamic Reticular Nucleus

TRN

The Thalamic Reticular Nucleus (TRN) 'forms a thin shell of neurons that cover the lateral and anterior surface of the dorsal thalamus' (Saalmann & Kastner, 2011, p. 209).   The TRN receives signals from all of the sensory modalities (Fulton, 2004; Mcalonan, Cavanaugh, & Wurtz, 2006), so this structure serves as a nexus for interactions between the thalamic nuclei and a variety of cortical areas (Fitzgibbon, 2006; Sherman & Guillery, 2000).   As such, it appears to play an important role in modulating single modality processing, and also providing linkages across modalities *(e.g. linking sight and sound)* (Saalmann & Kastner, 2011).

In terms of the visual modality, the TRN appears to contain 'topographically organised representations of the visual field' (Saalmann & Kastner, 2011, p. 217)   and this information is applied to influence other processing areas (Min, 2010), such as the LGN and pulvinar (Fitzgibbon, 2007; Min, 2010; Shipp, 2003).   For this reason, it is believed that the TRN influences 'selective attention by regulating thalamo-cortical information transmission' (Saalmann & Kastner, 2011, p. 217), and also appears to support important aspects of shaping attention in multi-modal communication *(e.g. matching sight and sound)* (Cavanaugh, Mcalonan, & Wurtz, 2008; Mcalonan, et al., 2006).   In addition to shaping and controlling attention, the TRN appears to fulfil the role of 'filtering irrelevant signal processing in conscious perception' (Min, 2010, p. 8).

To conduct the visual attention modulation, the TRN receives inputs from V1 *(Layer 6)*, the Superior Colliculus, the LGN (Wurtz, et al., 2011), and other related cortical areas (Min, 2010).

1.3.3.1.3. The Pulvinar

Thalamus/ Pulvinar

Although there are a range of other thalamic areas that support visual processing, this thesis will only focus on one of these, because of its importance in visual perception.   This is the pulvinar, which 'can be regarded as much farther up the visual pathway than are the LGN and TRN' (Mcalonan, et al., 2006, p. 4449), 'because it forms input-output loops almost exclusively with the cortex' (Saalmann & Kastner, 2011, p. 209).   This includes connections to both the occipital lobes, and the posterior parietal cortex *(that are both associated with vision)* (Smith, et al., 2010).   These connections provide both feed-forward and feed-back communication (Saalmann & Kastner, 2011).   For example, the pulvinar appears to send and receive information from areas V1 (Berman & Wurtz, 2011; Briggs & Usrey, 2011), and V5 (Breitmeyer, et al., 2008; Ffytche, Blom, & Catani, 2010; Zeki & Ffytche, 1998), and also the Superior Colliculus (Wurtz, et al., 2011).

In addition to providing connectivity for higher order visual processing, the pulvinar appears to play a key role in shaping visual attention, localising visual stimuli, filtering distractors, orienting responses, searching visual space, binding/segregating[45] visual information *(e.g. linking colour and shape)* (Saalmann & Kastner, 2011), managing

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45.   Binding is the process related to combining the sensory information that belongs to one object, whereas segregation is the process of disassociating information between objects (Mcgovern, Hancock, & Peirce, 2011).

aspects of salience (Fecteau & Munoz, 2006), and moving attention (Desimone & Duncan, 1995).

1.3.3.2. *Suprachiasmatic Nuclei*

Although this element is not specifically represented within Figure 1.1, the Suprachiasmatic Nuclei (SCN) are included in this discussion, because they have significant implications for the level of arousal experienced during visualised presentations.   The SCN are located on the anterior of the hypothalamus, and they are responsible for regulating the circadian rhythm[46] (Schwartz, 2002).   This cycle is moderated by the presence, or lack, of luminance reaching specialised ganglion cells in the retina (Berson, Dunn, & Takao, 2002; Moore, 2007).   For example, higher luminance received by the ganglion cells creates stimulation that is received by the SCN (Garrett, 2003).   In turn the SCN generate signals that cause arousal within the brain (Moore, 2007). On the other hand low light conditions can reinforce lower levels of arousal and induce sleepiness (Ospeck, Coffey, & Freeman, 2009).

Additionally, research conducted by Berson, et al. (2002) to isolate the ganglion responsible for generating the signals for the SCN, identified that they were optimally stimulated by blue (500 nm) light frequencies.   Later experiments carried out by Figueiro, Bierman, Plitnick & Rea (2009, p. 105) indicated that the 'higher level of blue light resulted in a reduction in melatonin[47] levels relative to the other lighting conditions'.   However, higher levels of red light also appeared to generate stimulation (Figueiro, et al., 2009), so the level of luminance may be the most important factor in determining the effects of lighting on the SCN.

1.3.4.   *Midbrain Region*

According to Francisco, Javier & Vladimir (2007), and Merker (2007), the midbrain region *(which sits at the top of the brain stem)* plays an important role in controlling attention and consciousness. For the purposes of this thesis only three elements of the midbrain will be discussed, because of their importance in visual processing.

1.3.4.1. *Superior Colliculus*

Superior
Colliculus

The superior colliculus (SC) appears to be intrinsically involved in visual control, spatial orientation and localisation (Sprague, 1972). For example the SC:

•   is involved in generating pursuit (Schutz, et al., 2011) and *(predominantly reflexive)* saccadic eye movements (Lisberger, 2010; Ludwig & Gilchrist, 2003), which shift the eye to points of attention *(e.g. target selection (Francisco, et al., 2007; Krauslis, 2007))* by directly projecting efferent signals to pre-motor areas of

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46.   In this context the term circadian rhythm relates to the roughly 24 hour cycle of wakefulness and sleepiness, as specified by Garrett (2003).

47.   Melatonin is a sleep inducing neurochemical (Garrett, 2003).

the brain (Desimone & Duncan, 1995; Merker, 2007; Theeuwes, Devries, & Godijn, 2003);

- appears to be the source of Corollary Discharges (CD) that compensate for the disruption of perception during saccadic eye movements, and thus assist in providing stable vision (Wurtz, et al., 2011);

- is associated with the implementation of multi-modal attention, monitoring, and control (Arieh & Marks, 2008; Bizley & King, 2008);

- may be responsible for mediating motion detection (Merker, 2007) and saliency processing (Fecteau & Munoz, 2006; Saalmann & Kastner, 2011);

- influences the level of alertness based on the level of luminance being received (Miller, Obermeyer, Behan, & Benca, 1998);

- is important in pattern discrimination (Cardu, Ptito, & Dumont, 1980);

- appears to play an important part in learning (Sprague, 1972), which may be due to attention issues *(as cited above)*, or due to the mesodiencephalic bottleneck *(of which the SC is a key part)* on the size of working memory (Merker, 2007); and

- shows responses to reward dependent effects (Schutz, et al., 2011), which are important for shaping attention and visual processing, as a part of the top-down and bottom-up processes.

To assist in achieving these objectives the SC receives retinal input, and may provide a second route to the cortex that bypasses the LGN (Breitmeyer, et al., 2008) using either direct connections, or connections through the pulvinar (Merker, 2007), to areas such as V5 (Bizley & King, 2008; Skottun & Skoyles, 2006; Zeki & Ffytche, 1998), the Forward Eye Fields (FEF) (Wurtz, et al., 2011), and the posterior parietal cortex (Merker, 2007)[48].

1.3.4.2. Pretectum

<div style="float:right; border:1px solid #888; padding:4px; color:blue;">Pretectum</div>

The pretectum is closely associated with the SC (Merker, 2007; Sprague, 1972), and it is therefore similarly linked to most of the functions of the superior colliculus, which were cited earlier.   In fact it may be more important than the SC for some aspects such as perception of luminance and learning (Sprague, 1972).   However, the main reason that the pretectum is cited separately is its role of pupillary control (Tsujimura & Tokuda, 2011).   The pretectum is predominantly responsible for initiating changes in pupil dilation and constriction with changes in luminance (Kourouyan & Horton, 1997). These changes are achieved by sending efferent signals through the Edinger-Westphal nucleus (Kourouyan & Horton, 1997).   Such changes in the size of the pupil then have implications on the eye's ability to focus, as specified in Section 1.3.1.1.

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48.   There are a range of other connections, such as the midbrain cerebral aquaduct *(in particular the periaquaeductal grey)*, and hypothalamus (Merker, 2007).   These have been omitted for the purpose of simplicity.

1.3.4.3. Reticular Formation

The Reticular Formation (RF) 'is an extremely important part of the human central nervous system' (Wang, 2009).   In terms of this thesis the importance stems from the RF's critical role in visual discrimination tasks, and modulating arousal, vigilance and attention (Puryear & Mizumori, 2008).   In particular, the RF is directly involved within the network that:

• assists in the bottom-up processing of salience (Fecteau & Munoz, 2006); and

• forms an important element in the brain's management of reward *(e.g. dopamine response rewards)* (Puryear & Mizumori, 2008).

1.3.5. Occipital Lobes

Occipital Lobe

The occipital lobe has long been nominated as the visual cortex, and it comprises a number of key regions, which are shown in Figure 1.18[49].
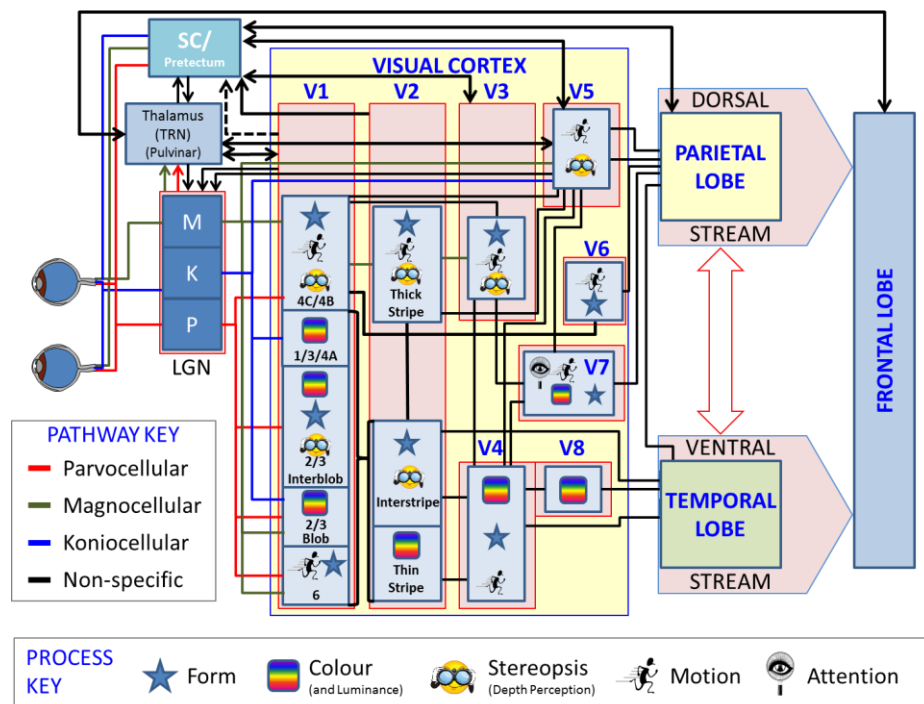
Figure 1.18:   A simplified model of regions, roles and feeds within the visual cortex

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49. This model was developed by the author from information provided in Kandel, et al. (2000); Skottun & Skoyles (2006); Martin (2004); Shipp (1995); Saalmann & Kastner (2011); Briggs & Callaway (2001); Briggs & Usrey (2011); Zeki & Ffytche (1998); Cloutman (2012); Clifford, Spehar, Solomon, Martin & Zaidi (2003); Grill-Spector & Malach (2004); Tootell et al. (1998); Brouwer & van Ee (2007); Levy, Schluppeck, Heeger & Glimcher (2007); Fattori, Pitzalis & Galletti (2009); Seymour, Clifford, Logothetis & Bartels (2010); Arcaro, McMains, Singer & Kastner (2009); Schendan & Stern (2007); Fecteau & Munoz (2006) and Norman (2002).

On the left of the visual cortex within this model[50] is area V1, which is also commonly referred to as the striate cortex, because of the striations within this area (Kandel, et al., 2000). The remaining areas (V2 to V8) are collectively referred to as the extrastriate areas (Grill-Spector & Malach, 2004; Kandel, et al., 2000). These areas work together through a staged process *(a partially hierarchical processing model)*, in which different areas handle diverse functional aspects *(the functional specialisation model)* (Grill-Spector & Malach, 2004), as shown in Figure 1.18. However, there is also significant intra-cortical connectivity between these areas (Koulakov & Chklovskii, 2001; Wurtz, et al., 2011), and these cortical regions therefore handle and share a wide range of different stimuli types, to develop percepts and representations about the environment (Grill-Spector & Malach, 2004).

In terms of this thesis the following key points related to the visual cortex are pertinent:

- The visual cortex utilises a retinotoptic framework[51] (Grill-Spector & Malach, 2004; Ward, Macevoy, & Epstein, 2010) for handling the information, so it is analysing a representation of the environment (Kandel, et al., 2000). However, it is also utilising non-retinotopic aspects within the processing continuum (Grill-Spector & Malach, 2004). In practical terms, this means that the stimuli is predominantly handled in a more abstract way in the higher processing areas (Kandel, et al., 2000).

- Each area handles both central *(foveal and parafoveal)* and peripheral vision feeds, but central vision is magnified to optimise the quality and acuity of the information received (Duncan & Boynton, 2003). This means that visual acuity declines for stimuli further away from the fovea, which reinforces the issues related to the distribution of photoreceptor cells in the retina *(as discussed in Section 1.3.1.2.1)*. There is therefore a strong bias toward processing central vision. For example, Azzopardi & Cowey (1993) showed that the amount of cortical tissue in V1 allocated to the processing foveal information was 3.3 to 5.9 times more than that allocated to peripheral vision. When this is also equated to the cone to ganglion ratios within the retina, it means that there is between 12 and 24 times more cells within the primary visual cortex, which are allocated to processing central vision, than there is to support peripheral vision (Duncan & Boynton, 2003). Additionally, it is likely that this focus on foveal and parafoveal

50. Some areas within this model are actually located within, or on the boundary of, the temporal and parietal lobes. For example, area V5 is located at the juncture of the temporo-parietal occipital lobes (Grill-Spector & Malach, 2004). For the purposes of simplification, all of the areas from V1 to V8 have been discussed within the region of the occipital lobe. Additionally, this is a highly simplified model and the functional and hierarchical connections within this model do not fully reflect the complex interconnections applied within this area, such as those identified in McDonald, Mannion, Goddard, & Clifford (2010).

51. This retinotopic map is represented in a log-polar form, so it is not an exact mapping, but stretched by the visual processing. This takes into account the magnification aspects created by the curved shape of the retina and the bias toward the foveal area (Grill-Spector & Malach, 2004). The mapping therefore 'preserves the qualitative spatial relations but distorts quantitative ones' (Grill-Spector & Malach, 2004, p. 251).

vision to improve acuity extends to the higher cortical *(extrastriate)* areas as well (Duncan & Boynton, 2003).

- Because of the physiology of this area *(particularly in the striate cortex)*, the cells typically respond well to:

  ➢ ***Edges.*** Neurons in the 'visual cortex respond best to edges in their receptive field' (Koulakov & Chklovskii, 2001, p. 519). For example, 'the interblob pathway sketches boundaries' (Shipp, 1995, p. 118). In particular, edges are defined by boundary contrast, which can be caused by differences such as luminance, colour, spatial frequency, or disparity (Grossberg, 1994). It is these aspects that make an object stand out (Grossberg, 1994)[52].

  ➢ ***Orientation.*** Cells within the visual cortex respond to a 'narrow range of orientations of elongated bars or gratings presented within a certain spatial position of the visual field.' (Okamoto, Ikezoe, Tamura, Watanabe, & Aihara, 2010, p. 151).

  ➢ ***Other Aspects.*** In addition to edges and orientation, there are a range of other aspects, which are pertinent in developing visual perception. For example, colour, form and movement are of particular importance (Grossberg, 1994; Sasaki & Watanabe, 2004, 2012; Seymour, et al., 2010; Shipp, 1995)[52].

- Within the visual cortex 'colour and form and motion are inextricably linked as properties of objects' (Shapley & Hawken, 2011, p. 701). In particular, colour and form are linked reciprocally, because colour and shape *(spatial relationships)* are so important in the perception of objects (Shapley & Hawken, 2011).

- There is a strong bias within the cells in V1 to manage colour opponent information, with around two thirds (2/3) of the cells allocated to this task (Friedman, Zhou, & Von Der Heydt, 2003; Johnson, Hawken, & Shapley, 2008).

- Conscious awareness of what is seen appears to occur higher in this processing than V1 (Pylyshyn, 2002), so in the early stages of processing the viewer is probably not consciously aware of the visual stimuli (Skottun & Skoyles, 2006).

- It appears that area V4 plays an important role in linking top-down and bottom-up processes (Mazer & Gallant, 2003). This 'convergence of bottom-up and top-down processing streams in area V4 results in an adaptive dynamic map of salience that guides oculomotor planning during natural vision.' (Mazer & Gallant, 2003, p. 1241)

- Area V5[53] plays a very important role in perception processing within the visual cortex. Key attributes of this area are:

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52. These equate to key salience factors as discussed in Chapter 2 of the thesis.

53. Area V5 is often referred to by other terms in various publications. For example it is also called the Middle Temporal (MT) area (e.g. Merchant, Battaglia-Mayer, & Georgopoulos (2001), or by McGraw & Roach (2008)), or the human Middle Temporal + (hMT+) area (Grill-Spector & Malach, 2004), or sometimes the Dorsolateral Occipital (DLO) area (Wandell, Dumoulin, & Brewer, 2007).

- ➢ This area contains direction selective cells (Huk, Ress, & Heeger, 2001), which are attuned to perceive coherent, patterned (Grill-Spector & Malach, 2004), and biological movement (Grossman & Blake, 2002), as a part of global motion detection (Castelo-Branco et al., 2002).

- ➢ V5 appears to play an important role in shaping attention within the visual cortex (Hupe et al., 1998; Zeki & Ffytche, 1998).   For example, Foxe & Simpson (2002) indicated that V5 can be activated prior to V1 *(e.g. during the presentation of fast or slow movement (Zeki & Ffytche, 1998))*, and the two areas then appear to interact to modulate attention.

- ➢ V5 is also important within the process for driving optical flow (Morrone et al., 2000), which affects pursuit tracking (Schutz, et al., 2011) and saccadic eye movements (Kandel, et al., 2000).   As explained in Section 1.6 this has important implications for shaping attention.

- There are direct feed-back loops from the visual cortex *(in particular V1 and V5)* to areas such as the LGN, pulvinar and superior colliculus, which appear to provide visual maps which may be used for afferent attention shaping and efferent control (Shipp, 2003).

- Although the visual cortex initially supports bottom-up processing of the visual stream, perception is also modulated through top-down processing (Dodwell & Humphrey, 1990; Ludwig & Gilchrist, 2003; Pourtois, Rauss, Vuilleumier, & Schwartz, 2008; Rauss, Schwartz, & Pourtois, 2011).   In particular, processing through the visual cortex is specifically modulated by attention (Briggs & Usrey, 2011; Karns & Knight, 2008), and this appears to be shaped by feed-back systems within the visual cortex, other areas within the interbrain and midbrain, and the temporal, parietal and frontal lobes (Foxe & Simpson, 2002).

1.4.   *From Perception to Cognition*

From the visual cortex in the occipital lobe, the visual stimuli take two paths to the frontal cortex (Cloutman, 2012), where higher level cognition primarily takes place (Buchsbaum, 2004; Gilbert & Fiez, 2004).   These two paths are known as the dorsal and ventral streams (Crick & Koch, 2003; Mishkin, Ungerleider, & Macko, 1983) [54].

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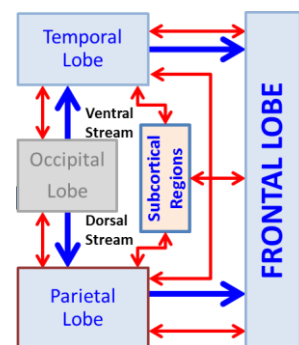
54.   The dual stream approach discussed in this section is designed to merge a range of models used to describe this phenomenon.   For example Milner & Goodale (2008) refer to these using the terms 'vision for perception' and 'vision for action'.   Fulton (2003a) refers to these as the 'Awareness' and 'Analytical' channels.   As another alternative, Crick & Koch (1998) talk about 'on-line' and 'seeing' systems, and in an earlier paper they refer to 'awareness' (Crick & Koch, 1995).   In particular, the terminology used in this paper is designed to merge these models with the affordances (Gibson, 1966, 1979) approach cited by Young (2006), the linked 'ecological-dorsal' or 'constructivist-ventral' model specified by Norman (2002), the 'Spatial Relationships' and 'Object Recognition' paths explained by Essen, Anderson, & Felleman (1992), and the 'Object Recognition'

A simplified model of the paths that these two streams take is illustrated in Figure 1.19[55].
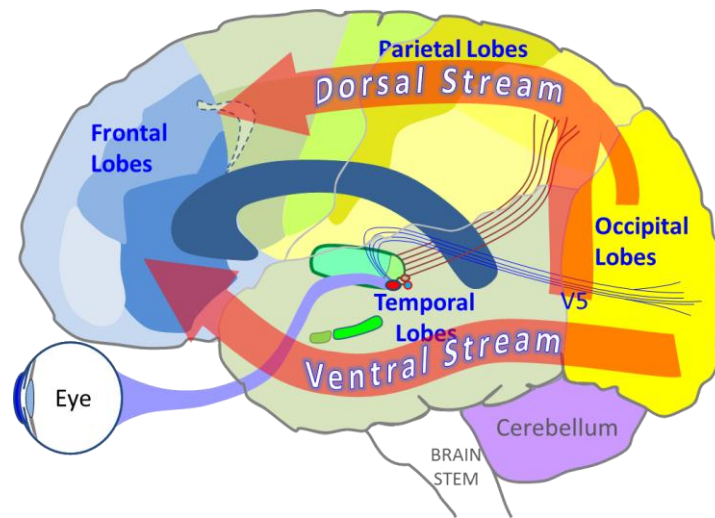
Figure 1.19: A simplified model showing the generalised pathways for the two streams

These two streams appear to be functionally specialised (Ikkai, Jerde, & Curtis, 2010; Kandel, et al., 2000; Norman, 2002), and can be generally characterised as follows:

• ***Ventral Stream.*** The ventral stream 'has been functionally conceptualised as the "what" stream, responsible for visual and auditory stimulus identification and object recognition, the mapping of information into conceptual representations, and the sound-to-meaning (and written word-to-meaning) mapping underlying the comprehension of spoken (and written) language' (Cloutman, 2012, p. 1). The ventral stream is typically dominated by the processing of the parvocellular information (Lamme & Roelfsema, 2000; Shipp, 1995), and also some aspects from the koniocellular pathway *(possibly colour and spatial frequency related stimuli (Van Essen & Gallant, 1994))* (Brown & Goodale, 2008; Nassi & Calloway, 2009; Simmons et al., 2009).

• ***Dorsal Stream.*** This second pathway 'constitutes the "where/how" stream, responsible for spatial processing (including location, relative position, and motion), sensorimotor mapping and the guidance of action towards objects in space' (Cloutman, 2012, p. 1). The dorsal stream appears to predominantly handle the magnocellular path stimuli (Sehatpour P et al., 2010) and some aspects of the koniocellular information *(e.g. motion related (Kaas & Lyon, 2007)).*

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and 'Context' model applied by Bar (2004). The pertinent aspects of these models are described in the appropriate sections of this thesis.

55. This model was developed by the author from information provided in Garrett (2003); Merchant, et al. (2001); Bisley (2011); Cloutman (2012); Hickok & Poeppel (2004) and Schendan & Stern (2007). The model is designed to be indicative only, and does not contain all of the linkages and connections that are related to the two streams. More of these connections are illustrated in Figure 1.2, Figure 1.3, and Figure 1.18.

Although the two streams are explained within this framework as independently handling the visual information, there is substantial cross pollination and sharing of information across the two streams (Skottun & Skoyles, 2006), as explained in Section 1.4.4. Additionally, some of the subcortical elements *(e.g. hippocampi, striatum, limbic system, etc., which are discussed below)* support both streams.

The following subsections explain some of the key neural mechanisms utilised within these two pathways and their interaction.

1.4.1.   Ventral Stream

As illustrated in Figure 1.18 the ventral stream is mainly receiving information from areas within the visual cortex that are dominated by the processing of aspects such as colour and form (Ninomiya, Sawamura, Inoue, & Takada, 2011). The ventral stream therefore appears to utilise these visual cues to create detailed mental representations of the world (Cloutman, 2012). For this reason the ventral stream is linked to the provision of awareness (Crick & Koch, 2003; Mazer & Gallant, 2003), and object categorisation (Gallese, 2007).
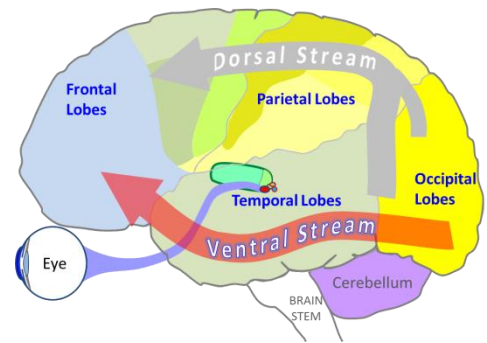
Within the context of this thesis, key physiological elements utilised within this stream can be categorised in terms of their processing activities, as discussed in the following subsections.

1.4.1.1.   Overview of the Temporal Lobe Functions

The temporal lobes (TL) appear to play an important role in object
recognition (Bartolomeo & Chokron, 2002; Mishkin, et al., 1983) and constancy (Ffytche, et al., 2010). Some of the regions within these two lobes are also highly focussed on responding to specialised features, such as faces[56] or hands (Kandel, et al., 2000). Additionally, the TL appear to be actively involved in linking new information with other memories, such as the recognition of familiar places (Ffytche, et al., 2010), colour recognition (Kandel, et al., 2000), recognition of lists of information *(e.g. declarative[57] memory recall)* (Aggleton, Sanderson, & Pearce, 2007), the processing of semantic[58] information (Mason & Just, 2007), and orientation *(in conjunction with*

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56.   The associated Fusiform Face Area (FFA) is not discussed in detail in this thesis, as it is considered less important in terms of the hypotheses.

57.   The term declarative memory relates to the storage and recall of factual information *(e.g. specific facts like dates, names, faces, etc.)* (Feldman, 2005). Declarative information appears to be stored as either semantic *(see Footnote 58)*, or episodic *(see Footnote 63)* memory (Feldman, 2005). Further information on declarative memory and the differentiation with non-declarative memory is provided in Footnote 65.

58.   'Semantic memory is the subcomponent of memory that is responsible for the acquisition, representation, and processing of conceptual information. This critically important system

areas within the dorsal stream) (Brocki, Fan, & Fossella, 2008).   The temporal lobes therefore play an important role in cognitive discrimination (Magnussen & Greenlee, 1999).

In particular, this area is linked to the processing of foveal and parafoveal vision, although some aspects of peripheral vision are also processed in these lobes (Grill-Spector & Malach, 2004; Larson & Loschky, 2009).   This utilisation of the peripheral vision may be associated with scene[59] 'gist' analysis (Larson & Loschky, 2009; Shimozaki, Chen, Abbey, & Eckstein, 2007).   This aspect is important when considering layout issues, such as those required to optimise the design of PowerPoint[®] slides for teaching.

This area also demonstrates persistent stimulus-selective activity, and it also appears to play an important role in working memory (Bellgrove & Mattingley, 2008; D'esposito, 2007).

Additionally, other regions in this area are linked to language (Hickok & Poeppel, 2004), and the recall of words (Kandel, et al., 2000).   In particular, fluent reading that draws on lexical memory[60], has been associated with this region of the brain (Borowsky, et al., 2006).   For instance, much of the passive *(e.g. reading/listening)* language related functions appear to be linked to Wernicke's area.

1.4.1.2. Wernicke's Area

In about 90% of people, Wernicke's area is located in the posterior portion of the left temporal lobe (Hickok & Poeppel, 2004)[61], and it also extends up into the area of the parietal lobe (Tanner, 2007) *(see Figure 1.3)*.   This region is linked with developing understanding and comprehension of both written and verbal language (Johnson, Williams, Pipe, Puppe, & Heiserman, 2001; Tanner, 2007).

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of brain function is implicated in a wide range of cognitive functions, including the ability to assign meaningful interpretations to words and sentences, recognize objects, recall specific information from previously learned concepts, and acquire new information from reasoning and perceptual experience' (Saumier & Chertkow, 2002, p. 516).

59.   A scene is a 'semantically coherent (and often nameable) view… comprising background elements and multiple discrete objects arranged in a spatially licensed manner' (Henderson & Hollingworth, 1999, p. 244).   Often this term is used to denote scenes in the real world, but for the purpose of this thesis the term will be utilised for any form of visual construct that will be viewed by an observer.

60.   The term lexical memory refers to the storage of language related words and sounds, which are recalled during the process of comprehension (Wise et al., 2001).   Some articles delineate this further into lexical and sublexical categories (Giroux & Rey, 2009). Lexical memory relates to familiar words, which have already been encoded for recall, and the sublexical systems are used to phonetically decode words (Borowsky et al., 2006).   The development and utilisation of lexical memory is associated with the ventral stream, and the sublexical processes are associated with the dorsal stream (Borowsky, et al., 2006; Saur et al., 2008)

61.   In the remainder of the population it is located in a similar location in the right hemisphere.

In terms of fluent reading, Wernicke's area draws on lexical memory, by linking to the hippocampus, thalamus, frontal cortex, and other cortical areas (Mason & Just, 2007; Wise, et al., 2001).

1.4.1.3. Subcortical Regions

Subcortical Regions

The following subcortical areas are pertinent to the processing of visual information within the framework of this thesis.

1.4.1.3.1. Parahippocampal Place Areas

The Parahippocampal Place Areas (PPA) respond more strongly to scenes and pictures of places, than other types of visual stimuli (Arcaro, et al., 2009; Dickinson & Intraub, 2009; Epstein, Harris, Stanley, & Kanwisher, 1999).   In particular, there is evidence that these areas assess the whole scene, rather than lower order bottom-up aspects (Doran & Hoffman, 2010), or individual visual objects within the scene (Epstein, 2005). For instance, the two PPA 'represents the geometric structure of scenes as defined primarily by their background elements' (Epstein, 2005, p. 954).

Additionally, the PPA are involved with encoding new information about the appearance and layout of what is being viewed (Epstein, et al., 1999).   To achieve this objective, the PPA appear to be important in linking the visual stimuli in representations with memories provided by the associated hippocampus *(see below)* (Ffytche, et al., 2010).

Although Shipp (2003) indicated that the PPA are predominantly processing information received through the foveas *(the fixation point)* they also appear to receive significant inputs from peripheral vision (Epstein, 2005).   The PPA and the associated Transverse Occipital Sulcus (TOS) also seem to play important roles in salience mapping (Ward, et al., 2010).

Processing within the PPA has also been strongly linked to the application of attention, with:

•   the provision of novel visual material increasing processing attention; and

•   repetition of visual material reducing the level of attention, and the amount of processing that is applied (Yi & Chun, 2005).

1.4.1.3.2. Hippocampi

The two hippocampi receive convergent afferent information 'from virtually all cortical association areas'[62] (Eichenbaum, 2004, p. 110).   These structures appear to be very important in visual processing (Meyer, 2002), and managing both short term storage

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62.   The hippocampi receive projections from, and provide inputs to, both the dorsal and ventral streams (Wang, Gao, & Burkhalter, 2011), the frontal lobe (Brogaard, 2011; Pennartz, Ito, Verschure, Battaglia, & Robbins, 2011) as well as other elements within the midbrain (Sprague, 1972) and interbrain areas (Mason & Just, 2007; Parikh & Sarter, 2008).

and the retrieval of information (Eichenbaum, 2004). Most importantly *(in terms of this thesis)*, the hippocampi seem to be 'critically involved in the rapid encoding of events as associations among stimulus elements and context' (Eichenbaum, 2004, p. 117). The following key points related to the hippocampi are important in terms of the hypotheses being investigated:

- ***They support top-down Processing.*** The hippocampi may be utilised to 'rapidly encode high-fidelity representations' of semantic elements (Ezzyat & Olson, 2006, p. 38), and link these with episodic memories[63]. In doing this, the hippocampi provide associations with episodic and other forms of memory to generate understanding through top-down processes (Eichenbaum, 2004). For example, the hippocampi are intrinsically involved in relational processing, and providing linkages to generate meaning (Sullivan Giovanello, Schnyer, & Verfaellie, 2004), so this affects aspects such as object recognition. Additionally, the hippocampi are intrinsically involved in generating plans (Lisman & Redish, 2009) and other top-down signals (D'esposito, 2007).

- ***They aid understanding.*** The hippocampi link knowledge 'in support of the flexibility of their expressions through comparisons and generalisations across memories' (Eichenbaum, 2004, p. 114). Such linkages assist in the rapid development of understanding, by relating new information to what is already known.

- ***They play an important role in learning.*** The two hippocampi play a critical role in learning (Schnotz & Kurschner, 2007; Tamminga, 2005), and in particular:

  - ➢ structural learning[64] where the stimuli are bound by their relationships with each other *(e.g. temporal relationships)* (Aggleton, et al., 2007);

  - ➢ the utilisation and memorisation of declarative information (Jurd, 2011; Sokolov, 2002), and the interconnection of explicit *(declarative)* memory (Rowland & Kentros, 2008) and non-declarative *(implicit)* memories[65] (Rose, et al., 2010);

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63. The term episodic memories 'refer to our ability to recall specific past events about what happened where and when. Episodic memory is distinct from other kinds of memory in being explicitly located in the past and accompanied by the feeling of remembering, whereas other knowledge that we acquire is purely factual, without any personalised pastness [sic] attached to it' (Clayton, Salwiczek, & Dickinson, 2007, p. 189). Episodic memory does not just include information of a specific event or situation, but also includes links to other related events *(e.g. ones that precede or follow the episode)* (Ferbinteanu, Kennedy, & Shapiro, 2006; Tulving, 2002).

64. Structural learning is the process of 'binding stimulus elements to make unique arrays (as in all configural learning), the relationship of these elements to each other, be it spatial or temporal, is specified' (Aggleton, et al., 2007, p. 723).

65. In traditional models 'explicit (declarative) memory is thought to be accessible to awareness, whereas the contents of implicit (non-declarative) memory are unconscious' (Berry, Shanks, & Henson, 2008, p. 367). In traditional models these memory types were seen to be disassociated. However, the research conducted by Berry, et al., (2008) has indicated that there are significant synergies between the two types. To avoid ambiguity generated by using this term in relation to explicit and implicit learning *(which was discussed earlier)*, this thesis will use the terms declarative and non-declarative.

> ➢ learning information that requires the application of spatial relationships (Maviel, Durkin, Menzaghi, & Bontempi, 2004); and

> ➢ understanding information that needs to be assessed in terms of its context (Eichenbaum, 2004).

- ***Repetition plays an important part in learning.*** The repetition of experiences, or visual inputs assists in developing declarative memory, because of the biophysiological constructs within the hippocampi (Nakazawa, Mchugh, Wilson, & Tonegawa, 2004; Salimpoor, Chang, & Menon, 2009).

- ***They assist in making inferential judgements.*** The hippocampi draw on a range of memories collected from a network of cortical areas, to assist in making inferential judgements (Eichenbaum, 2004).

- ***They play an important role in sequential management of memories.*** The hippocampi appear to play a significant role in ordering both semantic and episodic information (Eichenbaum, 2004; Levy, 1996). For this reason, the hippocampi are important in supporting the ordering of semantic information in learning. (Levy, 1996).

- ***They link emotions to new information.*** As a part of the relational and association processes supported by the hippocampi, emotional memories are also stimulated (Nalloor, Bunting, & Vazdarjanova, 2012). Such connections are facilitated within the limbic system (Rajmohan & Mohandras, 2007) *(see Section 1.4.1.3.4)*, and through connections with the frontal cortex *(see Section 1.4.3)*.

- ***The input order affects the quality of memory.*** Typically the most recently presented item in a sequence is best remembered (Eichenbaum, 2004).

1.4.1.3.3. Striatum and Basal Ganglia

Whereas the hippocampi are associated predominantly with declarative memory, the striatum is more closely associated with non-declarative *(procedural)* memory (Jurd, 2011), and habit formation (Yin & Knowlton, 2006). In particular, the striatum and basal ganglia[66] appear to interact to support the utilisation of procedural memory for behaviour related motor activity (Pennartz, et al., 2011). Additionally, areas within the striatum mediate:

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66. The basal ganglia were not illustrated in Figure 1.3, because their inclusion cluttered the diagram. The basal ganglia consist of a range of different nuclei, which are located in the vicinity of the mid-brain and 'receive inputs from the neocortex, and by way of their output nuclei, the basal ganglia project massively to thalamic nuclei, which in turn project to the frontal cortex. This anatomy means the basal ganglia are in a prime position to influence the executive functions of the forebrain, such as planning for movement and even cognitive behaviours' (Graybiel, 2000, p. 509). Additionally, 'the basal ganglia send outputs to brainstem nuclei involved in motor control, including the superior colliculus, which controls axial orientation and saccadic eye movements' (Graybiel, 2000, p. 509). The striatum acts as the gateway for the basal ganglia (Kreitzer & Malenka, 2008) and the basal ganglia also communicate with the cerebellum (Carras, Feger, Hoshi, Strick, & Tremblay, 2005).

- stimulus-response learning[67] (Voorn, Vanderschuren, Groenewegen, Robbins, & Pennartz, 2004);

- motivational and affective learning[68], which has direct implications for cognitive assessments of value and reward within top-down processes (Balleine, et al., 2009; Schmidt, Lebreton, Clery-Melin, Daunizeau, & Pessiglione, 2012); and

- goal seeking behaviours, appear to be generated through interaction between the striatum and hippocampi (Pennartz, et al., 2011).

To facilitate these aspects, the striatum and basal ganglia also interact with limbic system elements such as the amygdala (Everitt, Morris, O'brien, & Robbins, 1991), so feelings, fears and aspirations are intrinsically involved in goal seeking behaviours *(e.g. top-down processes such as plans, or the assessment of value and reward)*.

1.4.1.3.4.   Other Limbic System Areas

The limbic system includes a range of physiological structures, which include the hippocampi[69].   Other elements within the limbic system are associated with a range of fundamental behaviours *(e.g. hunger and reproduction)* (Feldman, 2005) and emotions, which include fear, rage, placidity, and motivation (Rajmohan & Mohandras, 2007).

Elements within the limbic system, such as the amygdala appear to have a moderating effect on regions within the mid-brain area *(e.g. thalamus)* (Fitzgibbon, 2007; Rowland & Kentros, 2008), interbrain (Merker, 2007) and ventral stream, which shape attention (Behrendt & Young, 2004; Mohanty, Gitelman, Small, & Mesulam, 2008). Additionally, the limbic system seems to modulate goal oriented behaviours and motivation (Goto & Grace, 2008), which has implications for reward systems (Gilbert & Fiez, 2004).   For example, the limbic systems respond strongly to reward signals, and link these to a wide range of salient and arousing events, which include reactions to high intensity and novel stimuli (Boksem & Tops, 2008).

Additionally, the limbic system seems to directly affect cognitive processing within the prefrontal cortex (Behrendt & Young, 2004; O'reilly, 2010; Parikh & Sarter, 2008). Just as importantly, the limbic system elements have key implications related to feelings

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67.   This can be equated to simplistic learning, such as the generation of pavlovian responses *(e.g. ring the bell and the dog salivates)*, which are aligned to the classical conditioning approach to learning.   Classical conditioning indicates that people and animals will respond in predictable ways if there is some stimulus *(e.g. reward, pain, etc.)* provided from within their environment (Biggs & Telfer, 1987).

68.   This approach links to the instrumental conditioning model.   Instrumental conditioning posits that humans and animals learn through encoding the consequences of their actions, which then leads to goal driven behaviours (Balleine, Liljeholm, & Ostlund, 2009).

69.   Although different papers utilise varying lists of the physiological structures involved in the limbic system (Rowland & Kentros, 2008), the elements in the following list are fairly widely accepted: (1)   The limbic cortex, comprising the cingulate gyrus, the parahippocampal gyrus; (2)   The hippocampal formation, which contains the dentate gyrus, hippocampus *(including the fornix)*, and subicular gyrus; (3)   Amygdala; (4) Septal Area; and (5) Hypothalamus (Rajmohan & Mohandras, 2007).

and emotions (Changeux, 2012; Rowland & Kentros, 2008; Van Honk, Morgan, & Schutter, 2007; Wood & Grafman, 2003) that the viewer might have in relation to the visual information that is provided (Behrendt & Young, 2004).

1.4.1.3.5. Insula

The insula are located in each hemisphere within the inner part of a fissure between the temporal and parietal cortices[70] and they also extend into the frontal lobe (Kandel, et al., 2000). These regions receive strong 'inputs from the sensory thalamus and from parietal, occipital and temporal association cortices' (Jones, Ward, & Critchley, 2010, p. 611) and exchange information with the frontal cortex, striatum, limbic system (Pennartz, et al., 2011), broca's area (Kljajević, 2011), and the cingulate gyrus (Koch, 2011; Mason & Just, 2007; Mohanty, et al., 2008). The two insular regions are implicated in 'language[71], auditory processing, pain processing, taste and flavour perception in addition to, or in conjunction with, autonomic[72] processing' (Jones, et al., 2010, p. 611). Additionally, the two insula appear to support the assessment of value and reward within goal-directed behaviour (O'doherty, 2011), and the application of focussed attention (Nelson et al., 2010).

Most importantly *(in terms of this thesis)* the insula appear to be primary nodes for integrating cognitive and emotional processing (Gu, Liu, Van Dam, Hof, & Fan, 2013). These physiological regions may therefore provide one of the key areas in which the first two dimensions of the first unifying model[73] *(comprehension and impressions)* are directly integrated within the human brain.

1.4.1.3.6. Broca's Area

For most people Broca's area is located in the left hemisphere of the brain, within the inferior frontal gyrus in the frontal lobe (Garrett, 2003)[74]. Although Figure 1.3 shows this as a specific region, it is not an isolated anatomical area and appears to be a much more diffuse neural zone than was originally thought (Kljajević, 2011).

It has long been known that Broca's area 'controls speech and provides grammatical structure to language' (Garrett, 2003, p. 64). However, more recent research has shown

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70. Although this region is listed as a cortical area (Fulton, 2011), it has been included in this Appendix as a sub-cortical area for simplicity, and because it is sometimes listed as a part of the limbic system *(e.g. Mier et al (2010))*.

71. In particular the insular regions appear to be sensitive to phonological processing, with particular emphasis on sublexical spelling translation in reading (Borowsky, et al., 2006) and the processing of lexical ambiguity (Mason & Just, 2007). This infers linkage to the dorsal sublexical processing stream.

72. The term autonomic refers to the automated regulation of general activities in the body *(e.g. heart rate, metabolic rate, etc.)* (Garrett, 2003). These are controlled through the autonomic nervous system, and emotional responses have a direct influence on arousal generated through this system (Feldman, 2005).

73. See Figure 2.1 in Volume 1 of this thesis for a description of this model.

74. For others it is located in similar areas within the right hemisphere.

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that this area contributes to many other aspects, which include 'phonetic, phonological, lexical, semantic and syntactic tasks; in rhythmic perception, harmonic incongruity perception, tonal frequency discrimination, comprehension of artificial languages, time perception, calculation tasks, memory tasks, action observation and mental imagery of movement, musical syntax, processing of complex geometric patterns, in prediction of sequential patterns' (Kljajević, 2011, p. 20), and even in body language (Yu & Ballard, 2005).

1.4.2.   Dorsal Stream

Whereas the ventral stream appears to be dominated by the processing of focussed information provided mainly by the parvocellular pathway (Doniger, Foxe, Murray, Higgins, & Javitt, 2002), the dorsal stream appears to predominantly handle information supplied through the magnocellular pathway (Mendes et al., 2005) [75].   Information managed within the dorsal stream is directly involved in visuospatial perception (Chan & Newell, 2008), which assists in the development of awareness *(and particularly conscious awareness (Gallese, 2007))* about the environment (Madary, 2011), and then uses this information to apply visuomotor guidance (Mcintosh & Lashley, 2008) *(e.g. generating attention focussed saccades and/or other physical movements).*
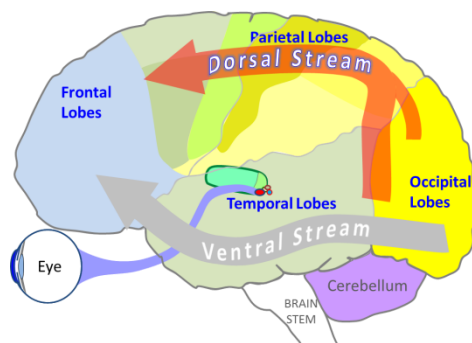
The dorsal stream passes through the parietal lobes to the frontal cortex. Rather than define each region independently, it will be more useful in terms of this thesis to aggregate the processes managed within the parietal lobe[76].   The following subsections therefore describe the key features of the dorsal stream activity.

Parietal Lobe

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75.   The key to this statement is the word 'dominated'. There is significant evidence that the ventral stream also handles some stimuli provided through the magnocellular pathway and the dorsal system also receives inputs from the parvocellular path (Laycock, Crewther, & Crewther, 2007; Madary, 2011; Skottun & Skoyles, 2006).

76.   For the purposes of simplicity adjoining neural regions to the parietal lobes, such as the intraparietal sulcus, have been handled conjointly within this thesis.   Additionally, aspects such as the split dorsal stream model developed by Rizzolatti & Matelli (2003) have not been included for the purposes of brevity. A discussion of the somatosensory cortex has also not been included. This neural region is responsible for processing skin senses, such as touch, warmth, cold and pain, and is also integral to body positioning and movement (Garrett, 2003). As these senses are not directly pertinent to the thesis, a discourse on this region has not been included. This merging of the regions, and the omission of the more complex aspects of the parietal structures within the dorsal stream, does not make any material difference to the hypotheses, or the findings.

1.4.2.1. This Stream is Very Fast

The dorsal stream transfers stimuli information more quickly to the frontal cortex than the ventral stream (Fattori, et al., 2009; Foxe & Simpson, 2002).   This is partly due to the fact that this dorsal neural feed of information is:

•	predominantly receiving inputs from the faster magnocellular and koniocellular pathways, as discussed earlier;

•	the percepts are originally not interpreted through the types of detailed cognitive processes applied to the ventral stream (Norman, 2002); and

•	the initial fast processing is predominantly unconscious (Irvine, 2011)[77].

This rapid processing supports the provision of feed-back and feed-forward systems *(see Section 1.4.4)* that modulate attention within the occipital (Pins & Ffytche, 2003) and temporal lobes (Singh-Curry & Husain, 2009).   For example, Figure 1.20[78] illustrates the approximate timeframes for activation of the various regions within the visual pathways.

77.	However, this is not true for all aspects, and some properties of the dorsal stream are consciously perceived, just as some stimuli within the ventral stream are processed unconsciously (Norman, 2002). This statement is therefore a generalisation based on dominant aspects within each stream.

78.	The timeframes are based on the research conducted by Foxe & Simpson (2002), and these results are based on the presentation of primed *(pre-cued)* visual stimuli. These figures are therefore probably indicative of the fastest likely timings. Other studies, such as the work published by Clementz, Brahmbhatt, McDowell, Brown & Sweeney (2007) showed slower activations. For instance, they identified that elements of the striate and extrastriate visual cortex appeared to be processing the stimuli within around 150ms after presentation. However, in spite of this slower start, they still indicated that volitional top-down processes were triggered at around 200ms. Their experiments therefore still indicate a dorsal stream transfer speed of less than 50ms, even for volitional activity *(e.g. active attention).*

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1. 0ms – Onset of stimulus within the eye
2. ~ 30ms – Activation of V1
3. ~ 56ms – Activation of Visual Cortex (Striate & Extrastriate areas)
4. ~ 80ms – Activation of Frontal Cortex via Dorsal Stream
5. ~ 110ms – Activation of areas in Ventral Stream
Range for information processing response periods

Timeline of Activation in Milliseconds (1/1000 second)
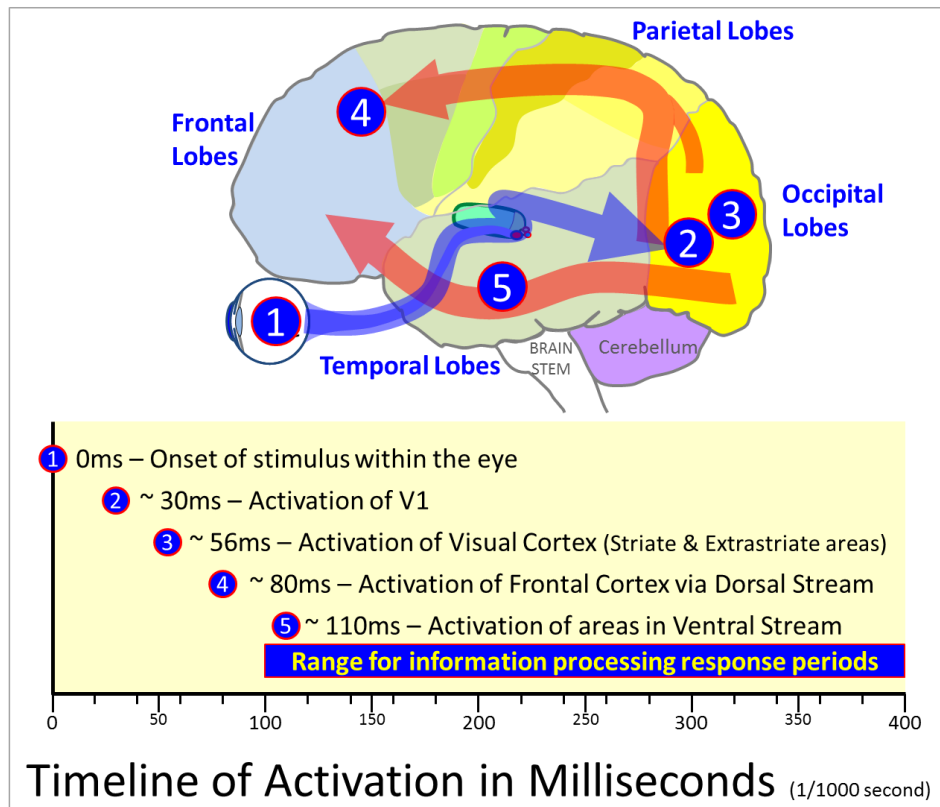
Figure 1.20:   Timeframes for activation of various areas for visual processing

Therefore, as pointed out by Foxe and Simpson (2002, p. 145):

'The rapid flow of activation through the visual system to parietal and prefrontal cortices (less than 30ms), provides a context for appreciating the 100-400ms commonly needed for information processing prior to response output in humans.   It demonstrates that there is ample time for multiple cortical interactions at all levels'.

It is these priming feeds that typically also trigger the transition from preconscious to conscious processing, as discussed in Section 1.2.3.2.

1.4.2.2.   Focussed on Change and Motion

The dorsal stream is also designed to manage rapidly changing stimuli, and for this reason many of the regions in this stream tend to be more plastic[79] (Au & Lovegrove,

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79.   Neural plasticity 'describes the brain's ability to be formed and moulded' (Muscolino, 2011, p. 68).   In practical terms, this describes 'the ability of the neuronal tissue to adjust activities and physical characteristics in order to adapt to changes in the environment or changes in their use' (Jensen & Overgaard, 2011, p. 1).

2007). This plasticity allows human awareness to keep up with the rapidly changing environment, so that new salient content can be detected more rapidly (Singh-Curry & Husain, 2009).

The plastic nature of some of the parietal regions is utilised to achieve motion perception (Ffytche, et al., 2010), and in particular the discernment of coherent motion[80] (Skottun & Skoyles, 2006).

1.4.2.3. Facilitation of Bottom-up and Top-down processes

Tapia & Breitmeyer (2011, p. 934) identified that the information passed through the dorsal stream had a direct bearing on conscious attention 'via top-down modulation of reentrant activity in the ventral object-recognition stream'. This means that the dorsal stream appears to trigger the ventral stream (Singh-Curry & Husain, 2009) to implement active attention *(e.g. focussing central vision on the object of interest, which then utilises the high definition parvocellular path feeds)* (Rawley & Constantinidis, 2010; Zimmer, 2008)[81]. Such activations can create either overt (Domagalik, Beldzik, Fafrowicz, Oginska, & Marek, 2012), or covert (Fischer & Weber, 1998) attention through bottom-up and top-down processes (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004).

Neural regions such as the Lateral Intraparietal (LIP) area also act 'as a priority map, in which objects are represented by activity proportional to their behavioural priority' (Bisley & Goldberg, 2010, p. 1). The resultant 'priority map combines bottom-up inputs like rapid visual response with an array of top-down signals like a saccade plan' (Bisley & Goldberg, 2010, p. 1). In conjunction with the Parietal Eye Fields (PEF) these priority maps are utilised to target saccades and attention, and support goal-directed movements (Muggleton, Kalla, Juan, & Walsh, 2011) .

1.4.2.4. Spatial Awareness Focus

Spatial coordinates are processed within the parietal lobe (Zimmer, 2008), and these are utilised to:

• manage awareness of the surroundings (Pins & Ffytche, 2003); and

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80. The perception of coherent motion relates to a higher level within the processing of visual movement than is generated within the visual cortex (Adelson & Movshon, 1983). This is achieved through 'spatiotemporal interpolation by direction selective integration of spatial pattern information'(Nishida, 2003, p. 273). Coherent motion perception therefore includes the application of subjective judgements (Delicato & Derrington, 2005), so it goes beyond basic bottom-up perception processes.

81. However, as pointed out by Lambert, et al. (2003), salient aspects such as colour can also capture attention directly through the ventral stream, so the dorsal stream provides just one mechanism for quickly shifting attention *(albeit a very important one)*.

- provide spatial coordinates which support the rapid targeting of reflexive saccades *(see Section 1.6.1)* by providing direct input to the superior colliculus (Ludwig & Gilchrist, 2003)[82].

The spatial depth structures managed within this stream also provide important three dimensional (3D) cues (Ellison & Cowey, 2007; Mendes, et al., 2005). These 3D cues seem to feed into the ventral stream to support object recognition, and object positioning in a spatial context (Farivar, 2009). Spatial awareness of this type therefore appears to have a direct effect on the cognition of aspects related to shape, size, and orientation (Farivar, 2009).

Additionally, because the dorsal stream is predominantly handling magnocellular and koniocellular feeds, the granularity of the percepts and representations handled in this area are typically considered to be of lower definition. For instance, whereas the ventral stream predominantly applies central vision *(foveal and parafoveal)* with some feeds from peripheral vision, the dorsal stream is dominated by the processing of 'peripheral retinal input with a high temporal resolution' (Madary, 2011, p. 424).

1.4.2.5. Sublexical Language Analysis

As discussed in Footnote 60, the ventral stream predominantly manages fluent lexical reading (Saur, et al., 2008). However, for words that cannot be read fluently, sublexical mechanisms are utilised to decode the words phonetically, and these actions are associated with the dorsal stream (Borowsky, et al., 2006). Additionally, as identified by Cohen, Dehaene, Vinckier, Jobert, & Montavont (2008) the parietal lobe is also important in managing the reading of degraded text, which is handled sublexically.

1.4.2.6. Part of a Network

This region receives significant inputs from the superior colliculus, hippocampi, cerebellum (Clower, West, Lynch, & Strick, 2001), and the limbic system (Fulton, 2004). As discussed earlier in this appendix, these neural structures appear to provide stimulus for shaping attention. Areas such as the limbic system also support the integration of feelings, impressions, and motivations to this processing.

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82. The regions most commonly identified as providing these activations are the Parietal Eye Fields, which code salient stimuli within coordinate frames that are linked in relation to the point of gaze (Muggleton, et al., 2011). These regions are therefore an important driver in generating rapid saccadic eye movements, and this activity is facilitated by direct connectivity with the superior colliculus (Mcdowell, Dyckman, Austin, & Clementz, 2008).

1.4.3.   Frontal Lobe

The frontal lobe[83] consists of the motor cortex (MC), premotor cortex (PMC), the prefrontal regions (Yeterian, Pandya, Tomaiuolo, & Petrides, 2012), and the orbitofrontal (OF) cortex (Rolls, Everitt, & Roberts, 1996).

1.4.3.1. Motor and Premotor Cortex

The motor cortex and premotor cortex are specifically responsible for the learning and retrieval of motor related memories, which support movements within the human body (Kantak, Mummidisetty, & Stinear, 2012).   As these motor activities are beyond the scope of this thesis, these regions will not be discussed in detail, with the exception of a sub-element known as the Supplementary Eye Fields (SEF).

The SEF directly contribute to initiating saccadic controls[84] (Lachaux, et al., 2006), and pursuit eye movements (Missal & Heinen, 2004).   Additionally, the SEF facilitate these activities by monitoring the context and consequences of these actions (Stuphorn, Taylor, & Schall, 2000).   Research has therefore indicated that the SEF are intrinsically involved in the brain's value and reward systems, by appraising value based oculomotor decisions and then assessing the consequential rewards (So & Stuphorn, 2012).

1.4.3.2. Prefrontal Cortex

The prefrontal cortex (PFC) comprises a large proportion of the frontal lobe.   This area is important for cognitive processing, because:

- it plays a significant role in developing comprehension (Hashimoto & Sakai, 2002) and impressions (Baron, Gobbini, Engell, & Todorov, 2011; Cassidy & Gutchess, 2012);

- it is important in implementing top-down (Miller, 2000; Sawaki & Luck, 2010), attention focussing processes, which are related to the management of visual information (Vanderhasselt et al., 2007; Zanto, Rubens, Thangavel, & Gazzaley, 2011);

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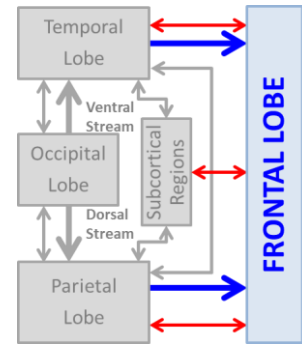
83. A simplified model of the frontal lobes has been utilised in this thesis. Different papers delineate the frontal lobes into a range of different regions, using a variety of models. For example, other naming conventions include regions such as the orbital, ventrolateral, lateral, anterior, medial and posterior.   The more complex aspects of these physiological models have not been applied, to avoid overcomplicating this non-material aspect of the content.

84. In particular the SEF is associated with anti-saccades (Lachaux, Hoffmann, Minotti, Berthoz, & Kahane, 2006).   These are consciously controlled eye movements, which suppress or inhibit typical attractions toward an object *(which are known as pro-saccades)* (Domagalik, et al., 2012).

- it appears to play a major role in planning (Crick & Koch, 1998; Kaller, Rahm, Spreer, Weiller, & Unterrainer, 2011; Oku & Aihara, 2008; Tanji, Shima, & Mushiake, 2007); and

- it affects numerous aspects of perception and cognition (Ciaramelli, Leo, Del Viva, Burr, & Ladavas, 2007; Foxe & Simpson, 2002; Libedinsky & Livingstone, 2011; Miller, Freedman, & Wallis, 2002).

For the purposes of this thesis[85], only key areas of the PFC are discussed. These areas are called the Frontal Eye Fields (FEF), dorsolateral (DL), and ventromedial (VM) regions. The functions of these regions can be broadly delineated as explained in the following subsections.

1.4.3.2.1. Frontal Eye Fields

The FEF form a part of the efferent systems utilised to shift the eyes to the appropriate location, to gather information from the environment (Muggleton, et al., 2003), and provide visual stability (Shin & Sommer, 2012). For example, the FEF receive feeds emanating in the superior colliculus, to create saccadic controls and stabilise vision (Wurtz, et al., 2011).

The FEF are therefore integral to visual search (Lane, Smith, Schenk, & Ellison, 2012; Muggleton, et al., 2003; Wurtz, et al., 2011). For example the FEF are intrinsically involved in both reflexive *(e.g. automatic eye movements responding to stimuli)* and goal-driven voluntary saccades *(e.g. the eyes are consciously moved to view specific objects in the environment)* (Ludwig & Gilchrist, 2003). These activities appear to utilise aspects of salience and priority (Ptak, 2012; Schutz, et al., 2011). For example, salience aspects such as colour appear to be important for efferent activations (Fecteau & Munoz, 2006; Muggleton, Juan, Cowey, Walsh, & O'breathnach, 2010).

1.4.3.2.2. Dorsolateral Prefrontal Cortex

The DL area receives information from the dorsal stream (Kravitz, Saleem, Baker, & Mishkin, 2011). Additionally, the DL maintains 'reciprocal connections with brain regions associated with motor control (basal ganglia, premotor cortex, supplementary motor area), performance monitoring (cingulate cortex), and higher-order sensory processing (association areas, parietal cortex)'[86] (Wood & Grafman, 2003, p. 140) . The DL also appears to play an important role in:

- working memory, because it directs 'attention to internal representations of sensory stimuli and motor plans' (Curtis & D'esposito, 2003, p. 415);

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85. A simplified model of the PFC has been utilised to minimise confusion, because the application of other more complex models would not be materially different within the context of this thesis.

86. The cingulate cortex plays a role in visuospatial orientation (Vogt, Vogt, & Laureys, 2006). The association areas referred to in this quote are linked to the somatosensory regions (Roland, O'sullivan, Kawashima, & Ledberg, 1996) described earlier in this appendix. These regions have not been covered in detail as their physiology and function have been grouped with other aspects for the purposes of simplicity.

- 'the decisional processes, preparing saccades by inhibiting unwanted reflexive saccades[87] (inhibition), maintaining memorised information for ongoing intentional saccades (short-term spatial memory), or facilitating anticipatory saccades (prediction), depending upon current external environmental and internal circumstances' (Pierrot-Deseilligny et al., 2003, p. 1460), which directly affect top-down processing; and

- 'the regulation of behaviour and control of responses to environmental stimuli' (Wood & Grafman, 2003, p. 140), which are modulated by emotional content (Ito et al., 2011).

1.4.3.2.3. Ventromedial Prefrontal Cortex

The VM receives sensory inputs from the ventral stream (Kravitz, et al., 2011), and also utilises reciprocal connections with the limbic system *(e.g. amygdala)* for the processing of emotions (Bechara, Damasio , Damasio , & Lee 1999).   Additionally, the VM interacts with the hippocampi and striatum to support memory related, and higher order, processing (Arco & Mora, 2009; Nieuwenhuis & Takashima, 2011), such as the direction of top-down control on goal directed behaviour (Arco & Mora, 2009; O'doherty, 2011). The ventromedial area is also closely linked with:

- 'the integration of information about emotion, memory, and environmental stimuli' (Wood & Grafman, 2003); and

- assessing aspects of value and reward (Kable & Glimcher, 2009).

1.4.3.3.   Orbitofrontal Cortex

The orbitofrontal area appears to be involved in self-evaluation behaviours (Beer, Lombardo, & Bhanji, 2009).   For example, the OF cortex is engaged in:

- **Reward Judgements.**   The OF manages reward and value related processes and the perception of negative reinforcers (Rolls, 2000), which are involved in 'motivational control and goal-directed behaviour' through conscious choice (Tremblay & Schultz, 1999, p. 704).

- **Associative Learning.**   The OF is responsible for linking stimuli across modalities to create associations that aid learning *(e.g. linking sight and taste stimuli with reward and punishment behaviour)* (Rolls, 2000; Schoenbaum & Roesch, 2005).

- **Influencing Planning.**   Associative learning helps to create expectations of predicted outcomes from actions, which link to limbic system areas such as the amygdala, and therefore emotionally affect goal directed behaviours *(e.g. plans)* (Saddoris, Gallagher, & Schoenbaum, 2005). Additionally, it appears that the OF and VM may interact when planning in terms of consequential behaviours (Zald & Andreotti, 2010).

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87.   This appears to work in conjunction with the FEF.

1.4.4.   Interaction between the Two Streams

1.4.4.1.   General Interaction

Although there is functional and anatomical separation of the dorsal and ventral streams (Yeterian, et al., 2012), which pass information between the occipital and frontal lobes, it is now widely accepted that there are numerous connections and synergies between them (Chan & Newell, 2008; Cloutman, 2012; Elliott, Tremblay, & Welsh, 2002).   For example, Weiller, Bormann, Saur, Musso, & Rijntjes (2011) illustrated how the dorsal and ventral streams need to interact to process language.   Three types of interaction between the streams have been proposed, and each has impacts on top-down and bottom-up processing.   These interactions can be categorised as follows:

- ***Independent Operation.***   In some situations the two streams appear to independently pass percepts to the prefrontal cortex (Lee & Donkelaar, 2002; Sanocki, Michelet, Sellers, & Reynolds, 2006) for integration (Yeterian, et al., 2012).

- ***Feed-back/Feed-forward Operations.***   In parallel with the independent processing, it appears that feed-back and feed-forward systems modulate the activities in the alternate stream.   For instance, dorsal stream information may reach the PFC much more quickly than ventral stream representations[88] (Laycock, et al., 2007).   Feed-back is then applied from the PFC to the visual cortex *(occipital lobe)*, which then moderates the attention within the ventral stream.   For example, Laycock, Crewther, Fitzgerald, & Crewther (2009) identified that the magnocellular *(dorsal stream)* information appear to play an important role in salience during word identification, because there is a feed-back system.   This feed-back then shapes attention within the parvocellular *(ventral stream)* (Laycock, et al., 2009).   Additionally, Foxe & Simpson (2002) identified that there are likely to be multiple iterations of feed-back and feed-forward between the two streams, and the frontal and occipital lobes, in the process of developing conscious awareness.   This is important, because it supports the implementation of both bottom-up and top-down processing within very short timeframes *(e.g. < 400 milliseconds)*.   As just one example, structures within the temporal lobe receive inputs from the prefrontal cortex to facilitate top-down processing of imagery (Kosslyn, Thompson, & Ganis, 2002).

- ***Cross-Talk Operation.***   There is also evidence of direct cross-talk between elements within the ventral and dorsal streams (Chen et al., 2007).   Such cross-talk appears to be strongly reciprocal (Felleman & Van Essen, 1991; Verhoef, Vogels, & Janssen, 2011).   This reciprocal communication directly moderates activities in the other stream and supports more effective cognition, such as the achievement of object recognition (Farivar, 2009).   Research indicates that the thalamus (Madary, 2011), pulvinar (Kaas & Lyon, 2007) and superior colliculus (Lyon, Nassi, & Callaway, 2010) are involved in such cross-talk activities.

These types of interaction support a 'flexible interactive system' that facilitates dynamic cognition (Cloutman, 2012, p. 3).   In fact this type of interaction is essential in

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88.   As explained in Section 1.4.2.1.

achieving numerous cognitive processes (Almeida, Mahon, Nakayama, & Caramazza, 2008; Koshino, Carpenter, Keller, & Just, 2005; Mcintosh & Lashley, 2008).

1.4.4.2. *Working Memory*

Much of the interaction described in the preceding section appears to take place within what is generically referred to as working memory. 'Working memory refers to the system or systems that are assumed to be necessary in order to keep things in mind while performing complex tasks such as reasoning, comprehension and learning' (Baddeley, 2010, p. 136). The role of working memory goes well 'beyond simple storage, allowing it to play an important role in cognition generally' (Baddeley, 2010, p. 138).

The key elements of, and connectivity associated with, working memory are illustrated in the model provided at Figure 1.21[89].
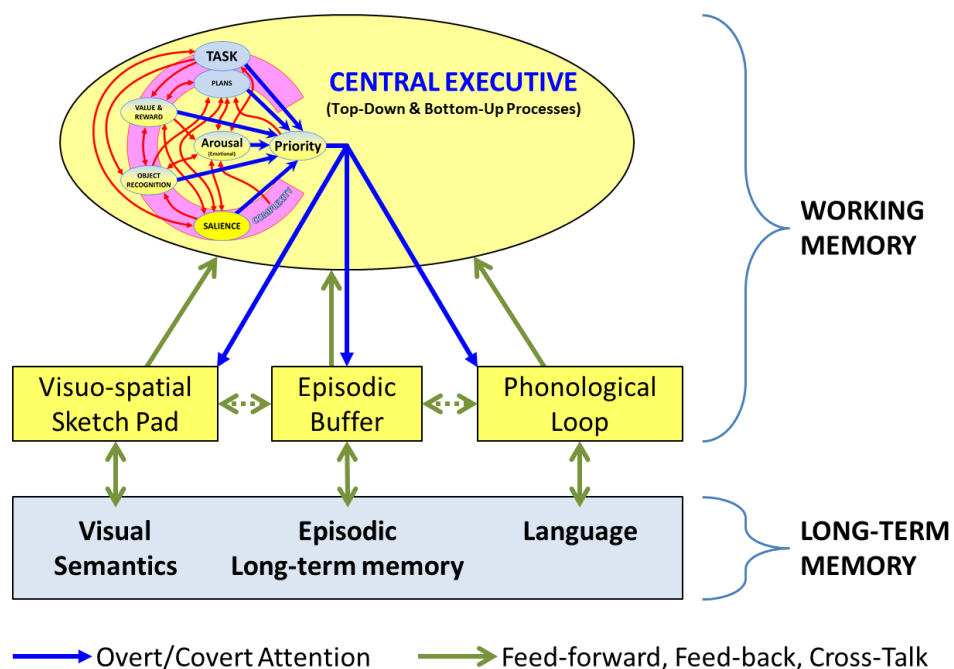
Figure 1.21:   Working Memory Model

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89.   This model has been adapted by the author from Figure 2 on Page 138 in Baddeley (2010). The significant changes made to this model are: (1) The separation between working and long term memory has been made more explicit in this model, than was achieved in Baddeley's version. (2) The top-down and bottom-up process model described in Section 2.2 in Volume 1 of this thesis has been explicitly placed into the central executive frame within this model. This allows the implicit aspects of the central executive mechanisms raised by Baddeley (2007, 2010) to be fleshed out more effectively. It is also noteworthy that this model does not illustrate other forms of working memory associated with the other senses such as; olfactory (smell) (Zelano, Montag, Khan, & Sobel, 2009), somatosensory (touch) (Savini, Brunetti, Babiloni, & Ferretti, 2012), and gustation (taste) (Savic-Berglund, 2004). For the purposes of this thesis, this oversight in Baddeley's (2010) model will not be significant, because this research is only focussed on visual input.

The key elements of this model are defined by Baddeley (2010) as the:

- **Central Executive.** The central executive is the attentional control system within this model (Baddeley, 2010), and it is responsible for managing the information within working memory (Baddeley, 1992). Although the processes applied for attentional control are not specified explicitly within Baddeley's model, they effectively align to the framework described in Section 2.2 *(in Volume 1)* of this thesis.

- **Visuo-spatial Sketch Pad.** This form of working memory handles and manipulates visual information and imagery (Baddeley, 1992).

- **Phonological Loop.** The phonological loop appears to include two components, which include the following:

  ➢ a store (storing speech-based information for about 1 to 2 seconds); and

  ➢ this is coupled with an articulatory control process *(which is 'analogous with inner speech')* (Baddeley, 1992, p. 255)[90].

- **Episodic Buffer.** The episodic buffer 'is capable of holding multidimensional[91] episodes or chunks[92], which may combine visual and auditory information possibly also with smell and taste. It is a buffer that provides a temporary store in which the various components of working memory, each based on a different coding system, can interface with information from perception and long-term memory. The episodic buffer is assumed to have limited capacity of about four chunks or episodes, and to be accessible through conscious awareness' (Baddeley, 2010, p. 138).

- **Long Term Memory (LTM).** In addition to the interactions between the elements of working memory, these active stores also:

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90. These functions are closely associated with Wernicke's areas *(see Section 1.4.1.2)* and Broca's area *(see Section 1.4.1.3.6)*.

91. Within the context cited by Baddeley (2007, 2010) the term 'multidimensional' is better aligned to the concept of being multimodal.

92. The concept of chunks was raised by Miller (1956) to represent the mental aggregation of bits of information. In Miller's (1956, p. 83) model a 'bit of information is the amount of information that we need to make a decision between two equally likely alternatives. If we must decide whether a man is less than six feet tall or more than six feet tall and if we know that the chances are 50-50, then we need one bit of information.' A bit is therefore not necessarily a single aspect *(e.g. a visual feature)*, but a conceptual linking of information for binary analysis, which in itself is an aggregation of discriminable variables *(e.g. points, colours, tones, etc.)* (Miller, 1956). Miller's (1956) chunk concept is therefore not a definitive measure, but a construct for understanding how information is organised or grouped, to allow it to be managed more effectively within working memory. This concept is important, because it explains how the mental aggregation of information through chunking can assist the brain to handle more information than would be possible for individual items or bits (Miller, 1956). Such aggregation may be influenced by aspects like relational pattern matching (Kirsch, Sebald, & Hoffmann, 2010) within representations.

> ➤ recall information from long term memory[93] to develop representations, which are utilised for cognition; and

> ➤ feed information into long term memory, so this can be recalled later (Baddeley, 2007).

As illustrated in Figure 1.21, each of the working memory and long term memory elements interact with each other through feed-forward, feed-back and cross-talk processes. The neural activations that support these interactions are known as synaptic reverberations (Mongillo, Barak, & Tsodyks, 2008), which are explained in the following section.

1.4.4.3. Reverberation – The Underlying Process for Working Memory Management

In practical terms, reverberation simply refers to the stimulation of neurons to keep them activated and processing the information within working memory *(known as persistence)* (Wang, 2001). This is a crucial activity, because it allows the information to be held on-line for long enough to:

• be utilised effectively for cognition (Mongillo, et al., 2008); and

• provide sufficient reverberations to initiate the 'the structural changes that underlie consolidation and formation of permanent LTM' (Nadel & Hardt, 2011, p. 252)[94].

Working memory related reverberations take place within specific areas such as the frontal lobes *(e.g. prefrontal cortex)*, and also between areas such as the thalamus, temporal lobe *(e.g. inferotemporal area within the ventral stream)*, and posterior parietal areas *(e.g. Posterior Parietal cortex/Lateral Intraparietal areas within the dorsal stream)* (Wang, 2001).

One of the key drivers that creates these reverberations is attention (Khan & Muly, 2011), and in the absence of attention the information within working memory will

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93. Long term memory refers to 'memory that stores information on a relatively permanent basis, although it may be difficult to retrieve' (Feldman, 2005, p. 226). The generic concept of long term memory can also be further delineated as 'long term' (LT) *(which lasts hours to months)*, or long lasting (LL) *(which lasts from months to a lifetime)* (Garrett, 2003). In either case, LT and LL memories are typically held as consolidations *(e.g. involving the melding of different memories and aspects of memory into a consolidated memory structure)* (Garrett, 2003), which can be categorised as episodic *(see Footnote 63)*, semantic *(see Footnote 58)*, or non-declarative *(procedural)* memories *(see Footnote 65)* (Feldman, 2005). At the biological level, the development of long term and long lasting memories is supported through the process of Long Term Potentiation (LTP), which entails creating new connections between brain cells (Garrett, 2003). These LTP connections are a critical element of the biological processes underlying learning (Garrett, 2003). Alternatively, the process of forgetting is associated with Long Term Depression (LTD), in which the synaptic connections between brain cells are weakened, or lost (Garrett, 2003).

94. See Footnote 93 for more information on consolidation and long term memory.

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typically be lost very quickly (Chua, 2009; Ptak, 2012). The generation of the top-down and bottom-up processes described in Chapter 2 *(in Volume 1)* of this thesis are therefore very important in terms of ensuring that the pertinent information will be held in working memory, and then transferred to LTM.

Having addressed the matter of general interactions and working memory, the following section returns to a description of the remaining element of the visual processing model provided in Figure 1.1. This element is the metencephalon.

1.5.   Metencephalon

The metencephalon contains structures within the hindbrain, such as the pons and cerebellum (Raz et al., 2003). The pons forms a bulbous part of the brainstem, which influences sleep and arousal (Garrett, 2003). Such arousal is in turn affected by neural regions like the Suprachiasmatic nucleus (Mistlberger, 2005) *(See Section 1.3.3.2 for more details on the SCN)*.

The cerebellum plays an important role in efferent control (Glickstein & Doron, 2008), and is implicated in maintaining balance and refining 'movements initiated in the motor cortex by controlling their speed, intensity and direction' (Garrett, 2003, p. 438). Additionally, the cerebellum is also involved in shaping aspects related to attention, language, and working memory (Glickstein, 2007; Strick, Dum, & Fiez, 2009). However, these activities within the cerebellum do not appear to be aligned to cognition directly, but predominantly to the efferent controls related to these activities (Glickstein & Doron, 2008), and the functional automation of cognitive activities (Merker, 2007; Miller, 2000).

To achieve these activities, the cerebellum is closely linked with key structures within the interbrain and midbrain regions (Kandel, et al., 2000), and through these (Wurtz, et al., 2011), to areas within the frontal lobe such as the FEF (Li, Medina, Frank, & Lisberger, 2011; Schutz, et al., 2011). Such connections support the cerebellum to play an important role in reading *(and in particular sub-lexical reading)* (Borowsky, et al., 2006; Schurz et al., 2010), and writing (Katanoda, Yoshikawa, & Sugishita, 2001). Of greatest importance for this thesis is the efferent saccadic control (Salman et al., 2006), and smooth eye tracking control (Lisberger, 2010) provided by the cerebellum.

1.6.   Eye Control Process

As illustrated in the preceding sections of this appendix, numerous physiological elements within the human brain contribute to top-down and bottom-up processes, which then affect comprehension and impressions. There are two additional physiological operations, which are important within the context of this thesis, because they are integral to shaping attention. These processes relate to:

•   ***Saccadic Eye Movements.*** Saccades are used to move the fovea within the visual field (Leigh & Zee, 1999), so the eye can fixate on specific objects (Liversedge & Findlay, 2000). These saccadic eye movements are therefore rapid movements of the eye, which are happening most of the time, to generate awareness of the

environment and focus attention on specific objects (Casey, 2004; Vanrullen & Koch, 2001) .

- ***Smooth Pursuit Eye Movements.*** Smooth pursuit eye movements support continual clear vision of objects, which are moving within the visual environment. (Leigh & Zee, 1999). In this form of eye movement the fovea is aligned to the object on which the person is focussing their attention, and the eye then tracks the movement (Lisberger, 2010).

Figure 1.22[95] provides a simplified explanation of the differences between these two types of eye movements.
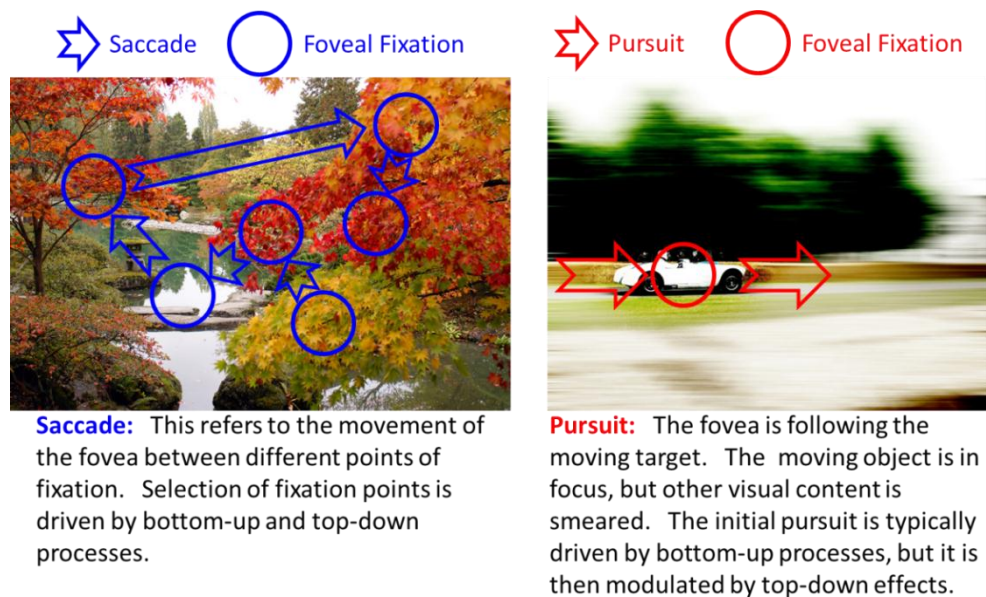
Figure 1.22: Illustration of the difference between saccades and pursuits.

These eye movements are controlled by interrelated systems (Fulton, 2003a; Orban De Xivry & Lefevre, 2007; Schutz, et al., 2011), and they are designed to shift the high definition foveal vision to important locations within the field of view (Schutz, et al., 2011), to facilitate awareness and attention (Reynolds & Chelazzi, 2004).

Drivers for these aspects appear to be remarkably similar for most people (Rothkopf, Ballard, & Hayhoe, 2007). However, the conscious or unconscious implementation of saccades and smooth pursuits is also task and context dependent (Mcdowell, et al., 2008; Rothkopf, et al., 2007). For example, the controls utilised to hit a nail with a hammer *(active engagement in the task)* will be different from those applied to view a presentation *(passive reading and viewing)* (Flanagan & Johansson, 2003). This thesis will therefore focus only on those aspects that are pertinent to the hypotheses which relate to passive reading and viewing.

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95. Concepts illustrated in these diagrams and the associated text are drawn from Schutz, et al. (2011); Ludwig & Gilchrist (2003); Liversedge & Findlay (2000); Au & Lovegrove (2007); Lisberger (2010) and McDowell, Dyckman, Austin, & Clementz (2008).

Both types of eye movement are pertinent to this thesis, because saccades are utilised to view information on the screen *(e.g. reading)*, and smooth pursuits are used to track moving objects *(e.g. viewing animations)*. The following subsections explain these eye movements, and their implications in more detail.

1.6.1. Saccades

Saccades pertinent to this thesis can be classified as either reflexive or volitional (Leigh & Zee, 1999), and these can be categorised as follows[96]:

- ***Reflexive.*** Reflexive saccades are made in response to visual stimuli (Leigh & Zee, 1999) and these reposition the fovea in response to external cues, which are typically initiated by bottom-up processing, but can then be modulated by top-down processes. (Mcdowell, et al., 2008).

- ***Volitional.*** This type of saccade is related to purposeful behaviours, which are normally linked to top-down processes (Leigh & Zee, 1999; Mcdowell, et al., 2008). Some examples of volitional saccades include; shifts of active attention based on plans *(remembering a scene and the location of objects in the view)*, object recognition *(recognising a shape and scanning it in a standard way)*, or on command *(consciously controlling the point of fixation)* (Leigh & Zee, 1999; Mcdowell, et al., 2008).

Within these two categories, the most important form of eye movement for this thesis is the pro-saccade[97], which involves the repositioning of the fovea to specific locations or

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96. Different articles also utilise other related terms. In particular, the terms stimulus and goal driven are commonly used. Stimulus driven is best aligned to reflexive saccades, whereas goal driven best aligns to volitional eye movements *(See Ludwig & Gilchrist (2003) and Mazer & Gallant (2003) for examples of the use of these terms)*. However, there also appears to be some ambiguous aspects related to the use of these terms, because some goal-driven behaviours may be better aligned to reflexive saccades *(e.g. it is not clear if low-level goal-driven reward mechanisms utilised within the SEF are specifically just volitional or reflexive)*. For this reason, the model used in this thesis utilises the reflexive and volitional paradigm, because the differentials and thresholds for stimulus/goal driven saccades are not directly material to the hypotheses being tested.

97. Leigh and Zee (1999) also describe three other types of saccade, which they call: (1) Express saccades: Very short latency saccades that can be elicited when the novel stimulus is presented after the fixation stimulus has disappeared (gap stimulus). (2) Spontaneous saccades: Seemingly random saccades that occur when the subject is not required to perform any particular behavioural task. (3) Quick phases: Quick phases are nystagmus *(this is where the eyes reset during prolonged rotation and direct gaze toward the oncoming visual scene)* generated during vestibular *(this is where the eye holds the image steady when briefly rotating the head)* or optikokinetic *(this is where the eyes rotate to hold the scene steady during sustained head rotation)* stimulation, or as automatic resetting movements in the presence of spontaneous drift of the eyes. *(This footnote contains intermingled quotes from Pages 4 and 91 within Leigh and Zee (1999))*. For the purposes of this thesis the express saccades are being grouped with the other reflexive pro-saccades, because they are created by changes in the content within the visual field, and are therefore covered within the standard bottom-up and top-down

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objects within the visual scene (Amlôt & Walker, 2006; Desouza, Iversen, & Everling, 2003). Alternatively, there are anti-saccades, which are inhibiting eye control processes which suppress pro-saccades (Domagalik, et al., 2012). Whereas, pro-saccades can be either reflexive or volitional *(reflecting bottom-up and top-down processes)*, anti-saccades are volitional (Domagalik, et al., 2012; Mcdowell, et al., 2008).

The last important saccadic influence within the context of this thesis relates to the gap effect. The gap effect is generated when visual stimulus is removed for a short period (Coubard, Daunys, & Kapoula, 2004). For example this can be achieved by blanking a screen, or removing the objects from a screen for a short time, before showing other objects on the screen. There are two important outcomes related to the application of the gap effect in terms of this thesis, and these are:

• the following saccade toward the new object becomes much faster, so the point of attention is moved to the new object more quickly after a gap stimulus is used (Anderson & Carpenter, 2007); and

• when all visual stimuli are removed *(such as a cut between scenes in a film, or the use of blank separators during a presentation)* then the gaze is typically shifted back to the centre of the screen (Schutz, et al., 2011).

1.6.2. Smooth Pursuits

Smooth pursuits are typically initiated reflexively (Tavassoli & Ringach, 2009), and are generated by the perception of object motion within the visual field (Berryhill, Chiu, & Hughes, 2006). Once the fovea has reflexively fixated on the movement it is 'a high probability' that the eye will start to track the moving object (Schutz, et al., 2011, p. 19). To facilitate this tracking, top-down processing can also be applied (Santos, Gizzi, & Kowler, 2010; Thier & Ilg, 2005).

The first part of the smooth pursuit is therefore referred to as open loop *(responding directly to the stimulus)*, but for extended tracking, feedback systems within the brain close the loop to optimise the fixation on the moving target (Schutz, et al., 2011).

1.7. Practical Implications

The preceding sections of this appendix have illustrated some key aspects of psychophysics and biopsychology, which support top-down and bottom-up processing of visual stimuli. The following points are of particular importance in terms of the hypotheses being investigated within this thesis:

• ***External stimuli can shape attention.*** As explained in Section 1.2, exogenous stimuli can shape the level of attentiveness applied by the viewer. This is important, because it can drive the way in which the viewer processes the information. The intent of effective visual design should be to present the

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processes. The spontaneous saccades and quick phase saccades are not covered explicitly as they are not germane to the hypotheses being investigated.

information in ways that motivate higher levels of awareness for the key information being provided.

- ***Comprehension and impressions are linked.*** Limbic system connectivity ensures that impressions[98] are interwoven with the cognitive processes discussed in this appendix. These interactions must therefore be taken into account when designing visual materials.

- ***The neural mechanisms are critical to design.*** As illustrated in the preceding information, there is now a significant level of understanding of the mechanisms utilised to process visual information. Failure to take into account these mechanisms can lead to visual design solutions that are counterproductive, and inhibit effective communication.

This thesis is therefore designed to apply the psychophysical, biopsychological, and physiological principles discussed in this appendix to identify optimal visual design principles. This approach therefore supports a deliberate design process, which is based on relevant theories, principles and guidelines, rather than an iterative subjective process. However, it is not intended that such design would be ultimately deterministic, or that prototyping would not be useful in the development of optimised visual materials.

General Note by the Author

Due to the substantial advances in neural scanning and monitoring techniques, which have been achieved over the past few years, there have been significant enhancements in the general understanding, and specific functionality, of various elements within the human brain. These advances have assisted in developing knowledge within the fields of psychophysics, biopsychology, and cognitive science. In particular, the expansion of knowledge in these fields within the last five years has been an important facilitator for the development of the concepts that are being addressed within this thesis. The author therefore wishes to take this opportunity to thank the other researchers who have made this current analysis feasible.

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98. The term impressions refers to the subjective feeling about the presentation, which results from the way the material is presented. This concept is explained in more detail in Chapter 1 of this thesis.

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