



Computational Modeling of Visual Selective Attention

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By

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Περίληψη

Η μελέτη της διατριβής στοχεύει να συνεισφέρει σημαντικά στη μελέτη της **ανθρώπινης προσοχής**, και πιο συγκεκριμένα της **οπτικής επιλεκτικής προσοχής** κυρίως μέσω της δημιουργίας ενός γνωστικού υπολογιστικού μοντέλου βασισμένο σε πληροφορία και γνώση που πηγάζει μέσα από μια διαθεματική προσέγγιση.

Συγκεκριμένα, οι επιστημονικές συνεισφορές της εργασίας προέκυψαν μέσα από τη μελέτη κατάλληλων προσομοιώσεων τριών σημαντικών πειραματικών μελετών. Πιο συγκεκριμένα, το υπολογιστικό μοντέλο προσέφερε λύσεις και επεξηγητικές υποθέσεις στις διάφορες διαφωνίες και αντιδράσεις που προκάλεσαν τα πειράματα αυτά στην επιστημονική κοινότητα βασισμένες στα αποτελέσματα προσομοίωσης. Το υπολογιστικό μοντέλο αναπτύχθηκε συνδυάζοντας τεχνικές συμβολικής προσέγγισης οι οποίες βασίζονται σε αλγόριθμους υψηλού επιπέδου με υποσυμβολικές τεχνικές οι οποίες χρησιμοποιούν πιο απλουστευμένα αριθμητικά μοντέλα. Επομένως το υπολογιστικό μοντέλο έχει την δυνατότητα να δέσει αποτελεσματικά τις αλληλοεπιδράσεις στο επίπεδο ομάδας νευρώνων με συμπεριφοριστικά δεδομένα, το οποίο δίνει ένα σημαντικό πλεονέκτημα στην προσπάθεια δημιουργίας θεωρητικού υπόβαθρου επεξήγησης αναφορικά με το πώς προκύψαν τα τελευταία.

Επιπρόσθετα, μέσα στα πλαίσια της διατριβής αυτής, νέες πειραματικές μελέτες διεκπεραιώθηκαν σε συνεργασία με το εργαστήριο της πειραματικής ψυχολογίας του Πανεπιστημίου Κύπρου ούτως ώστε να επεκταθεί η γνώση μας όσον αφορά την συμπεριφοριστική αντίληψη της προσοχής καθώς επίσης για να προσφέρουν καινούργια δεδομένα για σκοπούς σύγκρισης και βελτίωσης του μοντέλου. Ακόμη, η προσπάθεια δημιουργίας ενός ρεαλιστικού υπολογιστικού μοντέλου, σε συνδυασμό με τις επιτυχείς προσομοιώσεις των σημαντικών αυτών πειραμάτων, δημιούργησαν μια αξιόλογη βάση για μετέπειτα κοινωνικές και ιατρικές εφαρμογές αλλά και εφαρμογές σε θέματα που αφορούν την υπολογιστική νοημοσύνη.

Η δομή της μελέτης χωρίζεται σε τέσσερα κυρίως μέρη. Στο πρώτο μέρος δίνεται μια εισαγωγή για τον ρόλο της πληροφορικής στην ανάπτυξη της γνωστικής επιστήμης καθώς επίσης και ένα εισαγωγικό υπόβαθρο για την ανθρώπινη προσοχή από ψυχολογική και νευροφυσιολογική σκοπιά (Κεφάλαια 1, 2 και 3). Το δεύτερο μέρος αφιερώνεται σε μια συγκριτική μελέτη μεταξύ διάφορων υπολογιστικών μοντέλων υπολογιστικής προσοχής τα οποία είχαν σημαντική επίδραση στον τομέα αυτό και κυρίως στις διάφορες ιδέες που είχα. Στο τρίτο μέρος παρουσιάζεται μια λεπτομερής μαθηματική ανάλυση του μαθηματικού/υπολογιστικού μοντέλου που ανέπτυξα, καθώς και οι διάφορες εφαρμογές του με κατάλληλες προσομοιώσεις. Τέλος, στο τέταρτο μέρος, οι διάφορες επιστημονικές συνεισφορές που προέκυψαν από αυτή τη μελέτη συνοψίζονται, και αναπτύσσονται ορισμένες νέες ιδέες για την επέκταση και συνέχιση της μελέτης.

Abstract

The main goal of this research is to collect and integrate information and knowledge from different disciplines into a new computational model that will be able to provide contributions in the research of “*visual selective attention*”.

The contributions derived from this thesis, have been mostly associated with the computational simulations of three behavioral experiments related with visual selective attention that initiated discussions and controversies in the scientific literature regarding their underlying explanations. These are the **attentional blink phenomenon** by Raymond, Shapiro and Arnell (1992), the behavioral experiment that inspired the **perceptual load theory** by Lavie (1995) and the experiment that initiated a controversial debate on the **relation between attention and consciousness** by Naccache, Blandin and Dehaene (2002). In accordance, guided by the simulation results, a theoretical framework has been developed and presented on how the behavioral responses for each of the corresponding experiments were obtained, based on low level neural interactions, something that has not been clearly presented in the literature so far. The methodology behind the implementation is based on a new approach that combines the detail representations required in a connectionists spiking neural network model with more abstract concepts from cognitive psychology. As a result, the computational model effectively links the low level neural interactions with behavioral data, thus providing concrete explanations on how the latter were obtained.

Furthermore, within the scopes of this thesis, new experimental tasks related with the simulated experiments have been carried out in the Experimental Psychology Lab of the University of Cyprus in an attempt to extend our knowledge about the behavioral aspects of attention as well as to provide data that are necessary for comparison and supplementary improvement of the model. Finally, the biologically inspired structure of the model, together with successful predictions and simulations of the corresponding behavioral experiments have created a concrete backbone for future utilization of the model in social, medical and computational intelligence applications.

The structure of this thesis is divided into four main parts. In the first part, introductory information regarding the role of computer science in cognitive modeling is given, along with some background information related to visual selective attention. The second part is dedicated to a comparative literature review on relevant computational models of prevalent scientific impact in the field.

In the third part a detailed description of the proposed model is presented along with the simulation results of the three behavioral experiments. Finally, in the fourth part, the contributions and conclusions of the present study are summarized and the possible research paths and applications that can be effectively linked for future work with this study are explained.

Table of contents

1.	Introduction.....	18
1.1	The human brain from the computer science perspective.....	18
1.2	Cognitive modeling.....	20
1.2.1	Methods of computational-cognitive modeling	21
1.3	Cognitive modeling of visual selective attention- motivations.....	22
1.3.1	Approach to cognitive modeling of visual selective attention	24
2.	Theoretical background on human attention.....	26
2.1	The attentional system.....	27
2.2	Exogenous and endogenous orienting of Attention	28
2.3	Theories of selective attention	29
2.3.1	Early Selection Theories	30
2.3.2	Late Selection Theory (an alternative of Selection Theory, the “divided theory”).....	31
2.3.3	Perceptual Load Theory	32
3.	Visual selective attention	33
3.1	The visual system.....	33
3.2	The visual pathway	33
3.3	The Receptive field concept.....	37
3.4	Measuring Brain Activity.....	39
3.4.1	Functional Magnetic Resonance Imaging, Computer Tomography and Electroencephalography.....	40
3.5	Neural basis of selective attention.....	48
3.5.1	Cortical areas involved with visual selective attention	48
3.6	Neural mechanisms of Selective Attention	51
3.6.1	Bottom-Up neural mechanisms.....	55
3.6.2	Top-down neural mechanisms for attentional selection.....	59

4.	Computational models of visual selective attention - A review.....	66
4.1	Models simulating behavioral data	66
4.1.1	Corollary Discharge of Attention Movement model (Taylor & associates, 2000+) ..	66
4.1.2	The Simultaneous Type/Serial Token model (ST ₂)-(Bowman and Wyble, 2007)....	67
4.1.3	The global workspace model, (Dehaene Sergent and Changeux 2003).....	69
4.1.4	Neural Theory of Visual Attention (Bundesen, Habekost, Kyllingsbæk 2005).....	70
4.2	Models simulating visual saliency	71
4.2.1	A Model of Saliency-Based Visual Attention for Rapid Scene Analysis (Itti et al., 1998))	71
4.2.2	The Selective Tuning Model – Tsotsos 1990+.....	72
4.3	Algorithmic Models	74
4.3.1	The Adaptive Resonance Theory (ART) – (Grossberg 1987+).....	74
4.4	Modeling the underlying Neurobiology of Attention.....	75
4.4.1	A model for the neuronal implementation of selective visual attention based on temporal correlation among neurons (Niebur & Koch 1994)	75
4.4.2	The Biased Competition model- Desimone and Duncan (1995)	77
4.4.3	Setting the path towards the proposed model.....	78
5.	The proposed computational model of visual selective attention	80
5.1	An overview of the proposed computational model	82
5.1.1	RSVP model.....	83
5.1.2	The spatial attention model	90
5.2	Mathematical formulations of the proposed model units.....	91
5.2.1	Integrate and fire neuron models.....	91
5.2.2	Synaptic currents.....	92
5.2.3	Coincidence detector nodes.....	94
5.2.4	Working memory nodes.....	95
5.3	The computational model’s network mathematical representation.....	98
5.3.1	Neural representation of incoming stimuli.....	98
5.3.2	Mathematics of the RSVP	102

5.3.3	The spatial attention model	109
5.4	Network dynamics	111
5.4.1	Testing different input stimulus conditions in the proposed model	113
5.5	Justification on the adoption of the proposed implementation.....	116
6.	Applications of the model	119
6.1	The Attentional Blink paradigm (Raymond, Shapiro and Arnell (1992)).....	119
6.1.1	Simulation results.....	121
6.1.2	How the model reproduces the experimental data	122
6.2	The Perceptual Load Theory behavioral experiment (Lavie, (1995)).....	126
6.2.1	Method of the PLT task.....	127
6.2.2	Experimental and simulation results	128
6.2.3	How the model reproduces the experimental data	130
6.2.4	A comment on the simulation results.....	137
6.3	A behavioral experiment regarding the relation between attention and consciousness by Naccache, Blandin and Dehaene, (2002)	137
6.3.1	Method and experimental results of the Naccache, Blandin and Dehaene, (2002) task 138	
6.3.2	Simulation results of the Naccache, Blandin and Dehaene, (2002) task.....	139
6.3.3	How the model reproduces the experimental data	139
6.3.4	A comment on the simulation results.....	141
7.	Conclusions, contributions and future work	145
7.1	Contributions of the research work.....	145
7.2	Future work	147
7.3	Concluding remarks	147
	References.....	149

List of figures

Figure 1-1 The role of computer science in the study of the human brain.....	19
Figure 1-2 The schematic representation of a “white – box”	20
Figure 1-3 The schematic representation of a “white – box”	20
Figure 1-3The hybrid configuration of the proposed computational model	22
Figure 1-4 Computational modeling as a tool for better understanding of the attentional mechanism as well as to enhance the inspiration of new computational intelligence algorithms.....	24
Figure 1-5 The multi-disciplinary approach for cognitive modeling of visual selective attention. ..	25
Figure 2-1 Broadbent's model. Source from: <i>Perception and communication</i> . (Broadbent, D. E., 1958).	30
Figure 2-2Schematic representation of the attenuation theory by Treisman (1960).....	30
Figure 2-3 Schematic representation of the late selection theory by Deutsch and Deutsch (1963) ..	31
Figure 3-1 The six layers of the retina	34
Figure 3-2 The route to the primary visual cortex	34
Figure 3-3 The retina and cortical areas for visual processing in primate from van Essen et al (1992). V1 denotes visual area 1, the primary visual cortex and the largest visual area containing detailed representation of the visual input; V2 for visual area 2; LGN for lateral geniculate nucleus; FEF for frontal eye field , SC for superior colliculus, IT for inferotemporal cortex, MT for middle temporal area and LIP for lateral intra-parietal area. The lower case letters ending some of the abbreviations often denote spatial locations of the cortical areas, e.g., v for ventral, d for dorsal. ..	35
Figure 3-4 The two main visual pathways after the projection of the visual stimuli to primary visual area V1 (http://thebrain.mcgill.ca)	36
Figure 3-5 Receptive fields of the on and off retinal ganglion cells when the center or the background is illuminated, or when both center and surround are illuminated, Hubel (1963) – left image; Response of complex cells in the primary visual cortex (right image).	38
Figure 3-6 Increasing complexity of the receptive field properties along the visual pathway. Image from: Yantis (2005).....	39
Figure 3-7 The physical setup for recording from awake, moving monkeys. Image by Evarts (1973).	40
Figure 3-8 A layer of pyramidal cells in the cortex which can be seen as a current dipole generating an orthogonally oriented magnetic field.	41
Figure 3-9 The MEG sources generated by similar orientation pyramidal neurons	42
Figure 3-10 The SQUID sensor (Hamalainen 1992)	43
Figure 3-11 The gradiometer (Hamalainen et al., 1992).....	44

Figure 3-12 Measuring the total brain activity from the sources that generate it (forward problem) and the inverse problem to identify the localization of those sources based on the measurements..45

Figure 3-13 Equivalent Current Dipole assumption. The red arrow in the rightmost figure represents the assumption of an equivalent current dipole. Then based on the activations that it is calculated to produce in the MEG sensor it can be combined with the actual measurements and to provide an estimate of the source position.....46

Figure 3-14 The MFT solutions from the four source spaces are combined into one (center) for estimating the source of the brain activity. Image by Yuka Okazaki PhD thesis (2007).....47

Figure 3-16 The alerting, orienting and executive systems of the attentional mechanism according to Posner and Petersen (1990). Image from Posner and Rothbart, (2007).....48

Figure 3-5 Interaction between bottom up processing and top down control signals.....49

Figure 3-17 Regions generating top down signals and visual areas that interact with these signals.50

Figure 3-18 One basic possible control system of visual selective attention.....51

Figure 3-19 Neural activity of a V2 neuron, from Reynolds and Desimone (1999).....52

Figure 3-20 The response of a V4 neuron in the three different stimuli conditions by Reynolds et al (2000).53

Figure 3-21 Response of a V4 neuron when a preferred and a poor stimulus are presented alone and in pair at the same receptive field. Figure adapted by Reynolds and Desimone (2003).54

Figure 3-22 Reaction time analysis of the experiment by VanRullen et al, (2003).55

Figure 3-23 Experimental results by Nothdurft, Gallant and Van Essen (1999)56

Figure 3-24 An example of iso-orientation suppression.58

Figure 3-25 An example showing the effect of saliency.....59

Figure 3-26 A) Shows the two stimuli with the lower being the one that is placed within the receptive field of the neurons being recorded. The spike recording site is shown with the green square and the LFP recording site with the yellow square. B) Shows the firing rate in the two conditions (monkey attending on the stimulus inside the recorded receptive field – red line- and monkey attending on stimulus outside the recorded receptive field – blue line). C) Shows the respective power spectra. Image designed based on the data by Fries et al. (2001)61

Figure 3-27 A) The stimulation of pairs of neurons with common and independent components. B) A typical ρ_T versus c curve as estimated from a pair of neurons according to de la Rocha et al (2007).64

Figure 4-1 A schematic of the CODAM model (Taylor & Rogers 2002).67

Figure 4-2 The schematic representation of the ST2 model by Bowman and Wyble (2007).68

Figure 4-3 Processing pathways in the neuronal global workspace model of conscious access. Image by Dehaene et al (2003).69

Figure 4-4 A schematic Architecture of the proposed model by Itti et al. (1998)	72
Figure 4-5 The pyramidal architecture of the selective tuning mode (Tsotsos 1990+).....	73
Figure 4-6 The basic ART structure (Carpenter and Grossberg, 1987).....	74
Figure 4-7 The Architecture of the proposed model by Niebur and Koch (1994).....	76
Figure 4-8 The modulation of the early neural activity before entering area V2. In the proposed model, the output from V2 projects into neuronal "stacks" in V4, where it excites pyramidal cells as well as inhibitory interneurons. These V4 interneurons, in turn, inhibit the pyramidal cells of opposing feature selectivity and thus contribute in the general mechanism of selection.....	76
Figure 4-9 A simple connectivity representation for the biased competition model. Figure adapted by Reynolds et al (1999).	78
Figure 5-1 The RSVP and spatial attention tasks.....	81
Figure 5-2 Diagram of the RSVP proposed computational model.	83
Figure 5-3 The different modules that interact in the second stage of processing.....	87
Figure 5-4 A possible relation between ERPs and the RSVP model implementation	89
Figure 5-5 Spatial attention model schematic representation	90
Figure 5-6 Discrete computations in a simple example of neural processing. Each black represents a neuron and the red area corresponds to the synaptic activity caused by presynaptic neurons.	94
Figure 5-7 Representation of the coincidence detector mechanism.....	95
Figure 5-8 Working memory module functionality	97
Figure 5-9 The Itti and Koch (2000) architecture of the saliency map model, based on the Koch and Ulfman (1985) implementation. Image from Itti and Koch (2000).....	99
Figure 5-10 An example of image processing by the saliency map model.....	100
Figure 5-11 Generation of the input neurons spike trains.....	101
Figure 5-12 Generation of an output neuron spike train in the endogenous goals module.....	102
Figure 5-13 A schematic representation of the RSVP model implementation	103
Figure 5-14 Interaction of perceptual (temporal) cue in the early stages of processing	104
Figure 5-15 The temporal filter mechanism.....	106
Figure 5-16 The correlation control module mechanism.	107
Figure 5-17 A schematic representation of the spatial attention model.....	110
Figure 5-18 Changes in the spike-triggered average power spectrum based on the g_{AMPA}/g_{NMDA} ratio as presented in Buhmann and Deco (2008).	112
Figure 5-19 The three stimuli conditions that the model was tested.....	113
Figure 5-20 Initial firing rate representation of the two stimuli according to the saliency map model	114
Table 1 The measurement of synchronization between the three different conditions tested on the proposed computational model.	115

Figure 5-21 Neural response at the three different stimuli conditions for the two layers under investigation. In the above plots, the y axis corresponds to a different neuron in the corresponding layer and the x axis the time. A red dot means that two or more neurons have fired synchronously.115

Figure 6-1 The use of the RSVP methodology in attentional blink studies. Participants are asked to identify targets T1 and T2 that are presented, within a sequence of distractors.119

Figure 6-2 The basic curve from attentional blink studies based on the behavioral data from Chun and Potter (1995) showing the percentage of correct T2 identification given the successful identification of T1 as a function of SOA.120

Figure 6-3 Simulation Data from the proposed model.....121

Figure 6-4 The neural activations initiated by the processing of the target when measured from the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing SL₂).123

Figure 6-5 Processing of the second target falls within the time window that the P300 signal of the first target interacts. Therefore the second target, although it has strong correlations with the endogenous goals, the control signal is contradicted by the P300 inhibitory interaction.124

Figure 6-6 The coupling inhibitory interactions between stimuli125

Figure 6-7 High-load trial with incompatible distractor128

Figure 6-8 Low-load trial with compatible distractor128

Figure 6-9 Median latency for high load condition (error bars represent standard errors)129

Figure 6-10 Median latency for low load condition (error bars represent standard errors)129

Figure 6-11 Simulation results for high load condition130

Figure 6-12 Simulation results for low load condition130

Figure 6-13 Low and high load conditions together with the saliency map output131

Figure 6-14 a) shows the level of activations of the neurons that correspond to each stimulus in the high load condition as these are calculated according to the saliency map without taking into consideration the spatial attention interactions and b) with the spatial top down signal interactions. c) Shows the level of neural activity after the semantics top down interactions in the second stage of processing133

Figure 6-15 The neural activations that correspond to the target and the flanker when measured from the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing SL₂) in the high load condition.134

Figure 6-16 a) shows the level of activations of the neurons that correspond to each stimulus in the low load condition as these are calculated according to the saliency map without taking into consideration the spatial attention interactions and b) with the spatial top down signal interactions.

c) Shows the level of neural activity after the semantics top down interactions in the second stage of processing135

Figure 6-17 The neural activations that correspond to the target and the flanker when measured from the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing (SL₂) in the low load condition.136

Figure 6-18 The experimental setup by Naccache et al., (2002).....138

Figure 6-19 Basic pattern of findings from Naccache et al., (2002).....139

Figure 6-20 Median reaction times from the simulations, (error bars represent standard errors)...139

Figure 6-21 The neural activations that correspond to the prime when measured from the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing (SL₂).140

Figure 6-22 The neural activations that correspond to the prime in the cued conditions, when measured from FS₂ and SL₂.141

List of acronyms/abbreviations

AB	Attentional Blink
ADHD	Attention Deficit Hyperactivity Disorder
ANOVA	Analysis of Variance
ART	Adaptive Resonance Theory
CCM	Correlation Control Module
CD	Coincidence Detector
CDN	Coincidence Detector Network
CI	Computational Intelligence
CODAM	Corollary Discharge of Attention Movement
CT	Computer Tomography
ECD	Equivalent current dipole
ECG	Electrocardiograph
EEG	Electroencephalography
EOG	Electrooculograph
ERP	Event Related Potential
FEF	Frontal eye field
FIT	Feature Integration Theory
fMRI	functional Magnetic Resonance Imaging
FS _i	First stage of processing, layer i
GCL	The ganglion cell layer
ICA	Independent component analysis
INL	Inner nuclear layer
IPL	Inner plexiform layer
IPS	Intraparietal sulcus
IT	Inferotemporal cortex
LFP	Local Field Potentials
LGN	Lateral geniculate nucleus
LIP	Lateral intra-parietal area
LPFC	Lateral prefrontal cortex
MEG	Magnetoencephalography

MFT	Magnetic Field Tomography
MST	Medial superior temporal area
MT	Middle temporal area
N2pc	N2- posterior-contralateral
NTVA	Neural Theory of Visual Attention
ONL	Outer nuclear layer
OPL	Outer plexiform layer
PET	Positron Emission Tomography
PFC	Pre-Frontal Cortex
PLT	Perceptual Load Theory
PPC	Posterior parietal cortex
PRL	Photoreceptor layer
RF	Receptive Field
RSVP	Rapid Serial Visual Presentation
RT	Reaction time
SC	Superior colliculus
SL _i	Second stage of processing, layer i
SM	Saliency Map
SNN	Spiking Neural Networks
SOA	Stimulus Onset Asynchrony
SQUID	Superconducting Quantum Interference Device
ST	Selective Tuning
ST ₂	Simultaneous Type/Serial Token model
VSTM	Visual Short Term Memory
WM	Working Memory
WTA	Winner-Take-All

1. Introduction

1.1 The human brain from the computer science perspective

The human brain is one of the most extraordinary and complex creations in the universe. It is estimated to consist of by about 50 to 100 billion neurons that are interconnected and pass signals to each other through around 100 trillion synaptic connections. This highly non-linear and complex manner of neural communication in the brain provides us with the fascinating experience of human life as we know it. Our understanding of the world, and our ability to understand it the way we do, is based on the proper control and manipulation of data throughout the brain.

One of the fundamental functions of the human brain is to control the massive amount of information coming from external stimulations and received by the various sensory systems (e.g. mechanoreceptors, photoreceptors, chemoreceptor, thermo receptors) and to output the corresponding relevant responses that provides us with the ability to think, talk and generally to experience human life.

One can think of the brain as the closest to perfect information system known, therefore it has traditionally been the source of inspiration in the field of computer science. Artificial intelligence which is defined as the human-created, non-biological intelligence and more precisely computational intelligence (CI) which is the intelligence that emerges through some form of computation is today a major branch of computer science.

Studying the brain from the computer scientists' perspective has always been a great challenge, and is usually divided under two main paths within the CI field. On the one hand, to understand and mimic in a sense the functionality of the human brain has triggered the design and implementation of artificial intelligent systems such as robotics, expert systems etc. On the other hand, the understanding of certain brain functions can be facilitated with the implementation of relevant cognitive computational models that use techniques that are often drawn from the field of CI. Nevertheless, it is very important to have many channels of communication between these two paths, for the exchange of new information and knowledge for enhancing their independent evolution (Figure 1-1).

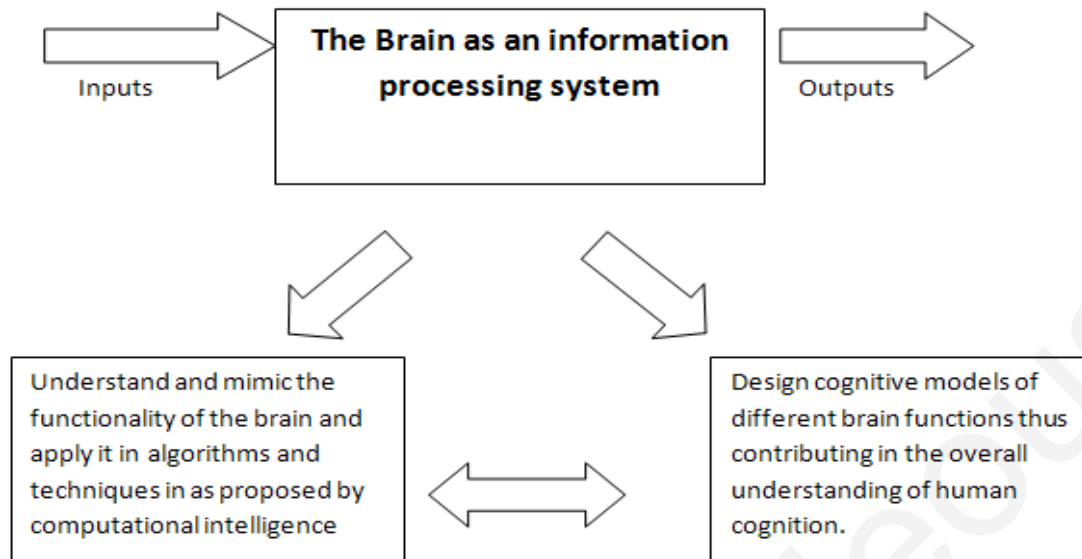


Figure 1-1 The role of computer science in the study of the human brain.

CI is usually defined with emphasis on the specific path that is involved with. For instance, the central goal from the engineering point of view is to specify methods and to provide the necessary tools to build intelligence.

Although it is not always necessary to perfectly mimic human behavior in the attempt to design computational intelligence systems, the main focus of this direction of research is usually human-centered. Consequently the main objective of the engineering perspective of CI is to develop and use techniques and algorithms mostly inspired from the human brain, for solving difficult problems that will help and improve our lives as humans or even to create cognitive systems that could compete and perform better than humans. In some restricted domains, such as pattern recognition, processing of large amounts of numerical information, classification, high precision control, cognition enhancement, brain-computer interfacing for human assistance, and many other tasks that generally need to process large sets of data, CI has made impressive progress.

For a machine however, to demonstrate intelligent behavior comparable to that of humans is a target still far from reality. Despite the great engineering progress in CI, to design and build artificial systems capable of solving higher-level cognitive functions, such as the understanding of language, reasoning, recognition, problem solving and generally to exhibit some sort of intelligent behavior is still in primitive stages. This is perhaps one of the ultimate goals of the scientific perspective of CI, which is focused the understanding of the basic principles that could develop intelligent behavior, in natural or artificial systems. This direction of research can be seen under the umbrella of cognitive science and more explicitly under the field of computational neuroscience. One of the fundamental techniques to explore and understand human cognition is to follow a computational modeling approach with simulations of different mental tasks. In this direction of

research however, it is very important to obtain information related to the internal functionality of the designed model. Therefore, it is necessary to “open” the “black box” and pay attention to the internal details, which is a typical characteristic of the “white box” models.

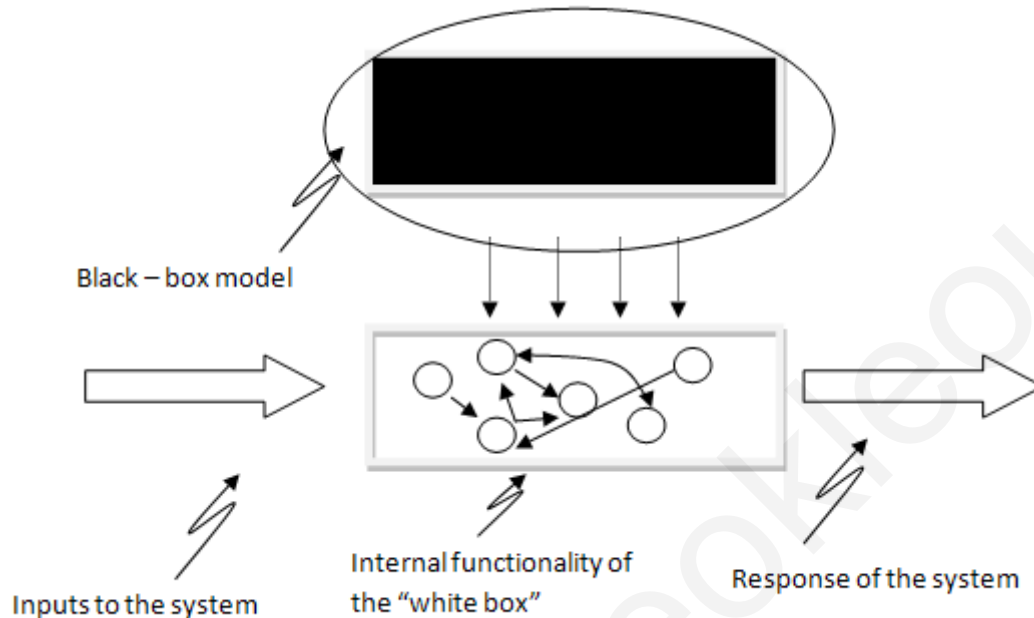


Figure 1-2 The schematic representation of a “white – box”

For the development of these types of cognitive models, it is necessary to collect information that explains, on a theoretical basis, the possible connections and interactions of the various components that comprise the system under development. Following that, the technological and research advances especially from the fields of computer science will provide the appropriate environment for their implementation.

1.2 Cognitive modeling

Modeling of cognitive processes has always been an interesting challenge for the scientific community, mostly because it aims in answering questions that belong to more theoretical disciplines like cognitive psychology, and in explaining neurophysiological findings. Cognitive modeling is a very essential tool of cognitive science nowadays and this can be proved by the rapidly increasing number of articles appearing in journals of Cognitive Science that involve cognitive modeling. In addition, cognitive modeling approaches are beginning to spread into other fields such as clinical psychology, medicine, economics, and many others.

Mathematical/computational modeling can help to comprehend the functional organization of a particular cognitive phenomenon since the development of explicit mathematical descriptions of the various processes that take place in the brain, require the investigation of fine details that cannot be understood purely on the basis of behavioral and neurophysiological experiments. For

example, one possible way to study a certain function of the human brain can be done through appropriate measurements of behavioral responses while subjects perform a relevant experimental task. Another way would be through neuroimaging techniques that locate areas of activity in the brain during the execution of a specific task and observe their connectivity in relation to a cognitive function, or through single cell recording techniques that offer significant information about the firing of individual or groups of neurons. Despite the useful amount of information received, none of these experiments on their own can fully explain how the specific cognitive function operates in the brain, unless the links between the two levels of experimentation are completely understood. This connection can be effectively examined through the implementation of specific and plausible computational models capable of providing a platform of communication between the different sources of information.

1.2.1 Methods of computational-cognitive modeling

There are two basic approaches for developing cognitive models. These involve the symbolic and sub-symbolic modeling. Symbolic modeling operates by representing abstract mental functions into symbols. This approach has evolved from the computer science paradigms that use technologies of knowledge-based systems and particularly systems that are based on logic rules according to methods and techniques from the field of classical artificial intelligence. The sub-symbolic approach includes the connectionists/neural network models that follow the neural and associative properties of the human brain. Connectionism relies on the idea that the human brain is composed of simple heavily interconnected nodes and that the whole operation of the system is mainly based on the connections between the nodes. Artificial neural network models are perhaps the closest mathematical implementations of this approach.

Neural network models, in terms of cognitive modeling are mostly used to describe the actual neural substrates and neural interconnections that implement different cognitive processes. Therefore, these models are usually evaluated by comparing their results with the neural activity observed in multiple cell recording studies. As a consequence, neural network models typically provide predictions related to the coupled interactions and the low level neural mechanisms that are necessary to create the observed firing patterns. However, the extensive level of analysis required to build neural models, and especially their complicated and numerous interconnections, makes them too difficult as modeling tools to address behavioral cognitive tasks. Alternatively, symbolic modeling can provide an abstract level of analysis for predictions of complex cognitive tasks and multiple measures of behavior, yet, avoiding the details on the low level neural interactions. One can see that both ways of modeling have their own important contributions based on what they try to predict and thus are equally needed in the field of cognitive science.

In line with the latter proposition, an innovation of this research is the development of a hybrid cognitive model that uses a combination of symbolic and sub-symbolic structures and therefore offers novel research potentials and the opportunity to contribute from a different perspective in the field of cognitive science (Figure 1-3).

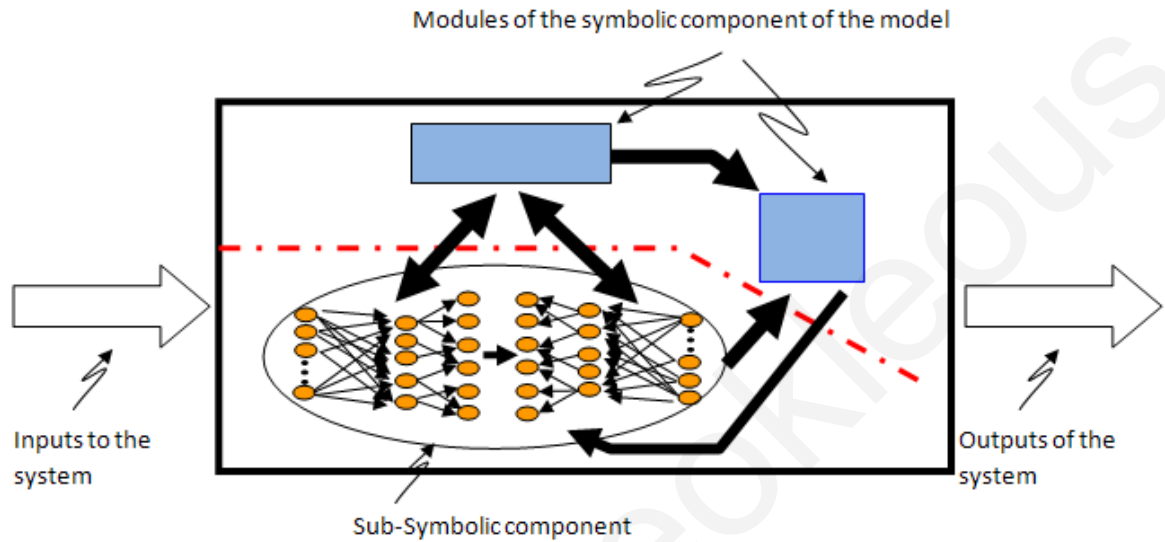


Figure 1-3 The hybrid configuration of the proposed computational model

Because of its nature, the model is able to simulate important behavioral experiments and at the same time to provide explanations related to the underlying low level neural mechanisms, since its internal functionality is designed according to the most recent neuroscientific findings.

1.3 Cognitive modeling of visual selective attention- motivations

In order to effectively investigate the complicated nature of the human brain it is suggested to concentrate independently on specific cognitive subsystems that contribute in the creation of human cognition. Accordingly, as noted in the abstract, the focus of this research is placed on the cognitive modeling of the system that is responsible for the proper control and filtering of the massive amount of information that enters into the human brain and it is defined as “human attention”. More specifically, after a preliminary study on human attention at large, I concentrated in the direction of *visual selective attention* motivated by the applications and results that such studies could have.

A comprehensive example of the role of human attention in general, can be seen by thinking that for every instant of conscious life, each person receives millions of external stimulations from his/her sensory systems. In fact, in each eye there are about 125 million photoreceptors that are estimated to provide information down the optic nerve in the range of $10^8 - 10^9$ bits per second. This amount of information exceeds by far what the brain is capable to fully process and

consciously experience and therefore, the role of visual selective attention is to maintain the stability in the brain by biasing only the relevant and essential information for further processing in the visual cortex, while at the same time to discard the redundant stimulations.

Indeed, if every stimulus was allowed to pass into perception, one would have been soon overflowed and be in constant distraction. Adding to that the internal thoughts, a person would end up in a totally unstable state. Rightfully then, selective attention is defined as the main control mechanism, necessary for keeping the brain system in stability.

How is this limited amount of information categorized as important and selected through simple neural interactions? How are our internal thoughts and previous experiences coupled to the overall process of attention? Or even, how is the attentional mechanism linked to conscious experience and human behavior? These are all challenging questions that stimulated and motivated the progression of the current research study. The most fascinating and inspiring thought however, is that, in my opinion, a complete understanding of how cortical neural activity is manipulated by selective attention will offer the basic foundations to realize how intelligent behavior is created.

In addition, selective attention has important behavioral implications in our everyday life and thus, a deeper understanding of its role could benefit the general public. For example, failure to sustain selective attention while driving to the road, when a distracting stimulus appears (e.g., an attractive advertisement board) may cause the driver to induce an accident. If however, attention is too focused and cannot be flexibly disengaged from the main stimulus or task, the driver may not perceive and react to the sudden appearance of danger (e.g., a car failing to obey a stop signal, or a human crossing the road).

Furthermore, deficits in the selective attention mechanism have been linked to fundamental brain disorders. For instance, the failure to inhibit distracting information in order to remain focused on a task is considered by many psychologists as the underlying cause of a disorder known as Attention-Deficit Hyperactivity Disorder (ADHD), which is often associated with adverse life outcomes (Barkley, 1997). Yet, perhaps the most important brain deficit directly connected with selective attention is schizophrenia. Abnormalities of attention have long been considered as core features of the cognitive dysfunction associated with schizophrenia. It has been shown by many studies that schizophrenics cannot modulate attention and they maintain consistently high levels of arousal during selective attentional tasks (Mirsky and Duncan, 1986; Laurens et al., 2005).

Finally, computational modeling of visual selective attention, can offer a twofold channel of communication between cognitive science and engineering intelligent systems. The field of “intelligent systems” can significantly profit from any newly acquired knowledge that cognitive modeling brings to surface, since combined with knowledge from computer science, can provide a good basis for CI applications. Robots and other engineered systems that mimic biological capabilities as well as brain-computer interfaces are some of the potential areas of applications that

can benefit from this twofold connection. At the same time, an improvement of the intelligent systems algorithms brings more sophisticated tools to study the brain (Figure 1-4).

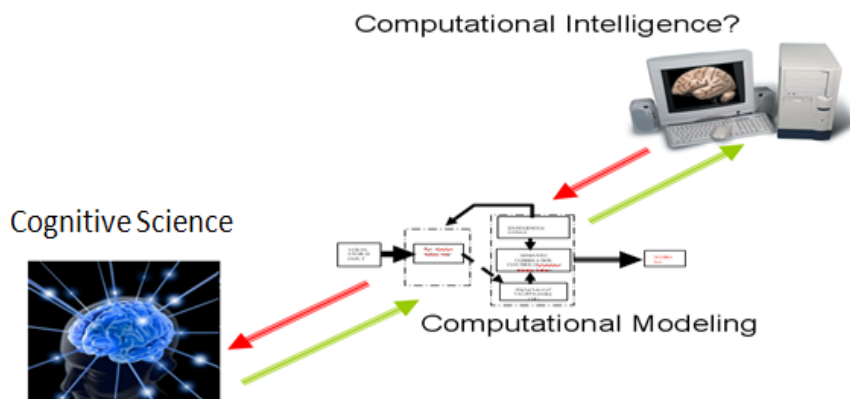


Figure 1-4 Computational modeling as a tool for better understanding of the attentional mechanism as well as to enhance the inspiration of new computational intelligence algorithms.

In the following section a description of the procedure and the different steps that have been followed during the design of the computational model is presented.

1.3.1 Approach to cognitive modeling of visual selective attention

As hinted earlier, visual selective attention is studied under the multidisciplinary field of cognitive science. Understanding the role of selective attention in intelligent behavior could be facilitated by looking at attention from different angles and areas of study.

In fact, a lot of information about the behavioral aspect of selective attention is coming from the field of cognitive/experimental psychology, in which the primary research methods involve experimentation with human participants. In these experiments, the measurement of behavioral response time to a specific stimuli, can give a lot of information and help to understand how the respective stimuli are processed.

In addition, the direct observations of the detailed mechanisms of the system that create intelligent behavior are equally significant. These observations are closely tied to the field of cognitive neuroscience and usually provide considerable information related to the low level mechanisms and the connectivity between different parts of the brain system (Kastner & Ungerleider, 2000). Similarly, with cognitive psychology, the primary research method is still based on controlled experiments, with the difference being that the emphasis is given on observations of the neural activity at different levels in the brain of humans (or animals) while performing these experiments. Therefore, to cope with the specific goals that are set, and to investigate the areas of visual selective attention that are somehow controversial, it is necessary to combine knowledge and methods from the fields of traditional cognitive/experimental psychology, cognitive neuroscience, and computer science.

With all these in mind, the **first step** in the process of implementing the computational model was to create a collaborative network between scientists that are involved with these disciplines and set the specific goals that the computational model will focus on. The **second step** was to take from the involved disciplines an abstract theoretical framework, and reformulate its assumptions into a simple mathematical or computer language description. However, often the conceptual theories are not sufficient enough to build the necessary foundations for a complete model. Thus, in the **third step** it is typical to make some assumptions that will allow a more detail and proper implementation. The **fourth step** was to configure several unknown parameters of the model, based on observed data, and evaluate its performance with existing experimental studies. It is highlighted that in this stage is important to examine predictions from the simulations and design new experiments for their proper evaluation. Finally, the **fifth** and last step is to go back and reformulate the theoretical framework in the light of the feedback obtained from any new experimental results. This is a never-ending iterative loop between the involved disciplines, since new experimental findings are continuously emerging and thus putting new challenges to previous models while predictions from cognitive models bring the need for performing new and different experiments. This circular process is in fact the mechanism that produces evolution in cognitive science and makes cognitive modeling more powerful over time (Figure 1-5).

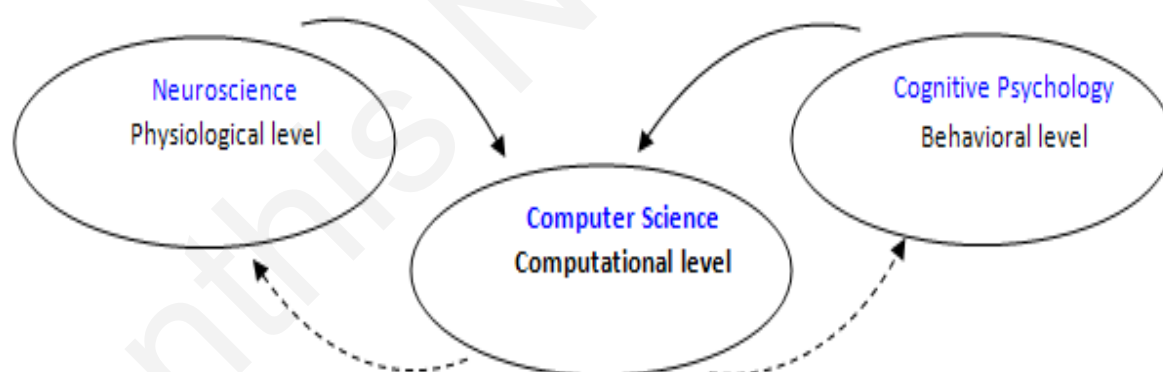


Figure 1-5 The multi-disciplinary approach for cognitive modeling of visual selective attention.

Cognitive models however, are constructed as simple representations of a cognitive system that only capture the essentials or a fraction of its complete operation. A sufficient amount of experimental data will always prove that a model is not completely true; yet the question is not to replicate exactly the human brain, but rather to design models that will give as close as possible representations of the cognitive system that is studied.

Along the lines explained in this section for a more effective and methodical research, an introduction to the basic concepts related with visual selective attention from the viewpoint of cognitive psychology and neuroscience is presented in the following two chapters.

2. Theoretical background on human attention

A commonly used statement for attention has been originally stated by William James in 1890, who said: “Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought.” (James, 1890).

More than a hundred years later, and with a large number of distinguished scientists dedicating a lot of effort in the study of attention, it is more appropriate now to say that still no one really knows exactly what the complete functional role of attention is, or how the underlying neural mechanisms allow attention to interact with the sensory information. Evidently, the primary role of attention is to sustain the focus of cognitive resources on a specific source of information, while filtering or ignoring any unrelated extraneous stimulation. At the same time however, attention is believed to be a precursor to many other neurological/cognitive functions such as working memory (Fukuda & Vogel, 2009), learning (Grossberg, 1999) and consciousness (Koch & Tsuchiya, 2006) and as a consequence, there are several contradictions on theoretical concepts behind the overall character of attention in primates. While many questions have been answered regarding the underlying neural mechanisms behind the attentional interactions on external and internal stimulations, new and more complicated issues are continuously coming up. For example, the functioning role of attention implies that there is an internal mechanism able to categorize stimulations based on their importance for “survival” at every instance. Moreover this mechanism is essential for the development of the learning mechanism and the optimum organization of memory. For instance, if it were not possible to distinguish an important stimulus from the rest, a newborn would probably not be able to begin the learning process and evolve. Or even without a mechanism that emphasizes the neural activity of a certain stimulus, it would probably not be possible to successfully register and store the characteristics of that stimulus in long term memory and to be perceptually aware of its existence. These, and many more, are some ideas that highlight the complicated role of attention in human cognition and that still have not been clearly understood. Therefore many specialized aspects of selective attention are still in the need of novel research.

In the following sections of this chapter, some basic concepts of human attention are presented, followed by a more concentrated analysis on selective attention.

2.1 The attentional system

Attention according to Posner and Dehaene (1994) can be described as “an arousal or an alerting system, an executive control system, or a system for orienting”.

From the Darwinian perspective, an increase in the arousal is necessary for survival. For example, higher levels of arousal or alertness, can allow an animal to hear and locate easier a threat, or a mother to protect her child. The executive control mechanism is essential for human behavior for resolving conflicts, error detection or task switching, while the orienting aspect of attention refers to the mechanism that turns our sensory receptors towards one set of stimuli and away from another.

One characteristic of the orienting process is that it can be distinguished to **overt** and **covert** changes. **Overt orienting** can be described as the act of directing sense organs, like for example the head and eye movements, towards a stimulus source. **Covert orienting** is the act of mentally focusing on one of several sensory stimuli. One typical example of covert orienting is the case in which we are looking at a person that we are having a conversation, yet our attention is focused on a different source. Covert and overt shifts of attention were first defined by Helmholtz (1989).

Covert attention orienting is usually studied separately from overt orienting behavior, although some studies suggest that the mechanisms of overt and covert attention may not be separate. For instance, the pre-motor theory of attention, initially proposed by Rizzolatti et al. (1994), suggested that these attentional systems are supported by the same neuronal mechanisms. On the other hand, more recent and detailed examination of the behavioral and physiological data indicates that although the two systems probably share some neural mechanisms, they are not identical (Corbetta & Shulman, 2002).

Covert and overt shifts of attention are usually categorized in the scientific literature, in **space-based** and **object-based** attention. In the space-based mode, locations in the visual field are selected while in the object-based mode, organized symbols of visual information are selected independently from their location in space. Evidence for spatial selection comes mostly from spatial cueing studies (e.g., Posner, 1980) in which the shift of attention in space was manipulated by cues that predispose the targets location. Evidence for object-based selection comes from a variety of different experimental studies (e.g., Scholl 2001; Cave & Bichot, 1999) in which their corresponding results cannot be theoretically explained only on the basis of space-based theories. In fact, many different studies have shown that attention can be split among multiple moving objects that do not occupy a connected region of space (e.g., Berhmann et al., 1998) and other studies emphasized the fact that object-based features are possible to modulate the spatial cueing effects, (e.g., Brawn & Snowden, 2000). These studies are some of the many examples in the corresponding literature that support the independent study of these two complementary modes of

selection. The most prevailing reason however, that triggered the independent study of **spatial** and **object** based attention came from neuroscientific evidences regarding the neurophysiology of attention (see Chapter 3).

2.2 Exogenous and endogenous orienting of Attention

One more central distinction in the physical orientation of attention involves the endogenous and exogenous reallocation of the attentional focus.

Top-down or **endogenous attention** refers to the volitional modulation of neural activity that corresponds to an object or a location in space, and it functions in response to signals initiated by internal goals, that most likely originate in the parietal and frontal lobes of the brain (Buschman & Miller, 2007). Bottom-up or **exogenous attention** on the other hand is a faster and more automatic process that relies on the sensory saliency of stimuli registered by subcortical structures and the primary sensory cortices (Corbetta & Shulman, 2002; Beck & Kastner, 2005; Buschman & Miller, 2007).

The exogenous process involves a physiological shift of attention that relies on a characteristic that most living creatures are born with and is referred to as orienting reflex. **Orienting reflex**, is defined as the movement of the eyes, the skin conductance change, or even the increase in heart rate that may occur automatically, with the appearance of a loud noise, a flashing light or any stimulation that distracts our internal model of the world, as it is created in that moment.

For example consider the case, in which a person is reading this text on a computer screen. The focus of attention will most probably be in the spatial area of the visual field that the sentence appears. At the same time, while reading the sentence, imagine a red flashing dot appearing on the left top corner of the screen. The rapid change of the previously processed image combined with the fact that the white background is significantly different from the red dot, will make the red dot become more salient compare with all the other stimulations on the computer screen. Thus, the reader will reflectively orient the focus of attention in an exogenous manner to the red dot's spatial location. On the contrary, if the sentence on the screen was: *Please concentrate and look for the little red dot that will shortly appear on the top left of the screen*, then, the focus of visual attention will orient towards the top left corner of the screen but this time voluntarily. In other words, the comprehension of the sentence by the reader in our example will trigger and generate some endogenous signals (possibly from parietal and frontal lobes of the cortex) that will manipulate the visual information and reallocate the attentional focus voluntarily.

Attention in human cognition however, has also been investigated clinically in patients with different neurologic pathologies and introduced some specialized aspects of its functionality. Some attention related deficits have been observed only at certain tasks, while in other conditions, the

patients responded normally and therefore, different attentional categories were defined. For instance, *focus attention* corresponds to the ability to respond separately to specific stimuli, *divided attention* defines the ability to simultaneously focus the cognitive resources on multiple tasks and *sustained attention* to maintain consistent attention to specific tasks during continuous and repetitive activity. In the next sections more emphasis will be given however on another major aspect of the orienting system, the *selective attention*.

2.3 Theories of selective attention

Our daily cognitive functioning relies heavily on our ability to select and process a very small subset of the information that is registered from our sensory organs and at the same time to ignore the rest. The cognitive process that allows us to carry out such selective processing is referred to as *selective attention* and has been extensively studied under many disciplines and different methods, such as behavioral experiments, electrophysiological and imaging studies, and computational modeling. The basic concepts of selective attention have been given detailed descriptions and scientific explanations over the last years; nonetheless many issues are still remaining to be clarified and many others to be confirmed, since several questions about fundamental issues are still debated among researchers.

The theoretical study on selective attention began in the 1950s with the classical concepts of selective attention being inspired mostly via auditory perception, when Colin Cherry (1953) first performed experiments on dichotic listening. In those experiments, the subjects had to listen to two separate streams of words in each of their ear through a headphone set, but to selectively attend only to the one. Following the task, the experimenter would inquire about the content of the unattended stream by asking specific questions to the subjects. The results from those experiments had a significant impact on the development of many theoretical concepts related with the attentional processing, and at the same time sparked a long debate around a central topic in the field of selective attention about the locus of the attentional filtering within the stream of information processing. Early selection theories of attention (e.g., Broadbent, 1958; Treisman, 1960) placed selection at an early stage of processing claiming that the attentional mechanism stops completely or attenuates processing before the mind can analyze its semantic content, while late selection theories (e.g., Deutsch & Deutsch, 1963) propose that selection occurs at a later processing stage and after all stimuli have been processed semantically in the short-term memory.

A more detailed analysis of the most prevailing theories related to selective attention is presented in the next section.

2.3.1 Early Selection Theories

The *“Filter theory”* is one of the major models of early selective attention and was initially proposed by Broadbent (1958). The main idea behind the first of the so-called "bottleneck" theories is that attention can be modeled as a physical channel that could allow only one message to pass into perception and short-term memory, based on its characteristics. In accordance to the results of the dichotic listening experiments (Cherry, 1953), Broadbent suggested that the unattended messages were apparently stored in a temporary memory buffer, and only their physical properties could be retrieved after a short period of time (Figure 2-1). The filter theory despite being one of the first models on selective attention, it still remains valid, since it is clear that the information processing capacity of human perception system is limited.

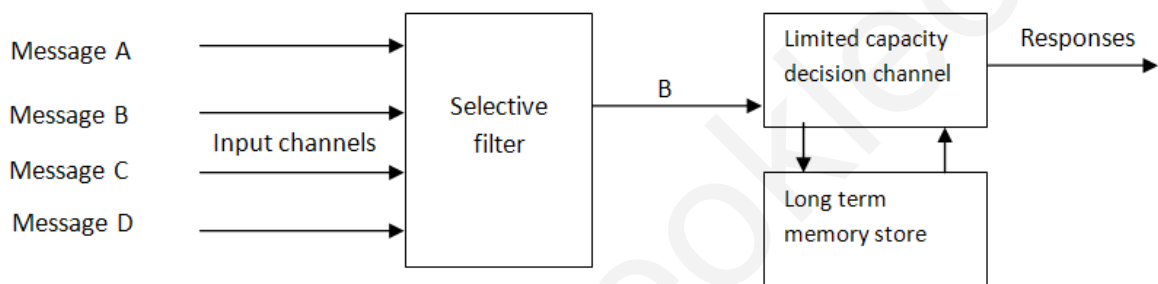


Figure 2-1 Broadbent's model. Source from: *Perception and communication*. (Broadbent, D. E., 1958).

More experiments on dichotic listening, such as those of Moray (1959) revealed that certain words, (like for instance a subject's name), seemed to pierce from the unattending ear to the selective filter. But, according to the filter theory, selection is due to the physical quantity of stimuli and thus switching attention should be unrelated to the content.

To explain this and solve the problem of the detection of subtle information through an unattended channel, Treisman and her colleagues (1960) suggested a new theory called *the attenuation theory*. According to the attenuation theory, some important words or sounds for each subject are activated and directed into perception more easily than less important stimuli. The unattended information, although it will be attenuated, it is possible under certain conditions for some messages to receive a certain degree of processing (Figure 2-2).

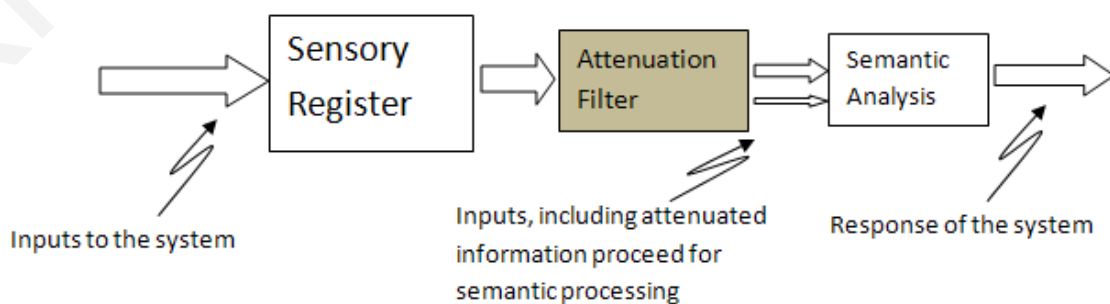


Figure 2-2 Schematic representation of the attenuation theory by Treisman (1960)

The last of the major bottleneck theories of attention was proposed in 1963 by Anthony and Diana Deutsch. The main argument that pushed them into a further modification of Treisman's (1970) theory was based on some new experiments they performed. Together with Donald Norman (1968) they showed that some words from the unattending stream could influence semantically the meaning of the attending sentences. One of the most famous examples was the sentence: *"They threw rocks at the bank yesterday"* which according to the sentences in the unattending ear, "bank" was realized as the bank of the river or bank as a financial institution. The late theories are thus suggesting that all incoming information is semantically processed before being filtered out.

2.3.2 Late Selection Theory (an alternative of Selection Theory, the "divided theory")

The Late Selection Theory (Deutsch & Deutsch 1963; Norman 1968), often called the automaticity is proposed against the Broadbent's (1953) and Treisman's (1960) theory. This theory suggested that no filtering or attenuation takes place. Instead all inputs are fully processed. It is assumed that perception is an unlimited process that can be performed in an automatic and parallel manner. According to this theory selection occurs after full perception and that is why is referred as to as "late selection".

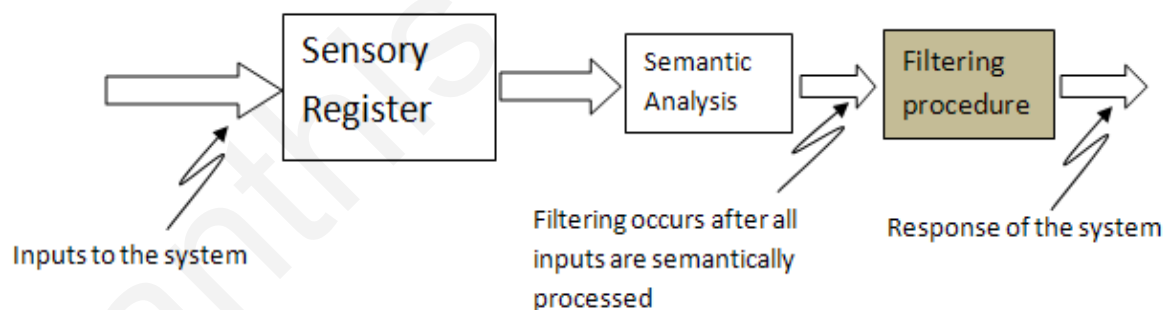


Figure 2-3 Schematic representation of the late selection theory by Deutsch and Deutsch (1963)

A promising way of reconciling the debate concerning the locus of selection has been more recently proposed by Lavie and colleagues (Lavie & Tsal, 1994; Lavie, 1995; Lavie & Fox, 2000). According to Lavie, attention is viewed as a pool of limited resources that are engaged by attentional tasks based on the processing demands they entail. Hence, Lavie's study proposed a possible determination on the early- late debate by suggesting that perceptual load of relevant information could determine the selective process of irrelevant information.

2.3.3 Perceptual Load Theory

Perceptual load theory (PLT) in respect to the previous theories is based on studies of visual selective. More specifically, this theory is based on a study in which participants were asked to respond to a specific target after the effect of a distractor. The behavioral results revealed that participants could efficiently filter out task-irrelevant distractors when performed under high levels of perceptual load (e.g., large display size), but fail to do so under low levels of perceptual load (e.g., small display size). The perceptual load theory thus, explains the modulation of selectivity by the processing capacity. When the load is high, capacity is exhausted and there are no available resources left to process irrelevant distractors and thus it can be inferred as early selection; while alternatively, when load is low the irrelevant distractor is processed and consequently influencing the reaction time of the response (late selection).

Perceptual load hypothesis, although offers an interesting approach concerning the early late debate, it has still being criticized and challenged and today researchers are continuing to investigate both early and late selection models searching for the true limitations of cognitive processing.

In accordance, the proposed computational model was used for simulations of the corresponding PLT experiment, aiming at clarifications regarding the theoretical concepts behind this theory (see Chapter 6) and to propose a possible theoretical framework regarding the selection process.

One important distinction of PLT with the previous experimental studies is that it strictly involves visual processing. In fact from the 1970s, the focus of attentional research has moved from the auditory to the visual domain, mainly because visual attention is easier to study experimentally. Despite the many common parallels between the two domains there are also some major differences, and therefore it is important to study selective attention with reference to the domain it refers to.

In the next chapter information about the visual system, the brain areas involved and what is currently known about the underlying neural mechanisms of visual selective attention from the most recent studies in the field of neuroscience is presented.

3. Visual selective attention

This chapter presents the basic concepts of visual selective attention from the neurophysiological perspective. Some introductory information about the visual system will be given before the corresponding cortical mechanisms that compose visual selective attention are analyzed.

3.1 The visual system

The visual system is the part of the central nervous system that is responsible for assimilating information from the environment and interpreting it into visual perception. More precisely, the human visual system accomplishes many complex tasks like the detection and discrimination between stimuli that have diverse features, the perception of distance to and between objects, and guides the corresponding body movements in relation to visual object.

The act of seeing begins primarily with the reception of light by a light-sensitive membrane in the back of the eye, called the retina. The light patterns are then converted into neuronal signals. The photoreceptive cells of the retina are able to detect photons of light and to produce the proportional neural impulses. These signals are then processed in a hierarchical fashion by different parts of the brain during their progression in the visual pathway.

3.2 The visual pathway

The term visual pathway implies that there is a hierarchy of levels for information processing in the visual system. More specifically, light that leaves an object enters the eye through a transparent portion of its external membrane (the cornea), pass through the lens and the vitreous space, and form a pattern on the retina that represents the viewed image.

Light then falls onto the photoreceptors of the retina and is transduced into electrical signals that are processed through layers in the retina. The retina consists of six layers: the photoreceptor layer (PRL), the outer nuclear layer (ONL), the outer plexiform layer (OPL), the inner nuclear layer (INL), the inner plexiform layer (IPL), and the ganglion cell layer (GCL) (Figure 3-1). The photoreceptors of the retina are responsible for transducing light into electrical signals that are then processed by the local neurons of the retina. The retinal ganglion cells are the output cells of the retina, so all visual information available to the brain is transmitted by the axons of these neural cells. The transduced signals are then processed in part of the cerebral cortex that is dedicated in some way to the processing of visual information.

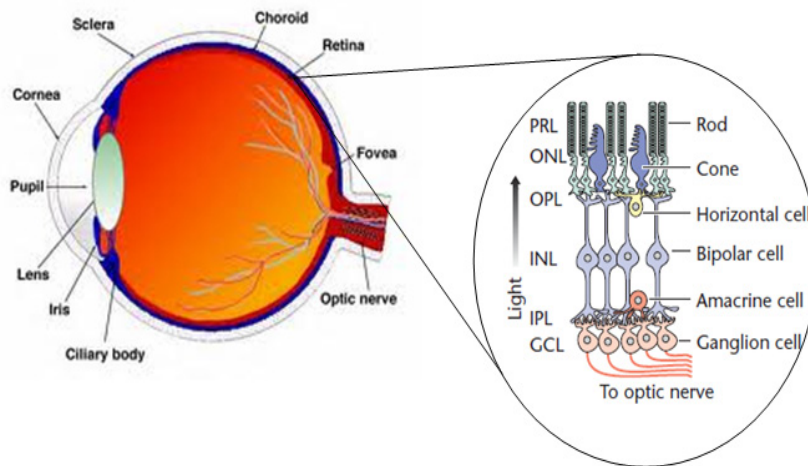


Figure 3-1 The six layers of the retina

The transduction of light into electrical activity occurs in two types of photoreceptors named rods and cones. In the human retina there are approximately 100 million rods and 5 million cones. The rods are specialized in the detection of low intensity (scotopic) light, and are homogeneous in their wavelength sensitivity while the cones appear in three different forms, each to be sensitive in different wavelengths of light and are specialized for the detection of higher intensity (photopic) light. The fovea, which is the most sensitive portion of the retina, contains exclusively cones.

The signals produced by the photoreceptors are transmitted to synapses directly on bipolar neurons that are sensitive to specific light contrast and these in turn synapse to the retinal ganglion cells. As mentioned, the retinal ganglion cells are the only output cells of the retina, so these cells convey all the necessary information to perform the various visual functions such as the detection of shape, color, motion etc. The output signals of the retinal ganglion cells are propagated into the brain through the optic nerve until they reach a major relay station, the lateral geniculate nucleus (LGN) as can be seen in Figure 3-2.

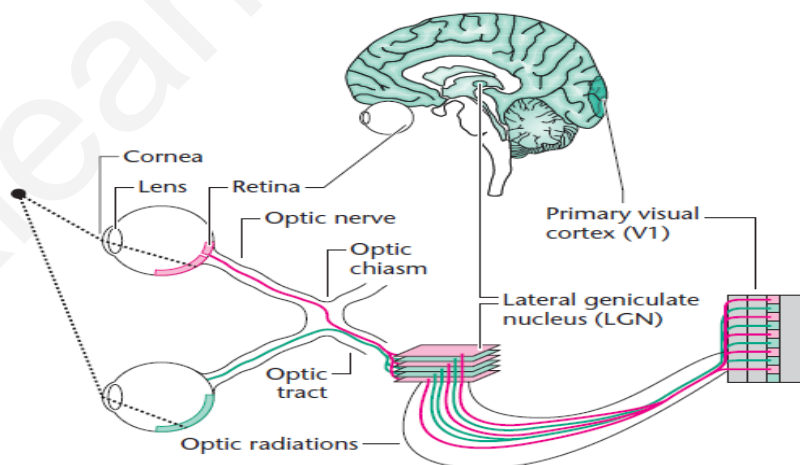


Figure 3-2 The route to the primary visual cortex

Many ganglion cells have their axons connected to other structures apart from the LGN, such as the superior colliculus (SC) which in humans is known to be mostly involved with eye and movements. The neurons of the SC influence another structure which is involved in visual attention and motion perception, the pulvinar, which is located in the thalamus.

Following the visual hierarchy, the cells from the previously mentioned cortical structures are projected to the primary visual cortex which is also known as the striate cortex, or V1. Studies performed on macaque monkey, have shown that after the signals are processed in V1 they are communicated via multiple pathways to more than thirty visually responsive extrastriate cortical areas (Figure 3-3).

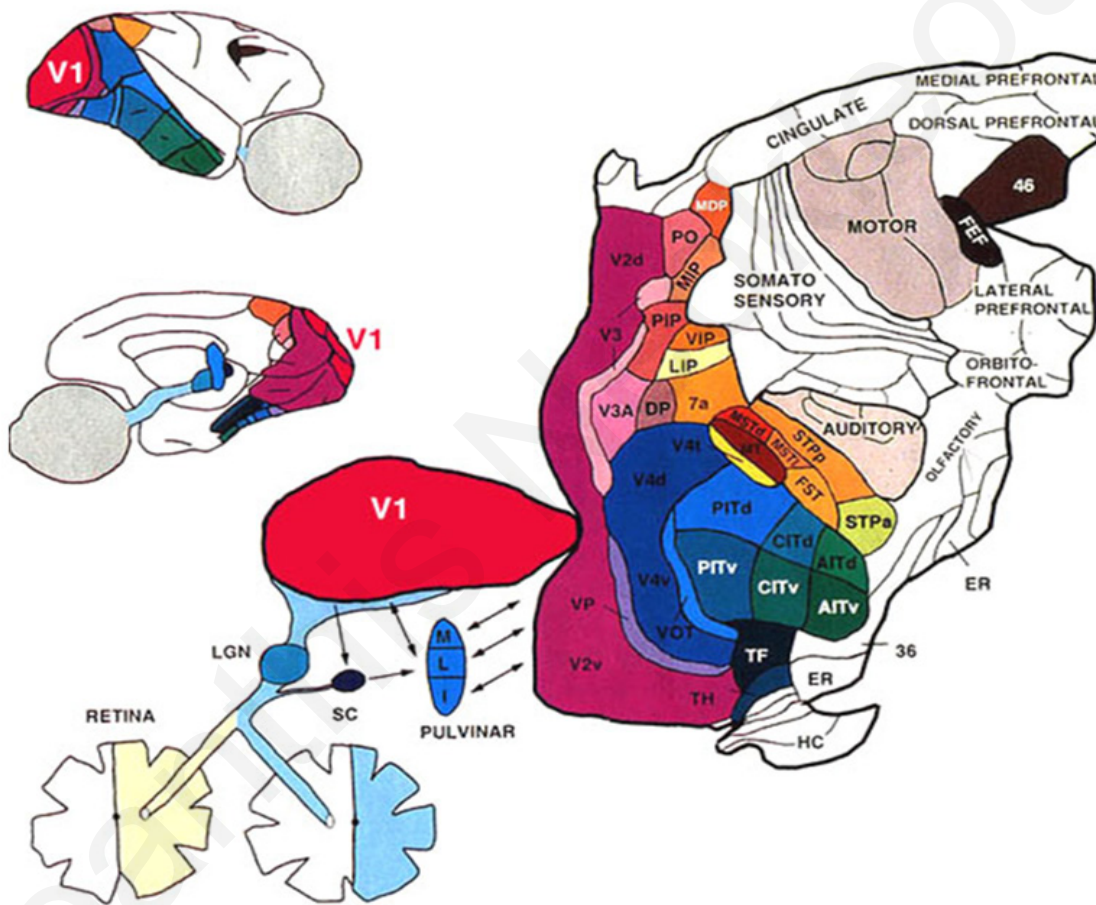


Figure 3-3 The retina and cortical areas for visual processing in primate from van Essen et al (1992). V1 denotes visual area 1, the primary visual cortex and the largest visual area containing detailed representation of the visual input; V2 for visual area 2; LGN for lateral geniculate nucleus; FEF for frontal eye field, SC for superior colliculus, IT for inferotemporal cortex, MT for middle temporal area and LIP for lateral intra-parietal area. The lower case letters ending some of the abbreviations often denote spatial locations of the cortical areas, e.g., v for ventral, d for dorsal.

guidance of our actions in real time towards objects in the visual world. Therefore, one can infer that it executes motor control over objects; yet most probably in an unconscious manner.

Another region involved in the visual processing is area V3 that mainly receives information mainly from area V2. Most of the V3 neurons have properties similar to those in V2. After passing through areas V1, V2, and V3, a large part of the visual information continues ventrally to area V4. The exact role of area V4 is still under investigation, however it is probably involved in recognizing shapes, and it appears to be essential for perceiving colors (Moran & Desimone, 1985). Continuing up in the visual hierarchy, information passes to the inferotemporal cortex (IT) (Figure 3-4). The cells of area IT receive many connections from area V4 and respond to a very wide range of colors and simple geometric shapes. Additionally, the IT cells seem to play an important role in visual memory.

It is pointed that between all the cortical areas involved in the visual processing of the incoming stimuli, there are complicated feedforward and feedback projections. For example only a small subset of direct and indirect projections of signals involve the direct feedforward projections from V1 to pulvinar, V2, V3, V5 or middle temporal area (MT), and frontal eye fields (FEF) as well as feedback projections to V1 that originate from V2, V3, V4, V5 or MT, FEF and inferotemporal cortex (Ungerleider & Desimone, 1986). Moreover, lateral connections inside separate areas, such as in area V1 are influencing the process of the information, and thus formulate a complicated communication system.

3.3 The Receptive field concept

Each neuron in every area of the occipital cortex typically responds to light within a restricted area of visual space. This area is called the receptive field of the specific neurons. For retinal neurons, the receptive field is small, in the range of approximately 0.06 degrees of diameter, measured as a visual angle in the center of vision. This area is very small to cover most complete recognizable visual objects, but only a portion of it. Ascending along the visual hierarchy, in area V4 the neural receptive field becomes larger, in the range of 10 degrees in visual angle diameter, and 20-50 degrees in IT. That is in the IT, it is possible that a single neuron to signal the recognition of a small visual object (Rolls, 2004).

The receptive fields of the bipolar neurons respond best to a light/dark or to a dark/light contrast between their centre and surrounding areas and similarly, this information is transferred to the retinal ganglion cells. The cells that response to a light/dark contrast are called ON cells, while those that respond to a dark/light contrast between the centre and surround are called OFF cells.

In the primary visual cortex or area V1, the receptive fields of the corresponding neurons are much more diverse and complicated than in the retina and thalamus. For example, some neurons in the primary visual cortex can respond selectively to different attributes of the visual scene such as line

orientation, direction of movement, luminance contrast, stimulus velocity, color, retinal disparity and spatial frequency (frequency of black and white stripes in a degree of visual space).

The first characterization of receptive fields in the primary visual cortex was given by Hubel and Wiesel (1962) and it was made on the basis of two main categories. The first category involves the simple cells, which are cortical cells that respond to light and dark spots in different subregions of their receptive field. Due to this arrangement the simple cells are possible for encoding visual stimuli such as lines, bars or squared shapes. The other category involves the complex-cells (the majority of cells found in the visual cortex) that do not have separate subregions (Martinez & Alonso, 2003). For a complex-cell to act in response, it might be necessary not only to have a correctly oriented bar of light within their receptive field, but also to move in a particular direction or even for the bar to be of a particular length (Figure 3-5).

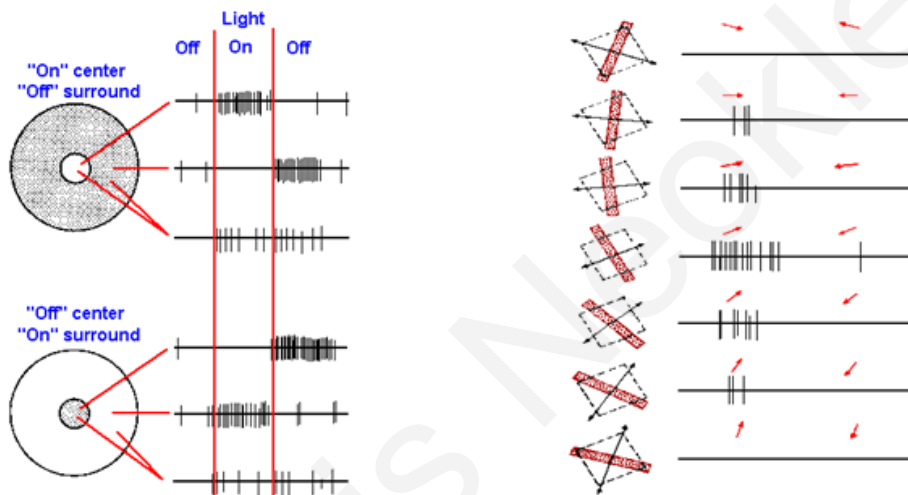


Figure 3-5 Receptive fields of the on and off retinal ganglion cells when the center or the background is illuminated, or when both center and surround are illuminated, Hubel (1963) – left image; Response of complex cells in the primary visual cortex (right image).

Many neurons of the secondary visual cortex V2 and V3 have receptive field properties similar to those of the neurons in the primary visual cortex, yet many others respond to far more complex shapes. For example, some of these cells are sensitive to color and movement.

Neurons in higher cortical areas as explained have larger receptive fields and can be more selective to the identity of the stimulus than to its physical location.

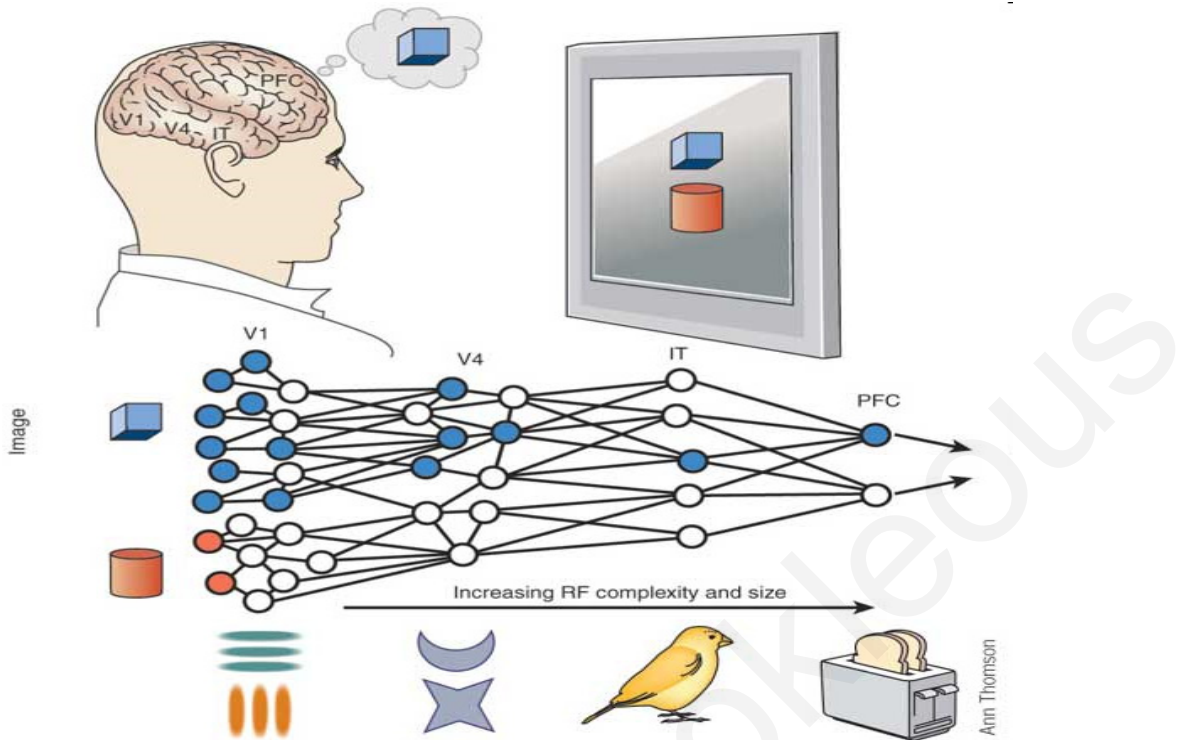


Figure 3-6 Increasing complexity of the receptive field properties along the visual pathway. Image from: Yantis (2005)

The concept of the receptive field is very important in the neurophysiologic study of visual selective attention for the reason that it gives a plausible explanation about the low level interactions during attentional tasks as will be explained in following sections.

3.4 Measuring Brain Activity

The technological achievements during the last years in the design and commercialization of sophisticated equipment specialized to the collection of brain activity data, together with the development of very efficient algorithms for their analysis, have given researchers important insights about the basic functionality of attention, from the neurons level until large cortical areas.

The measurement of brain activity can be performed with either invasive or non-invasive techniques. Single neuron recordings are the most common invasive techniques that are usually performed on living animals. This technique involves the placement of electrodes in specific cortical areas of the animal and therefore it allows the observation of the electric activity from a single neuron or a small group of neurons in a region of interest. Single neuron recordings have provided important insights on how the brain processes information especially on the neural behavior and the low level interactions.

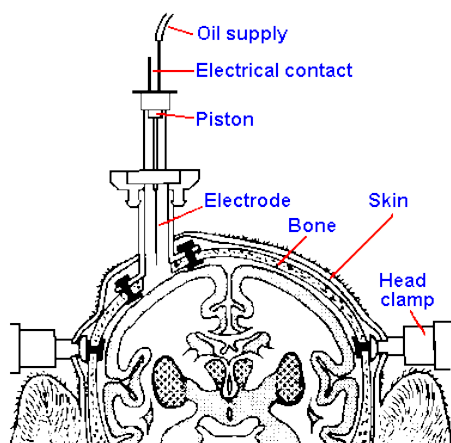


Figure 3-7 The physical setup for recording from awake, moving monkeys. Image by Evarts (1973).

Alternatively, neuroimaging techniques are mostly non-invasive and their basic characteristic is that they provide a wide field of view by summarizing simultaneous activity across the whole brain. Non-invasive techniques, although they cannot offer the specificity and detail that single cell recordings provide, have one significant advantage, since due to their nature are usually performed on humans. The most common methods of functional neuroimaging are functional Magnetic Resonance Imaging (fMRI), Computer Tomography (CT), Positron Emission Tomography (PET), Electroencephalography (EEG) and Magnetoencephalography (MEG). Some basic concepts of each of these techniques are presented below. During the progression of my PhD studies however, I was given the opportunity to prepare and complete an experiment related with visual selective attention with the use of Magnetoencephalography in the Laboratory of Human Brain Dynamics of the Brain Science Institute in RIKEN-Japan, therefore more emphasis will be given in the description of the specific neuroimaging technique.

3.4.1 Functional Magnetic Resonance Imaging, Computer Tomography and Electroencephalography

Functional magnetic resonance imaging (fMRI) works by detecting the changes in blood oxygenation and flow that occur in response to neural activity. The theoretical background of this technique is based on the fact that when a brain area is more active it consumes more oxygen. Thus in order to meet this increased demand of oxygen, blood flow increases to the active area. fMRI uses suitable techniques to measure and process the blood flow in the brain, and it can be used to produce activation maps that show which parts of the brain are involved in a particular mental process.

Computed Tomography (CT) scanning is mainly based on the differential absorption of X-rays. An x-ray source rides on a ring around the inside of a tube, with its beam aimed at the subjects

head. CT scanning uses a computer program that performs a numerical integral calculation on the measured x-ray series to estimate how much of an x-ray beam is absorbed in a small volume of the brain. Bone and hard tissue absorb x-rays well, air and water absorb very little, and soft tissue is somewhere in between. Thus, CT scans reveal the gross features of the brain.

Electroencephalography (EEG) is the measurement of the electrical activity in the brain through recording electrodes that are placed on the scalp. The resulting electrical signal from a large number of neurons is known as an electroencephalogram (EEG). EEGs are frequently used in experimentation because the process is non-invasive to the subject under study and can provide good timing resolution in the analysis of the collected data. EEG is one of the few techniques available for detecting changes in electrical activity in the brain on a millisecond-level. The EEG activity which is time-locked to the presentation of a stimulus is referred to as evoked potential and is widely used in cognitive science research.

3.4.1.1 Magnetoencephalography (MEG)

Magnetoencephalography (MEG) is another non-invasive neuroimaging method for detecting, analyzing, and interpreting the magnetic fields generated by the electrical activity in the brain. Similarly with EEG, MEG has also the advantage of the sub-millisecond temporal accuracy, and therefore helps to a better understanding of the dynamics of cortical function.

MEG signals derive from the net effect of ionic currents flowing in the dendrites of neurons during synaptic transmission. In accordance with Maxwell's equations, any electrical current will produce an orthogonally oriented magnetic field. These net currents can be thought of as current dipoles and thus can be associated with position, orientation, and magnitude but not with spatial coordinates in the cortex (Figure 3-8).

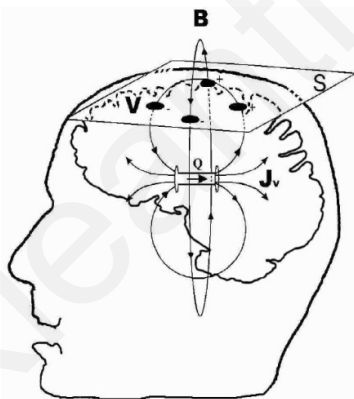


Figure 3-8 A layer of pyramidal cells in the cortex which can be seen as a current dipole generating an orthogonally oriented magnetic field.

For the brain activity to generate a signal that is detectable, approximately 50,000 active neurons are needed. Furthermore, the neurons must have similar orientations to generate magnetic fields

that reinforce each other. Therefore, it is often the layer of pyramidal cells in the cortex, which are generally perpendicular to its surface, that give rise to measurable magnetic fields (Figure 3-9).



Figure 3-9 The MEG sources generated by similar orientation pyramidal neurons

The MEG measurements span a frequency range from about 10 mHz to 1 kHz and can register field magnitudes from about 10 fT (femtotesla) for spinal cord signals to about several pT (picotesla) for brain rhythms. These magnetic fields are about a billion times smaller than the earth's magnetic field which is in the range of 50 μ T (microteslas). Additionally the brain fields are many orders of magnitude smaller than the environmental magnetic noise for about a factor of 1 million, therefore a prerequisite for useful MEG measurements is the availability of sensors that can detect the weak magnetic fields generated by the brain.

3.4.1.1.1 Sensing Magnetic fields

High-quality detection of brain magnetic fields is the first step in the MEG signal processing chain. As mentioned, the measured brain fields are extremely small and the only detectors presently available with adequate sensitivity are the Superconducting Quantum Interference Device (SQUID) sensors.

SQUIDs are coupled to the brain fields by means of flux transformers. SQUIDs and their flux transformers are superconducting and must be operated at low temperatures, usually immersed in cryogen. The cryogen is contained in a thermally insulated container (dewar), which must be electromagnetically transparent so that the brain signals can reach the flux transformers and the SQUID detectors (Figure 3-10).

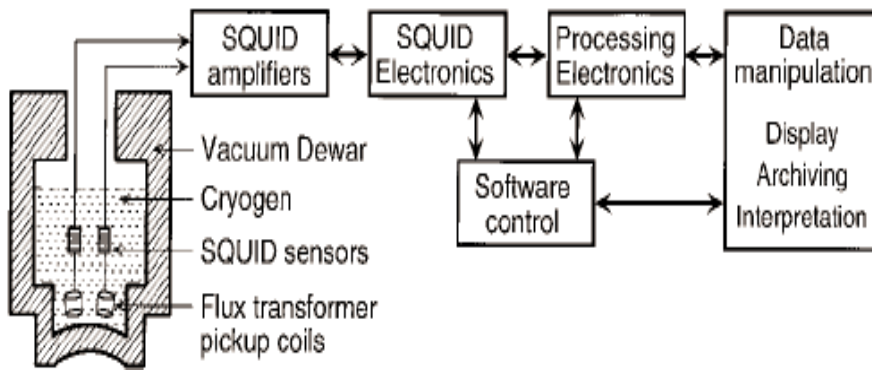


Figure 3-10 The SQUID sensor (Hamalainen 1992)

3.4.1.1.2 Noise Sources

Perhaps the most important part of the MEG data acquisition and system analysis is the distinction of the useful data, from the many other noise sources that contaminate them. In that sense, it is important to define the possible noise sources that might have an effect on the measurements in order to be able to eliminate them with an appropriate methodology.

The most important noise sources arise from four main categories. First, is the *environmental noise* that might be due to fluctuations in the earth's magnetic field, moving cars, elevators, power lines etc. Another important noise source is the *noise originating from the sensor itself*, such as from the electronics, thermal interactions or from vibrations that could possibly interfere with the brain activity. Then it is the *biological noise* from the heartbeat, or the eye blinks and even respiration that creates artifacts in the collected data and it is necessary to be filtered out. Finally, brain activity that it is not of interest should be taken into consideration and if it is possible to be removed from the collected data.

3.4.1.1.3 Noise Cancellation

After identifying the noise sources then a more appropriate technique is used to try and increase the signal to noise ratio as much as possible. Usually, a different approach is used to eliminate noise coming from different sources in order to have closer to optimum results.

3.4.1.1.3.1 Magnetically shielded room

For reducing the environmental noise, the most commonly used method is the magnetically shielded room. This room is enclosed with the layers of high ferromagnetic metal. Usually, the shielded rooms in many MEG labs are enclosed in a capsule made of layers of permalloy and one aluminium. A typical attenuation of the external fields is approximately 100 dB at 1 Hz.

3.4.1.1.3.2 Gradiometer

For eliminating noise from distance sources such as the environmental noise, a gradiometer is usually adapted on the sensor. The sensor consists of two or more coils, taking the difference between the fields measured by the coils. This arrangement is insensitive to a homogeneous magnetic field and sensitive to nearby signal sources. Since brain magnetic fields are not homogeneous, are retained and thus gradiometers only reduce the noise originating from a long distance.

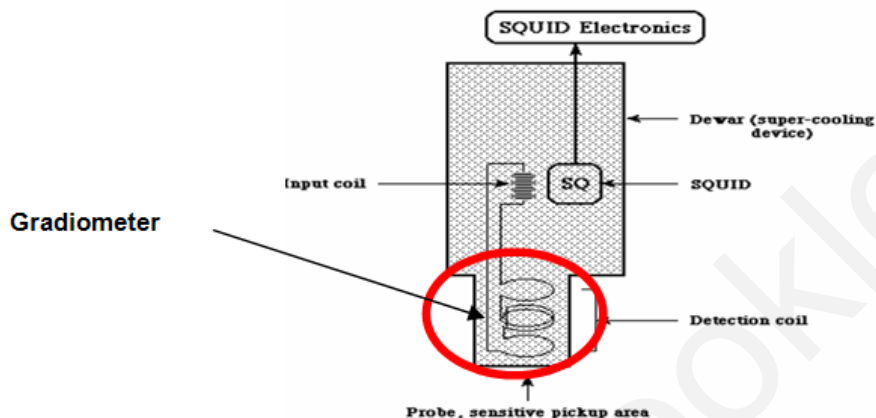


Figure 3-11 The gradiometer (Hamalainen et al., 1992).

3.4.1.1.3.3 Filtering and averaging

Another characteristic technique for eliminating noise is by filtering and averaging the collected data. The typical cut-off frequency in MEG measurements is 0.03 – 1.0 Hz for high pass filter, and 40 – 400 Hz for low pass filter. Averaging is also a simple way for measurement of evoked responses. By averaging, noises are cancelled out, and the signal that remains, is that which is synchronized with the stimuli. However, this approach, cannot remove the noise which is synchronized with the stimuli.

3.4.1.1.3.4 Reference sensor

Some MEG systems have extra sensors only for noise measurement. These sensors are usually positioned far away from the subject's head and thus they can detect distant noise sources. From a noise sensor's output, one can compute some of the gradient field and thus this configuration of the distance sensors can be seen as a virtual gradiometer. For eliminating unwanted artifacts generated by the biological noise, usually the electrical activity generated by eye movements and cardiac systole is monitored by simultaneous recordings of Electrooculograph (EOG) and Electrocardiograph (ECG). Then the concatenated single-trial signal for each run is generally analyzed with independent component analysis (ICA) (Jahn & Cichocki 1998).

3.4.1.1.3.5 Independent Component Analysis

Independent Component Analysis (ICA), is a signal processing solution that separates different signals that are statistically independent in time. Consequently it is possible to identify and remove strong ICA components correlated with either EOG or ECG.

3.4.1.1.4 Source Localization

Finally, for determining the location of the activity within the brain, advanced signal processing techniques are used that use the magnetic fields measured outside the head to estimate the location of that activity's source. Despite the fact that EEG and MEG have the great advantage that they reflect brain electrical activity within millisecond temporal resolution, there are however limitations in the spatial resolution for principal physical reasons. For instance in order to determine the electroencephalography (EEG) and magnetoencephalography (MEG) signal from the knowledge of the sources, as well as the electrical properties of their biological environment, it is feasible and is known in the literature as the forward problem. This can be achieved with unique solutions based on the analysis of the Maxwell equations for electromagnetism. However, even with an infinite amount of EEG and MEG recordings around the head it is not possible to recover uniquely the source localization of the primary current distribution mainly generated by the electric activity of the pyramidal neurons. This limitation is referred to as the inverse problem and many algorithms and methodologies have been developed for providing good estimations of the sources. One interesting description used for the inverse problem is the attempt to reconstruct an object from its shadow. It is necessary to have additional information to be able to do that since only some features such as the objects shape are uniquely determined.

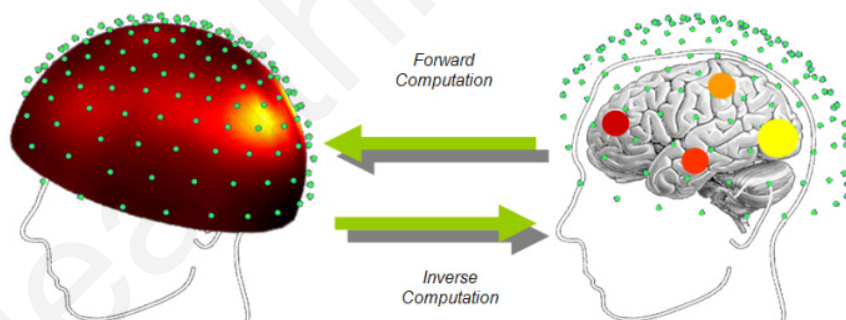


Figure 3-12 Measuring the total brain activity from the sources that generate it (forward problem) and the inverse problem to identify the localization of those sources based on the measurements

Nevertheless, various solutions to the inverse problem have been developed and obtained as a probabilistic estimate under suitable constraints. Some of the most important and commonly used probabilistic solutions are presented in the next sections.

3.4.1.1.4.1 Dipole model source localization

One of the most popular solutions is by making the assumption that the solution can be modelled as just a few focal sources. These sources are interpreted as representative of their neighbourhood and are referred to as equivalent current dipoles (ECDs). Based on that, many algorithms have been developed for fitting the equivalent current dipole into a position in the brain (e.g. Marquardt, 1963). Then it is possible to calculate the best fitting current dipole compared with the obtained data, by using standard non-linear least-squares optimization methods. Nonetheless, there are some important drawbacks based on the limitations of dipole models in the attempt to characterize neuronal responses. One significant difficulty concerns the problem of accurately estimating the total number of dipoles that could provide the minimum error in the evaluation of the algorithm. Another problem would be the sensitivity of dipole location, especially with respect to depth in the brain.

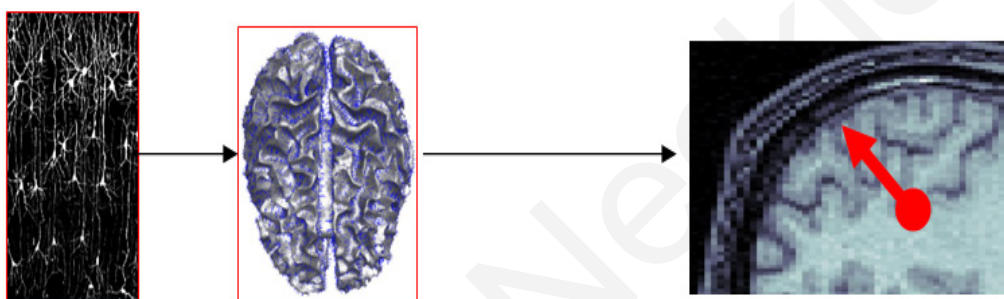


Figure 3-13 Equivalent Current Dipole assumption. The red arrow in the rightmost figure represents the assumption of an equivalent current dipole. Then based on the activations that it is calculated to produce in the MEG sensor it can be combined with the actual measurements and to provide an estimate of the source position.

3.4.1.1.4.2 Lead-field-based imaging approach

Another popular approach is based on the assumption that the continuous current density can be written as a linear sum of functions, each defining the sensitivity profile, or lead field, of the sensors. Lead-field-based modeling divides the source space into a grid containing a large number of dipoles. Since the lead fields decay fast away from each sensor the superficial sources are biased with respect to the deep sources. Therefore a weighted function matrix is usually applied to the data. The inverse problem would then need to calculate the dipole moments for each grid node (Hamalainen, 1994). One important weakness of this approach is the very poor spatial resolution.

3.4.1.1.4.3 Magnetic field tomography

One other technique to estimate current sources to localize neural activity is the Magnetic Field Tomography (Ioannides et al., 1990). MFT has proven to a large extent to be an accurate technique and provide good spatial resolution as it has been demonstrated in many experiments (Moradi et al., 2003).

The basic principle of MFT is based on the separation of the brain into four main source spaces. Typically each source space is defined by $17 \times 17 \times 11$ grid points in size, in a way that they partially overlap and completely cover the left, right, top, and back part of the brain for each subject as can be seen in figure 3-14.

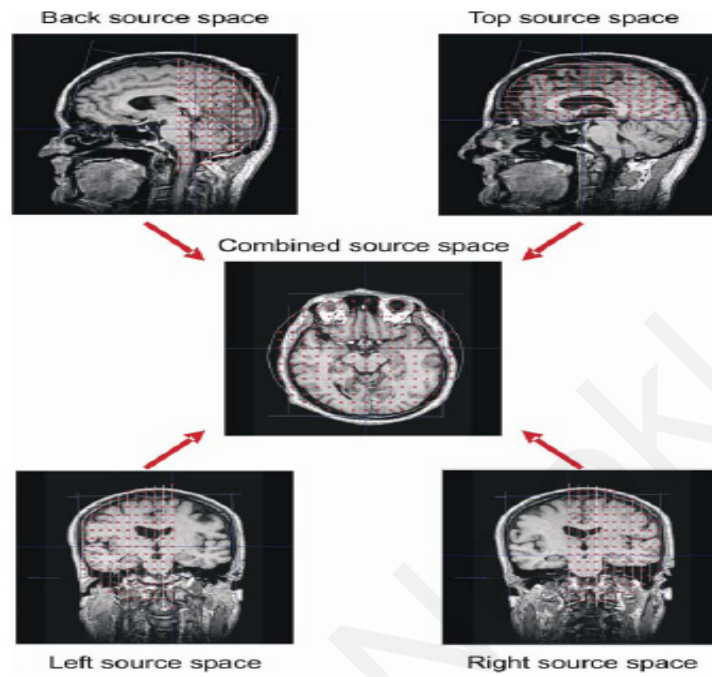


Figure 3-14 The MFT solutions from the four source spaces are combined into one (center) for estimating the source of the brain activity. Image by Yuka Okazaki PhD thesis (2007)

By measuring separately the primary current density of each of the four source spaces (using the closest channels to each source space) it is possible to combine and compute the three-dimensional distribution of primary current density, \mathbf{J} of the entire brain, in an array of $(17 \times 17 \times 17)$ grid points or voxels. Consequently, each voxel typically represents the activity in three-dimensional space. The size of a voxel typically represents a volume of 343 mm^3 (a cube with 7 mm sides) although it might vary depending on the size of the subjects head.

The localizing algorithms presented briefly are some among the plethora of algorithms and methodologies that have been developed and optimized during the last years for the identification of cortical areas and their interacting roles in human perception. In line with that, a brief analysis of the cortical regions that have been shown to be involved with visual selective attention as well as the underlying neural mechanisms that construct the channels of information transfer are presented in the next section.

3.5 Neural basis of selective attention

3.5.1 Cortical areas involved with visual selective attention

All the cortical regions that are involved with visual processing can be influenced from the attentional mechanism; however, it is possible to categorize these regions based on their functional role in the attentional system or on the various aspects of selective attention.

Posner and Petersen (1990), and later on Posner and Dehaene (1994) have proposed that the attentional control system is comprised by an alerting system, an executive control system, and an orienting system. The cortical areas they proposed to be involved in the different aspects of controlling attention are shown in figure 3-16. These areas have been correlated with each of the attentional subsystems based on several studies of humans exhibiting brain deficits in specific cortical areas. More specifically, they proposed that the parietal cortex is responsible for disengaging attention, the superior colliculus for moving attention, and the thalamus for engaging attention. These propositions have shown to be consistent with lesion studies in primates, which show that deactivation of the pulvinar (part of the thalamus) decreases an animal's ability to filter out irrelevant stimuli from a scene (e.g. Snow et al. 2009).

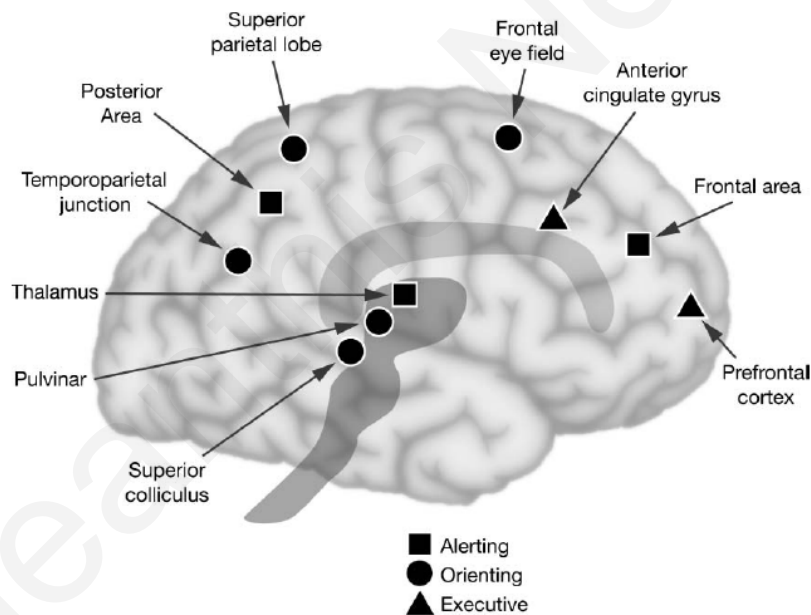


Figure 3-16 The alerting, orienting and executive systems of the attentional mechanism according to Posner and Petersen (1990). Image from Posner and Rothbart, (2007)

However, the most important distinction of the attentional role involves the automatic and volitional operation as previously explained. In terms of cortical organization, this distinction is mainly performed in regions that are coupled with information from sensory inputs (in the case of visual attention from retinal ganglion cells) and support the exogenous or automatic attention tasks,

and regions that are responsible for generating and directing control signals towards the cortical areas that receive the sensory inputs in the case of the endogenous or volitional attention. Posner and Rothbart (1991) have hypothesized that control is subdivided among posterior and anterior networks in the brain. More specifically they explained that the posterior network is more concerned with the automatic control or bottom up visual attention, while the anterior network is more closely associated with the top-down control signals of attention. This hypothesis was later on confirmed by many other neurophysiologic studies (e.g. Corbetta & Shullman, 2002; Buschman & Miller 2007).

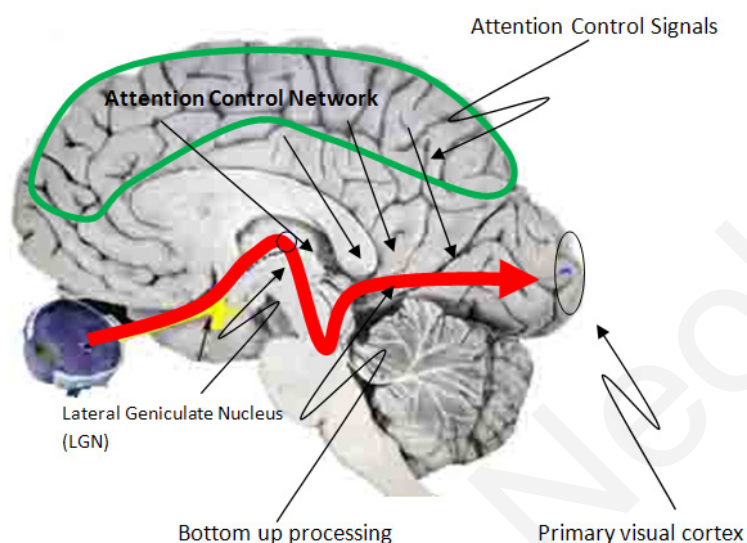


Figure 3-5 Interaction between bottom up processing and top down control signals

In the case of solely bottom up attention, the brain visual areas that receive the sensory inputs are divided into the **ventral** or **dorsal** processing pathways beyond the primary visual cortex V1. As previously mentioned, *space based attention* is primarily concerned with the spatial localization and the direction of attention towards objects of interest in space and obviously it involves the cortical areas along the “dorsal stream” including the posterior parietal cortex (PPC).

Object based attention involves the cortical areas along the “ventral stream” including the inferotemporal cortex (IT) and it mainly concerns the recognition and identification of visual stimuli. Of course although the two paths are distinct, they can operate in concert to influence the allocation of attention since many of the visual cortical areas are heavily interconnected.

In the case of top-down attention, several studies of patients suffering from attentional deficits due to brain damage as well as studies of healthy subjects performing attentional tasks have given insights into a distributed network of higher-order areas in frontal and parietal cortex that appear to be involved in the generation of the top-down feedback control signals.

More specifically, it has been documented that damage to the right PPC (due to stroke, for example) often leads to unilateral visual neglect, which is thought to be a disorder in the ability to

deploy spatial attention. Even more, many sub-regions of the PPC have been studied in detail and believe to have significant contributions to attentional control, like for instance the lateral intraparietal area (LIP, Bisley & Goldberg, 2003), the intraparietal sulcus (IPS), (Silver, et al., 2007) and the superior parietal lobule. Sub-regions of the prefrontal cortex have also suggested to participate in the generation of the control signals such as the frontal eye field (FEF), and the supplementary eye field (Hagler & Sereno, 2006), as well as the superior colliculus. For a detailed overview on the brain regions involved with visual selective attention see Kastner and Ungerleider (2000), Yantis (2008).

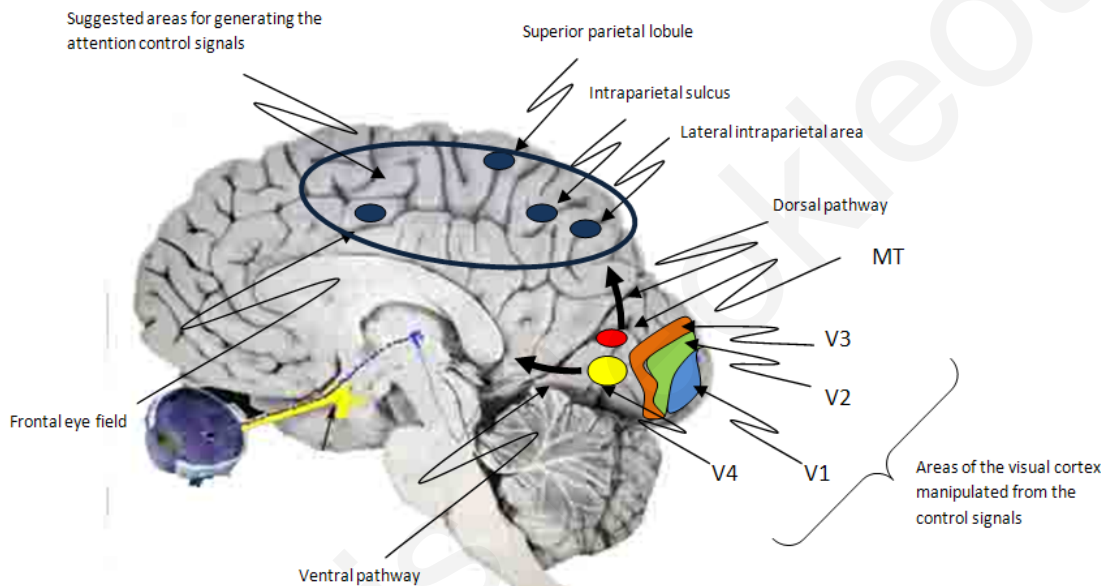


Figure 3-17 Regions generating top down signals and visual areas that interact with these signals.

Another interesting issue regarding the relation between the cortical areas involved with the control of attention, concerns the timing and sequence of the cortical regions activation. More specifically, in a study by Buschman and Miller (2007), information recorded from multiple electrodes simultaneously implanted on the lateral intraparietal area (LIP) in the parietal cortices and the lateral prefrontal cortex (LPFC) and frontal eye fields (FEF) in the frontal cortex of Macaca monkeys, was presented. This information revealed a significant difference in the timing of the activations within the specific cortical areas depending on the nature of the task. For example when top –down tasks were involved, modulations have shown to originate from the parietal and frontal cortex in order to manipulate the neural activity in the occipital cortex, while in the case of salient stimuli and bottom up tasks, the corresponding areas in the occipital cortex were activated first and the information was transferred to higher cortical areas afterwards.

The later observation has been suggested earlier by other studies (Giteleman et al, 1999; Kastner & Ungerleider 2000) and is of great importance in view of the fact that the mode of the action of

attention can be realized as a collaboration and exchange of signals between cortical areas. It is therefore important to incorporate this type of neural network communication in the design of a computational model, especially when considering both aspects of visual selective attention (endogenous and exogenous). One can explain the interaction between the two subsystems using basic concepts of control theory. More specifically, the parietal and frontal cortices can take the role of the controller in the system while visual areas in the occipital cortex to be the controlled regions that are involved in a bottom up manner (Figure 3-18).

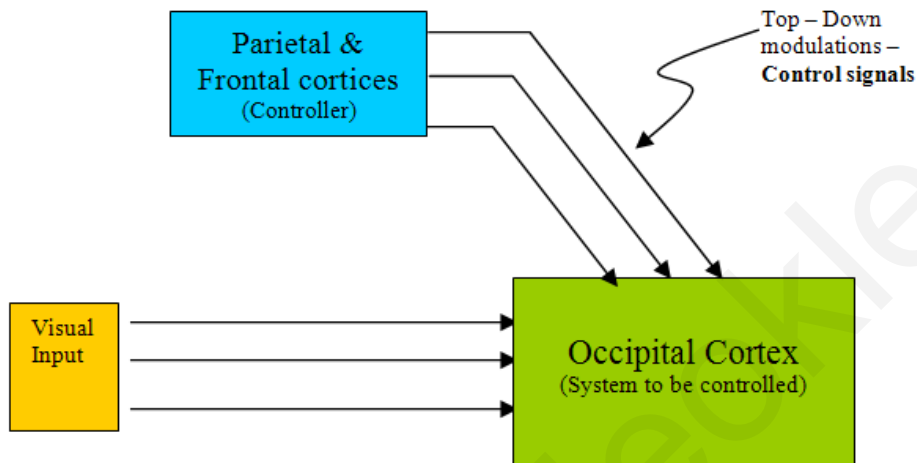


Figure 3-18 One basic possible control system of visual selective attention

Besides however, the interactions between different cortical areas in the networks level, it is of equal importance to consider the underlying neural mechanisms that allow this communication from the single neurons perspective, when attempting a more realistic and plausible implementation of a computational model. Therefore some theories related with the low level neural interactions that prevail in the scientific literature are presented in the next section.

3.6 Neural mechanisms of Selective Attention

The complete realization about how attention selects one stimulus from another based on the low level neural interactions seems to be the key to decode the general behavior of this cognitive function. Indeed, it is necessary to understand how organisms manipulate the neural activity of a stimulus in their visual field. For example at one occasion a stimulus can be presented in which its context determines that it should be attended (like a red traffic light) and in a different occasion a similar stimulus (like for instance a red light on a Christmas tree) might not be considered as important to be attended. Thus, the neuronal representations of a stimulus cannot be determined entirely by its physical properties, but there must be an additional process that distinguishes the attentional state of a stimulus such as knowledge, associated with previous experience.

Attention in the neuronal level can better be portrayed as a competitive process. This is a hypothesis that was originally inspired from single cell recording studies on monkeys. In particular, some studies observed the responses of a cell when elicited by the presence of visual stimulus in the cell's RF. The responses were then compared with responses of the same cell when a second stimulus was presented simultaneously within its RF (Moran & Desimone 1985, Reynolds & Desimone, 1999).

Figure 3-19 by Reynolds and Desimone (1999) shows the response of a V2 neuron when measured by an invasive electrode in the monkey's visual cortex. It is assumed that the specific V2 neuron is tuned to respond better towards the vertical orientation as can be seen from the top dotted line. When the horizontal bar was presented alone in the neurons receptive field, the response of the neuron was reduced (solid line below). When both bars were presented simultaneously the neurons response was shown to be a weighted average of the responses to the individual stimuli presented alone. Finally, when attention was directed towards the preferred stimulus the interaction from the second was reduced. This sensory suppressive interaction among multiple stimuli has been interpreted as competition for neural representation and can be expressed on the basis of lateral inhibitory interactions among neurons in the visual cortex (Reynolds & Chelazzi 2004).

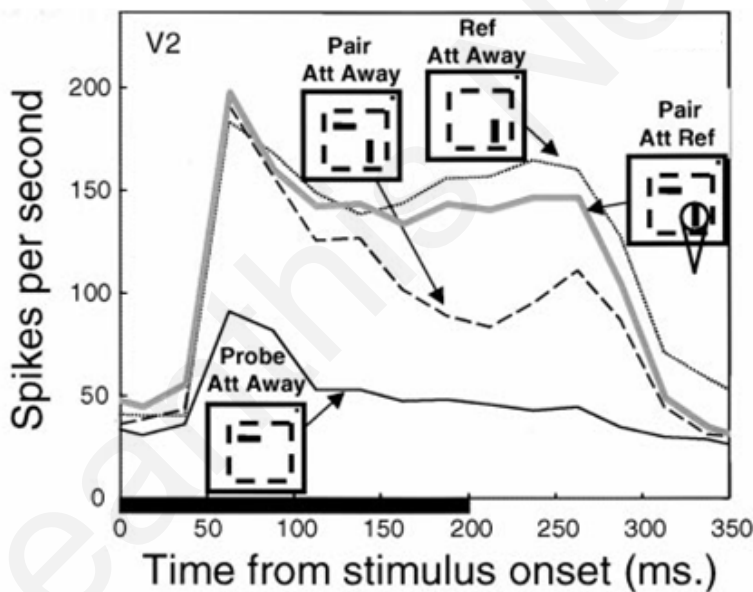


Figure 3-19 Neural activity of a V2 neuron, from Reynolds and Desimone (1999)

Similar observations were made even earlier on areas of the visual cortex with larger receptive fields such as area V4 and IT (e.g. Moran & Desimone, 1985), as well as in the middle temporal area MT and medial superior temporal area MST (e.g. Treue & Maunsell, 1996). Although the size of the receptive field in early areas of the visual cortex is not adequate to capture two simultaneous

stimuli, still several recent studies have shown similar attentional effects even in area V1 (e.g., Shibata et al., 2007).

Consistent with these observations, single-unit recording studies in monkeys have shown attentional interaction due to spatial selection combined with luminance contrast when a single stimulus appeared within the receptive field of a single cell (Treue & Maunsell 1996, Roelfsema & Spekreijse 2001). An example of this attention-dependent response facilitation is illustrated in figure 3-20, that shows data by Reynolds et al. (2000) taken by invasive measurements from a V4 neuron in the visual cortex of monkeys. The role of contrast in the visual response is considered according to three different stimulus conditions as can be seen in the right part of Figure 3-20.

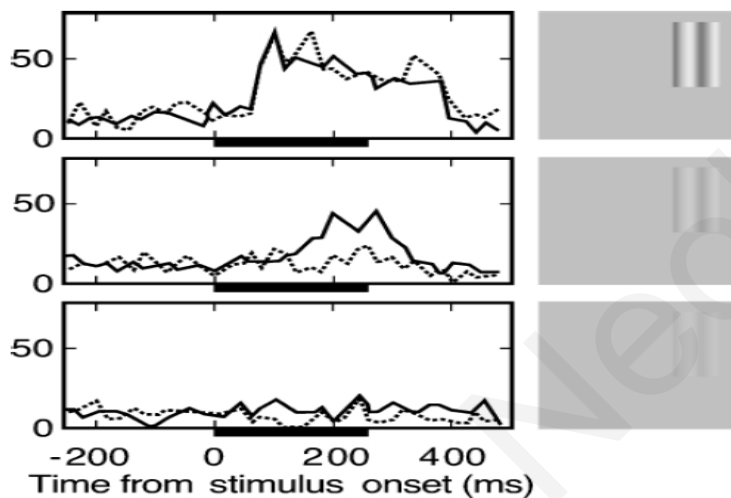


Figure 3-20 The response of a V4 neuron in the three different stimuli conditions by Reynolds et al (2000).

More specifically, the dashed line in each panel shows the response elicited by a stimulus when appeared within the V4 neuron's receptive field, but with the monkey's attention to be directed away from the corresponding spatial location. The solid line shows the response of the same neuron only this time with spatial attention to be directed to the stimulus. Each panel of figure 3-20 corresponds to one of three levels of luminance contrast of the stimulus and as can be seen this differentiation of contrast is reflected on the neurons response in both conditions (with and without spatial attention). The most interesting observation however is in the condition with the medium contrast (10% contrast stimulus) in which the neuron did not elicit any response above the baseline when attention was directed away from the receptive field, yet elicited a clear response when attention was directed to its location in the receptive field.

Another interesting single cell study that revealed important information about the underlying neural mechanisms was by Reynolds and Desimone (2003) that recorded data from a neuron in area V4 of a macaque. In that study, two stimuli with difference in orientation and contrast appeared simultaneously within the monkey's receptive field. As can be seen by figure 3-21 the

effect of increasing contrast is qualitatively different when two stimuli appear within the receptive field. By increasing the contrast of one of them, amplification or suppression of the neurons response can result, and this variation is mostly based on the neurons selectivity for orientation. More specifically in this example, the V4 neuron is shown to be tuned or to have a “preference” in the vertical orientation. Thus the equivalent stimulus is taken to be the strong stimulus while the horizontal spatially superimposed gratings although elicited an excitatory response when presented alone still are specified as the “poor” stimulus.

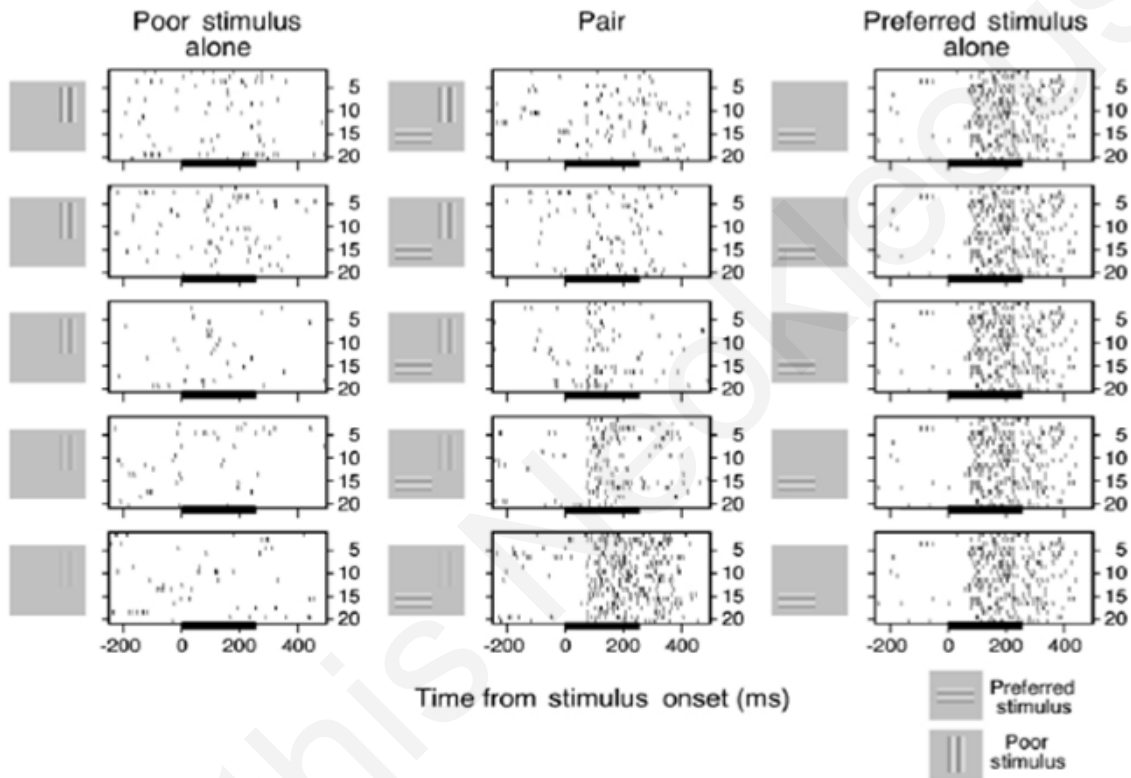


Figure 3-21 Response of a V4 neuron when a preferred and a poor stimulus are presented alone and in pair at the same receptive field. Figure adapted by Reynolds and Desimone (2003).

The response of the V4 neuron when the poor stimulus was presented is shown in the first column with variations in the stimulus contrast from 5% (top panel) to 80% (bottom panel). The right column shows the response elicited by the preferred stimulus, with fixed contrast. The second column shows that by increasing the contrast of the poor stimulus at one location suppresses the response elicited by the preferred stimulus (with fixed contrast) at a second location, when both stimuli are presented in the same receptive field of the V4 neuron. Therefore, one observation that can be inferred based on the corresponding study is that whenever two or more stimuli appear in the same receptive field of a single cell, competition can result, or in other words, attention is responsible to bias the stimulus that is about to be selected in respect to its competitive stimuli.

However, one question that naturally emerges at this point is how the attentional bias is generated and where it initiates? The answer is that both, the automatic mechanisms that construct bottom up attention and the voluntary driven top-down attention process can create these biases as it is explained in more detail in the following section.

3.6.1 Bottom-Up neural mechanisms

Bottom up attention is a primitive fast and automatic mechanism that depends on the saliency of each sensory input. This mechanism is performed at very early stages of visual processing before the interference of any top-down signals and without taking into account the internal state of the organism.

Many theories about the functionality and the underlying mechanisms of bottom up attention were inspired from experiments related with visual search, in which the main task is to identify a target among several distracters. In these tasks, the target differs from the distracters usually along one or more dimensions (e.g. Shiffrin & Schneider, 1977). One such example is a more recent version of visual search by VanRullen et al., (2003) in which subjects had to identify the target letter X among the L's (in the first condition) and the target letter T among the L's (in the second condition).

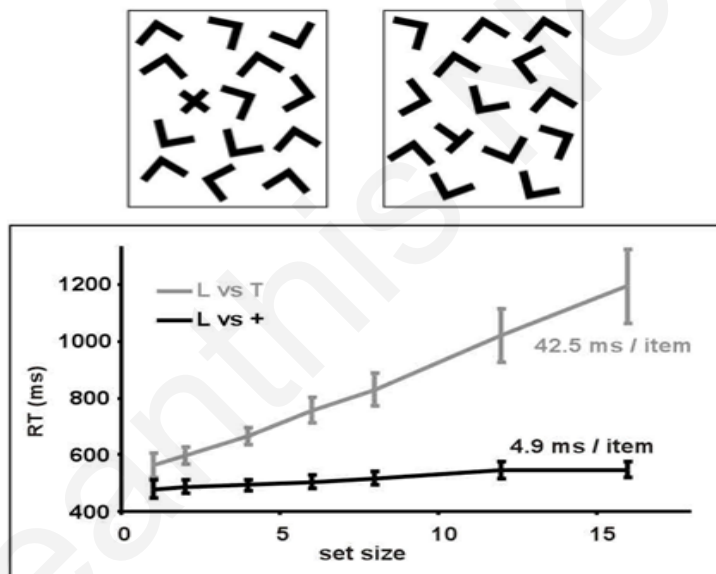


Figure 3-22 Reaction time analysis of the experiment by VanRullen et al, (2003).

From the experimental results shown in figure 3-22 (by VanRullen et al., 2003) the response time compared with the number of objects in the first condition (black line), does not significantly increase while in the second condition (grey line) there is an increase of about 42.5 ms for every new item (distractor) that is presented in the visual field. The most prevailing explanation for these experimental results and similar older studies is based on the feature integration theory (FIT) by Treisman and Gelade in 1980. The FIT suggested that search performance results from a two-stage

process. The first and pre-attentive stage (is considered to occur before the influence of attention) and is utilized upon different maps that are specialized to capture and register specific features such as color, orientation, motion and spatial frequency. Each of these maps is suggested to be correlated with neurons that are tuned on the same features and the processing of the elements across the display in this stage is assumed to be in a parallel and simultaneous manner. If selection occurs only according to the first stage, the search times are independent with the number of items in the visual field. The conjunctions between features however, might not allow the isolation of the target, and therefore the feature integration theory suggested a second, limited capacity and serial stage that is required to focus attention on single items in turn based on a separate master map. In this case, the response time increases with respect to the number of items.

The FIT had a significant impact on the scientific society and provided the foundations for developing many other computational models for bottom up processing. More specifically, it inspired an idea originally proposed by Koch and Ullman (1985) that is based on a 2 dimensional retinotopic map defined as the saliency map.

The proposal of the saliency map is based on the assumption that different possible factors can participate in determining visual saliency. In fact, many neuroscientific studies have indicated how the saliency of a visual object does not depend only on its features but mostly on the context in which the object is presented, like for instance its surrounding background.

Stimuli that stand out from their background are processed preferentially at nearly all levels of the visual system. For example the response of a cell that had increase activity when a “preferred” stimulus was presented in its receptive field, has been completely suppressed when similar stimuli appeared within a large surrounding region (Allman et al 1985, Desimone et al 1985). Even more, the suppression of the specific cell is larger when the density of the stimuli in the surround is greater (Knierim & Van Essen 1992).

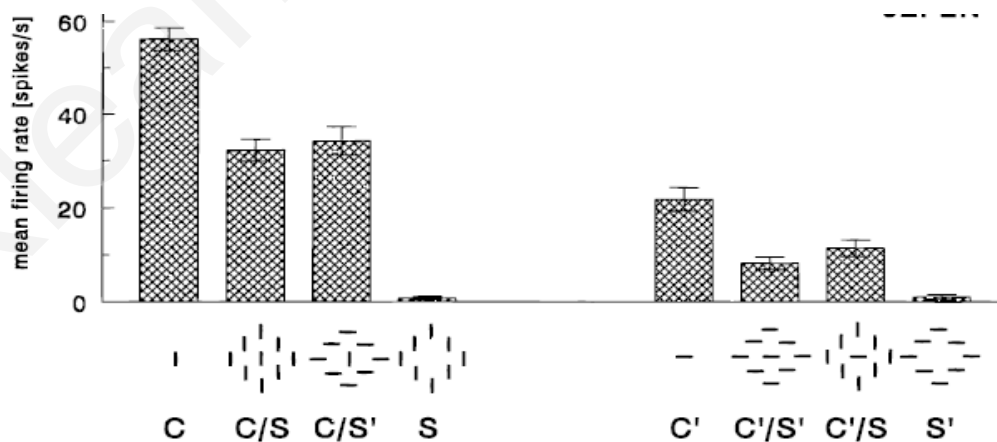


Figure 3-23 Experimental results by Nothdurft, Gallant and Van Essen (1999)

For example Figure 3-23 shows the responses of a V1 cell when tested to different texture conditions by Nothdurft et al., (1999). In this study, an optimal bar over the “classical” receptive field (RF) was presented alone or together with a texture surround located outside the RF. The y axis of figure 3.23 shows the firing rate of the V1 cell in eight different conditions. The x axis shows the different stimuli conditions that are based on combinations of center lines (C) and texture surrounds (S) between preferred (vertical bar) and non-preferred stimulus (horizontal bar). As can be seen the responses to the optimal center vertical bar (condition C) as well as the responses to the horizontal center bar (condition C') have been suppressed by texture surround (conditions C/S,C/S'; and conditions C'/S',C'/S) , which is an observation that supports the saliency map hypothesis.

The anatomical location of the saliency map, (if it exists as an independent component), was suggested to be located somewhere in the very early stages of visual processing. Koch and Ullman (1985) proposed that it may be located in the lateral geniculate nucleus of the thalamus, an area previously suggested as playing a major role in attentional control by Crick (1984). The pulvinar that is known to be involved in attention (Robinson & Petersen 1992) has also been suggested as a candidate for housing the saliency map. Another possibility is the superior colliculus, likewise known to be involved in the control of eye movements (Kustov & Robinson 1996). Several neocortical areas have been suggested as well, including V1 (Zhaoping 2002), V4 (Mazer and Gallant 2003), and posterior parietal cortex (Gottlieb 2007). In fact, the proposal of the existence of a salient map in very early stages of visual processing was motivated by the finding that in the primary visual cortex and specifically in the visual area V1, a neuron's response can be significantly suppressed by contextual inputs outside, but near its receptive field (Sillito et al., 1995; Nothdurft et al., 1999; Wachtler et al., 2003). Indeed, the response to a preferred input feature, i.e. in orientation, color, or motion direction etc., is much more suppressed when there are similar rather than very different input features in the nearby context. Specific examples of such iso-feature suppressions include iso-orientation suppression (e.g., Knierim & van Essen, 1992), iso-color suppression (Wachtler et al., 2003), and iso-motion-direction suppression (Jones et al., 2001).

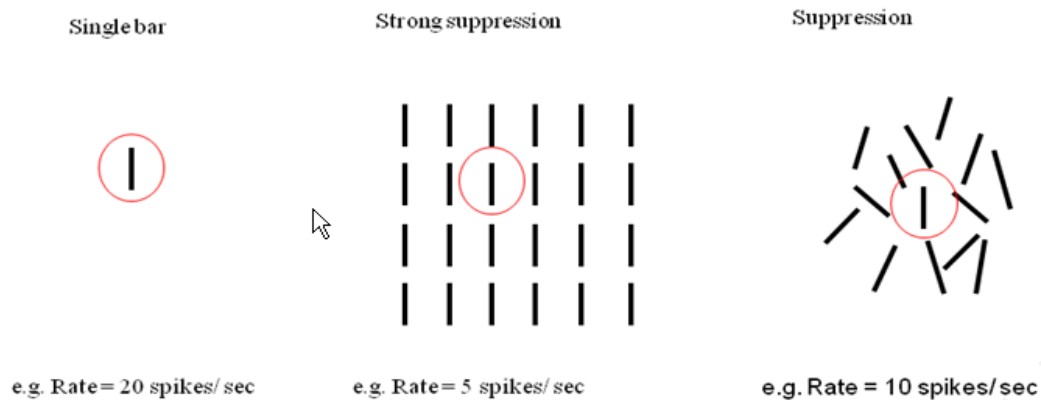


Figure 3-24 An example of iso-orientation suppression.

This generalization however, holds also for visual “features” at a much higher level of complexity like semantic contrast, for example. Therefore it is more likely that the saliency map, does not arise in one particular location but it rather interacts as a functional map whose components are distributed over many brain areas. Presumably, the calculation of visual saliency begins from the very early stages of visual processing and information from each layer is then conveyed to the following layers during the progression of neural activity in the visual stream.

One comprehensive example of how the bottom up mechanisms contributes in visual perception can be seen in the two figures below. In figure 3-25 (left image), the neurons whose receptive field correspond to the spatial location of the red tulip, will increase their activations resulting for the red tulip to pop-out and capture our attention immediately. The pop-out effect can be explained according to the competitive interactions among neurons that correspond to a certain stimulus, since the inhibition from each stimulus towards all the other in its vicinity is analogous to its “strength”. In the example of figure 3-25 the inhibitory mechanisms between the neurons of the similar surrounding stimuli (the white tulips) result to a mutual suppression of their neural activity, thus their integrated inhibition towards the neurons that capture the red tulip is limited. In the right image of figure 3-25 the same neurons that previously had an increase response for the red tulip will now be significantly suppressed.

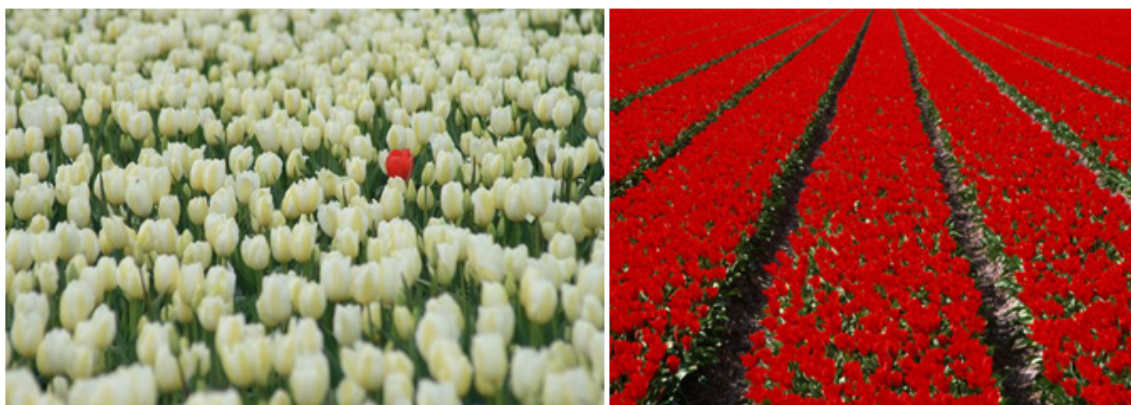


Figure 3-25 An example showing the effect of saliency

3.6.2 Top-down neural mechanisms for attentional selection

Plenty of scientific evidence from single-cell recording studies in monkeys and functional brain imaging along with event-related potential studies in humans have shown that attention related top down signals modulate the visually evoked activity. In particular, top-down signals have been shown to facilitate the information processing of stimuli at attended locations, or the information processing of features that belong to the attended stimuli (Desimone & Duncan 1995). This facilitation has been observed to affect neural processing in several ways, like for instance through the enhancement of an attended stimulus neural response. Top down signals initiated from the presence of perceptual cues (e.g spatial cues), have shown to increase the baseline activity in the attended location even before the appearance of a visual stimulation (Shibata et al., 2008; Poghosyan & Ioannides 2008).

Although response modulation by selective attention provides probably the best-studied example, and numerous studies have established that attention shifts can influence the levels of neuronal activation, during the last years, there is increasing evidence that modulator top-down effects might influence not only the average neuronal firing rates, but also the temporal structure of neural responses (Gruber et al., 1999; Fries et al., 2001). Therefore, the extensive experimental work, mainly done in the single neuron level, has emerged two hypotheses related to the possible underlying mechanisms of top down visual selective attention. These are the rate based mechanism and the most recent theory of neural synchronization.

3.6.2.1 Rate-based mechanism of selection

The most prevailing theory related with the rate-based mechanism, is referred to as biased competition (Moran & Desimone, 1985; Chelazzi et al., 1993) and has been inspired from the plethora of single-cell recordings mentioned previously that showed enhanced firing rates in neurons that represent the attended stimuli and suppressed firing rates of neurons encoding unattended stimuli. The basic principle of the biased competition theory is that behaviorally

relevant stimuli will receive an attentional bias reflected with an increase on their neural activity (and thus to gain priority in the visual cortex processing) whereas irrelevant stimuli will be filtered out due to coupled inhibitory interactions between them. Despite the fact that the rate based mechanism for selection seems to be convenient and plausible in the attentional process, it raises some questions related to the interference that might come up with the neural coding that is based on the firing rate. That is, supposing that there is information contained in the firing rate that has been initiated by a certain stimulus, then any modifications of those rates on the purpose of selection would seem to obstruct the broadcast of that information in other cortical regions. This problem can be resolved if another degree of freedom is considered, such as the level of synchronization among groups of neurons that represent a certain stimulus. More precisely, although the biased competition theory, in its original form was limited to studying rate effects (e.g. Deco & Rolls, 2005) it has recently examined neural synchronization and the possible interactions that may induce this phenomenon during attentional tasks (Buehlmann & Deco, 2008).

3.6.2.2 Synchronization as a neuronal mechanism of selection

The second more recent hypothesis related to the mechanisms of selection, places emphasis on the synchronization of neural activity during the process of attention.

The theoretical basis for synchrony as a mechanism for attentional selection was originally proposed by Crick and Koch (1990). The basis of this theory is that neurons that correspond to the source of the attended information, will present an increase of synchrony between their corresponding spike trains. Crick and Koch (1990) suggested that visual selective attention functions in a way that there is a change in the temporal structure of the neural spike trains representing the source that is about to be selected. The latter suggestion possibly derives from the basic hypothesis that temporal patterns are necessary in order for synchronization to appear. The neural synchronization hypothesis was later on supported by many recent experiments showing that neurons selected by the attention mechanism have enhanced gamma-frequency synchronization (Gruber et al., 1999; Fries et al., 2001). More specifically, Fries et al. (2001) in a study of visual attention have recorded multi-unit activity and local field potentials (LFPs) in area V4 of monkeys while performing tasks of selective attention between behaviorally relevant visual stimuli and distracters. They showed an increase in high frequency (>35 Hz) synchronization, and a decrease of low frequency (<17 Hz) synchronization, when the monkeys attended the stimulus within the receptive field of the neuron in respect to the condition in which the monkey attended to a stimulus outside the recorded receptive field (figure 3-26).

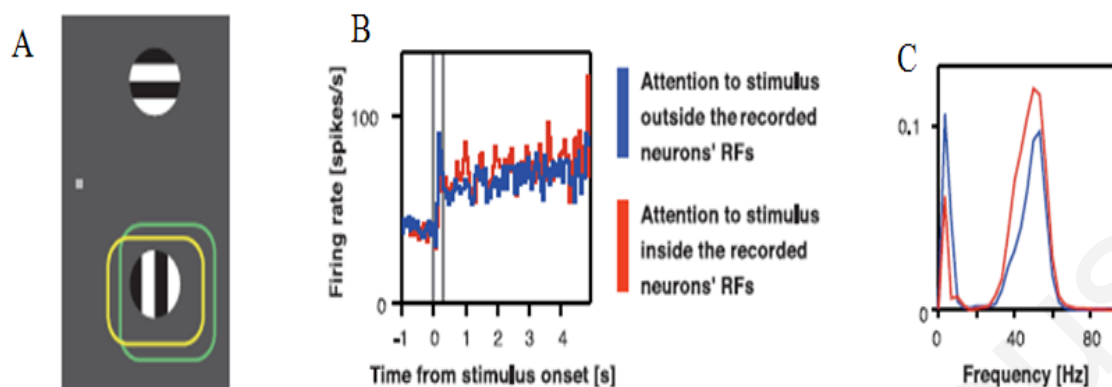


Figure 3-26 A) Shows the two stimuli with the lower being the one that is placed within the receptive field of the neurons being recorded. The spike recording site is shown with the green square and the LFP recording site with the yellow square. B) Shows the firing rate in the two conditions (monkey attending on the stimulus inside the recorded receptive field – red line- and monkey attending on stimulus outside the recorded receptive field – blue line). C) Shows the respective power spectra. Image designed based on the data by Fries et al. (2001)

Synchrony can be seen as a powerful selection mechanism considering that action potentials that arrive synchronously can increase the impact of the involved neurons on the postsynaptic targets (Azouz & Gray, 2003) and thus to have a greater effect at the next processing stage than do asynchronous action potentials. In addition, recent evidence has suggested that the coding of stimulus contrast in V1 involves synchronization (Henrie & Shapley, 2005) which is an important finding given that response synchronization is not limited by the saturation of neuronal spike rates at high contrasts. In this sense, spike rates which may be potentially limited by response saturation at high contrast can be avoided if attentional modulations are based on the coherence of neural population. Studies that emphasize the significant role of synchronization in the brain, have underlined the great importance that temporal structure of neuronal spike trains might have in terms of information processing and consequently have increased the interest in the scientific society around the role of temporal information in neural coding although this is still a controversial issue (see Deco & Rolls 2011, for a recent review).

Nevertheless, if we consider that in (complex) nervous systems, behavior is influenced by internal cognitive or perceptive state of the animal combined with the immediate sensory input; temporal structures of spike trains could play a critical role in the binding of the involved cortical areas by conveying information through neural synchronization. In particular, cross-area synchrony may be a general mechanism for regulating information flow through the brain, since findings from MEG and fMRI studies in human subjects support this idea (e.g. Tallon-Baudry et al, 2005).

Furthermore, cross-area synchrony has been investigated by many recent studies that emphasize the direct connection of top-down attention with neural synchronization (Niebur et al., 2002; Gross

et al., 2004). More specifically, Saalmann et al. (2007) performed neural recordings simultaneously from the posterior parietal cortex and an earlier area in the visual pathway (V4) of macaques monkeys while performing a visual matching task and they observed neural synchronization between these two regions in the case when the monkey selectively attended to a specific location. More recently, Gregoriou et al. (2009) have provided evidence for enhanced oscillatory coupling between area V4 and an area in the prefrontal cortex known as the frontal eye field (FEF) when attending a stimulus. Thus one can infer that parietal neurons which presumably represent neural activity of the endogenous goals can selectively increase neural synchronization in earlier sensory areas.

3.6.2.2.1 How is synchrony induced?

Two possible mechanisms prevail in the literature so far related with the mechanisms that can induce neural synchronization during the deployment of attention. The first mechanism is based on the assumption that lateral inhibitory interactions between networks of neurons can rearrange the timing of impulses and stimulate synchronous activity. The second possible mechanism is based on the common input hypothesis which implies that a neuronal population whose activity is to be selected is already identified, and the attentional mechanism can induce synchronization by sending simultaneous action potentials to all neurons in that population. These proposed mechanisms are mainly based on the neuron's dynamics as well as on the relation between the excitatory and inhibitory input spikes (Salinas & Sejnowski, 2001).

Cortical structures have a wide range of intrinsic mechanisms that could generate synchronous activity with the most plausible to be through inhibitory interneuron networks that can control the gain of spiking responses (Azouz & Gray, 2003; Tiesinga & Toups, 2005). Inhibitory interneurons have been observed to connect between them with GABAergic inhibitory synapses and electrical gap junctions with the result to form networks (Galarreta & Hestrin, 2001) that contribute in the generation of synchronous gamma-frequency oscillations observed in the cortex (Deans et al., 2001; Hormuzdi et al., 2001). Therefore inhibitory cells are considered as good candidates for mediating the effects of attention observed in cortical neurons by generating synchronized oscillations in the 20–40 Hz range.

The second proposed mechanism on how synchronization is induced is mostly based on the contribution of the temporal information in neural processing. For example, it has been shown that neurons with overlapping receptive fields in the lateral geniculate nucleus, have extracted from their spike trains around 20% more information when the synchronous spikes were taken into account separately from the non-synchronous ones (Dan, et al 1998). Even more, in an example that is usually associated with the binding problem (i.e. how primitive features bind together to construct an object) Kreiter and Singer, (1996) stimulated the receptive fields of two visual neurons

in two conditions. In the first condition, a single object was presented within their receptive field and in the second two objects. In the second condition however, the neurons response evoked practically the same firing rates as in the first condition. The synchrony between these neurons reflected whether one or two stimuli were presented, even when the firing rates in both conditions did not vary.

These examples show that, temporal information has significant contribution in sensory coding and therefore, if neurons are sensitive to correlations, it is possible to extract and integrate similar information from different sources, and convey this correlation in the network. In fact, the sensitivity of neurons in correlated inputs has been extensively studied and neurophysiologic evidence confirmed by computational implementations supported this notion (Binder & Powers 2001; Galan, et al., 2006).

In particular, in the study by de la Rocha et al., (2007) the spike train correlation coefficient of in vitro cortical unconnected pairs of neurons has been calculated when injected with levels of correlated fluctuating currents (that resemble synaptic activity) into their somata. The input current for example into one pair of neurons was defined by equation 3.1 below, in which the first term μ_i is the temporal average of the current. In the second term the weighting factors ζ_i are independent for each cell, while ζ_c is common to both cells (figure 3-27(a)). The input correlation coefficient c ($0 \leq c \leq 1$) is then responsible to set the degree of shared fluctuations whereas σ_i set the variance of the input current.

$$I_i = \mu_i + \sigma_i(\sqrt{1-c}\xi_i(t) + \sqrt{c}\xi_c(t)) \quad \text{eq.3.1.}$$

To quantify the output spike train correlation between two cells (e.g. n_1 and n_2), the correlation coefficient of the spike counts was computed, over a sliding window of length T as represented by equation 3.2.

$$\rho_T = \frac{Cov(n_1, n_2)}{\sqrt{Var(n_1)Var(n_2)}} \quad \text{eq.3.2.}$$

Cov in eq 3.2 is the covariance between n_1 and n_2 while Var the variance. The correlation coefficient ρ_T is thus a dimensionless quantity that can range between 0 and 1 (0 corresponds to independent spike trains and 1 for fully correlated spike trains). Therefore, as can be seen in figure 3-27(b) below, ρ_T increases with c and thus emphasizing the sensitivity of neurons when receiving correlated inputs.

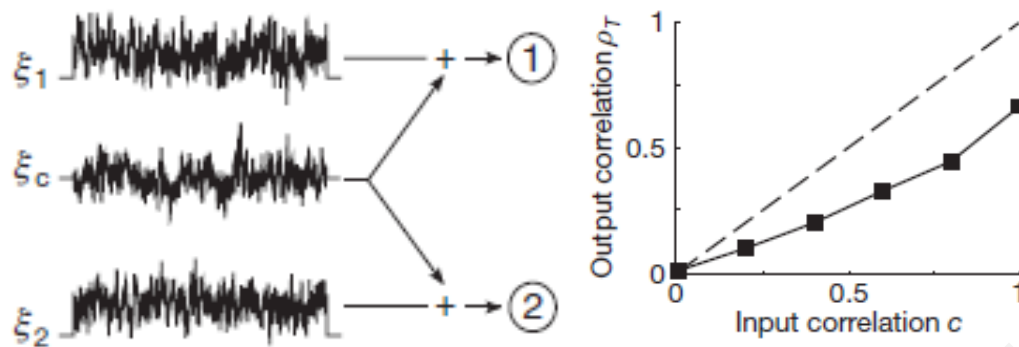


Figure 3-27 A) The stimulation of pairs of neurons with common and independent components. B) A typical ρ_T versus c curve as estimated from a pair of neurons according to de la Rocha et al (2007).

The sensitivity in correlated activity observed in neurons however implies that neurons might be exquisitely sensitive to certain temporal input patterns and in particular to be sensitive to the arrival of spikes from two or more inputs within a short time window. This type of process which is defined as coincidence detection, in theory could be achieved by having neurons with a very short membrane time constant so that the membrane potential can change rapidly. Thus the post synaptic neuron could respond best when two or more input spikes appear simultaneously rather with a time difference. In fact there is considerable experimental evidence signifying that under certain conditions, such as high background synaptic activity, neurons can function as coincidence detectors (Niebur & Koch, 1994; Destexhe et al., 1998; Kempter et al., 1998).

More specifically, the main neurons found in several layers of the visual cortex are the Pyramidal cells and several recent studies about their function imply that these neurons respond best to coincident activation of multiple dendritic compartments. An interesting review about coincidence detection in pyramidal neurons can be seen in Spruston (2008) in which a variety of coincidence-detection mechanisms based on observations of single-unit recordings in pyramidal neurons of anaesthetized and awake animals are commented.

The two possible mechanisms explained in this section, although most probably have a combined contribution in the initialization of neural synchronization during attentional tasks; in the design of the computational model I have inherited the second mechanism mostly because it coincides with my personal thoughts. Even more, the complicated and large forward and feedback projections within each layer of the visual cortex could provide a more plausible anatomical basis for the second hypothesis.

The neurophysiologic analysis presented in this chapter was significantly important for the progress of this research considering that it provided ideas and suggestions about the basic building elements of the computational implementation. The various hypotheses concerning the low level neural interactions and cortical networks interactions have been carefully studied and evaluated along with

numerous discussions with cognitive psychologists and neuroscientists before incorporating them in the computational model.

Despite however the neurophysiologic guiding lines, another major source of inspiration for the design of the model came from a number of previous computational models presented by outstanding scientists in the field. A selection of visual selective attention computational models based on the influence they had on my research is presented in the next chapter.

4. Computational models of visual selective attention - A review

In this chapter, the most important computational models of visual selective attention are presented. They are briefly explained and analyzed so that they are classified into four categories based on the purpose that each model was designed.

In the literature there are also many other relevant computational models. The ones presented here have been selected according to their scientific impact as well as on their influence, mostly through inspiration and guidance towards the proposed model. A wider and extended review of computational models of visual selective attention can be found in Tsotsos et al. (2005).

4.1 Models simulating behavioral data

4.1.1 Corollary Discharge of Attention Movement model (Taylor & associates, 2000+)

One assumption that is considered in the Corollary Discharge of Attention Movement (CODAM) model is that the mechanism of attention in the brain, functions in a manner analogous to a control system and therefore in the implementation a control engineering approach has been followed. The model in its initial form is composed of several modules on the basis of neurobiological theories of attention (Figure 4-1). The Input Module represents the neural activity at very early stages of visual hierarchy and it has its output directly connected to the Object Map, where the specific neural activity representing information is registered. The input module also activates the Goals Module which guides the top-down deployment of attention. An Inverse Model Controller is also included to generate an attention control signal for the amplification of the attended stimulus activity based on the activity in the goals module. The model also has a Working Memory (WM) buffer whose contents define what information is available for report as well as a Corollary Discharge buffer which uses a copy of the attention control signal to predict forthcoming input by pre-activating the buffer working memory site. Finally, a Monitor Module provides a measure of the error occurring during an attention movement by comparing actual and desired attentional movements. The CODAM model was used for simulations of many behavioural experiments with more important the Posner benefit effect in vision (Taylor & Rogers, 2002) and the attentional blink phenomenon by Raymont, Shapiro and Arnell (1992) in Fragopanagos et al., 2005.

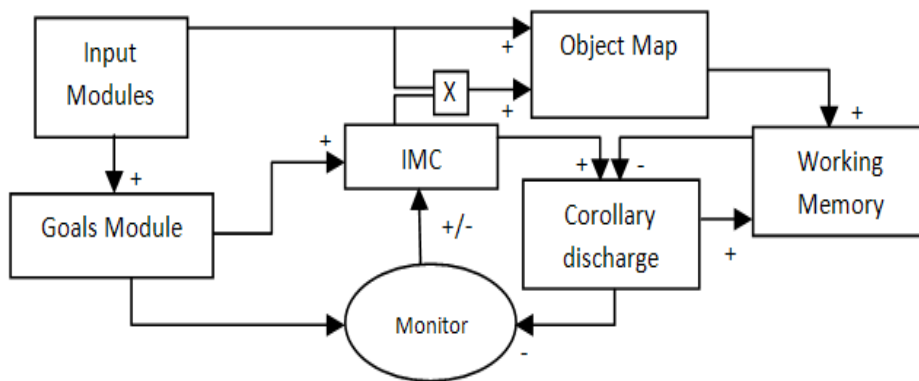


Figure 4-1 A schematic of the CODAM model (Taylor & Rogers 2002).

In more detail, the GM is responsible for biasing the IMC either endogenously by receiving information from other sources in a top-down manner, or exogenously causing attention to be directed to new and more salient inputs of greater importance. The inverse model controller module causes amplification of the attended stimulus activity while reducing that of the distractors. This signal generated by the controller, responsible for changing the focus of attention, is applied in an alerting way to the early visual cortices which in a sense receive the neural activity caused from the input stimulus. A critical component of the CODAM model is the so-called “corollary discharge” or copy of the control signal. This term was originally introduced in Von Holst and Mittelstaedt (1950) to describe a copy of the oculo-motor control signal. This copy of the control signal is well known in control theory and it can lead both to speed-up and to increased accuracy in control systems. This copy is employed in the model in a way that it can reduce the effects from distractors, and to improve attention control by preventing errors in speeded response. The corollary discharge buffer is responsible for two main processes in the model. It allows the corollary discharge signal to give an early preparation to the working memory site as well as to activate any error signal if the goal set up earlier is not realized. Thus, it can be inferred that it acts as a crucial component in the prediction of forthcoming input to the buffer working memory site. The error monitor is used to generate an early error signal between the corollary discharge signal and the goals signal. Therefore, it is responsible for resolving conflict situations in a way that it allows attention to achieve its purpose, as well as to inhibit distractors from accessing the working memory site before the attended stimulus is reported.

4.1.2 The Simultaneous Type/Serial Token model (ST₂)-(Bowman and Wyble, 2007)

The Simultaneous Type/Serial Token model is a neural network model that simulates the encoding of stimuli into working memory and it has been used to simulate successfully the attentional blink phenomenon.

The model is comprised by two processing stages for the neural activity that represents visual stimuli. A first stage of parallel visual processing combined with a serial second stage tied to Working Memory (WM) encoding. Furthermore, in order for the model to encode the visual stimuli, two factors named as “types” that provide information about the feature properties of an item and “tokens” to mark the occurrence of visual stimuli are used.

In the ST2 model the first stage is responsible for extracting the visual features and to categorize semantically each incoming stimulus. The first stage allows parallel processing and thus provides the ability to concurrently process multiple items with little interference between them. In order for an item to obtain a more durable representation and thus to gain access to working memory, it has to make it through the second stage. Stage 2 can be considered as the entrance to WM, which in contrast to the first stage, it is constrained to sequential processing. These constraints according to the suggested methodology, arise because the system attempts to associate items with discrete episodic contexts.

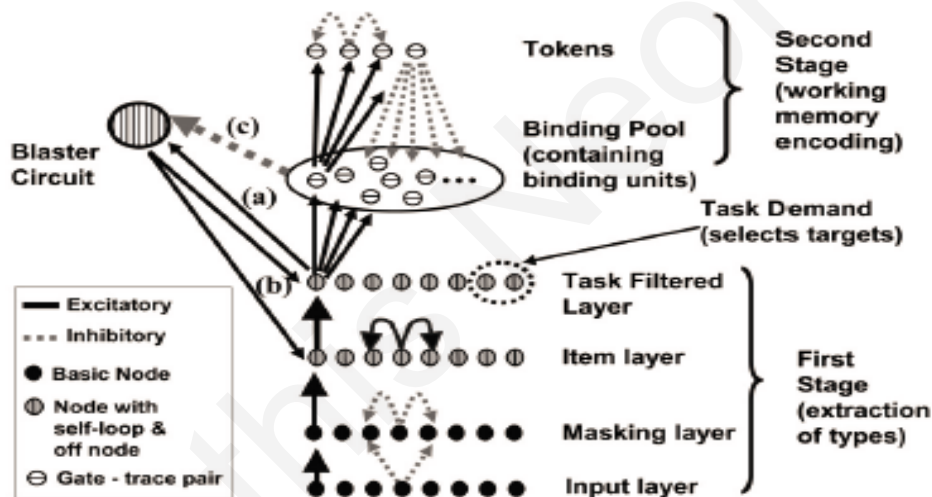


Figure 4-2 The schematic representation of the ST2 model by Bowman and Wyble (2007).

Other components of the model that contribute in the overall process are the saliency filter, the transient attentional enhancement module and the binding pool as shown in Figure 4-2. The saliency filter can be seen as the intermediate component between the first and the second stage since it is responsible for enhancing task-relevant items and thus enabling them to progress into the second stage. Additionally, the saliency filter ensures that task-irrelevant items do not reach Stage 2. However, despite the amplification of the neural activity of a salient item by the saliency filter, the authors of the model suggest an additional mechanism similar to the control signal suggested by the CODAM model. More specifically, when an item passes the saliency filter in a strongly active form, a separate mechanism represented by the transient attentional enhancement will provide it a temporally brief, but spatially specific, enhancement. Thus, it will help the item to elevate across

the later levels of Stage 1 and subsequently to encode into WM. In this sense, the mechanism can be considered as exogenous in character, since it is activated by the occurrence of a salient environmental stimulus.

Finally, perhaps the most important process in the model is the binding of the types with tokens. In particular, a dedicated pool of binding nodes is suggested in the model, which forms a self-sustaining pattern of activity during encoding in order to store the coincidence of types and tokens. Thus, the binding pool satisfies the requirement that WM does not commit type representation space, and with this manner it allows a type to be processed even if it is already present in the memory set.

4.1.3 The global workspace model, (Dehaene Sergent & Changeux 2003)

Another interesting model is the Global Workspace Model (GWM) of Dehaene, Sergent and Changeux (2003). This model is biologically detailed and anatomically prescribed and similarly with the previous models, was successfully used to reproduce the data of the attentional blink (Figure 4-3).

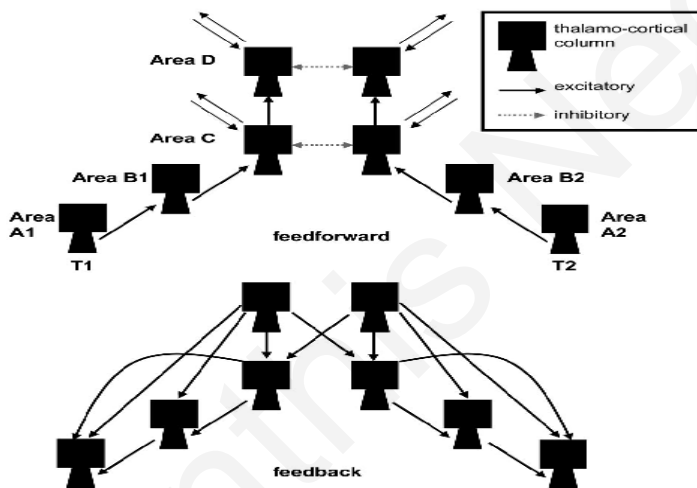


Figure 4-3 Processing pathways in the neuronal global workspace model of conscious access. Image by Dehaene et al (2003).

The general functionality of the model is based on the competition between stimuli to engage a global workspace access. However, stimuli first need to pass through neural processing pathways that originate from early sensory regions to higher association areas of the temporal, parietal, frontal, and cingulate cortex. The authors suggest that when a stimulus accesses a sufficient number of workspace neurons, the activity of the neurons becomes self-sustained. Thus, it can be broadcasted via long-distance connections to different areas and create therefore a global and exclusive availability for a specific stimulus. At this point, the stimulus is considered as having reached consciousness. Another important characteristic of the model is the inhibition that is exerted by neurons which process a stimulus that has accessed workspace towards other

surrounding workspace neurons, which makes the latter unavailable for processing other stimuli. The Global Workspace Model has no control signal to amplify neural activity. Instead, when intrinsic fluctuations are in phase with stimulus presentation, the total activation is enhanced. This results in biasing neurons of adjacent areas and therefore increasing the probability for the entire network to fall in a global active state. Furthermore, it is proposed in the models description that global activity can be more easily achieved when there is ‘‘resonance’’ between bottom-up sensory information and top-down signals.

The previous models described in this section have been specifically selected for presentation because both of them try to simulate data from the ‘‘attentional blink’’ experiment by Raymont, Shapiro and Arnell (1992) which provides good justification and evaluation for any model. A simulation of this specific behavioural experiment was made by the proposed computational model and thus a comparison between the results of these models is feasible and will be presented in Chapter 6.1.

4.1.4 Neural Theory of Visual Attention (Bundesen, Habekost, Kyllingsbæk 2005)

The Neural Theory of Visual Attention NTVA is a neural interpretation of C. Bundesen’s (1990) theory of visual attention. NTVA was used to account data from many attentional effects in human performance by simulating reaction times and error rates, as well as it was used to simulate effects observed in the firing rates of single cells in the primary visual cortex and thus according to the authors it provides a bridge between cognition and neurophysiology.

In TVA, in order for an object to be encoded in the short term memory, it is necessary to have two characteristics. The first is for the object to have visual identification based on the category it belongs and the second to be selected from the attentional mechanism when presented in the visual field. According to the theory of visual attention, visual categorization of an object has the form ‘‘object x has feature i ’’ or, equivalently, ‘‘object x belongs to category i ’’. When visual categorization of an object completes processing, then this object can enter the visual short term memory (if memory space for the object is available in VSTM). More precisely after the object identification, a race among objects in the visual field begins in order to become encoded into VSTM thus it can be inferred that the theory of visual attention is based on a two stage model.

The way that each object is encoded according to NTVA is based on the central equation 4.1 below that calculates the total firing rate that each object will have based on its saliency.

$$u(x, i) = \eta(x, i) \beta_i \frac{w_x}{\sum_{z \in S} w_z} \quad \text{eq.4.1.}$$

In eq 4.1, the rate at which a particular visual categorization, “x belongs to the category i ”, is defined by $u(x, i)$ and as can be seen is given by the product of three terms. The first term, $\eta(x, i)$ corresponds to the strength of the sensory evidence that object x belongs to the category i . The second term β_i is a perceptual decision bias associated with category i which can be thought of as a factor indicating the contribution that a certain feature has in the classification of an object category and is bounded between 0 and 1, ($0 \leq \beta_i \leq 1$); with zero being the minimum and one the maximum contribution. The third term is the relative attentional weight of the object x , (w_x) in respect to the sum of weights across all objects in the visual field, (S), $\sum_{z \in S} w_z$ and therefore gives a reflection of a filtering mechanism in the equation. Therefore, each object that will be presented in the visual field will have a calculated corresponding firing rate based on the parameters that are considered in eq 4.1 and based on their firing rate a race to access working memory begins.

4.2 Models simulating visual saliency

4.2.1 A Model of Saliency-Based Visual Attention for Rapid Scene Analysis (Itti et al., 1998)

The model has been developed on the basis of a previous biologically plausible architecture proposed by Koch and Ullman (1985) which has been inspired from the so-called “feature integration theory,” by Treisman and Gelade (1980). More specific, selection in the model appears to be implemented in the form of a spatially circumscribed region of the visual field or more commonly known as the “focus of attention” and this attended region is selected based on theoretical background from neurophysiological studies.

The idea behind the implementation of the model is based on a suggestion by Koch and Ullman (1985) that explains how visual input is first decomposed into a set of topographic feature maps and the visual field is divided into several spatial locations. Each location then competes for saliency within each map and as a result, only the locations that appear to be more salient than their surrounding areas can persist and are further processed. Following the initial processing, all of the topographic feature maps feed, in a purely bottom-up manner, a master “saliency map,” which is responsible for coding individually and relatively with the combined saliency each location. Based on the coding of the master “saliency map,” a winner take all mechanism begins to process each location for performing shifts on the focus of attention as can be seen in Figure 4-4 below.

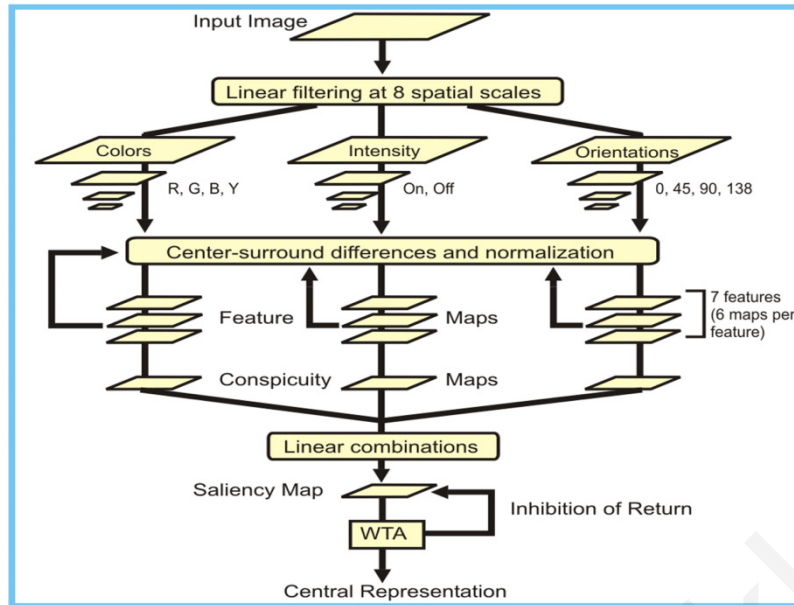


Figure 4-4 A schematic Architecture of the proposed model by Itti et al. (1998)

4.2.2 The Selective Tuning Model – Tsotsos 1990+

The Selective Tuning model (ST) was first described in Tsotsos (1990). In contrast with the previous model by Itti et al., selective tuning although is mainly a bottom up selection model of visual attention; task knowledge is able to bias the computations throughout the processing network. Thus the selective tuning can support both bottom-up and top –down modulations of attention.

The visual processing architecture in the selective tuning model is proposed to be pyramidal in structure as can be seen in figure 4-5 below, where the feed-forward and feedback connections between the units of the network provide the ability to adjust the selection based on bottom up or top-down information.

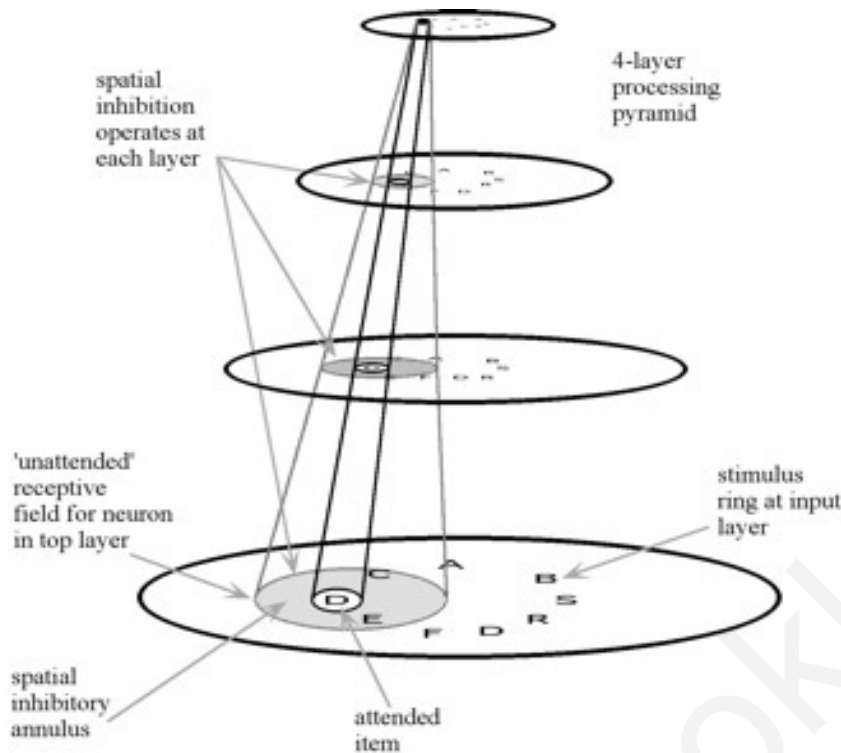


Figure 4-5 The pyramidal architecture of the selective tuning mode (Tsotsos 1990+)

The general functionality of this algorithm is mainly based on winner-take-all (WTA) processes between different layers of the visual hierarchy. WTA is a parallel algorithm for finding the maximum value in a set and is commonly used to simulate how a specific stimulus gains access into working memory. For example, when a stimulus is first applied to the input layer of the pyramid, it activates in a feed-forward manner all of the units within the pyramid to which it is connected (figure 4-5) that result in an inverted sub-pyramid of units and connections. The selection process is based on the importance of the content within a specific receptive field of each layer, measured by the response strength of each processing unit. In other words, the strongest activation a unit has the more probable is for the specific unit to be selected.

Therefore, the algorithm initially performs a WTA process across the entire visual field at the top layer, which means that the unit with the largest response in the top layer will be the global winner. In addition, the WTA can accept guidance for areas or stimulus qualities if there is top-down information related to a task; otherwise the algorithm operates independently and based on the salience of the input stimulus.

Following the selection of the winner node (in the top-layer), the selection process goes steps back to previous layers by activating a hierarchy of WTA processes. More specifically, the global winner activates a WTA that operates only over its direct inputs and thus localizes the largest response between the units of the immediate previous layer within the top-level winning receptive field. Next, all of the connections of the visual pyramid that do not contribute to the winner are

inhibited. This mechanism of selection and then inhibition of the un-attended receptive fields is then applied recursively through the pyramid. The end result is that from a globally strongest response, the focus of attention is concentrated and localized in the sensory field at the small receptive fields of the earliest levels.

4.3 Algorithmic Models

4.3.1 The Adaptive Resonance Theory (ART) – (Grossberg 1987+)

Adaptive Resonance Theory (ART) is a theory that first has been developed in 1987 by Stephen Grossberg and Gail Carpenter, however an interesting description can be seen in Carpenter and Grossberg (2005). The basic target of this theory was to provide an explanation on how the brain processes information, however although ART is a general theory it can be applied in attentional tasks with a very interesting and plausible manner.

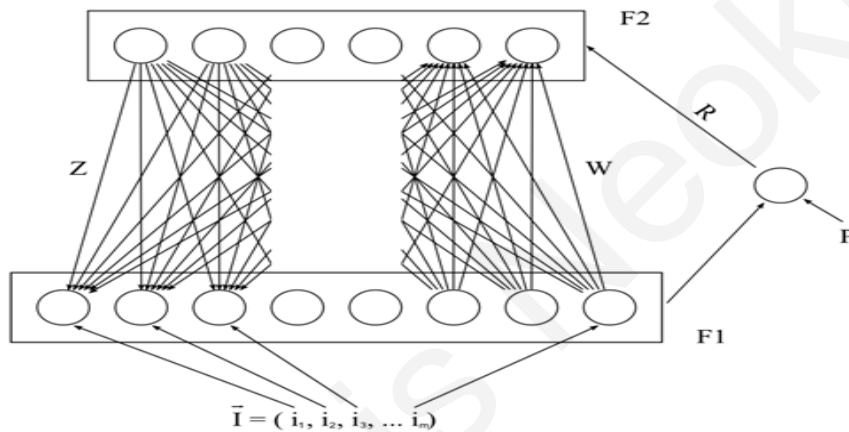


Figure 4-6 The basic ART structure (Carpenter and Grossberg, 1987).

The ART system is an unsupervised learning model that consists of a comparison and a recognition field. Those fields are composed by neurons, a vigilance parameter, and a reset module. ART performs recognition of a visual stimulus by transforming it into an input vector (a one-dimensional array of values) and then connects it to its best match in the recognition field according to a comparison field. The best match is the single neuron whose set of weights (weight vector) most closely matches the input vector. In other words, if we assume that we are searching for a visual stimulus in the visual receptive field, then the recognition field would be an array of values that correspond to the information coming from top-down signals. Thus the neurons whose input vector has the best match with the recognition field will be selected in a top-down manner. Furthermore, in the ART algorithm, each recognition field neuron outputs a negative signal (proportional to that neuron's quality of match to the input vector) to each of the other recognition field neurons and inhibits their output accordingly. This is a mechanism that reflects the possible competitive mechanisms of selective attention.

The vigilance parameter and the reset module are mostly responsible for training and producing memories. Vigilance parameter is responsible for producing memories which are relatively connected with the degree of vigilance. It is assumed that a memory of a certain stimulus will be retained with greater detail if that stimulus is accompanied with high vigilance compared to lower vigilance. For instance, an input stimulus will be represented by an input vector with an array of values. After the input vector is classified through the comparison field, the reset module compares the strength of the recognition match to a vigilance parameter. If the vigilance threshold is met, training commences. Otherwise, if the match level does not meet the vigilance parameter, the firing recognition neuron is inhibited until a new input vector is applied. In other words, training commences only upon the completion of a search procedure since the recognition neurons are disabled one by one by the reset function until the vigilance parameter is satisfied by a recognition match.

4.4 Modeling the underlying Neurobiology of Attention

4.4.1 A model for the neuronal implementation of selective visual attention based on temporal correlation among neurons (Niebur & Koch 1994)

The model proposed by Niebur and Koch (1994) has been developed in order to simulate the possible neural mechanisms behind selective visual attention based on the temporal correlation among groups of neurons. This theory fits relatively well with the recent findings that support the importance of synchronization as a selective mechanism, mainly due to the emphasis they place on the temporal information contained in an incoming stimulus.

The basic architecture of the model is shown in Figure 4-7 in which the interaction between the two cortical areas in the hierarchy of visual cortical processing is presented. The theory behind the model is based on the assumption that visual areas V2 and V4 are among the first areas of the visual cortex that have shown to be subjected to attentional modulations. Actually, recent neurophysiological research as it was mentioned in the previous chapter has shown activity in area V4 to be strongly and systematically modified by selective attention. Despite the fact that area V4 receives direct input from V1, the model considers the major input to be from area V2 because the former projection is limited to the central field representations.

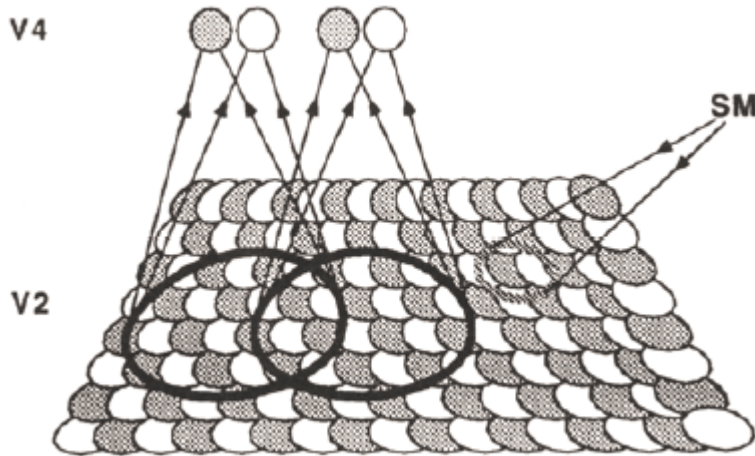


Figure 4-7 The Architecture of the proposed model by Niebur and Koch (1994)

More specifically, as it has been explained in the previous chapter, input from the two-dimensional retina is fed via the lateral geniculate nucleus (LGN) and V1 into area V2. Thus it can be inferred that the initial attentional modulation originating in the saliency map has already been applied to the neural activity before entering area V2 as can be seen in Figure 4-8 below.

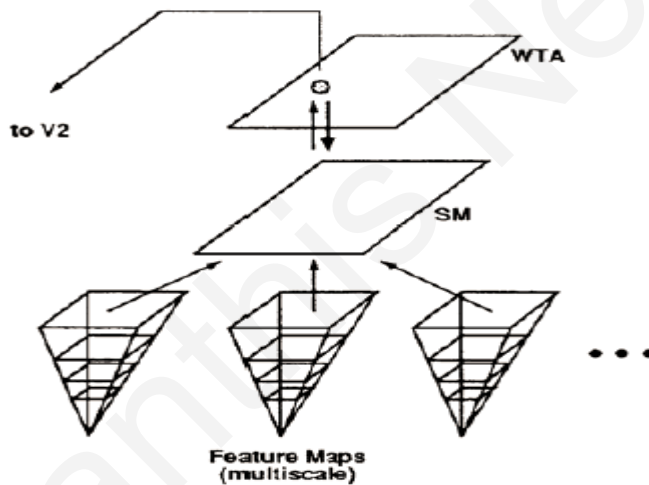


Figure 4-8 The modulation of the early neural activity before entering area V2. In the proposed model, the output from V2 projects into neuronal "stacks" in V4, where it excites pyramidal cells as well as inhibitory interneurons. These V4 interneurons, in turn, inhibit the pyramidal cells of opposing feature selectivity and thus contribute in the general mechanism of selection.

The receptive fields of V2 cells are represented in figure 4.7 by overlapping circles and specifically white and gray circles represent cells that are tuned to two different features. The two black circles correspond to the receptive fields of the V4 cells. That is a V4 cell will receive input from all V2 cells that appear within its corresponding black circle. Finally, the shaded unfilled circle in the figure represents the focus of attention. That is all V2 cells inside the circle are subjected to temporal modulation by the saliency map (SM), but without changing the average firing rate of those cells. With this manner they provide a plausible way to use the temporal parameters

contained in the V2 cells neural activity and to induce synchronization in the following stage of processing which would be in area V4 of the visual cortex.

This model was one of the first models that have been developed based on the hypothesis by Crick and Koch (1990) which suggested that visual attention at the single cell level manifests itself via “temporal tagging” in order to generate correlated neural activity. Indeed the architecture of the model by Niebur and Koch (1994) brought in the surface some possible mechanisms that can induce neural synchronization that have been considered in future models, including the proposed computational model presented in this thesis. Therefore in the next chapter some fundamental operations of this model that have been inherited with some modifications in the proposed model will be analyzed in more detail in the next chapter.

4.4.2 The Biased Competition model- Desimone and Duncan (1995)

The “biased competition model” is a very influential model in the attention mainly because it has been supported by a significant body of behavioural and neurophysiological experimental evidence. The key idea behind the model relies on the fact that neural processing is in general competitive among the brain systems responding to sensory input. Indeed, neurophysiological evidence as explained in chapter 4 emphasize that stimuli presented in the visual field will participate in a form of competition in order to “win” the shared attentional resources and access WM. Sustained signals from task context act to bias competition in the model, so that the stimulus relevant to the current task or behaviour will have more potentials to “win” the race to WM. The mechanisms for biasing a specific stimulus or the top-down modulations are suggested to arise from feedback connections between working memory and prefrontal cortex. Finally, according to the model, competition especially in object – based attention is integrated between one brain system and another. Therefore in the case that different objects are activating the same neurons and because the tendency is for the same object to assume dominance throughout the network, then due to the couple interactions, these neurons will be mutually suppressed.

More precisely, the model assumes that when two stimuli appear within the visual field, at some stage of visual processing will activate separate populations of neurons. If these two stimuli however appear close to each other, their neural response will converge to a common input neuron in a subsequent stage of cortical processing. In their model Desimone and Duncan (1995) assume that each input population will provide both excitatory and inhibitory signals to the output neuron through inhibitory interneurons. Thus, the response of the output neuron will depend on the corresponding excitatory and inhibitory input ratio and specifically its selectivity to a specific source will be based on the corresponding projection between the two inputs. In other words, the stimulus that will send proportionally more excitatory signals to the output neuron will elicit stronger response and thus define the selectivity neural path.

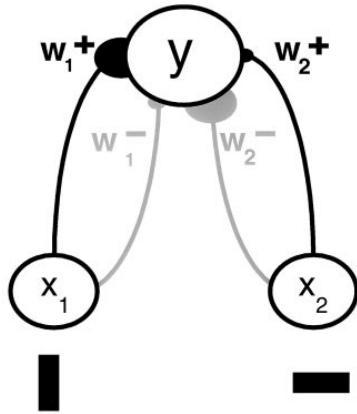


Figure 4-9 A simple connectivity representation for the biased competition model. Figure adapted by Reynolds et al (1999).

For example, Figure 4-9 shows the excitatory and inhibitory inputs initiated by two different stimuli (vertical and horizontal bar) from separate cells in the visual cortex (i.e. neurons in area V2) and mathematically expressed by eq.4.2 below. E is the total excitatory input and I the total inhibitory input, while X_1, X_2 correspond to the responses from the two cells. W_i^+ and W_i^- represent the corresponding excitatory and inhibitory weights.

$$E = X_1 W_1^+ + X_2 W_2^+, \quad I = X_1 W_1^- + X_2 W_2^- \quad \text{eq.4.2.}$$

The response of the output neuron y , it is then described by the basic equation that governs the neural response in the model (eq.4.3) in which y is the stimulus neural response, B the maximum response, E the total excitatory input, I the total inhibitory input and A reflects a passive decay.

$$\frac{dy}{dt} = (B - y)E - yI - Ay \quad \text{eq.4.3.}$$

4.4.3 Setting the path towards the proposed model

As noted in the introduction of the Chapter, the computational models that had been presented were the primary source of inspiration and guidance in designing the basic framework of the proposed model. Each of the presented categories corresponds to computational models that focus on specific research fields, like for instance the simulations of reaction times and error rates measured from behavioral experiments, or the effects observed in the firing rates of single cells in the primary visual cortex.

However, it is equally important to give emphasis on computational models that link these two fields of research and thus to provide mathematical frameworks that bridge cognition and neurophysiology. In line with this, the proposed computational model, as has been briefly

mentioned in Chapter 2, combines symbolic with sub-symbolic modeling that gives the potential to connect these specialized research fields, and hence to provide a new perspective in the research of selective attention. Therefore, one main difference and distinction that the proposed computational model has, compared to the majority of the models presented here, is that it is focused on the simulation of behavioral experimental data and at the same time it operates according to theories about neural mechanisms on the single neuron level. The global workspace model of Dehaene et al., (2003) and the model behind the neural theory of visual selective attention by Bundesen et al., (2005) are also models that bridge the two fields of research, however there are several differences in their overall operation compared to the proposed computational model as will be explained in the following chapter.

More specifically, the proposed model received influences from the global workspace model (Dehaene et al., 2003) and the model of Niebur and Koch (1994) concerning the mechanisms that induce neural synchronization and from the biased competition framework (Desimone & Duncan, 1995) about the competitive interactions among incoming stimuli. In fact, the combination and conjunction of these theories can provide a very optimistic view about the possible brain mechanisms that underlie selective attention and built the foundations for the proposed implementation as will be analyzed in the following chapter.

5. The proposed computational model of visual selective attention

The proposed computational model was built through an appropriate system of dynamical equations that were mostly implemented and simulated with the MATLAB/SIMULINK environment. This is a specialized programming platform for multi-domain simulations and model-based design of dynamical systems. SIMULINK provides a powerful and versatile interactive graphical environment that allows not only the implementation of time-varying systems, but also the observation of the system dynamics in a very comprehensive manner.

The proposed attentional system has many coupling signal interactions from multiple sources; therefore it is important to visually observe each phase and component while manipulating parameters of the model. SIMULINK offers such simulation capabilities. A theoretical and mathematical representation of the model is given in this Chapter, while the SIMULINK model and its various components with the underlying programming code are presented in Appendix A.

The methodology that has been followed to effectively implement the computational model was based on a recurrent process. Initially the model was designed according to the neurophysiological information about the low level neural interactions and after that; its performance was evaluated on the basis of several known behavioral experimental data. During the evaluation stage, any strange results or simulation predictions were re-examined through the design and execution of new behavioral experiments. The corresponding experimental data were then used for new modifications and detail corrections on the parameters of the model. This procedure was repeated until the credibility of the model's behavior was substantially confirmed. More specifically, four undergraduate and two graduate students (see Appendix C) have dedicated their diploma theses in the design and execution of behavioral experiments related with selective attention guided from the computational simulations.

Next the model was used for simulations of behavioral experiments that had immense impact in the scientific literature with the main objective to resolve any disagreements that these experiments have brought in the surface. The behavioral experiments that were used for simulations are placed under two main categories of visual attention tasks. The first category refers to tasks in which the deployment of attention is focused on the temporal appearance of visual stimuli, with a typical methodology frequently used in these tasks to be the rapid serial visual presentation (RSVP). RSVP is a method of displaying a sequence of visual stimuli in rapid succession at the same location (Figure 5-1), with one of the most famous attention related tasks of this tactic to be the attentional

blink paradigm by Raymond, Shapiro and Arnell (1992). This is a well-established experiment frequently referred in the attention literature. The AB was simulated through the proposed computational model, and the findings will be explained in more detail at the following chapter. The RSVP methodology is also used in attentional tasks that examine the influence of visual masking. **Visual masking** refers to the reduction or elimination of a specific stimulus (i.e. the target) visibility, when presented in a brief temporal window (~100ms) by the presentation of a second brief stimulus, called the “mask” and it can be either forward or backward depending on whether the mask precedes or follows the stimulus (Moore, 1998). Visual masking is an interesting technique introduced at the end of the 19th and beginning of the 20th century but extensively studied since then, for exploring the dynamics of visual information processing (Breitmeyer and Ögmen, 2006) and in particularly the relation between attention and perception. This is a research area that my thesis is also to some extent involved with.

The second category of attentional tasks refers to the presentation of multiple stimuli simultaneously in separated spatial locations of the visual field. One such behavioral experiment is the perceptual load task by Lavie (1995) whose findings were as well deeply analyzed in accordance to simulations from the proposed computational model.

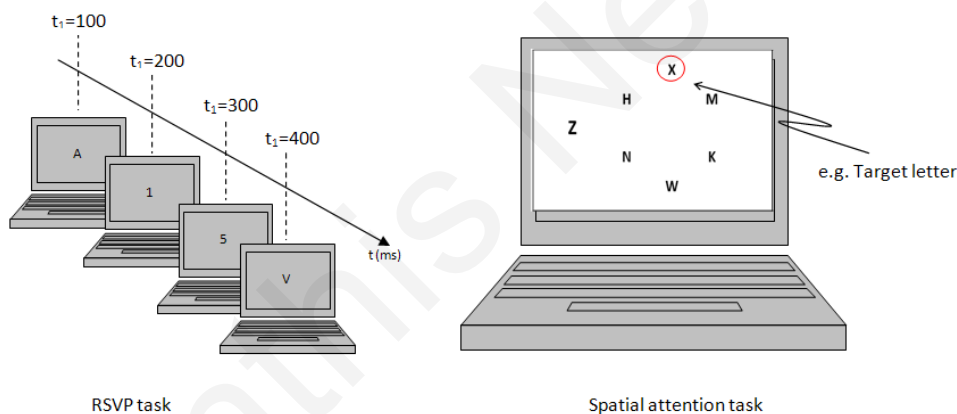


Figure 5-1 The RSVP and spatial attention tasks

In the following sections, a separate analysis is given on the basis of two sub-models, defined as the RSVP model and the spatial attention model. The justification for this comes mostly for the reason that the competitive interactions among stimuli at the neuronal level, occur relatively with the time that each stimulus is presented in every task. For example, in the RSVP tasks the competitive interactions between presented stimuli occur at different time windows since, (at least in the experiments that are studied in this report) only one stimulus appears at the same spatial location at any time instant (see figure 5-1.a). On the second category, the competitive interactions occur simultaneously and in parallel among each presented stimulus since multiple stimuli appear at different spatial locations, yet in the same temporal window.

Therefore even though a separate analysis is given, it is pointed that the proposed model is a system having a coherent structure and its operational units follow the same principles.

Separate modules however, in the proposed implementation should have been included in the cases where the requirements of the tasks were different. For example, if it was instructed by the task to identify and response a spatial location (spatial attention), a different pathway should have been integrated than in the case where the task demanded to response on a specific target (object attention) as this is explained on section 3.2.

The RSVP tasks that are considered and studied computationally with the proposed model do not involve spatial attention since every stimulus appears at the same location on the computer screen. However, in the behavioral task of perceptual load theory (see section 6.2), although it is instructed to identify and response towards a certain target, thus concerning object attention and neural interactions in the dorsal pathway, spatial interactions are also involved. Nevertheless, these spatial interactions are due to spatial cues that appear before the presentation of the visual stimuli and thus interact with the neural processing at very early stages of the visual pathway (e.g. in area V1) where the two pathways (dorsal and ventral) interact and communicate. Therefore although it would have been more realistic to include different modules for spatial and object attentional interactions, a simplified model is presented, given that the spatial interactions occur in a common visual area that is part of the neural pathway in the proposed model.

5.1 An overview of the proposed computational model

The structure of the model relies on previous literature about the neurophysiology of visual selective attention (Figure 5.2). The model involves two stages of processing implemented through spiking neural networks (SNN). The first stage simulates the initial bottom-up competitive neural interactions among visual stimuli, while the second stage involves top-down semantic modulations of neural activity. During the progression of neural activity through the two stages of processing, the encoded stimuli compete for access to working memory (WM) through forward, backward, and lateral inhibitory interactions which modulate the strength of their neural response. This implementation is based on the biased competition framework (Moran & Desimone, 1985) and on neurophysiologic findings showing that competition for neural representation in visual areas V1 and V2 is initiated when two or more stimuli fall within the receptive fields of the same or nearby cells (Reynolds & Desimone, 1999; Reynolds & Chelazzi, 2004- see Chapter 4). The first stage of the model corresponds to the early visual areas at the occipital regions of the brain (e.g., V1, V2) and the second stage of processing reflects the interaction between higher areas within the visual cortex accompanied with a fronto-parietal network responsible for maintaining goal-directed activity (e.g. Corbetta & Shullman, 2002; Posner & Rothbart, 2007). The interaction between these

two systems in the model produces enhancement and synchronization of neural activity that leads to the selection of a particular stimulus for further processing.

5.1.1 RSVP model

In the RSVP tasks, each incoming stimulus will receive inhibition from the stimuli that appeared before as well as by those that follow. This assumption is consistent with several studies of single cell recordings (Rolls et al., 1999; Keysers & Perrett, 2002) that show the effect of visual masking on the firing rate of neurons in the temporal cortex of monkeys. Thus, competition between the RSVP items, represented by backward and forward inhibition, will have the first impact on each of the neural responses in this model configuration. Even more, forward and backward masking in the proposed computational model, is intensified by a reverberatory activity between the first and second stage of processing. More specifically, these loops of neural activity between the two stages may indirectly interact with the processing of stimuli that appear in the visual field within different temporal windows (see Figure 5-2).

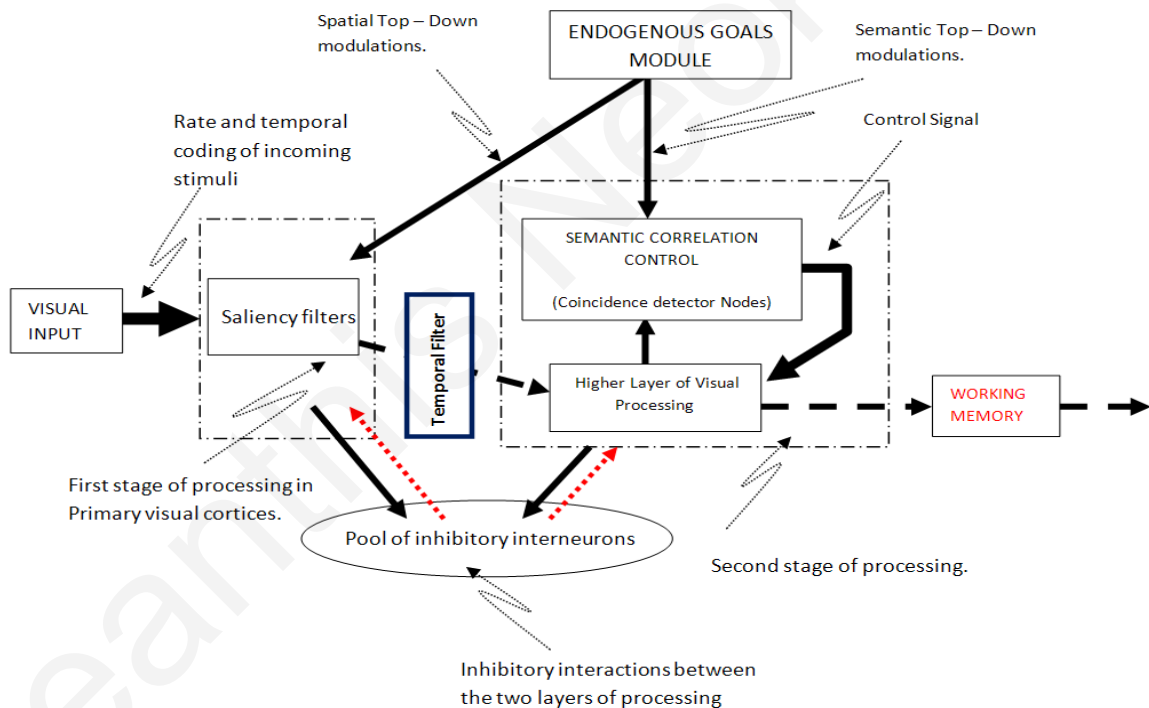


Figure 5-2 Diagram of the RSVP proposed computational model.

5.1.1.1 First stage of processing

The initial representations of stimuli that enter the visual field are created in the model on the basis of a saliency map. The manipulation of visual activity by means of a saliency map in the early stages of visual processing is supported by the finding that in the primary visual cortex and specifically in area V1, a neuron's response can be significantly suppressed by contextual inputs that lie outside but near its receptive field (Nothdurft, et al., 1999; Wachtler et al., 2003; Shibata et

al, 2008). In the model, a saliency map that was originally proposed by Koch and Ullman (1985) as a neuromorphic vision algorithm has been adopted. This algorithm was implemented by Walther and Koch (2006) into a Matlab toolbox (Saliency Toolbox - <http://www.saliencytoolbox.net>) which can be used to produce saliency values for every spatial location in the visual field. These values are used by the model to establish the initial firing rates of the neurons that correspond to visual stimuli (see section 5.3.1.1).

However, it should be noted that the importance of saliency in visual perception is a debated issue. On one hand, salient but irrelevant stimuli have been shown to automatically capture attention (Crick & Koch, 1990). On the other hand, in their recent review, Corbetta et al., (2008) claim that the behavioural relevance of a stimulus is more important than saliency for the activation of ventral frontoparietal network that is responsible for stimulus-driven attention. Corbetta et al., (2008) argue that exogenous orienting (i.e., orienting towards salient but non-relevant stimuli) activates a dorsal frontoparietal network that is involved in goal-directed attention.

Nevertheless, the use of saliency values to generate the initial representation of each incoming stimulus in the model is based on the assumption that different factors (at different levels in the visual hierarchy) may contribute to the saliency of a stimulus. For example, luminance contrast appears to be the initial variable on which saliency computation is based, since it is the first type of information extracted by our visual system in the retina (VanRullen, 2003). In higher levels of processing in the visual cortex, other feature dimensions such as orientation, color and motion are encoded and thus contribute to the visual saliency of a stimulus. At even higher levels in the visual pathway, “features” with increased level of complexity (e.g., semantic contrast) may influence visual saliency. VanRullen (2003) suggested that each level in the visual hierarchy processing builds its receptive field selectiveness based on the output of the preceding layers (Chelazzi, et al, 1993).

Thus, although the receptive fields of neurons in the higher layers of the visual pathway will be activated based on top-down activity; information about local contrasts from all previous layers is still maintained and should therefore be included in the computations.

The second stage of processing explained in the next section, accounts for the influence of top-down goals to neural activity when these are relevant to the task. Otherwise it simply behaves as an extension of the neural path towards working memory. However, the distinction in two stages of processing does not eliminate the possibility of having both bottom up and top down mechanisms to interact. In fact in several occasions in which perceptual cues are involved in attentional tasks the two systems operate simultaneously as will be presented in the detailed analysis that follows.

5.1.1.2 *Second stage of processing*

The neuroscientific literature and especially studies using single cell recordings (Chapter 4) have shown that the neural activity in the area V4 receives influence from top-down activity (Moran and Desimone, 1985; Fries et al., 2001; Reynolds & Desimone, 2003). Top-down signals in the second stage, are assumed to transfer information about the semantics of each stimulus, therefore, this level of processing handles the coupling interactions between the neural activity that represents visual stimuli and the activity that maintains semantic information.

Top-down interactions in the second stage of processing have been implemented in a way that can produce both neural amplification and neural synchronization as suggested by recent scientific evidence (e.g. Fries et al., 2001; Gregoriou et al., 2009). For example, attention will enhance the firing rates of the attended stimuli neurons and suppress the firing rates of neurons that encode unattended stimuli; while at the same time will force them to operate in a more synchronous rhythm.

More specifically, similar with the interference model of Isaak et al. (1999), in the presented model templates that contain features of targets are created and used for evaluating any visual input. These target representations are maintained in the endogenous goals module (Figure 5.2) and recalled when tasks demand it. More precisely, following the neural interactions of the first stage of processing, the spike trains that correspond to any incoming stimuli will pass through a “temporal filter” that reorganizes their spikes appearance without however altering their average firing rate. This mechanism is implemented in the model according to a pre-defined probability that reflects the degree of resemblance between the features of any incoming stimulus and those of a target. Thus only the spike train patterns of a stimulus that shares features with the target will change significantly and become closer to the distinct spike train pattern that maintains the semantic representation of the target. The temporal filter mechanism in the model is inspired by Crick and Koch (1990) who suggested that the selection of stimuli could be made on the basis of synchrony across neurons. Crick and Koch (1990) also claimed that visual selective attention could function in a way that it causes changes to the temporal structure of the neural spike trains that represent information to be selected and suggested that these temporal changes are a prerequisite for the presence of neural synchronization. This procedure modulates the timing of spikes within the spike train while the firing rate of the spike train remains unchanged.

After the temporal filter manipulation, neural activity is conveyed in the neural network layers of the second stage where semantic top down signals begin to exert their influence. The manipulation of neural activity in higher areas of the visual cortex by endogenous signals has been given great emphasis by many scientists as indicated by the great number of theories that exist on this topic. For instance, the Resonance Theory proposed by Grossberg (1999) claims that temporal patterning of neural activity could be ideally suited to achieve the matching of top-down predictions with

bottom-up inputs. Furthermore, in their Global Workspace model, Dehaene et al. (2003) suggested that global neural activity that represents the attended stimulus can be achieved more easily when there is “resonance” between bottom-up sensory information and top-down signals. In fact, several experimental studies that document the synchronization between cortical areas involved in top-down processing and early areas of the visual cortex are well-suited with many of those predictions and theories. For example, Engel et al. (2001) in their report argued that top-down effects which induce particular patterns of subthreshold fluctuations in the dendrites of a target population could be “compared” with temporal patterns arising from peripheral inputs. Along the same lines, Womelsdorf et al. (2007) suggested that synchronization of neural activity could be generalized as the “handshaking” between cognitive top-down control and the matching sensory bottom-up information.

In line with the above suggestions, a correlation control module (CCM) composed primarily of coincidence detection neurons is included in the model. Coincidence detection (CD) is a very simplified model of neuron whose output response depends on the number of synchronous or very temporally close action potentials that appear at its input (see section 5.2.3). The CCM is responsible for evaluating the correlation between the neural activity of encoded stimuli and the activity that represents the top-down signals that maintain the properties of the target in a given behavioral context (i.e., endogenous goals possibly held in prefrontal cortical areas). Based on the degree of correlation, a control signal will be generated for the amplification of the corresponding neural activity.

More specifically, the strength of the control signal can have many variations, mainly based on the total firing of the CD neurons of the CCM. That is, if two signals are correlated then the CD neurons will fire more frequently and will consequently elicit a stronger control signal. Furthermore, an increase in the degree of correlation will generate synchronization of neural activity in the spiking neural network (SNN) of the second stage of processing. A strong correlation between an incoming stimulus and the endogenous signals will result in a gradual increase of synchronous firing by the CD neurons.

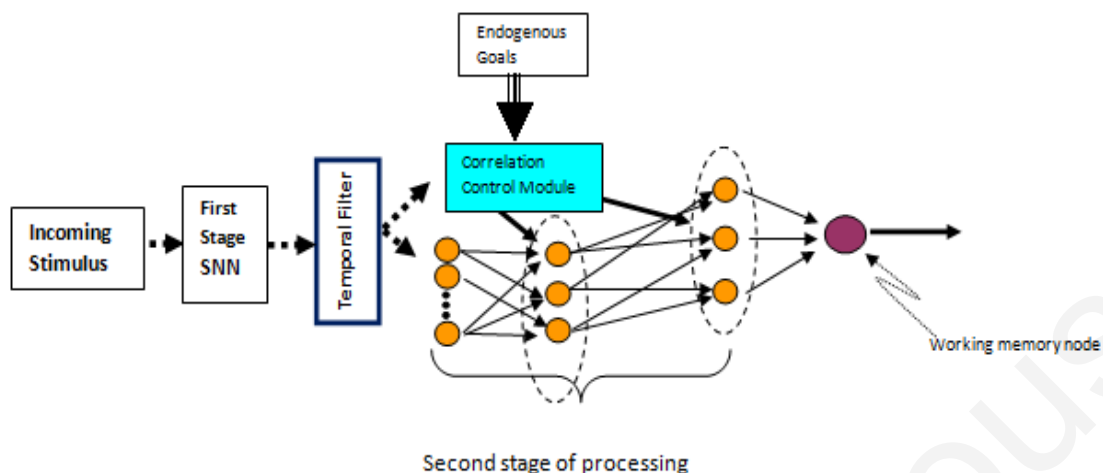


Figure 5-3 The different modules that interact in the second stage of processing

The implementation of the CCM in the model was inspired by what is currently known about the functional role of pyramidal cells, the main neurons found in the visual cortex. The pyramidal neurons have one large dendrite that branches upward into the higher layers of the cortex, as well as an axon which may be long enough to reach distant areas of the brain. Pyramidal neurons have been observed to respond best to the coincident activation of multiple dendritic compartments (Spruston, 2008). Therefore a network of CD neurons may function as a mechanism that controls the correlation between two streams of information that originate from different cortical areas. Based on that, the CCM may be cited in anatomical locations where interaction between top-down signals and bottom up sensory information has been observed. More specifically, spontaneous activity that is correlated with both networks has been observed in regions of the prefrontal cortex which poses as a possible site for the CCM in the brain (Fox et al., 2006). In addition, several studies have provided evidence for the interaction between signals containing sensory information in visual area V4 and signals of behavioral context (e.g., Treue, 2003; Reynolds and Desimone, 2003; Ogawa and Komatsu, 2004). The visual area V4 fits nicely with this model implementation as a possible cortical location for the existence of the CCM.

Finally, following the modulation of neural activity by top-down goals, the neural path leads to the working memory network. The working memory network will output a signal indicating perceptual awareness of an incoming stimulus if its neural activity is sufficient to activate the working memory nodes. The same working memory signal however, will act in an inhibitory manner towards any newly generated signals from the Correlation Control Module during that time window. This inhibitory process is necessary for preventing multiple stimuli entering working memory while it is still occupied.

However, the use of a separate controller in the model such as the CCM and the interaction of an inhibitory signal from the working memory network are two concepts that need to be discussed in more detail.

Both proposed mechanisms are inspired by a number of studies that concentrate on the chronometric analysis of the electric activity in the human cortex.

In fact, improved algorithms and techniques that have been developed during the recent years for filtering, analyzing and distinguishing brain signals while human subjects perform attentional tasks have contributed significantly in the understanding of possible attentional neural interactions.

Especially through EEG and MEG techniques that can provide a very detailed temporal analysis, it was possible to identify and categorize several event-related potentials related to attentional tasks.

Event-related potentials (ERPs) are signals that measure the electrical activity of neuronal firing in the brain that is generated upon an event such as the presentation of a stimulus. Over the years a number of ERP components related to attention have been identified in the literature and became even clearer with the use of MEG (Ioannides & Taylor, 2003).

The first distinguishable physiological signals are observed around 80-150ms post stimulus and are referred to as the P1/N1 signals. Several ERP studies have shown that stimuli at attended locations elicit greater positive (P1 at 80-130 ms) and negative (N1 at 150-200 ms) components over the posterior scalp compared to stimuli at unattended locations (e.g. Hillyard & Anllo-Vento, 1998, Luck & Hillyard, 2000).

The second group of distinguishable signals corresponds to the P2/N2 signals that appear at about 180-240 ms post-stimulus. The N2 in particular is a negative-going wave that peaks 200-350ms post-stimulus and is found primarily over anterior scalp sites (Folstein & Van Petten, 2008). More relevant however with selective attention has been found to be an ERP component in the time range of the N2 family components, labeled “N2pc” (N2- posterior-contralateral). In fact, several studies have pointed a strong correlation of the N2pc component with selective attention and specifically indicated that it reflects the allocation of attention (e.g Luck, et al., 1997; Luck 2005). Therefore, it has been proposed by several scientists as the control signal for the movement of attention (Hopf et al., 2000, Taylor 2002).

The N2pc component has been demonstrated to occur when attending to visual features and semantic features as well (Eimer, 1996, Luck and Hillyard, 2000), while MEG has been used to localize the N2pc primarily to lateral extrastriate cortex and inferotemporal visual areas, such as V4. Therefore the control signal of the CCM in the proposed model can be justified on the basis of the N2pc component.

Another important ERP is the P300 component which is observed at about 350–600 ms post stimulus and is taken to be an index of the availability for report or an indication of perceptual

awareness for the stimulus that triggered it (Kok 2001, Linden 2005). Thus, access to the working memory sensory site is expected to occur in that specific time window.

If we now consider the different temporal windows that these attention related ERPs have been identified, especially in accordance to RSVP tasks (that rely on brief stimuli presentation and therefore the time to process each stimulus by the working memory is critical and limited), then some interesting hypotheses can be inferred.

For example, in the case that two targets appear among distracters in a RSVP task (see section 6.1 for a more detail description of a relevant task) and the second in line target is not perceived, the corresponding P1/N1 components were still obtained even though the N2pc and P300 were not seen (Sergent et al., 2005). The N2pc component of the second target however, it is only suppressed when it falls within the temporal window of the P300 signal from the first target. In line with the latter evidence, one can infer that the P300 signal initiated by the first target, interacted with the N2pc component of the second target. More precisely, this is a mechanism that has been suggested to offer a protective prevention of any other stimulus getting through and interfering with the processing of the first target until a sufficient level of its activity has been reached (Fragopanagos et al 2005).

Therefore, the inhibitory signal from the working memory network which is used in the proposed implementation for the same purpose as in the latter hypothesis can be justified based on the electrophysiological evidence described here.

A possible relation between the ERPs explained here and the model RSVP implementation is shown in Figure 5-4.

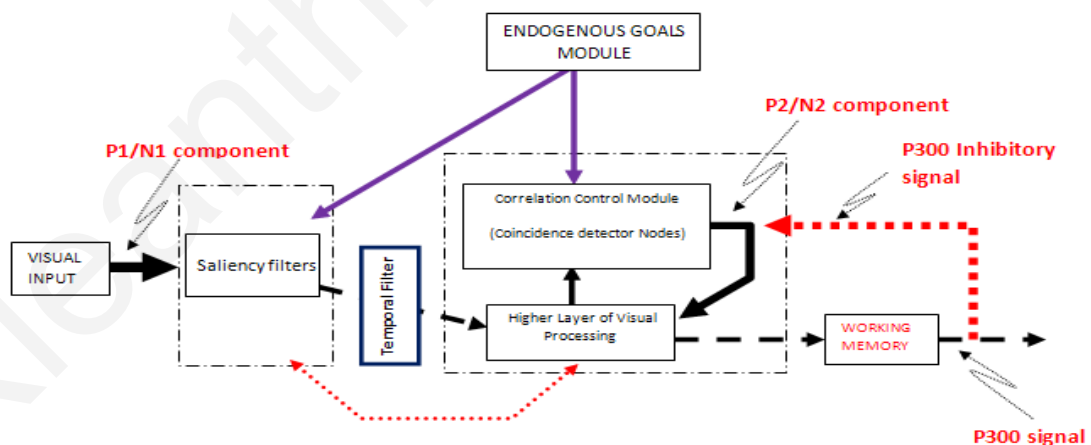


Figure 5-4 A possible relation between ERPs and the RSVP model implementation

5.1.2 The spatial attention model

The spatial attention model is very similar to the RSVP model, having some minor operational differences due to the nature of the tasks that the two models are designed to simulate. For example, forward and backward masking interaction does not influence the overall processing in the spatial attention model, since in strictly spatial attention tasks, usually all stimuli appear simultaneously. The spatial attention model however, utilizes lateral inhibition between neurons whose receptive field corresponds to separate spatial locations of the visual field. A graphical representation of the spatial attention model is depicted in Figure 5-5.

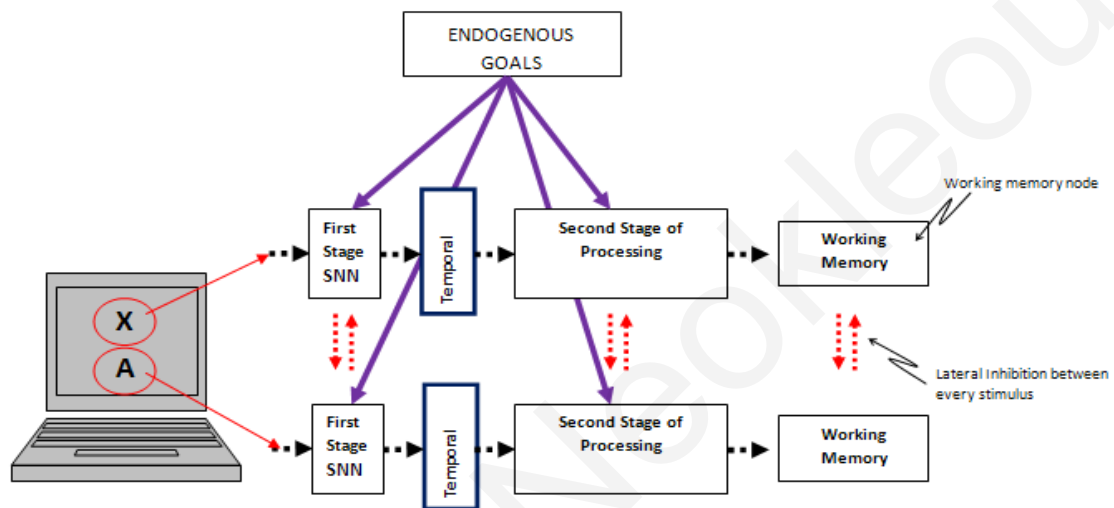


Figure 5-5 Spatial attention model schematic representation

Another important feature that is incorporated in both models concerns the way that perceptual cues influence the initial firing rate generated by the input neurons. For instance, in the spatial attention model, the top-down spatial factors (e.g., when cues are used to prime the spatial location of an upcoming stimulus) are allowed to exert their influence in the first stage of processing. This is compatible with the findings from several studies documenting that cues may increase the neural activity of neurons that correspond to visual stimuli immediately after the presentation of a stimulus, or even before the onset of the stimuli (e.g., Gandhi et al., 1999; Shibata et al., 2008; Silver et al., 2007).

Similarly in the RSVP model, temporal cues that prepare participants to anticipate a shortly appearing target can interfere with the initialization of the initial firing rate. In other words, a stimulus that appears in the time window immediately after the temporal cue, will receive an additional bias from the top down signals that interact during that time.

Perceptual cues interact in the model again through a **coincidence detector network** (CDN) module, similar in the implementation as the **correlation control module** (CCM) of the second stage of processing.

In the following sections, the basic computational units of the proposed computational model are first presented and then the overall neural network functionality based on the different modules involved is analyzed in detail.

5.2 Mathematical formulations of the proposed model units

5.2.1 Integrate and fire neuron models

The basic computational units used in the implementation are the “integrate and fire (I &F)” model of neurons, and the choice to design the model based on I&F neurons was made according to some thoughts. First, I believe that the level of modeling should be relevant with the level of the questions that one tries to address. For instance more realistic models of neurons with detailed biophysical restrictions such as the Hodgkin & Huxley (H&H) neurons would not be appropriate for this study, given that the main goal is to explain behavioral data through computational simulations. However, H&H neurons would have been more appropriate in studies that try to explain the dynamics of neural communication in the molecular level.

Another point that guided me into developing the model on the basis of I&F neurons concerns the dynamics of the I&F fire neurons, which can offer a proper level of description of the biological neurons dynamics in a very simplified manner and therefore one can experiment with realistic time scales and firing rates of spike trains that are the carriers of information in the brain. Therefore the capability to derive potential hypothesis about cognitive processes exists.

Furthermore, the non-linearity of the I&F neurons threshold can make the system sensitive to different spiking events and synaptic time courses and thus to be able to observe changes in the response of the system with minimum interactions (e.g. see section 6.3 where top down interference on very low neural activity was behaviorally relevant).

Finally, with the I&F implementation, one can easily incorporate noise due to the randomness of the neural spiking inherent by changing the threshold level or the resting potential after a spike occurrence, thus having more realistic simulations. More specifically, noise was incorporated in the experimental simulations of the attentional blink phenomenon (section 6.1).

A mathematical representation of the membrane potential dynamics of a neuron according to the I&F model is given in equation 5.1

$$\tau_m \frac{dV}{dt} = E_{leak} - V(t) + R_m I_s(t) \quad \text{eq.5.1.}$$

Where V is the membrane potential of each neuron, τ_m is the membrane time constant, and E_{Leak} is the resting potential of the membrane. The membrane potential can be seen as a measure of the extent to which a node is excited. $I_s(t)$ represents the total synaptic current and is a simple combination of pre-synaptic excitation and bias currents that increase the membrane potential, as

well as inhibition currents that reduce the membrane potential of the node. The total summation of the excitatory and inhibitory currents influences the actual membrane potential at each time instance. Finally, R_m is the membrane resistance of the neuron.

In brief, eq.5.1 determines how the membrane potential V of each neuron develops over time after an input current I_s is applied. The value of the membrane potential increases until it reaches a specific threshold (V_{th}) at which a spike is emitted and V resets to its initial condition or resting potential V_{reset} . Subsequently, a refractory period is applied before the neuron model is allowed to integrate any pre-synaptic currents again.

The sequence of output action potentials from a neuron (i) is defined as the neuron's output spike train and it is expressed by $y(t)_i$.

5.2.2 Synaptic currents

The term $I_s(t)$ in eq. 5.1, quantifies the synaptic currents that are mediated by the excitatory receptors AMPA and NMDA (activated by glutamate, g_{AMPA} and g_{NMDA}) and the inhibitory receptor $GABA_A$ and $GABA_B$.

$$I_s(t) = (I_{AMPA}(t) + I_{NMDA}(t)) + (I_{GABA_A}(t) + I_{GABA_B}(t)) \quad \text{eq.5.2.}$$

However, in the following analysis, the synaptic inputs will be considered as the total excitatory and inhibitory synaptic currents ($I_{exc}(t) + I_{inh}(t)$).

Indeed, in the framework of the integrate-and-fire model, each pre-synaptic spike generates a post-synaptic current pulse that is driven in the input of the following neuron as shown in eq. 5.3-5.5.

$$I_s(t) = (I_{exc}(t) + I_{inh}(t)) = g_{ext}(t)(E_{S_{ext}} - V) + g_{inh}(t)(E_{S_{inh}} - V) \quad \text{eq.5.3.}$$

Where

$$g_{exc}(t) = \bar{g}_{exc} w_{ext} P_s(t) \quad \text{and} \quad g_{inh}(t) = \bar{g}_{inh} w_{inh} P_s(t) \quad \text{eq.5.4.}$$

\bar{g} in equation 5.4 is the maximal excitatory or inhibitory conductance and w_{exc}, w_{inh} are the excitatory and inhibitory synaptic weights. $P_s(t)$: Reflects the fraction of open ionic channels that determine the synaptic conductivity and is expressed by eq.5.5 below.

$$\frac{dP_s}{dt} = -\frac{P_s}{\tau_s} + \sum_k \delta(t - t_k) \quad \text{eq.5.5.}$$

t_k is the time of spike appearance from a pre-synaptic neuron.

The parameters $E_{S_{exc}}$ and $E_{S_{inh}}$ of equation 5.3 describe the reversal potentials of the corresponding excitatory and inhibitory synapses. The reversal potential of the excitatory synapses $E_{S_{ext}}$ is much larger than the membrane resting potential, hence the current induced by a presynaptic spike at an excitatory synapse is positive and thus an increase in the membrane potential of the post synaptic neuron is induced. The reversal potential of the inhibitory synapses is

close to the membrane resting potential, thus an action potential arriving at an inhibitory synapse will drag the membrane potential of the post synaptic neuron down to its reversal potential. As the reversal potential of excitatory synapses is usually significantly above the firing threshold of spiking neurons and the inhibitory reversal potential is close to the membrane resting potential, each of the corresponding terms $(E_{s_{exc}} - V)$ and $(E_{s_{inh}} - V)$ can be fitted within the excitatory and inhibitory synaptic weight constants of eq.5.4.

Therefore, the total input current to a certain neuron is the sum over all current excitatory and inhibitory pulses from the total number of pre synaptic neurons and can be expressed by eq.5.6

$$I_s(t) = \sum_j^N \bar{g}_{exc} w_{exc} P_s(t)_j + \sum_j^M \bar{g}_{inh} w_{inh} P_s(t)_j \quad \text{eq.5.6}$$

N is the total number of excitatory input neurons and M the corresponding inhibitory input neurons. $P_s(t)_j$ determines the synaptic conductivity (eq.5.5) which can be modeled by a simple exponential decay with time constant τ_s (eq.5.7).

$$P_s(t) = \frac{1}{e^{t/\tau_s}} + \frac{(\Theta(t-t_k)e^{t/\tau_s})}{e^{t/\tau_s}} \rightarrow P_s(t) = f(\delta(t - t_k)) \quad \text{eq.5.7}$$

In eq.5.7 Θ represents the Heaviside step function (zero for negative arguments, unity for zero or positive arguments, eq. 5.8).

$$\Theta(n) = \begin{cases} 0 & n < 0 \\ 1 & n \geq 0 \end{cases} \quad \text{eq.5.8}$$

Finally, the total input current can be modeled as a function of the synaptic weights and the spike train time sequences of the pre-synaptic neurons.

$$I_s(t) = \bar{g}_{exc} w_{exc} \sum_j^N f(\delta(t - t_k))_j + \bar{g}_{inh} w_{inh} \sum_j^M f(\delta(t - t_k))_j \quad \text{eq.5.9}$$

The coupling computations and interactions in the model however, are performed in discrete time and therefore the corresponding mathematical expressions are formed analogously. In biological neurons, spike duration has a finite duration in the order of 1ms. Similarly each spike is represented in the model by a pulse of unity amplitude and 1ms duration. Therefore in the discretization process each time step δt is taken to be 1ms.

The simplification adopted in the time discretization, in a sense, bounds the depth of information that can be gained in the single neuron level compared to more elaborated models or to biological neurons. Nevertheless, as discussed in a number of papers, (Soula et al., 2006; Cessac 2008), this kind of modeling simplification, provides a rough yet realistic approximation of a biological neuron behavior.

In line with the above, the basic membrane potential differential equation (eq. 5.1) for a neuron i after a formal time discretization is given by 5.10

$$V_i(t + \delta t) = (E_{leak} - V)(1 + \frac{dt}{\tau_m}) + \frac{R_m}{\tau_m} I_s(t) \delta t \quad \text{eq.5.10.}$$

As mentioned, the sampling time was chosen to be the smaller than all characteristic time scales in the model which is the duration of the action potential. Therefore with $\delta t = 1 \text{ ms}$ eq.5.10 can be re-written to:

$$V_i(t + 1) = \frac{(E_{leak} - V)}{\tau_m} (\tau_m + 1) + \frac{R_m}{\tau_m} I_s(t) \delta t \quad \text{eq.5.11.}$$

Similarly the implementation of the synaptic currents is also in discrete time and therefore eq.5.5 takes the following form.

$$P_{s_i}(t + dt) = \frac{P_{s_i}}{\tau_s} (1 - \frac{dt}{\tau_m}) + \sum_k \delta(t - t_k) \delta t \quad \text{eq.5.12.}$$

A graphical representation of the discrete computations from a simple example implemented in MATLAB SIMULINK is shown in Figure 5-6 below. In the specific example and generally in the simulations of the model, the output of each neuron is assumed to be a discrete unity pulse with duration 1ms as previously mentioned.

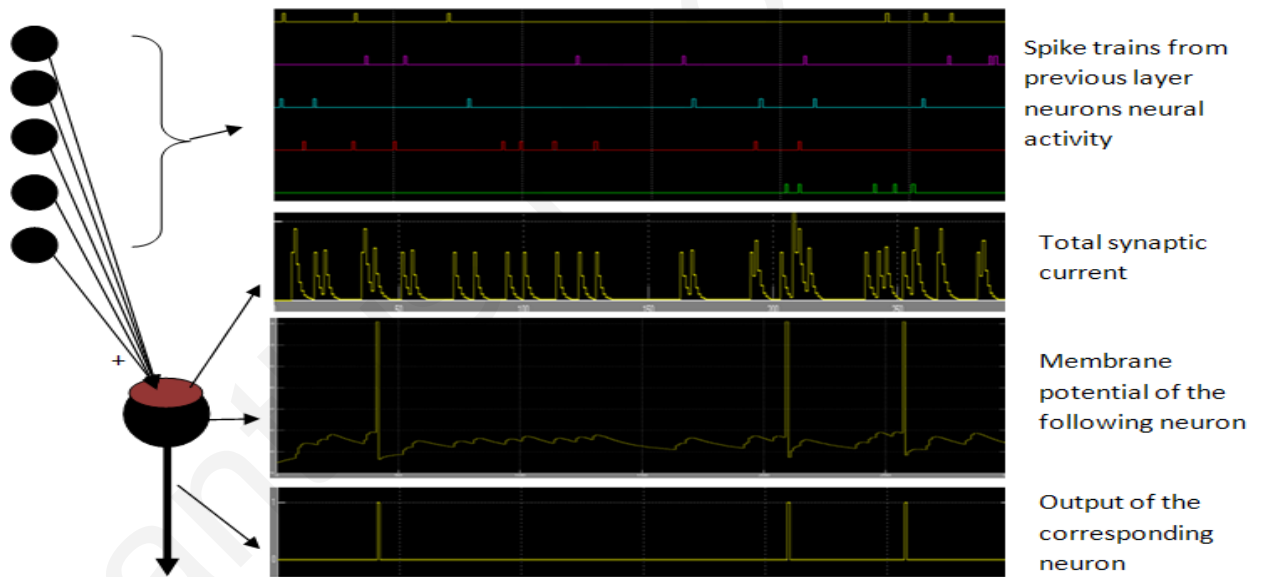


Figure 5-6 Discrete computations in a simple example of neural processing. Each black represents a neuron and the red area corresponds to the synaptic activity caused by presynaptic neurons.

5.2.3 Coincidence detector nodes

The proposed model includes a subsystem of coincidence detector neurons. One way to model coincidence detection can be based on separate inputs converging on a common target. Let us consider a basic neural circuit of two input neurons with excitatory synaptic terminals A and B converging on a single output neuron C (Figure 5-7). If it is assume that each spike is represented

by a pulse with amplitude equal to 1. Then the coincidence detector neuron C will fire only if the sum of its input is greater than 1.

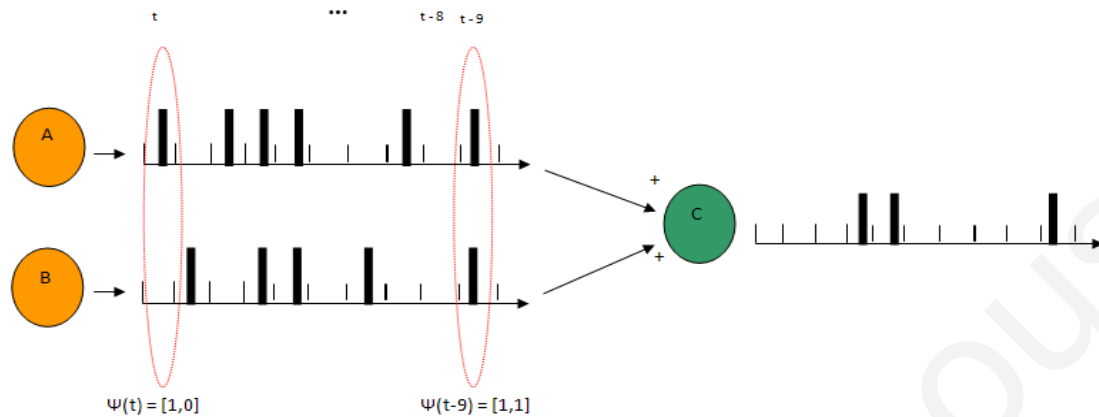


Figure 5-7 Representation of the coincidence detector mechanism

More precisely, let $\Psi(t)$ be a binary row vector denoting the states of neuron A and B at time t and $C(t+1)$ the state of neuron C at $t+1$ as in Figure 5-7.

Then the outcome of C at $t+1$ can be expressed by:

$$C(t+1) = \theta(\Psi(t) - \theta) \quad \text{eq.5.13.}$$

As usual, θ is the Heaviside step function with $\theta(x) = 1$ for $x > 0$, and $\theta(x) = 0$ otherwise. θ is the specific threshold in which a number of synchronous input spikes is necessary to cause an output spike of neuron C.

5.2.4 Working memory nodes

Working memory is defined as a brain system that provides selection, temporary storage, and manipulation of information necessary for supporting complex cognitive tasks such as language comprehension, learning, and attention (Baddeley, 1992). One possible neural mechanism for working memory is that information is stored in rapid short-term changes in the synaptic weights (Malsburg and Schneider, 1986; Schmidhuber, 1992). Another mechanism is based on the hypothesis that sustained neural activity can temporarily store the necessary information (Funahashi et al., 1989; Miyashita & Chang, 1988). The latter proposition is more widely accepted and is typically modeled through recurrent neural network models.

In addition, pre-frontal cortex (PFC) neurons or networks that have been confirmed by several studies about their involvement with working memory functions (e.g. Kesner et al., 1996; Owen 1997) seem to be equipped with a mechanism that enables them to hold active neural representations of goal-related information and to protect this goal-related delay activity against

interfering stimuli (Durstewitz et al, 1999). The latter has been proposed according to a number of single- cell recordings studies on macaque monkeys that demonstrated inhibitory interactions during interference of distracting stimuli while working memory networks have been involved with the processing of a previously presented target (e.g. Kessler & Kiefer 2005).

In line with that, the working memory network of the proposed computational model is designed in a way that it incorporates three important properties of the second working memory proposition. These are:

The neural activity from incoming information will be gradually built up through a recurrent procedure in the working memory nodes until a certain threshold is passed. Once this condition is fulfilled, perceptual awareness of the incoming information is assumed.

b) The working memory network has a safety mechanism that protects the processing of a certain stimulus once it has successfully accessed working memory.

c) Once the working memory network has processed and signaled the awareness of a stimulus, the protective mechanism is then released and the network is again available for any new stimulus to access it.

The proposed working memory network is comprised by two nodes, each representing a small neural network in the PFC with the membrane potential of the first to evolve according to eq. 5.14 below.

$$V_{WM_1}(t + 1) = \frac{(E_{leak} - V_{WM_1})}{\tau_m}(\tau_m + 1) + \frac{R_m}{\tau_m}(I_s(t) + I_s(t - 1)) \quad \text{eq.5.14.}$$

As can be seen by eq.5.14, the synaptic input of the WM₁ node is sustained and whenever a new synaptic input arrives it is summed up on the previous value. In other words, the total synaptic current at each time instance is:

$$I_s(t)' = I_s(t) + I_s(t - 1) \quad \text{eq.5.15.}$$

As a consequence, the response and specifically the frequency of the response of the WM₁ node will vary depending on the strength of the incoming neural activity.

The second working memory node is described by the next equation, in which the primary observation is that its response is explicitly dependent by the WM₁ node's response.

$$V_{WM_2}(t + 1) = \frac{(E_{leak} - V_{WM_2})}{\tau_m}(\tau_m + 1) + \frac{R_m}{\tau_m}I_{WM_1s}(t) \quad \text{eq.5.16.}$$

Within the working memory network framework, important inhibitory interactions are also considered. More specifically, the output of a WM₁ node is used for inhibition between other WM₁ nodes that correspond to competitive stimuli that might appear in a different spatial location of the visual field (as is the case in the spatial attention tasks). Additionally, the same output is used to

block the processing of a new stimulus that might appear in the same spatial location after a small window, as is verified by RSVP experiments.

Finally once the WM_2 has been given the signal of recognition and awareness, it automatically sends a release signal that brings the synaptic current at the input of the WM_1 node back to zero and thus the network is free again to receive information from any new stimulus (Figure 5-8).

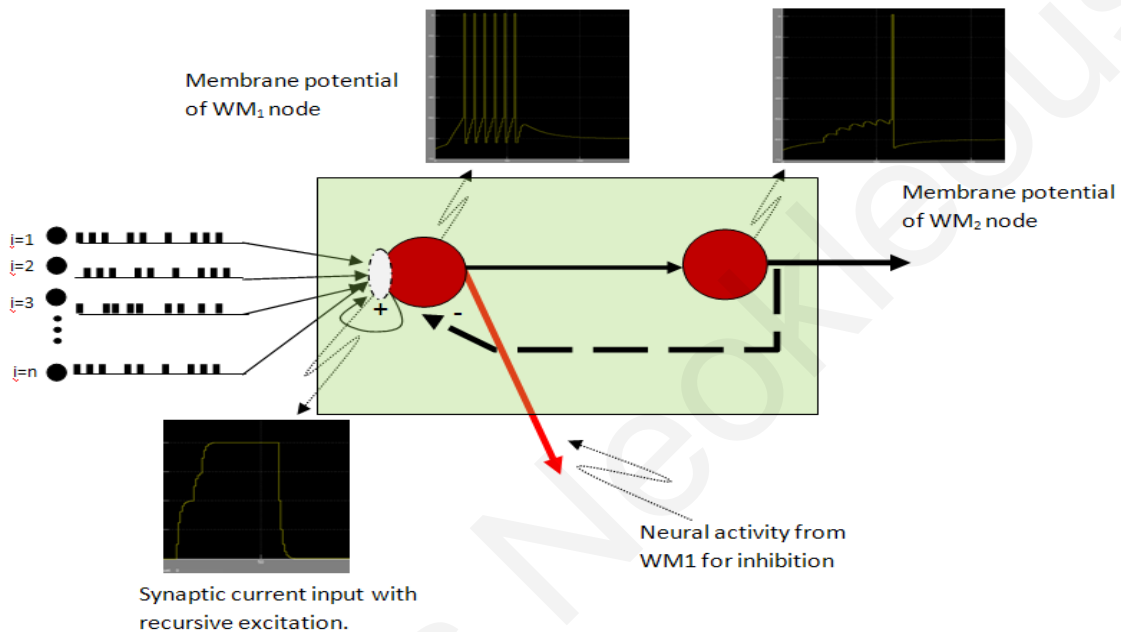


Figure 5-8 Working memory module functionality

The model explained here for representing WM neural interactions was intended in this manner, mainly for the reason that the proposed computational model was designed to simulate behavioral experiments that measure the response times as well as the accuracies of response. Therefore, relevant measurements had to be established from the computational simulations and more specifically from the working memory layer for comparison purposes. However, to do so several simplifications had to be considered like for example the representation of small PFC neural network by single nodes. For example, whenever the neural activity of a certain stimulus has forced the second working memory node (WM_2) to fire an action potential, perceptual awareness of that stimulus is assumed. In addition, the response time of the system's response is taken as the time that the corresponding node fires.

5.3 The computational model's network mathematical representation

5.3.1 Neural representation of incoming stimuli

Each stimulus in the visual field is encoded through 12 input neurons whose receptive fields are associated with the spatial positions at which the stimuli appear. These neurons encode stimuli as spike trains, i.e., series of discrete action potentials which are represented in the model as binary events (0's and 1's) denoting the absence or presence of a spike/action potential. For example, if the firing rate of an input neuron A is P_A , then the corresponding spike train can be seen as a Bernoulli process with probability P_A to have the value 1 in each time bin and 0 with probability $1 - P_A$, ($0 \leq P_A \leq 1$). The number of bins in a spike train is set in the model to equal the duration of each stimulus; that is, if a stimulus appears within the visual field for 100ms then the neurons whose receptive fields correspond to that stimulus will generate spike trains with 100 time bins.

5.3.1.1 Saliency map model

The initial settings of the input neurons firing rates in the model are determined based on the saliency map MATLAB toolbox of Walther and Koch (2006). The overall saliency at each location in the visual field results from the integration of information across individual feature maps and is represented by the firing of neurons whose receptive fields correspond to the particular location. The capability to compute center-surround differences of various features and scales is provided in the toolbox. In their model, Itti and Koch (2000) take into account nine different scales of the input image by sub-sampling it into a dyadic Gaussian pyramid.

Low-level vision characteristics such as channels tuned to different colors, orientations, and brightness are combined into seven different feature types. The computation of these feature types is based on evidence suggesting that they are detected by the mammalian visual system. For instance, one feature type encodes the image intensity contrast as (Leventhal, 1991), two feature types encode the double-opponent red-green and blue-yellow channels (Luschow & Nothdurft, 1993; Engel, et al., 1997), and four feature types encode the local 0o, 45o, 90o, and 135o orientation contrasts (DeValois, et al., 1982; Tootell, et al., 1988). Bottom-up saliency is computationally formulated according to evidence showing that the saliency of each location is a function of the surround (Leventhal, 1991). Therefore, in the model of Itti et al (2000) center-surround differences for every type of feature are calculated by a cross-scale subtraction \ominus between two maps at the center (c) and the surround (s) levels of the scaling pyramid (created by the input image), yielding the "feature maps". For every type of feature, six different feature maps are created, leading to 42 different feature maps as shown in eq.5.17-5.20.

$$I(c, s) = |I(c) \ominus I(s)| \quad \text{eq.5.17.}$$

$$RG(c, s) = |(R(c) - G(c)) \ominus (R(s) - G(s))| \quad \text{eq.5.18.}$$

$$BY(c, s) = |(B(c) - Y(c)) \ominus (B(s) - Y(s))| \quad \text{eq.5.19.}$$

$$O(c, s, \varepsilon) = |(O(c, \varepsilon) \ominus O(s, \varepsilon))| \quad \text{eq.5.20.}$$

I is the image intensity contrast, RG the double- opponent red and green channels, BY to the double- opponent blue and yellow channels and O the local orientation contrast. ε is taking the angles $0^\circ, 45^\circ, 90^\circ$ and 135° .

The feature maps are then combined into three “conspicuity maps,” I for intensity, C for color, and O for orientation at a center scale and then are normalized and summed up to form the final saliency map S (Figure 5-9).

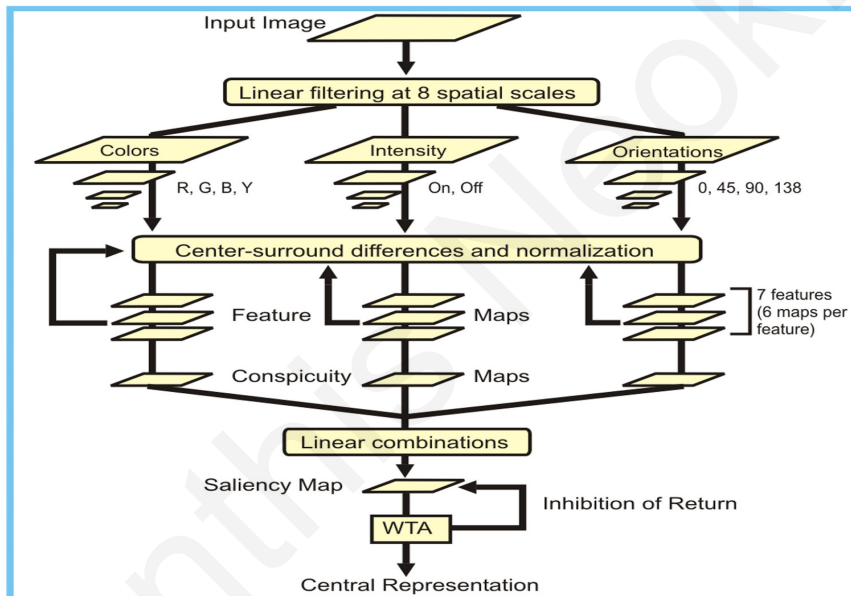


Figure 5-9 The Itti and Koch (2000) architecture of the saliency map model, based on the Koch and Ulfman (1985) implementation. Image from Itti and Koch (2000)

The saliency map model processes an image and produces saliency values for every pixel on the display as can be seen for example in Figure 5-10

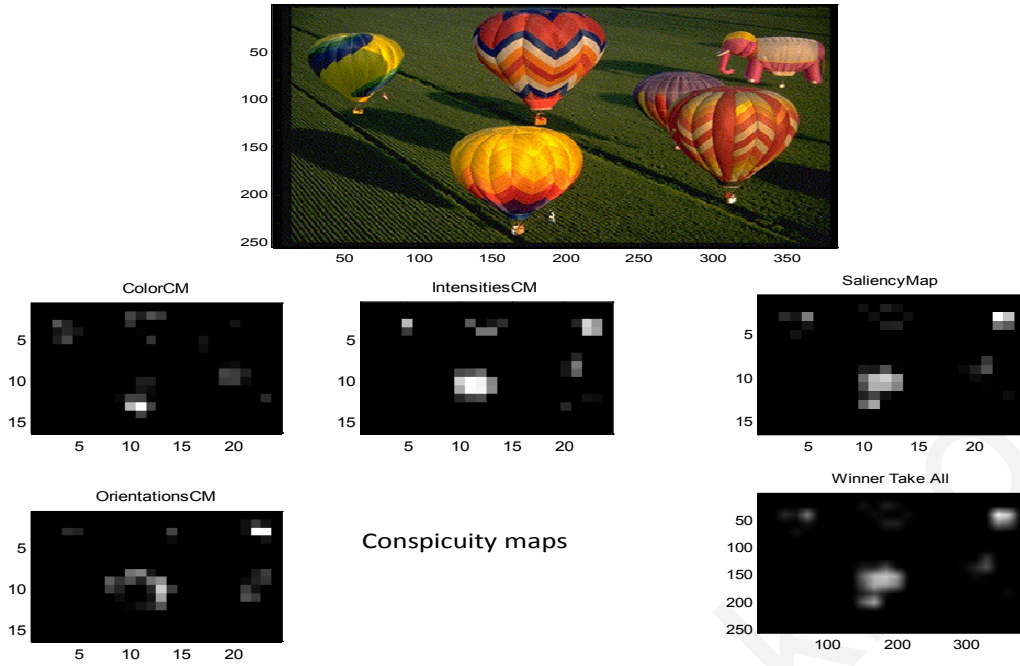


Figure 5-10 An example of image processing by the saliency map model

The output of the saliency map is then used to generate the initial firing rates of the input neurons whose receptive fields correspond to specific locations in the processed image according to eq. 5.21 (Figure 5-11). Equation 5.21, takes into account both the maximum pixel value and the sum of all pixel values that fall within the receptive fields of the neurons and outputs the firing rate of each neuron.

$$FR_{Si} = \alpha (Max(P_j)) + \beta \left(\sum_{j=1}^n P_j \right) \quad \text{eq.5.21.}$$

In eq.5.21, FR_{Si} represents the firing rate of each of the 12 input neurons that correspond to the receptive field of stimulus S_i , $(Max(P_j))$ is the maximum value of all the pixels that correspond to stimulus S_i , and $(\sum_{j=1}^n P_j)$ is the total summation of the n pixel values P_j that correspond to stimulus S_i . Terms α and β are weighting constants. The maximum value of the pixels for each stimulus reflects in a sense the general saliency of the stimulus while the summation value was used to incorporate the size of the stimulus in the calculations, since the model always uses 12 neurons to encode every incoming stimulus regardless of its size.

Therefore, following the analysis explained in the first paragraph of section 5.3.1, the initial firing rates of the input neurons whose receptive fields correspond to specific locations are generated.

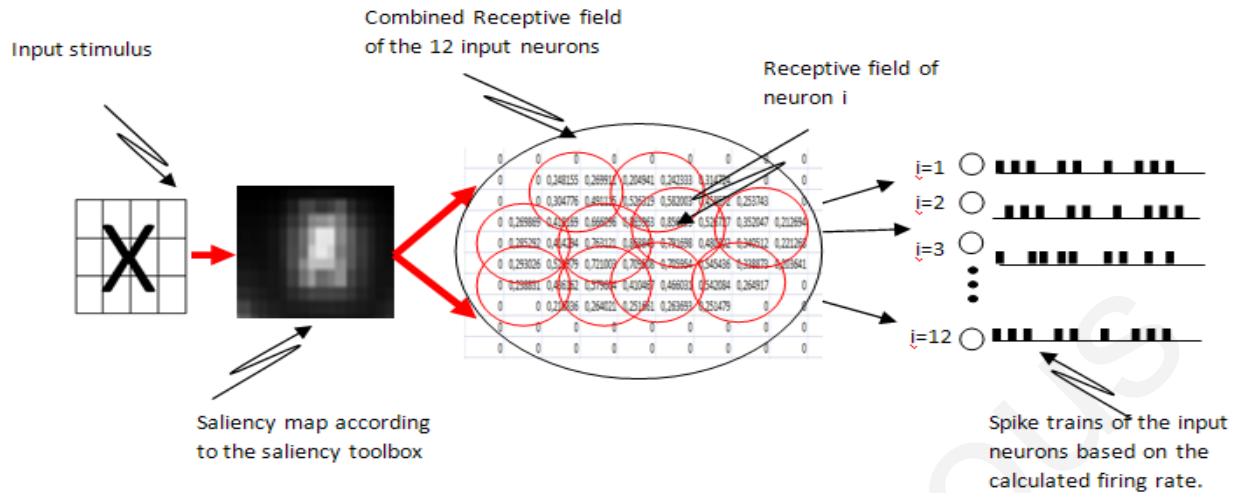


Figure 5-11 Generation of the input neurons spike trains

The values in the saliency map represent the extent to which locations in the visual field may attract attention in a solely bottom-up manner (Zhaoping, 2002; Zhaoping & Dayan, 2006). However, although no semantic modulation of neural activity takes place at early stages of processing, top-down spatial factors initiated by perceptual cues are allowed to influence neural activity. (Silver et al., 2007; Shibata et al., 2008).

Once the initial neural activity corresponding to each stimulus is set, neurons representing different visual inputs inhibit all others in an effort to win the race to working memory. The strength of the inhibition that is exerted on other stimuli depends heavily on the levels of saliency. Thus, stimuli with high saliency values are able to cause stronger inhibition towards the representations of other stimuli that are present in the visual field.

5.3.1.2 Generation of the endogenous Goals

In tasks that involve top down processing, it is important for the simulations to generate sets of synthetic spike trains with controlled rates and cross-correlations that will be stored in the endogenous goals module. These will represent the targets at each occasion. The methodology used for the generation of the spike trains that represent the endogenous goals, follows the algorithm proposed by Niebur and Mikula (2007). This algorithm generates spike trains whose mean rates as well as the cross-correlations between pairs of spike trains are free parameters that can be selected independently. The cross-correlation between any two of these spike trains can be selected to be minimal indicating completely independent spike trains or maximal representing identical spike trains. For example, considering two spike trains A and B, if it is desired that the two spike trains have a specific degree of correlation between them, then the state of A can be switched (with a probability q) to that of B.

Therefore, for the representation of a specific target in the simulations, a random spike train with a certain firing rate is generated according to the above procedure, and having that as the reference spike train, a number of correlated spike trains can be initialized. As a result, all the output neurons of the endogenous goals module will produce spike trains with the same degree of correlation between them.

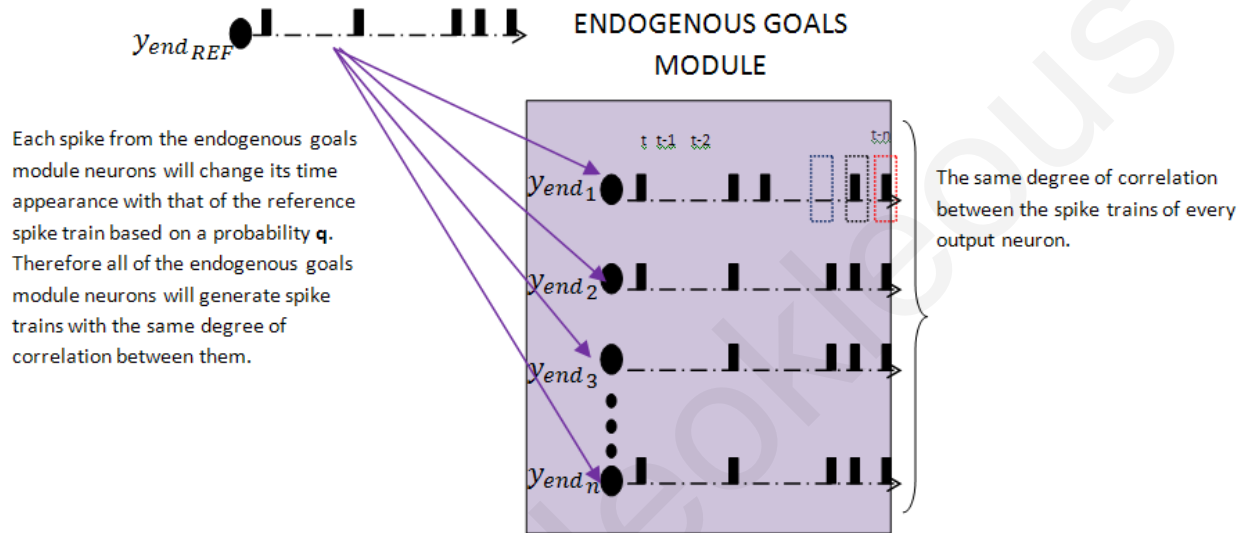


Figure 5-12 Generation of an output neuron spike train in the endogenous goals module

5.3.2 Mathematics of the RSVP

In this section, each layer of the neural network will be analyzed under the two specific model schemes, the RSVP and the spatial attention model.

As explained the output spike train of a specific layer's neuron is a function of its membrane potential at each time instance and the total synaptic input it receives. Therefore, in the following analysis a neuron's response will be denoted as below:

$$y_{(xx)_i} = f(V_{(xx)_i}, I_s(t)) \quad \text{eq.5.22.}$$

The subscript in the parenthesis of eq.5.22 defines the name of the layer that the specific neuron belongs to and the i subscript to the position of the neuron within the layer.

Figure 5-13 presents the different neural network layers and modules that complete the RSVP model implementation in which the following analysis is based.

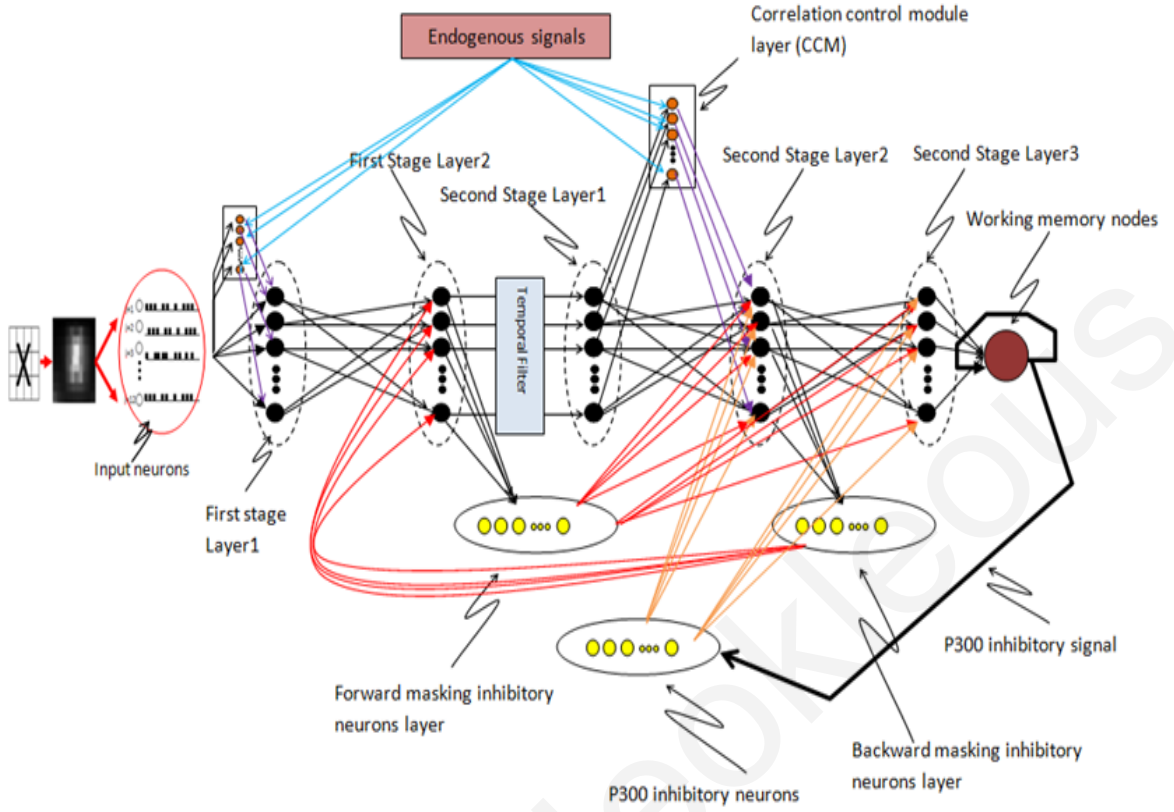


Figure 5-13 A schematic representation of the RSVP model implementation

5.3.2.1 Description of the first stage layer 1- (FS_1)

The response of a neuron i that belongs to the first stage layer1 can then be expressed by:

$$y_{(FS_1)_i}(t + 1) = f(V_{(FS_1)_i}, I_s(t)) = f(V_{(FS_1)_i}, \sum_j^N I_{exc_{IN}_j}(t)) = f(V_{(FS_1)_i}, \bar{g}_{exc_{IN}} w_{exc_{IN}} \sum_j^N f(\delta(t - t_k))_j) \quad \text{eq.5.23.}$$

with $P_s(t)_j = f(\delta(t - t_k))_j$

With N being the total number of excitatory input neurons that are linked to the first stage layer1 from the input layer ($I_{exc_{IN}}$). The subscript j shows the position of the pre-synaptic neuron in the layer it belongs, that initiated the corresponding synaptic current.

In eq.5.23 the Dirac function $\delta(t - t_k)$ can be replaced by the output spike train response of the pre-synaptic neuron (in this case from the input layer neurons, y_{IN_j}), as presented in the following equation, 5.24.

$$y_{(FS_1)_i}(t + 1) = f(V_{(FS_1)_i}, (\bar{g}_{exc_{IN}} w_{exc_{IN}} \sum_j^N f(y_{(IN)_j}(t)))) \quad \text{eq.5.24.}$$

In the case that perceptual cues prime the spatial location that a target will appear, high frequency endogenous signals will trigger the corresponding coincidence detector network that is linked with the neurons whose receptive fields fall within the spatial region specified by the cue (Figure 5-14).

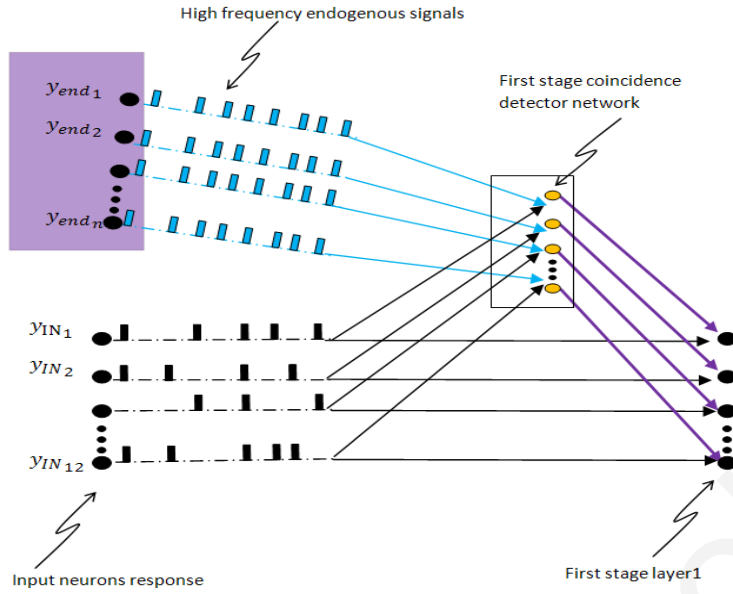


Figure 5-14 Interaction of perceptual (temporal) cue in the early stages of processing

In this condition, the response of a first stage layer #1 neuron will then be:

$$y_{(FS_1)_i}(t+1) = f(V_{(FS_1)_i}, (\bar{g}_{exc_{IN}} w_{exc_{IN}} \sum_j^N f(y_{(IN)_j}(t))) + (\bar{g}_{exc_{CDN}} w_{exc_{CDN}} \sum_j^N f(y_{(CDN)_j}(t)))) \quad \text{eq.5.25.}$$

It is important to note that in eq.5.25 $w_{exc_{CDN}}$ is greater than $w_{exc_{IN}}$ and therefore the contribution of the CDN to the progression of neural activity from the input neurons to the first stage of layer 1 is relatively higher.

5.3.2.2 Description of the first stage layer 2- (FS_2)

The response of a neuron i that belongs to the first stage layer #2 as explained is a function of its synaptic inputs. These are determined by the first stage layer #1 neurons and the inhibitory neurons of the backward masking layer.

$$y_{(FS_2)_i}(t+1) = f(V_{(FS_2)_i}, (\bar{g}_{exc_{FS_1}} w_{exc_{FS_1}} \sum_j^N f(y_{(FS_1)_j}(t))) + (\bar{g}_{inh_{BM}} w_{inh_{BM}} \sum_j^M f(y_{(BM)_j}(t)))) \quad \text{eq.5.26.}$$

N is the total number of excitatory input neurons that are linked to the first stage layer #2 from the first stage layer #1 ($I_{exc_{FS_1}}$) and M are the corresponding inhibitory inputs ($I_{inh_{BM}}$) from the pool of inhibitory interneuron's (defined as the backward masking inhibitory neurons layer).

5.3.2.3 Description of the second stage layer 1- (SL_1)

Following the neural interactions in the first stage of processing, the output spike trains will pass through a “temporal filter” that controls the change of temporal spike appearance of the incoming spike based on the predefined probability of resemblance $P(res)$ as explained in a previous section of this Chapter.

The response of a neuron i in the second stage of processing layer #1, $y(SL_1)_i$ is thus the result of the temporal spike appearance manipulation of the $(y(FS_2)_i)$ neuron when passed through the temporal filter block.

As briefly explained, the temporal filter block, is an algorithmic function with its inputs being the predefined probability of resemblance $P(res)$ for each incoming stimulus (i.e. for stimulus s_i that would be $P(res)_{s_i}$), the spike sequence of the previous layer neurons, and the spike train that corresponds to a semantic representation of a specific target (see Appendix A for the listing of the algorithm). The output of the algorithm is a new spike train with the same frequency of response but with an adjustment on the timing of spike appearance. The probability of resemblance is calculated according to a value-based matrix that is formulated according to the feature characteristics of a given stimulus (such as the number of line crossings, curves and orientation of lines) that are similar to those of the target. For example, if in a specific task the target is the letter X, and the letters O and A appear at the visual field, then the letter A will be awarded a higher probability of resemblance than the letter O as its features are more similar to those of the target.

More explicitly, a random number is generated and the algorithm compares this number with the probability of resemblance that corresponds to the stimulus responsible for this neural activity $P_{res_{s_i}}$. If the random number is smaller or equal to the specific probability, the time bin of the incoming spike $t_{k_{FS_{s_i}}}$ will change and will appear in the closest time bin that a spike appears within the endogenous spike train time sequence $t_{k_{end}}$. In the case of the opposite condition in which the random number is bigger than the $P_{res_{s_i}}$, the appearance of the incoming spike will remain in its original time bin. In this manner, it is possible to “re-organize” the temporal pattern of an incoming stimulus, without having to interfere with its firing rate, since the total number of spikes remains the same.

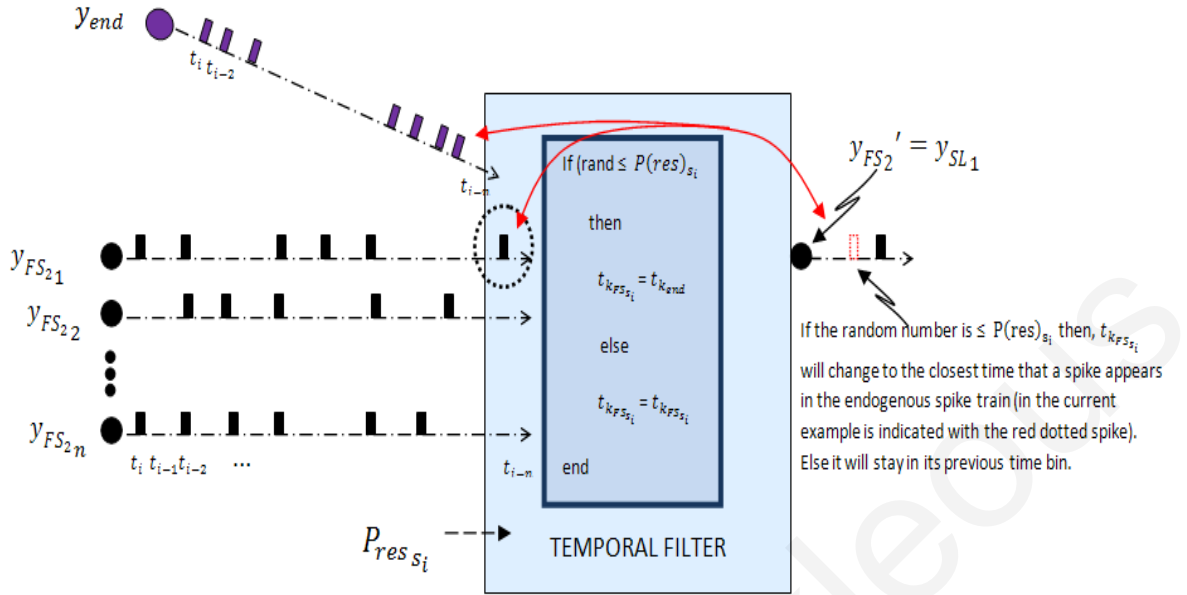


Figure 5-15 The temporal filter mechanism

The responses of the first layer neurons in the second stage of processing are then expressed by equation 5.27:

$$y_{SL_{1_i}} = f(y_{FS_{2_i}}, P_{res_{s_i}}) \quad \text{eq.5.27.}$$

5.3.2.4 Description of the correlation control module layer

Following the second stage of processing layer1 (SL₁), neural activity is gradually progressed towards the SL₂. The same neurons of the SL₁ however, are at the same time connected with the pool of coincidence detector (CD) neurons that comprise the correlation control module (CCM) (see Figure 5-13 of the RSVP design).

In the CCM, each CD neuron has a total of three neurons connected to its input. Two random inputs are from SL₁ and one input from the endogenous goals. The response of the CD nodes is explicitly dependent on the number of action potentials that arrive simultaneously in their inputs. In the current implementation, the threshold has been set to $\theta = 2$. That is, at least two spikes of the three inputs on each coincidence detector neuron must arrive synchronously for the CD neuron to fire (Figure 5-16).

Therefore, the response of the CD neurons can be expressed by eq.5.28.

$$y_{CCM_i}(t + 1) = \Theta(\Psi_i(t) - \theta) \quad \text{eq.5.28.}$$

$\Psi_i(t)$ is a binary vector that denotes the states of the spike trains from the endogenous goals $y_{end_i}(t)$ combined with the states from two neurons of the second stage layer #1 ($y_{SL_{1_i}}(t)$). The k

and m subscripts in eq.5.28 represent the two randomly selected neurons from the SL_1 that are driven in the i^{th} CD neuron.

$$\Psi_i(t) = \begin{bmatrix} y_{end_i}(t) \\ y_{SL_{1k}}(t) \\ y_{SL_{1m}}(t) \end{bmatrix} \quad \text{eq.5.29.}$$

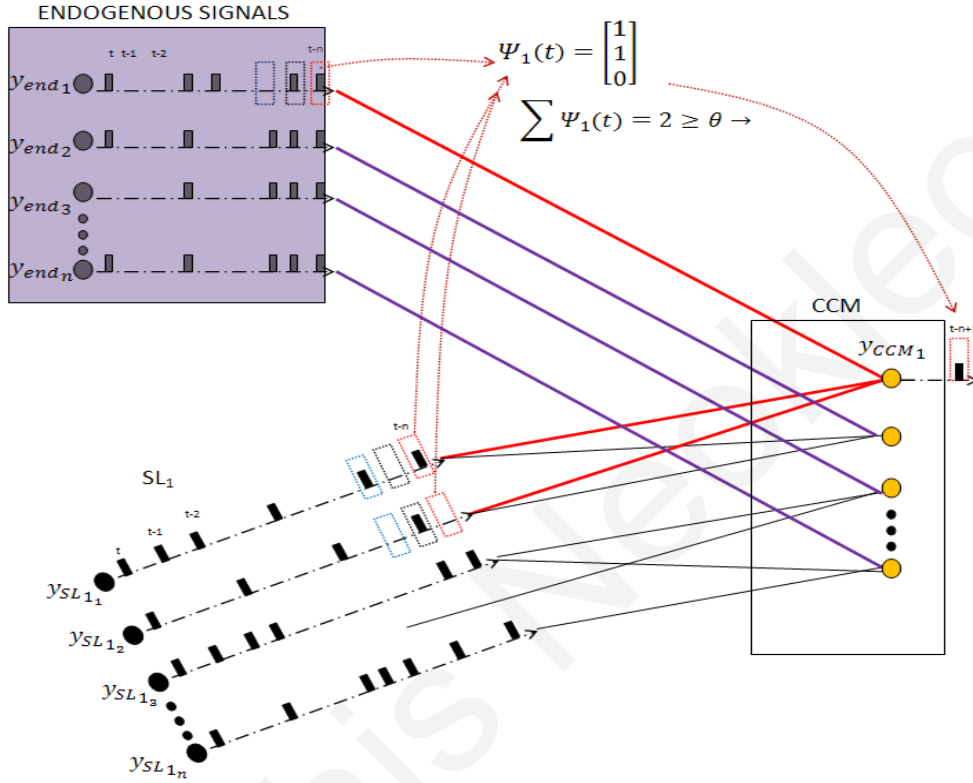


Figure 5-16 The correlation control module mechanism.

5.3.2.5 Description of the second stage of processing – second layer (SL2)

Neurons in the SL_2 receive excitatory inputs from the CCM and the SL_1 and inhibitory inputs from the P300 and forward masking pools of inhibitory interneurons.

$$y_{SL_{2i}}(t+1) = f \left(V_{SL_{2i}}, (I_{exc}(t) + I_{inh}(t)) \right) \quad \text{eq.5.30.}$$

Where,

$$I_{exc}(t) = \bar{g}_{exc_{SL_1}} w_{exc_{SL_1}} \sum_j^N f(y_{SL_{1i}}) + \bar{g}_{exc_{CCM}} w_{exc_{CCM}} \sum_j^N f(y_{CCM_i}), \quad \text{eq.5.31.}$$

$$I_{inh}(t) = \bar{g}_{inh_{FM}} w_{inh_{FM}} \sum_j^N f(y_{FM_j}) + \bar{g}_{inh_{P300}} w_{inh_{P300}} \sum_j^N a(y_{P300_j})$$

However, the inhibitory interactions from the P300 signal are stronger than the backward and forward masking inhibitions, while the backward masking will produce stronger inhibition than forward masking which implies that inhibitory signals for the neurons of the already presented stimulus towards the neurons of the proceeding stimulus are relatively lower than the other way around (Seiffert and Di Lollo, 1997). Indeed, according to a neurodynamic analysis on the biased competition framework by Deco and Rolls (2005), feedback connections have found to be about 2.5 times weaker than the feed-forward connections between inter-area cortical interactions. These experimental and analytical observations have been reflected in the proposed implementation by distinct weighting factors attached to the corresponding inhibitory synaptic currents. Similarly the excitation signals from the coincidence detector neurons have stronger weights attached to them than the excitatory spikes from the two stages of processing layers. Moreover, the excitatory connections in the second stage of processing are stronger than the excitatory connections in the first stage of processing. The latter assumption is based on neurophysiologic findings showing that the greater the degree of overlap between receptive fields, the stronger the inhibition. Therefore, given that the second stage of processing of the proposed model mainly corresponds to interactions between V4 neurons that have overlapping receptive fields while the first stage of processing is mostly V2 neurons that do not have overlapping receptive fields, the latter hypothesis has been incorporated in the model with the inequality of eq.5.32.

$$\begin{aligned} w_{exc_{CCM}} &> w_{exc_{SL}} > w_{exc_{FS}} \\ w_{inh_{P300}} &> w_{inh_{BM}} > w_{inh_{FM}} \end{aligned} \quad \text{eq.5.32.}$$

5.3.2.6 Description of the second stage of processing - third layer (SL₃)

The SL₃ neurons will receive excitatory inputs from the SL₂ and inhibitory inputs from the P300 and forward masking pools of inhibitory interneurons as is presented below.

$$y_{SL_3_i}(t+1) = f\left(V_{SL_3_i}, (I_{exc}(t) + I_{inh}(t))\right) \quad \text{eq.5.33.}$$

Where,

$$\begin{aligned}
 I_{exc}(t) &= \bar{g}_{excSL_2} w_{excSL_2} \sum_j^N f(y_{SL_2i}) \\
 I_{inh}(t) &= \bar{g}_{inhFM} w_{inhFM} \sum_j^N f(y_{(FM)_j}(t)) \\
 &+ \bar{g}_{inhP300} w_{inhP300} \sum_j^N f(y_{P300j}(t))
 \end{aligned} \tag{eq.5.34}$$

Along the same lines, the working memory nodes, and the response of the inhibitory neurons from the P300, forward and backward masking layers are shown with the equations in the following subsections.

5.3.2.6.1 Working memory layer

The response of the working memory node 1 (WM₁) and working memory node 2 (WM₂) is a function of the parameters given in eq.5.34 and 5.35 below that are based on the analysis presented in section 5.3.3 (working memory nodes).

$$y_{WM_1i}(t+1) = f(V_{WM_1i}, \bar{g}_{excSL_3} w_{excSL_3} f(y_{SL_3i}(t))) \tag{eq.5.35}$$

$$y_{WM_2i}(t+1) = f(V_{WM_2i}, \bar{g}_{excWM} w_{excWM} f(y_{WM_1}(t))) \tag{eq.5.36}$$

5.3.2.6.2 P300 inhibitory layer

$$y_{P300i} = f(V_{P300i}, \bar{g}_{excWM} w_{excWM} f(y_{WM_2i})) \tag{eq.5.37}$$

5.3.2.6.3 Backward masking inhibitory layer

$$y_{BMi} = f(V_{BMi}, \bar{g}_{excSL_2} w_{excSL_2} f(y_{SL_2i})) \tag{eq.5.38}$$

5.3.2.6.4 Forward masking inhibitory layer

$$y_{FMi} = f(V_{FMi}, \bar{g}_{excFS} w_{excFS} f(y_{FSLi})) \tag{eq.5.39}$$

5.3.3 The spatial attention model

As previously explained, the functionality of the spatial attention model, is similar to the RSVP, having only some minor differences concerning the inhibitory interactions. Indeed, in the spatial attention model, the P300, forward and backward masking inhibitory neurons, will not influence the overall processing. Lateral inhibitions from neurons whose receptive field capture different spatial location of the visual field will have the primary role in the competition process (Figure 5-17).

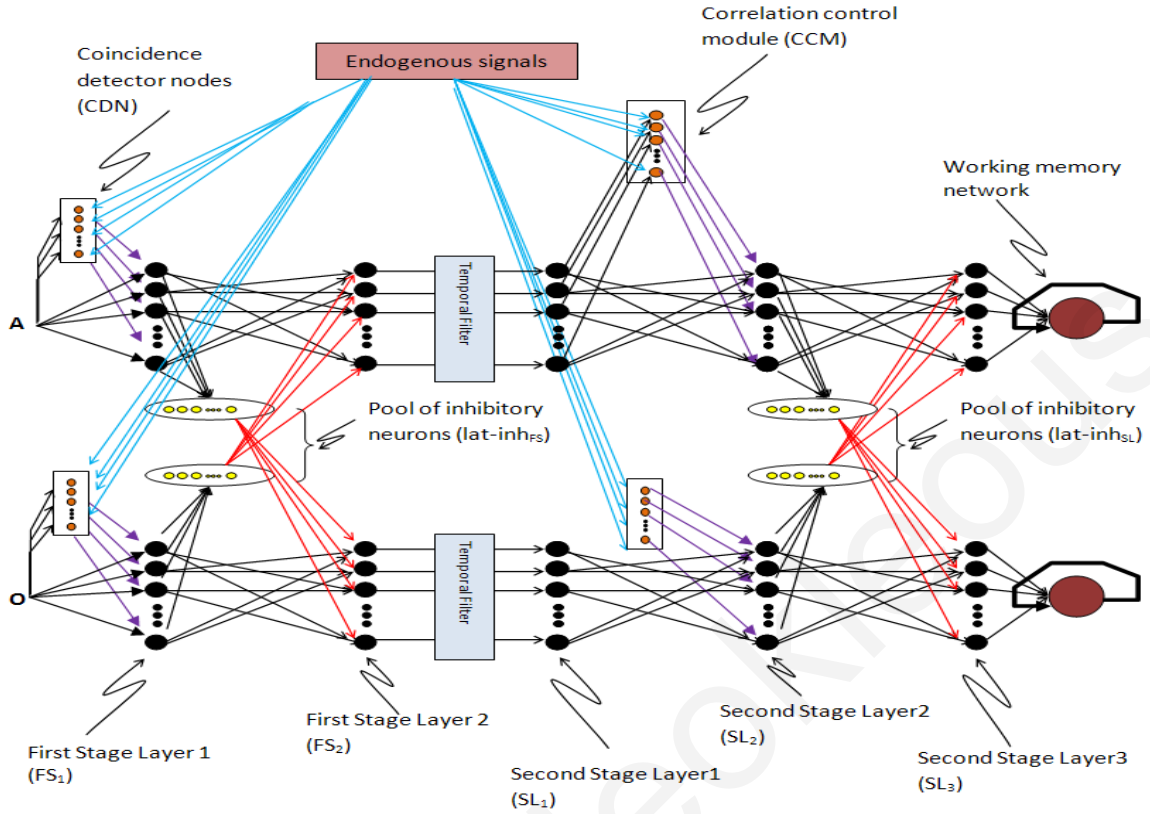


Figure 5-17 A schematic representation of the spatial attention model

For example, the response of the first stage layer 2 neurons that correspond to the target letter X in the above figure will be based on the function described by the equation below.

$$\begin{aligned}
 y_{X(FS_2)_i}(t+1) = & f(V_{X(FS_2)_i}, (\bar{g}_{exc_{FS_1}} w_{exc_{FS_1}} \sum_j^N f(y_{X(FS_1)_j}(t))) \\
 & + (\bar{g}_{inh} w_{lat-inh_{FS}} \sum_j^M f(y_{A(FS_1)_j}(t))))
 \end{aligned}
 \tag{eq.5.40}$$

where, $y_{X(FS_2)_i}$ corresponds to the output spike train sequence of the FS2 neurons that capture stimulus X and $y_{A(FS_1)_i}$ corresponds to the output spike train sequence of the FS1 neurons that capture stimulus A. $w_{lat-inh_{FS}}$ represents the synaptic weights that describe the lateral inhibition between the neurons whose receptive field capture each of the two stimulus.

Along the same lines will be the response of the SL₃ neurons that receive the neural activity that initiated by stimulus X as can be seen by eq.5.41 below.

$$\begin{aligned}
 & y_{X(SL_3)_i}(t + 1) \\
 &= f(V_{X(SL_3)_i}, (\bar{g}_{excSL_2} w_{excSL_2} \sum_j^N f(y_{X(SL_2)_j}(t))) \\
 &+ (\bar{g}_{inh} w_{lat-inhSL} \sum_j^M f(y_{A(SL_2)_j}(t))))
 \end{aligned} \tag{eq.5.41}$$

5.3.3.1 Some observations on the spatial attention model

The lateral inhibition weight between the neurons of the second stage of processing is stronger than the corresponding weight of the first stage of processing ($w_{lat-inh_{SL}} > w_{lat-inh_{FS}}$). This inequality is applied to the model, for the reason that the V4 neurons that comprise the second stage of processing have overlapping receptive fields and therefore produce stronger competitive interactions between them (Deco & Rolls, 2005).

In the case that perceptual cues prime the spatial location that a target will appear, in a similar manner to the RSVP model, high frequency endogenous signals will interact to the corresponding coincidence detector network. The main difference is that in the RSVP model these signals will appear at the specified time window that the cue signified, while in the spatial attention model the endogenous signals will interact with the coincidence detector network that is linked with the neurons whose receptive field falls within the spatial region specified by the cue.

5.4 Network dynamics

The attentional mechanism in the proposed computational model relies on the effect of saliency and endogenous bias on the incoming stimuli neural activity. These interactions have been implemented in the computational model with a network of integrate and fire neurons combined with coincidence detector neurons. This configuration supports the most recent scientific evidence related to the neural mechanisms that specifically emphasize the neural activity amplification and synchronization of the selected stimulus.

More specifically, it has been shown by several studies that oscillations in a neural network model can be generated by pyramidal-to-interneuron loops (e.g. Brunel & Wang, 2003; Whittington & Traub, 2003; Gieselmann & Thiele, 2008) and more importantly that the oscillation frequency depends on the relative timescales of the excitatory and inhibitory decay constants. For example it has been shown that faster excitation than inhibition, will favor this feedback loop and give rise to oscillations in the gamma range (Brunel & Wang, 2003).

Even more recently, Buehlmann and Deco (2008) explained how oscillations can be manipulated by adjusting the conductance of different synaptic currents. More precisely, in their model synaptic currents are mediated by the excitatory receptors AMPA and NMDA (activated by glutamate, g_{AMPA} and g_{NMDA}) and the inhibitory receptor GABA, (g_{GABA}). The two types of excitatory synapses (AMPA and NMDA receptors) have different time constants: AMPA decays very fast (2 ms), whereas NMDA decays slowly (100 ms), while the decay constant of GABA (10 ms) lies between the two.

In the specific study, an increase of g_{AMPA} and a decrease of g_{NMDA} cause the pyramidal-to-interneuron loop interactions to oscillate more strongly and thus resulting in increased gamma activity. Buehlmann and Deco (2008), in their report emphasize that the crucial parameter to generate oscillations in the network is the relative contribution of the slow NMDA and the fast AMPA receptors to the total synaptic currents and as can be seen by figure 5-18.

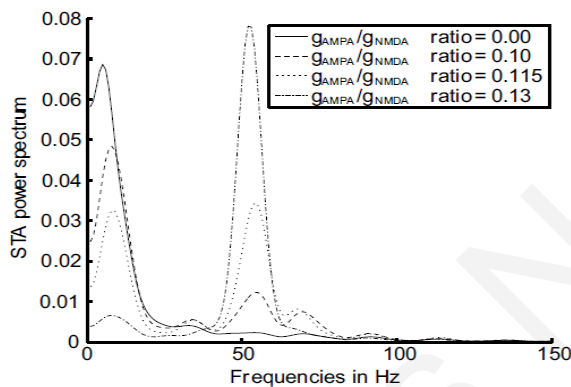


Figure 5-18 Changes in the spike-triggered average power spectrum based on the $g_{\text{AMPA}}/g_{\text{NMDA}}$ ratio as presented in Buehlmann and Deco (2008).

However, up to now the candidate molecule for performing coincidence detection has been the postsynaptic NMDA receptor (e.g. Sjöström et al., 2003; Dan & Poo, 2006; Sprunston 2008). Therefore, one can assume that a combination of coincidence detector neurons with basic integrate and fire neurons might induce neural synchronization as shown in the study above.

Furthermore, as explained in chapter 4 and in particular by the study of de la Rocha et al (2007), synchronization of neural activity in a cortical network is more probable to be induced when the synaptic current that is driven towards the networks neurons is correlated.

In line with the above hypothesis, a simple configuration on the basis of the proposed computational model has been put forward to test several conditions, and thus to examine the models dynamics in respect to the generation and propagation of synchronous neural activity in a cortical network.

5.4.1 Testing different input stimulus conditions in the proposed model

Following the above implementation, the complete model was tested on several conditions before simulating the experimental tasks explained in the following Chapter.

Parameters:

Some of the parameters for designing the dynamics of the system are presented here however, more detail description can be found in Appendix A.

$$\tau_m = 30 \text{ ms}$$

$$E_{\text{Leak}} = V_{\text{reset}} = -65 \text{ mV}$$

$$V_{\text{th}} = -50 \text{ mV}$$

$$R_m = 90 \text{ M}\Omega$$

An absolute refractory period (T_{Refract}) of 2ms has been applied with a rule.

Coincidence detector neurons threshold = 2

Gain of excitatory neurons:

V1 neurons = 20; V2 neurons = 20; V4 neurons = 30.

Gain of inhibitory neurons:

Second stage of processing pool of inhibitory neurons = -2

First stage of processing pool of inhibitory neurons = -1.2

The gain of the excitatory and inhibitory neurons in the experimental simulations has been slightly readjusted for every task accordingly. Nevertheless, without escaping the borders set by the restrictions explained in the subsections of 5.3.

The model was tested initially on three different ways of presenting a simple stimulus comprised by a red and black circle appearing simultaneously in the visual field. Referring to Figure 5.20, in condition A) the two circles appear alone and simultaneously in the computer screen. In condition B) a perceptual cue indicating the spatial location of the red circle appears a little shortly before the two circles appear in the computer screen, and finally in condition C) a written cue requests the subjects to search for the red circle when the two stimuli appear.

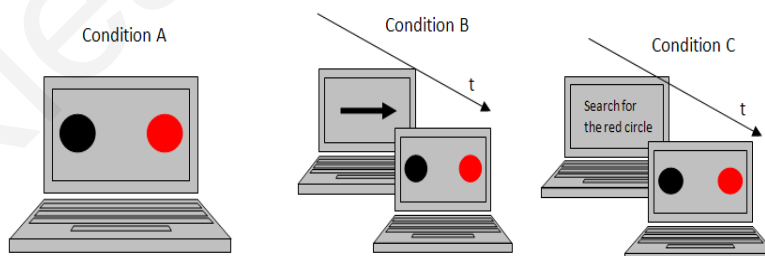


Figure 5-19 The three stimuli conditions that the model was tested

In all three conditions, the input neurons that capture the red and black stimulus were initialized according to the description given above with the use of the saliency map toolbox by Walther and Koch (2006).

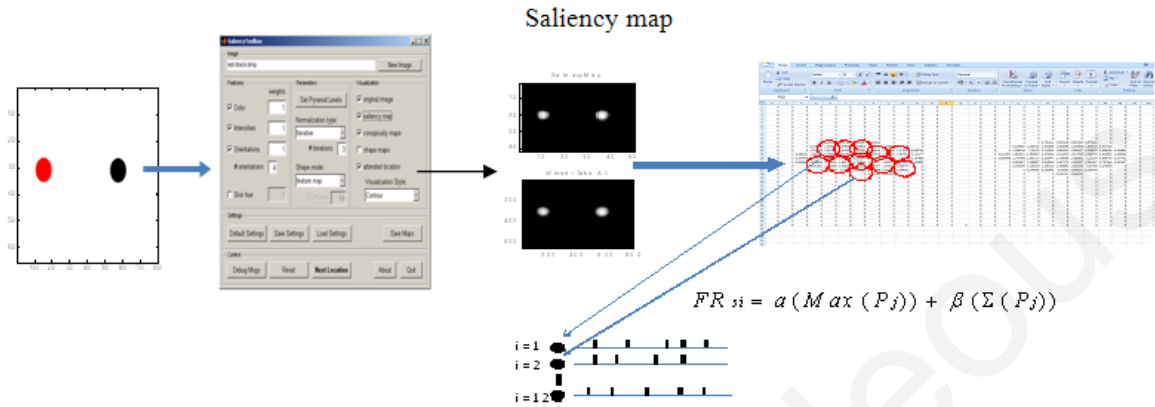


Figure 5-20 Initial firing rate representation of the two stimuli according to the saliency map model

Each layer in both stages of processing of the proposed model, comprises ten integrate & fire neurons. However, in the following analysis, only the response of the neurons in the first stage layer #2 (FS₂) and second stage layer #3 (SL₃) is considered.

The measurement of neural synchronization was made according to the “event synchronization” methodology proposed by Quian, et al., (2002), in which a simple description is given below.

For the following analysis, let x_1 and x_2 be two spike trains generated by two neurons and $t_i^{x_1}, t_j^{x_2}$ their corresponding spike time instances. The total number of spikes in each spike train are m_{x_1} and m_{x_2} , therefore $i = 1, \dots, m_{x_1}; j = 1, \dots, m_{x_2}$.

The number of times an event (or a spike) appears in x_1 shortly after it appears in x_2 , is then given by $c^\tau(x_1|x_2)$ as described in eq.5.42.

$$c^\tau(x_1|x_2) = \sum_{i=1}^{m_x} \sum_{j=1}^{m_y} J_{ij}^\tau \quad \text{eq.5.42.}$$

$$\text{With } J_{ij}^\tau = \begin{cases} 1 & \text{if } 0 < t_i^{x_1} - t_j^{x_2} \\ 1/2 & \text{if } t_i^{x_1} = t_j^{x_2} \\ 0 & \text{else,} \end{cases} \quad \text{eq.5.43.}$$

Similarly, the number of times an event appears in x_2 shortly after it appears in x_1 , is given by $c^\tau(x_2|x_1)$. Finally, the measurement of synchronization between the two spike trains is:

$$Q_{x_1x_2}^\tau = \frac{c^\tau(x_1|x_2) + c^\tau(x_2|x_1)}{\sqrt{m_{x_1} m_{x_2}}} \quad \text{eq.5.44.}$$

The same analysis is then performed for every two combinations of the 10 output neurons of the example, leading to 45 different combinations. Therefore the average degree of synchronization for each network layer is calculated as in eq.5.44.

$$\overline{Q^\tau} = \frac{1}{45} \sum_{k=1}^{10} \sum_{l=1}^{10} \frac{c^\tau(x_k|x_l) + c^\tau(x_l|x_k)}{\sqrt{m_{x_k}m_{x_l}}} \quad \text{eq.5.45.}$$

According to the above methodology, the analysis in the test example has given the results shown in Table 5.1 and Figure 5-22.

Table 1 The measurement of synchronization between the three different conditions tested on the proposed computational model.

	Condition A		Condition B		Condition C	
	FS ₂ layer	SL ₃ layer	FS ₂ layer	SL ₃ layer	FS ₂ layer	SL ₃ layer
Red circle ($\overline{Q^\tau}$)	0.5454	0.4773	0.4506	0.5931	0.5853	0.7507
Black circle ($\overline{Q^\tau}$)	0.5503	0.4819	0.2774	0.3103	0.5816	0.3125

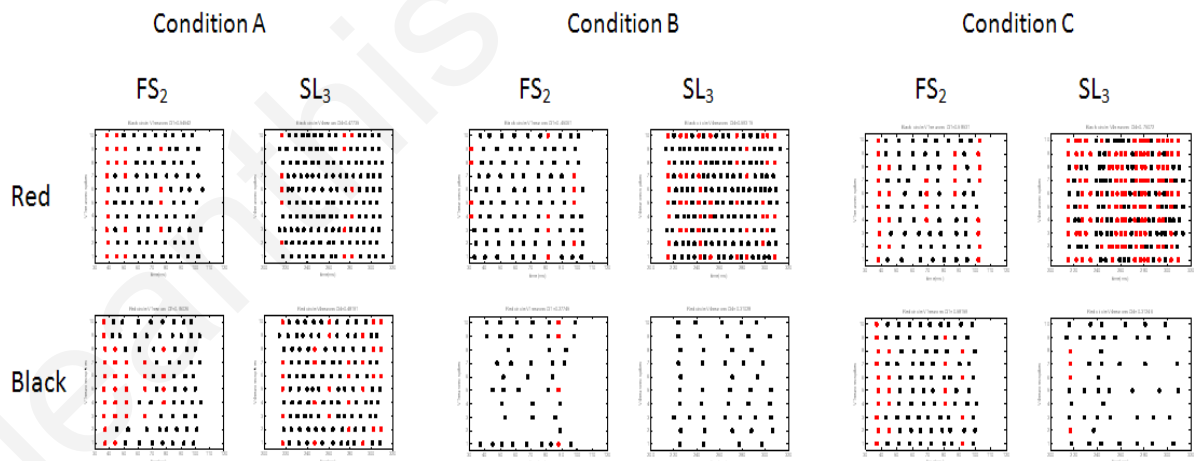


Figure 5-21 Neural response at the three different stimuli conditions for the two layers under investigation. In the above plots, the y axis corresponds to a different neuron in the corresponding layer and the x axis the time. A red dot means that two or more neurons have fired synchronously.

In condition A, it is expected that the two stimuli produce more or less a similar response in both stages of processing. This is mainly because there are not any external signals in favor of any of them and their initial saliency is almost the same. In condition B the FS₂ layer comprised by the

neurons whose receptive field capture the red circle, will have an increased activity compared with the neurons of the black stimulus. This behavior is mainly because endogenous signals containing spatial information will bias the neural progression of the red stimulus in FS_1 which will result in an increase of inhibition towards the corresponding layer of the black stimulus neurons. Finally in condition C, neural activity from both stimuli in the first stage of processing, will not have significant difference between them, however in the second stage of processing semantic information about the red circle will interfere. Endogenous signals describing the semantics of the red target will have increased correlation with the neural activity that corresponds to the red stimulus and as a result the coincidence detector module will be more active causing an increase of neural activity and synchronization in the SL_3 of the red circle compared with the same layer of the black circle.

This example indicates the basic operations that have been incorporated in the implementation of the model and thus enabling a better comprehension of its emerging behavior.

In the following section, I justify why I have chosen to adopt the specific neural mechanisms and operations.

5.5 Justification on the adoption of the proposed implementation

As noted in Chapter 3 (section 3.6.2), the low level neural mechanisms that describe the mechanism of selection are a debatable issue in the literature. More specifically, the synchronization of neural activity is based on a theory that generated several contradictions among prominent scientists that are experts in the field. The main point of contradiction is placed on the assumption that neural synchronization is more probably induced due to temporal information encoded in the stimuli spike trains, something that is still not widely accepted. In fact, in a recent review by Deco and Rolls (2011), strong scientific arguments are presented in favor of the rate coding versus the stimulus dependent synchrony. Also, in a study by Aggelopoulos et al. (2005), it was shown that about 95% of the information in the inferior temporal cortex was present in the firing rate, while only about 5% in any stimulus dependent on synchrony. Indeed, Deco and Rolls (2011) suggest that “firing rates rather than correlation are the main element of the population code for feature binding in primary visual cortex”. Oscillations, according to them are not needed for attention or decision making, but if synchronized oscillations were present in a network, then it is possible to have more spikes accumulating on average in the excitable phase of an oscillation than in the less excitable phase. Therefore they can speed information processing within a single network and thus to contribute in faster reaction times. To strengthen their theory, they point to the simulations by Buehlmann and Deco (2008) (see previous section) that explain how oscillations could be initiated according to the dynamics of connected networks and especially by altering the excitation/inhibition cycle. Therefore, a separate controller to produce synchronization, as this is

the case in my thesis, is suggested that is not necessary, and that oscillations, if they exist can increment the speed and efficiency of the transmission and are thus behaviorally relevant. However, although I find this theory very probable, I believe that at the end it depends on how one interprets some concepts.

To elaborate on this, a separate analysis is given first on my decision to include a separate controller and second to include neural synchronization in the neural processing.

About having a separate controller, what has to be clarified here is that in the proposed implementation, the same simulation results that are presented in the following chapter could have been obtained even if the Correlation Control Module was completely removed. Indeed, if the coincidence detector neurons that are included in the CCM have been incorporated accordingly in the second stage of processing, the simulation results would not have been altered. The question that arises then is why to use a separate controller. The justification of having a separate controller mostly comes from neuroscientific studies especially about attention related Event Related Potentials (ERPs) as it is analyzed in section 5.1.1.2. The second reason for including the CCM is based on scientific influences that I had while studying the relevant literature on computational modeling of visual selective attention. More specifically, several of my thoughts have been in the same lines with studies that attempt to approach the attentional system from an engineering perspective (e.g. Taylor & Rogers 2002), since to include a controller offers a more plausible interpretation on my understanding about the functionality and interaction of human attention on the neural activity of visual stimuli. For example, one could suggest that attention (as a control signal) is responsible for altering the excitation/inhibition cycle which results in oscillations, and these oscillations in their turn help to communicate more effectively the neural activity within the cortex, which to my understanding, is one of attention's roles in human cognition.

Concerning the debate about neural synchronization and firing rate manipulation as the principle mechanisms of the attentional system, I believe that both (neural synchronization and firing rate) contribute in conjunction to the overall process of visual attention, a point that has been reflected in my model. There are numerous scientific evidences that support this notion. However, the primary reason why I have incorporated this idea is based on my interpretation and supposition on how processing and selection of neural activity could be performed most effectively and optimally in the brain. In fact, considering the early years of modern neuroscience, until today, all of the new findings follow a logical interpretation blended with the nature's characteristics. In line with this thought, I hereby explain why I have been sympathetic to the synchronization theory, by pointing some neurophysiologic evidence through the following simple example.

Let us assume for a moment that a certain stimulus appears for the first time in one's visual field. Repetition of this stimulus would gradually end-up to combine successfully its various features into one "object" and to register it in the long-term memory. If again we assume that information about

the properties of that stimulus is encoded using rate and temporal coding, these features would have been stored in the memory as well. In the case, in which we are asked to identify this specific stimulus among several others, the top-down information containing these features will interact with the neural activity produced from all the stimuli that appear in the visual field. At the level of individual stimulus processing, this implies interaction between two sources of information, the one being from top-down signals and the other from the bottom-up stimulus neural activity. Therefore, if these two sources share a certain degree of correlation, the combination of specific neurons properties, such as their sensitivity in correlated activity, (de la Rocha et al., 2007) and their sensitivity in responding to the coincidence activation of presynaptic spikes (Spruston, 2008) can induce neural synchronization (e.g. section 5.4).

In conclusion, the realization of the model was tested and evaluated based on simulations of three relevant behavioral experiments. Therefore, taking into account the successful reproduction of the experimental data by the model, the theoretical structure in which the model has been built can be further justified. The computational simulations have also inspired recommendations for possible explanatory theories regarding the cognitive mechanisms that produce these behavioral results. A more detailed analysis concerning three very important behavioral experiments and the proposed explanations in connection to their results is presented in the next Chapter.

6. Applications of the model

In this chapter simulation of three intensely debated in the literature behavioral experiments are presented, as well as the relevant contributions derived from the proposed computational model. For each of the three experiments, an explanation concerning their output results is given, based on the simulations done and more precisely according to the neural interactions and coupling mechanisms that compose its internal functionality.

The first experiment presented here is the *Attentional Blink (AB)* paradigm, originally identified by Raymond et al. (1992). The AB task employs the rapid serial visual presentation (RSVP) method and has been selected for simulations because it presents some of the brain's limitations in processing visual information and thus had immense impact on the scientific society.

The second experiment is the behavioral task that inspired the *perceptual load theory* by Lavie (1995) that offered an appealing account on how selection of information within the processing stream can either occur early or late. However, despite the extensive acceptance of the theory, it has been recently criticized and challenged. Thus, a possible explanation on how the corresponding behavioral results were obtained is of importance.

Finally, one of the most influential tasks regarding the *relation between attention and consciousness* by Naccache et al (2002) is examined. This task was also very challenging for the proposed computational model, for the reason that it sparked an interesting debate among a number of scientists regarding the relation between the two cognitive processes.

6.1 The Attentional Blink paradigm (Raymond, Shapiro and Arnell (1992))

In the attentional blink (AB) task, different stimuli at a rate of about 100ms are sequentially presented and participants are asked for example to identify letter targets among number distractors within the sequence of the presented stimuli (Figure 6-1).

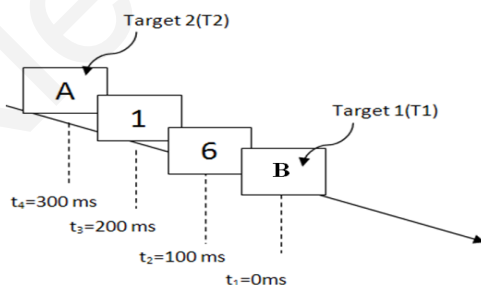


Figure 6-1 The use of the RSVP methodology in attentional blink studies. Participants are asked to identify targets T1 and T2 that are presented, within a sequence of distractors.

The AB refers to the findings that when 2 targets are presented among the sequence of distractors, the correct identification of the 1st target (T1) impairs the identification of the 2nd target (T2), provided that T2 appears within a brief temporal window of about 200-500ms following T1. In cases where T2 is presented before or after this temporal window, it is normally identified. Furthermore, although it might be expected that the AB should be maximal immediately following T1, a phenomenon referred to as lag-1 sparing often arises, where T2 accuracy is preserved even when T2 occurs immediately after T1.

The percentage of correct T2 reports as a function of the Stimulus Onset Asynchrony (SOA; i.e., the temporal interval between T1 and T2) is shown in Figure 6.2 (basic curve – red curve) according to the behavioral data from Chun and Potter (1995).

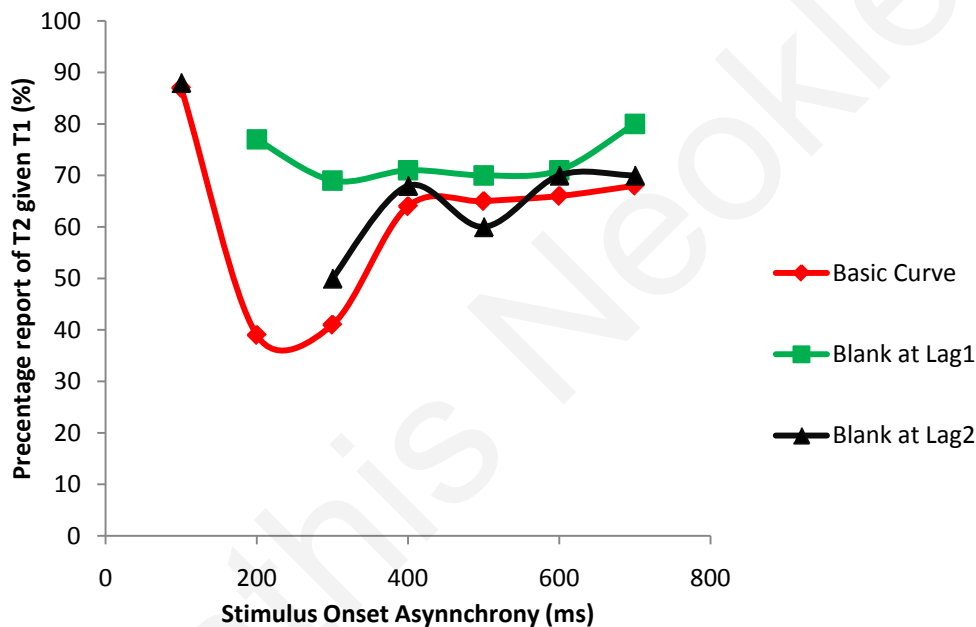


Figure 6-2 The basic curve from attentional blink studies based on the behavioral data from Chun and Potter (1995) showing the percentage of correct T2 identification given the successful identification of T1 as a function of SOA.

Another important finding from the AB paradigm is that if T1 is not followed by a mask (distractor), the AB impairment is significantly reduced. In other words, if lag 1 ($t=100\text{ms}$) or lag 2 ($t=200\text{ms}$) are replaced by a blank then the AB curve takes the form shown in the green and black series of Figure 6-2 accordingly.

The attentional deficit that came up through the AB paradigm, has given important insights regarding the possible signal interactions during the deployment of attention and on the same time it provided an interesting challenge in terms of computational modeling. Several theories as well as

computational models have been formulated to account for the basic U-shaped curve of the AB and the modification of the curve when masks are replaced by blanks at lags 1 or 2.

Because of the particularity of the AB's data, this task is occasionally taken to be a criterion for the evaluation of any new computational implementation. Indeed, for a model to successfully simulate and reproduce the corresponding data it must incorporate several neural signal interactions, yet it must not escape from what is known from neurophysiology regarding the neural mechanisms.

Similarly, the proposed model was used for the simulation of the AB phenomenon with and without the blanks and the corresponding results along with the theoretical framework behind them were published in Neokleous et al (2009a, 2009b, 2009c). A thoroughly description of the simulation results and how these were obtained is given in the next section.

6.1.1 Simulation results

The model was run under three conditions. One was the typical AB condition in which T2 follows the T1 after a fixed delay (SOA of T2) while distracting numbers are presented in-between the two targets as well as after T2. This is the no-blanks condition as all positions in the RSVP sequence were occupied by stimuli. In another condition, termed Lag 1 blank, neither a target nor a distractor was presented at Lag 1. In a third condition, Lag 2 blank, a blank was presented 200ms after T1 (i.e., after a distractor was presented at Lag 1). For the simulations, T1 was always presented at time $t=0$ and T2 at each of the subsequent time lags. For each lag that T2 was presented, the simulations were run for 50 times. Results revealed a clear match between simulations (Figure 6-3) and the patterns of finding obtained from previous studies (Figure 6-2).

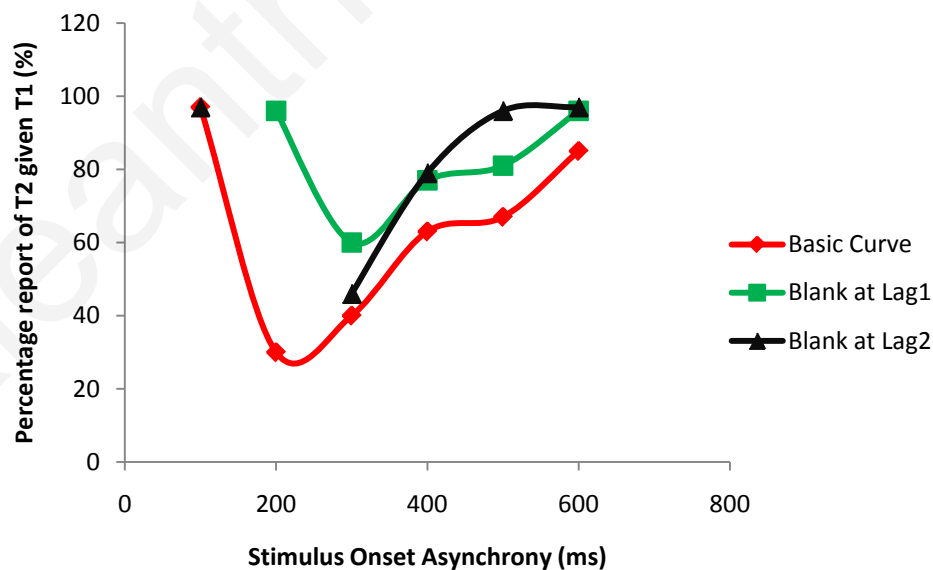


Figure 6-3 Simulation Data from the proposed model

As predicted by the literature, an AB effect was observed in the no-blanks condition when T2 was presented at Lags 2, 3, and 4 (i.e., the temporal window of 200-400ms). In addition, Lag 1 Sparing was observed when T2 was presented at Lag 1, while as expected based on the findings of Giesbrecht and DiLollo (1996) and Seiffert and DiLollo (1997), the AB effect was reduced in the Lag 1 and Lag 2 blank conditions.

6.1.2 How the model reproduces the experimental data

According to the model description of Chapter 6, all visual input will be initially encoded and generated with a specific firing rate relevant to their saliency. Selection of a certain stimulus will then occur gradually within the information processing stream. What is selected is influenced by the result of the inhibitory interactions among visual input at the first-stage of processing and is finally determined after the influence – facilitatory or inhibitory – of internal volitions at a subsequent stage (if these exist). In terms of the AB effects however found in the literature, specific features of the model are responsible for the successful simulations and these are numbered below.

The first feature of the model is the ability to handle competitive inhibition between any incoming stimuli during the whole process. More specifically, in the first stage of processing, the inhibition caused by the masking stimuli towards the two targets will modulate their initial neural activity. Indeed, the inhibition in the first stage of processing is critical for the simulations because it happens at very early stages of visual processing, before any top-down interference and thus makes no distinction between distractors and targets. The only criterion for setting the level of inhibition in the first stage of processing is explicitly based on the initial saliency of every incoming stimulus. Therefore given that the targets and distractors have more or less the same saliency (since all appear with the same contrast, size, and design) the initial inhibition will be equally distributed. Furthermore, as briefly mentioned in the previous chapter, feedback and feed-forward interactions due to a reverberatory activity among the first and second stage of processing will highlight the forward and backward masking interactions from the distracting items of the RSVP stream onto the two targets.

The second feature of the model that contributes to obtain the simulation results are the semantic top-down interactions in the second stage of processing. By definition, the AB task requires the identification and report of the two (letter) targets; thus, it is important in the implementation to include signals for the recognition and selection of the neural activity that corresponds to a target stimulus. This mechanism is performed in the model through the correlation control module (CCM) that generates a control signal relevant to the degree of correlation among the incoming neural activity (initiated from an input stimulus) and neural activity from the endogenous goals module representing the targets characteristics. As a consequence, the target stimuli will be biased in

respect to the distracting elements and subsequently will elicit stronger inhibitions. Figure 6-4 presents the neural activations that correspond to the target letter when measured from the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing (SL₂). Each black dot corresponds to a spike while the red dots show which spikes in the neural network layer have been produced synchronously. In line with the latter, the neural activations of the SL₂ clearly show the effect of the CCM in the neural progression.

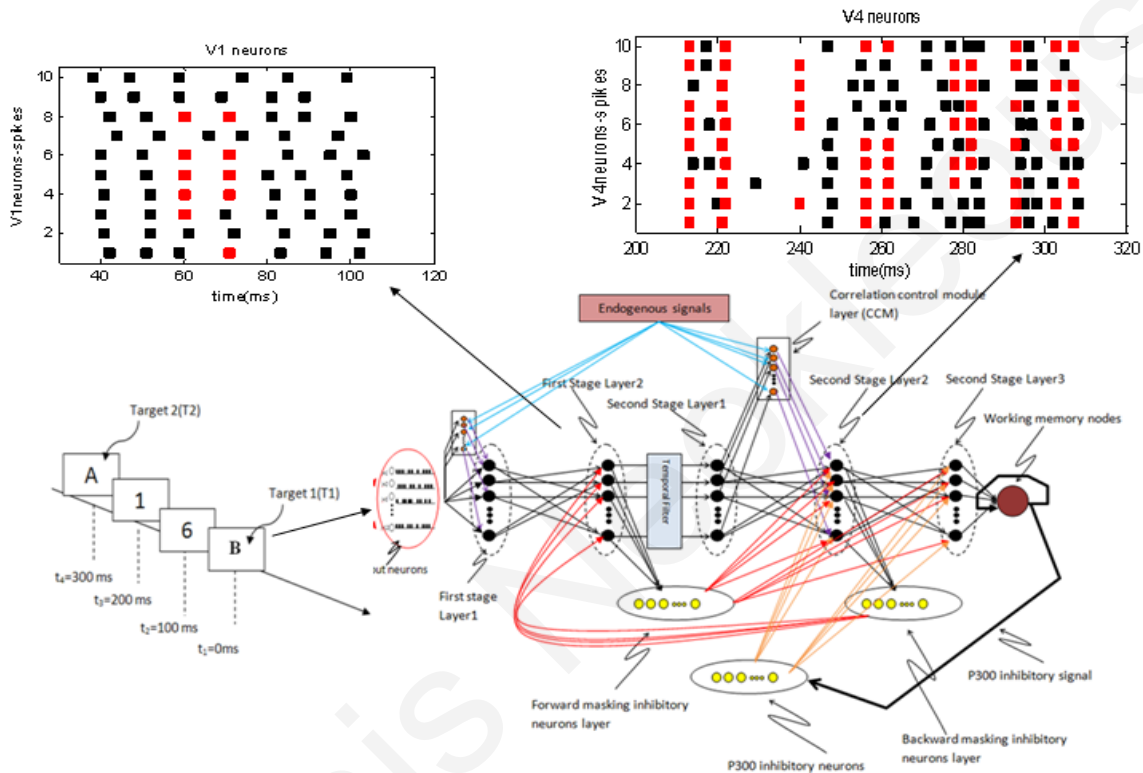


Figure 6-4 The neural activations initiated by the processing of the target when measured from the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing (SL₂).

The third feature inherited by the model necessary to get the proper simulation results, concerns the interaction between two attention event related potentials (ERPs). These are the P2/N2 signals that appear at about 180-240ms post-stimulus and have been proposed as control signals for the movement of attention and the P300 signal at about 350–600 ms post-stimulus which is associated with the working memory sensory buffer site and is taken to be the signal of the availability for report, as stated in the previous chapter.

Finally, by incorporating a certain level of noise due to the randomness of the neural spiking inherent, the model was able to exhibit similar behavior with the experimental data.

More specifically, how these features help to obtain the simulation results for each of the three characteristics observed in the experimental data is analyzed in the following sections.

6.1.2.1 Basic Blink

The explanation for the U- shaped curve despite the inhibitory interactions among distracters and targets, mostly lies in the assumption that the P300 signal generated by the first target falls into the time window that the P2/N2 component of the second target was about to be generated. Thus due to this interaction, the P2/N2 component that was about to bias the neural activity of the second target is strongly inhibited. As a result, the second target, fails to access working memory. A graphical representation of this possible interaction is shown in Figure 6.4.

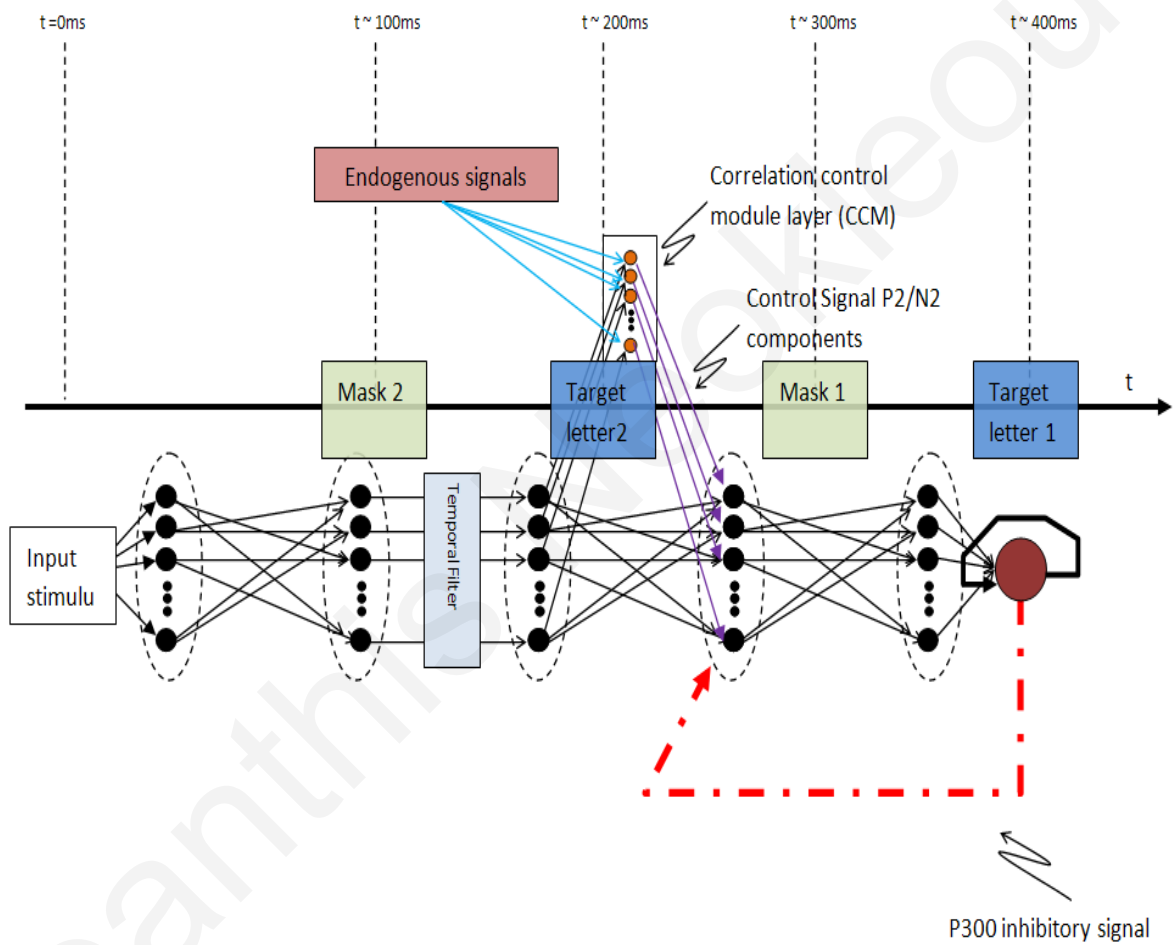


Figure 6-5 Processing of the second target falls within the time window that the P300 signal of the first target interacts. Therefore the second target, although it has strong correlations with the endogenous goals, the control signal is contradicted by the P300 inhibitory interaction.

6.1.2.2 Lag-1 sparing

As explained, lag-1 sparing refers to the high percentage of correct identification of the second target when presented immediately after the first target. One possible mechanism according to the proposed model that could be behind this finding, involves the competitive inhibitory interactions

between subsequent stimuli. More specifically, when the first target reaches the second stage of processing, it will cause inhibition towards the stimuli still processed by the first stage of processing. This inhibition will influence the strength of the masking distractor that appears immediately after the second target. Given that, the corresponding distractor which is in fact responsible for the primary masking effect acted on the second target will have reduced “strength” and thus will analogously extract reduced inhibition (Figure 6.6).

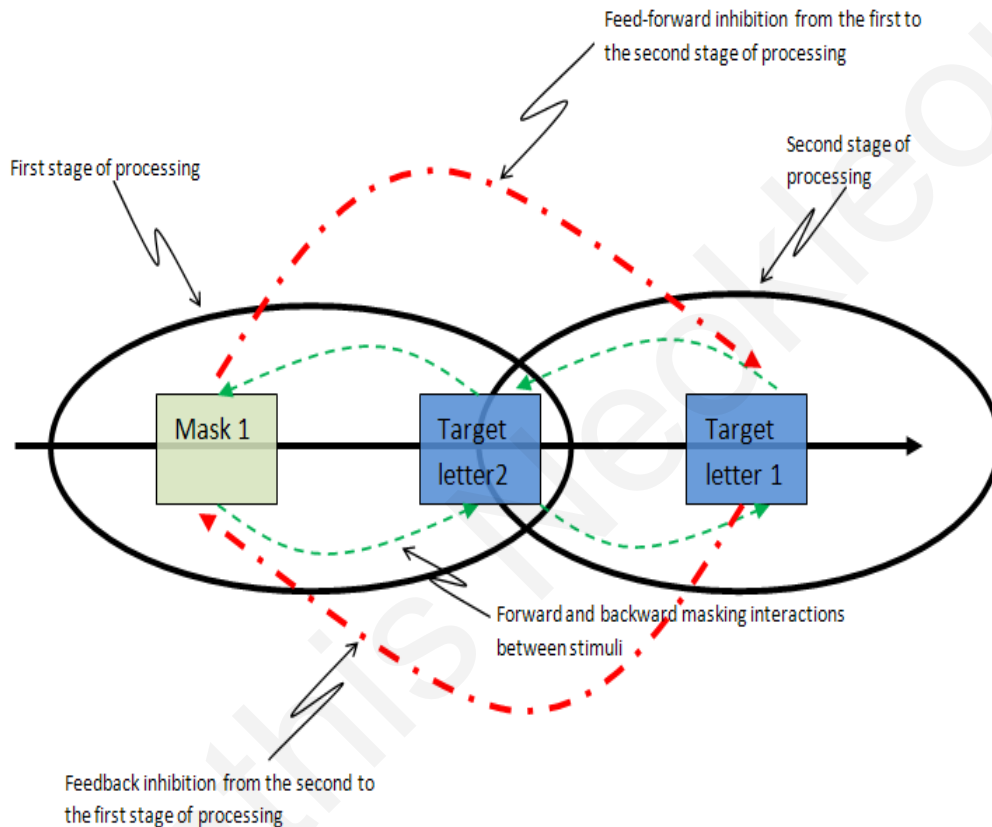


Figure 6-6 The coupling inhibitory interactions between stimuli

Furthermore, lag-1 sparing according to the model can also be explained on the basis of the short time gap between the two targets. The second target appears 100ms after the first target, which is outside the P300 signal of the first target interacting window. Therefore the amplification of the second target’s neural activity from the correlation control module signals will not be interfered. Hence, the second target will reach working memory with adequate strength to win perceptual recognition as well. An interesting observation however in this condition, is that although both T1 and T2 are identified, many times are perceived in the wrong order. In fact according to Chun and Potter (1995) when T2 appears at lag 1 temporal order judgment was only a little above chance. This finding is again consistent with the proposed implementation for the reason that the same

working memory node will be excited from the neural activity that corresponds to both targets. In other words it is like the two targets appeared as one stimulus.

6.1.2.3 Blanks at lag 1 and lag 2

The curves with blank at lag 1 (green series) and blank at lag 2 (black series) of Figure 6-1 are again consistent with the competition processes between various stimuli in order to access working memory. Indeed, the substitution of a forward or backward mask with a blank removes the inhibitory interactions that would have been induced otherwise from the distracting stimuli. Finally the informality of the adjoining synaptic weights between feed-forward and feedback neural activity (Chapter 6 – section 6.3) results into different levels of inhibition when forward or backward mask are substitute with a blank and therefore explains the difference between the green and black curve of Figure 6-3.

6.2 The Perceptual Load Theory behavioral experiment (Lavie, (1995))

In one of Lavie's studies regarding the perceptual load theory (PLT), participants were asked to determine whether a presented stimulus was the letter x or the letter z. In one condition, termed the high-load, the letter was flanked by 5 other letters. In another condition, termed the low-load condition, the target was presented accompanied by no flanking letters. In both conditions a distractor letter was presented nearby the target. In a subset of trials the distractor was incompatible to the target designating the alternative response (i.e., if the target was x the distractor was z and vice-versa). In other trials, the distractor was a neutral letter. Results revealed that the interference exerted by the incompatible distractor, evidenced as increased latency for identifying the target, was greater in the low than the high load condition. Lavie accounted for these findings by arguing that in the high-load condition all attentional resources are consumed by the main task leaving no spare resources to process the distractor; that is, the distractor is discarded at an early stage of processing. In contrast, in the low-load condition the task does not exhaust all available resources leaving spare resources to process the distractor. In this case, the distractor is discarded at a later-stage. Therefore, one can suggest that PLT has given a promising way of reconciling the debate concerning the locus of selection in the attentional mechanism (see section 3.2).

However, although the PLT offers an appealing account for how selection of information can occur either early or late, it has been later on criticized and challenged. For example, Johnson, McGrath, and McNeil (2002) have shown that an endogenous cue priming the location of the target (i.e., a central arrow presented prior to the target display) eliminates any distractor interference in the low-load condition. As the presentation of a cue does not alter the amount of spare resources, this result is problematic for at least a strong version of the PLT. Furthermore, Elitti, et al., (2005) provided

evidence that the critical variable might be the saliency of distractors and not perceptual load per se. In their experiments Elitti et al. manipulated the onsets and offsets of targets and distractors, showing that interference can be present with high-load provided that the distractor is made more salient. Finally, Torralbo and Beck (2008) have criticized the PLT on two grounds. First, they argued that the term perceptual load is not clearly defined. Second, they claimed that the concept of exhausted capacity of attentional resources cannot be reconciled easily with what is known about brain mechanisms. Torralbo and Beck (2008) proposed that the neural basis for perceptual load is the extent of competition among stimuli to gain representation in the visual cortex and the strength of a top-down biasing mechanism that is needed to resolve the competition and select a stimulus.

Considering the above, the PLT has placed a challenging framework for the proposed computational model, with the expectation to provide a biologically-plausible account of how perceptual load effects may arise in the corresponding behavioral experiments. The resultant simulations accompanied with an analogous discussion on how these were derived have been published in Neokleous et al., (2009c). Nevertheless, a comprehensive analysis on how the overall study on PLT was framed is presented in the next section.

More specifically, a behavioral experiment was carried out in an attempt to (1) replicate the basic pattern of findings obtained with perceptual-load experiments, (2) examine the interaction between cuing and perceptual load, and (3) to generate data that would allow a comparison with the model's output. The experiment conducted was similar to that of (Johnson et al., 2002) with the exception that an 80%-valid peripheral cue was used. In their experiment Johnson et al. (2002) have used a 100%-valid central cue.

6.2.1 Method of the PLT task

In the designed task, a 2 (perceptual load: high, low) \times 3 (cue: no cue, valid, invalid) \times 3 (distractor compatibility: neutral, compatible, incompatible) within-subject design was used. The experiment was designed and presented using the E-Prime software package. During testing participants were seated approximately 50-60cm from a computer screen.

Participants were asked to perform a visual search task in which 6 letters arranged in a circular array in the center of the screen were presented after a fixation cross. In the high load condition, the search array comprised of the target (X or Z) and 5 letters (M, K, N, H, W) that shared features with the two possible targets (Figure 6-7). In the low load condition the target appeared among 5 O's (Figure 6-8).

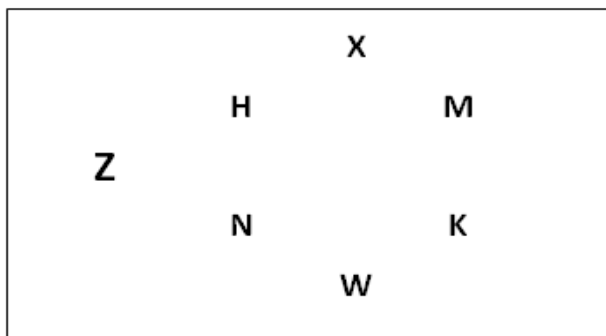


Figure 6-7 High-load trial with incompatible distractor

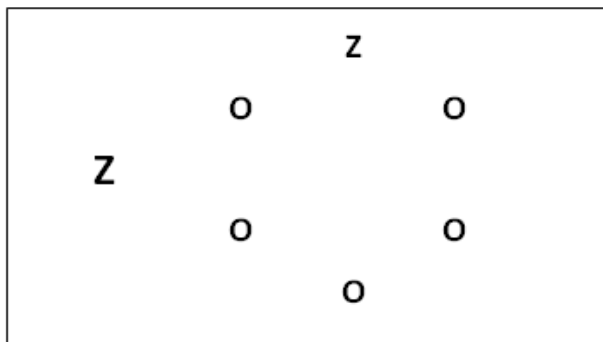


Figure 6-8 Low-load trial with compatible distractor

In both conditions, a larger distractor letter (X, Z or L) appeared simultaneously on the left or on the right of the circular array and it was compatible (identical to the target), incompatible (calling for the alternative response) or neutral (the letter L) in 1/3 of the trials. Participants were requested to ignore the distractor letter and focus on identifying the target (X or Z) in the 6-letter search array.

In cue-present trials an asterisk was presented for 150 ms after the offset of the fixation point. The cue was located either in the same location as the target letter (valid cue), or in another position in the circle (invalid cue).

Each participant carried out 216 experimental trials, 50% in the low load condition and the other 50% in the high load condition. In each load condition there were 96 valid cue trials (i.e., 80% of the total cue present trials), 96 no cue trials, and 24 invalid cue trials. Reaction time (RT) and accuracy scores were recorded and were used for data analysis.

6.2.2 Experimental and simulation results

Separate repeated-measures ANOVA were carried out for accuracy and latency data with load, cue type, and distractor compatibility as factors. Invalid cues were excluded from the analyses as they constituted only a small subset of trials. Perceptual load effects are typically found in latency data therefore, latency for correct responses was the primary measure of interest in our analyses. Yet, a more detail description on the experimental data analysis can be found on Neokleous et al. (2009c).

Median latencies for the high and low conditions, with and without cues are presented in Figures 6-9 and 6-10. In Figure 6-10 the interference exerted by the incompatible distractor can be clearly seen (indicated with the red line).

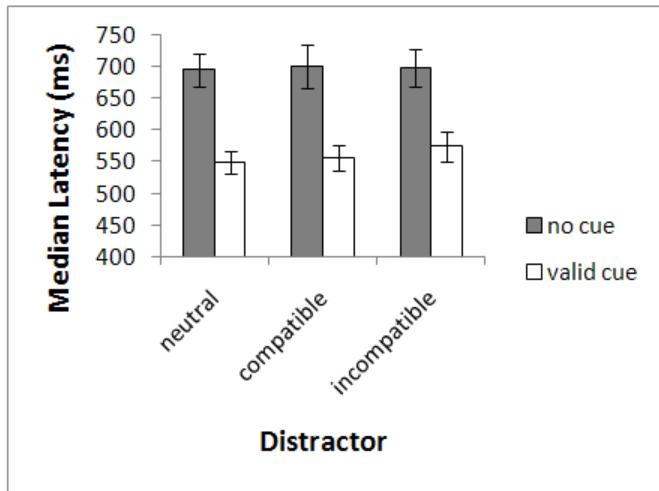


Figure 6-9 Median latency for high load condition (error bars represent standard errors)

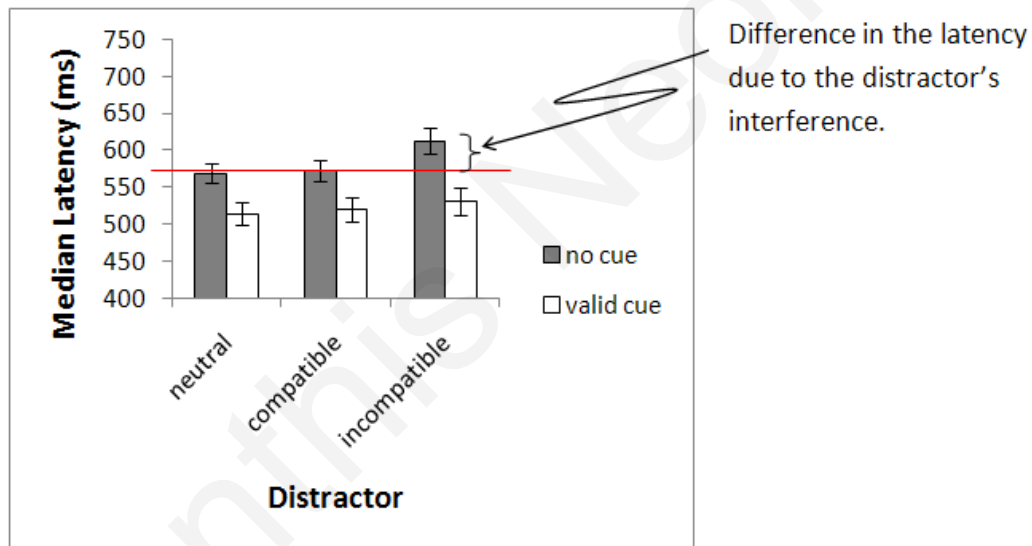


Figure 6-10 Median latency for low load condition (error bars represent standard errors)

The computational model was again implemented using the Matlab-Simulink environment and has been tuned to incorporate interactions according to spatial attention tasks as this is the case with the PLT. More specifically, fifty simulated trials in each combination of load and distractor compatibility were run using the model. Median latencies were computed for each condition and were subjected to a 2 (load: high, low) x 3 (compatibility: neutral, compatible, incompatible) repeated-measures Analysis of Variance (ANOVA) and presented in Figures 6-11, 6-12.

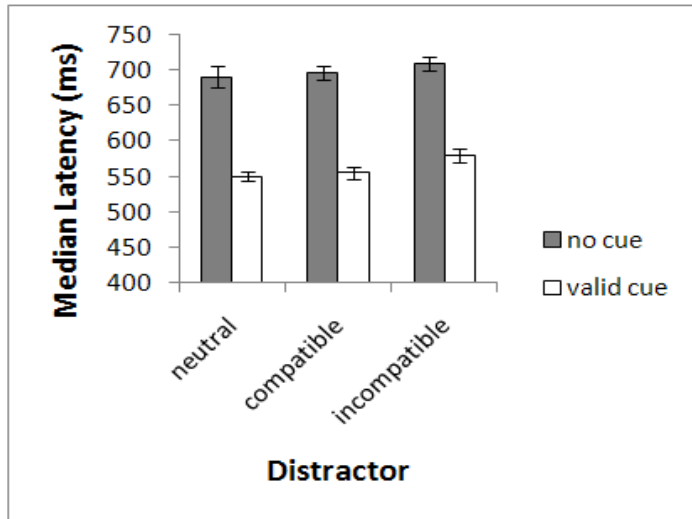


Figure 6-11 Simulation results for high load condition

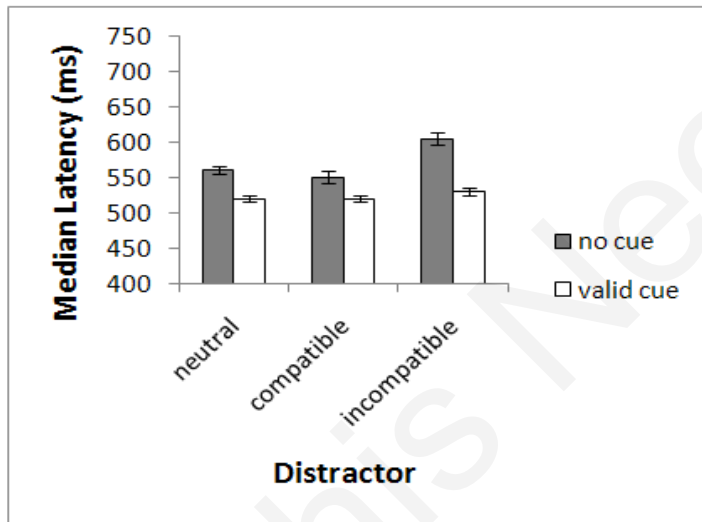


Figure 6-12 Simulation results for low load condition

As evidenced the pattern of results obtained in the experiment replicated the typical pattern of findings of perceptual-load studies (Lavie & Cox, 1997) but also verified the prediction of the model for no distractor interference in the cued low load condition.

6.2.3 How the model reproduces the experimental data

Generally, top-down interactions in both stages of processing, (spatial and semantic top-down interference) in conjunction with the competitive inhibitory interactions between each stimulus, are the primary factors responsible for the successful reproduction of the behavioural findings.

More precisely, images depicting conditions for high and low load like those used by Lavie and Cox (1997) were produced by taking screenshots from an E-Prime program of the perceptual load task. Following that, the example images were analyzed using the saliency map Matlab toolbox of

Walther and Koch (2006) and the saliency values were transformed into firing rates of the input neurons that encoded each stimulus in the display as explained in Chapter 6.

The saliency analysis in the low load condition yielded higher firing rates for neurons representing the target than those representing the other letters (the 5 O's) in the circular array. This was expected since in the low load condition the distracting O's in the circular area create a background that pushes the target letter (X or Z) to become more salient. Conversely, in the high load condition all stimuli that appear in the circular area have more or less the same saliency (Figure 6-13). In both conditions, the distracting flanker due to its increase size compared to all the other stimuli is represented with an increase initial firing rate according to the transformation equation 6.21-Chapter 6.

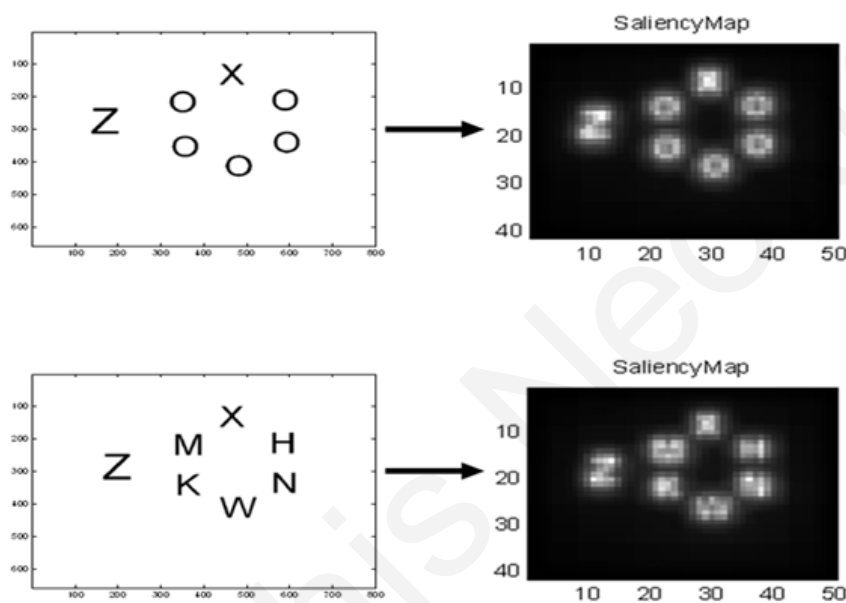


Figure 6-13 Low and high load conditions together with the saliency map output

Furthermore, given that the instructions of the task were telling to the subjects to concentrate only on the circular area, the stimuli presented in that specific region were biased compared to the distracting flanker. Spatial top down signals are driven towards the neurons whose receptive field coincides with the circular area and consequently induce an amplification of their corresponding initial firing rate.

As neural activity progress to the second stage of the proposed model, the semantics of every stimulus begin to have a more critical role in the overall processing. Accordingly, the neurons representing the target letters X and Z, due to their correlation with the semantic endogenous information will demonstrate high frequency spike rates accompanied with neural synchronization (see section 6.3). However, although the inhibition caused by each of the two stimuli is relevant to their neural activation, in the case where the flanker and the target are compatible, both (the target and the flanker) will stimulate reduced inhibition between them since both of them are semantically

similar. The same assumption applies in the first stage of processing between the stimuli which are presented by similar spatial top-down characteristics. Put differently, the distracting letters in the circular area will cause stronger inhibition to the flanker which is outside the circular area than between them.

In the cue conditions, an additional factor enters to the overall processing. The appearance of an asterisk before the presentation of the visual stimuli generates specific top-down spatial signals that are concentrated in a very small spatial area around the asterisk. Thus any stimuli that appears in that area immediately after, will gain a significant advantage in the competition process.

On the basis of the above analysis, a more detailed description about how the simulation results were obtained for each condition is presented below.

6.2.3.1 High load condition

In the high load condition, each stimulus in the circular area has a relatively high salience. This along with the spatial top down amplification results into high levels of neural activations for every stimulus and consequently high levels of inhibition towards each other. More importantly however the corresponding neural activity, results to a combined stronger inhibition towards the distracting flanker. The consequences of these interactions in the first stage of processing are reflected on two main observations of the simulation results. The first observation corresponds to the increased latency of the target's response in the high load condition compared with the low load condition (Figure 6-10). The model outputs a target response similar with the experimental data in this condition because the neural activity of the target is significantly reduced from the lateral inhibitions caused by all other stimuli and thus more time is required until it is fully processed from the working memory module.

The second observation concerns the absent of interactions from the flanker towards the target, an effect that according to the model is correlated with the flanker's strength in the second stage of processing. This phenomenon can be explained by the fact that the combined inhibitory interactions from the stimuli in the circular area towards the flanker in the first stage of processing almost neutralize its neural activity. Therefore in the second stage of processing, there no spare resources are linked to the flanker in order to extract any interference. A more comprehensive explanation of these interactions can be seen in Figure 6-14 in which the level of activation between the neurons that represent each stimulus at different stages of the overall processing (and consequently the analogous inhibition that each stimulus acts on all the other) is shown.

Figure 6-14.a corresponds to the level of activations of the input neurons as these are calculated according to the saliency map without taking into consideration the spatial attention interactions. Figure 6-14.b, shows the same neurons activation after the influence of the spatial top-down signals. Of course in the simulations, the spatial top-down signals interact to the presented stimuli even

before their appearance, thus the initial levels of neural activations that are applied to the model are those of figure 6-14.b. Nevertheless, Figure 6-14.a is presented only to point out the effect of the spatial interactions. Figure 6-14.c shows the level of neural activity after the semantics top down interactions in the second stage of processing.

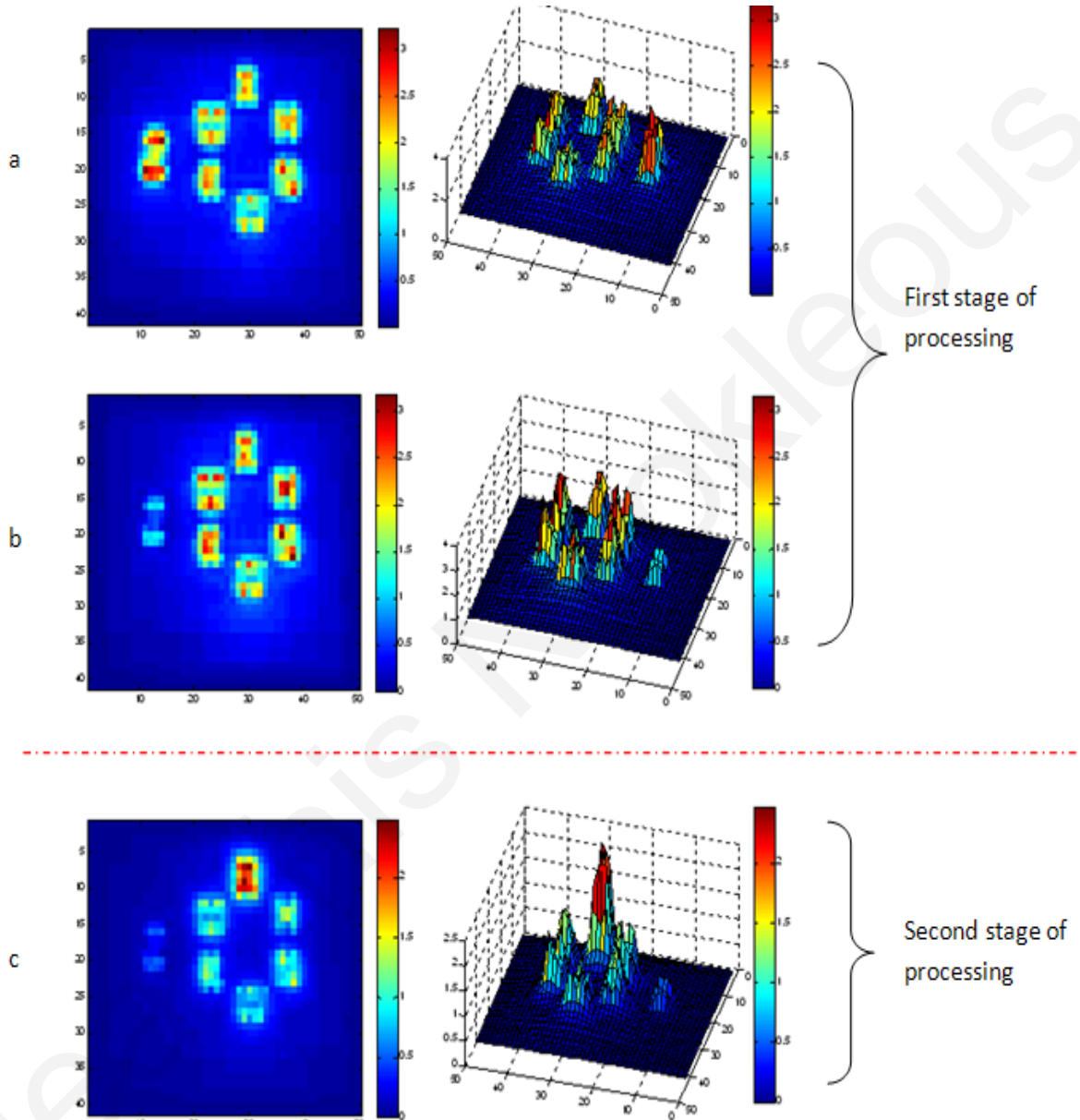


Figure 6-14 a) shows the level of activations of the neurons that correspond to each stimulus in the high load condition as these are calculated according to the saliency map without taking into consideration the spatial attention interactions and b) with the spatial top down signal interactions. c) Shows the level of neural activity after the semantics top down interactions in the second stage of processing

In Figure 6-15 one can observe the neural activations that correspond to the target and the flanker when measured from the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing (SL₂) in the high load condition. Each black dot corresponds to a spike while the red dots show which spikes in the neural network layer have been produced synchronously. From Figure 6-15 it is clear that the neural activations that correspond to the flanker have been significantly suppressed thus preventing any semantic interactions in the second stage of processing.

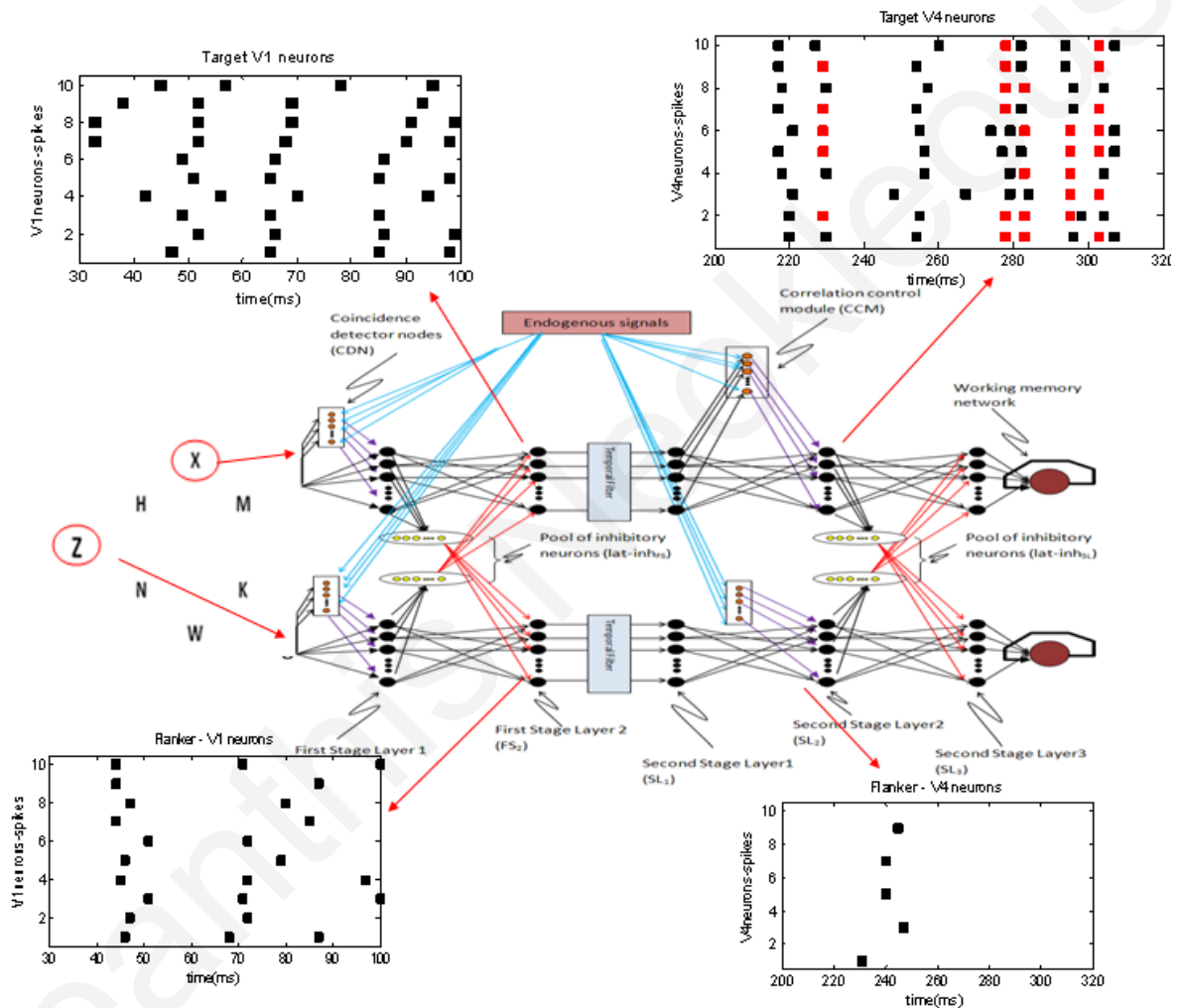


Figure 6-15 The neural activations that correspond to the target and the flanker when measured from the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing (SL₂) in the high load condition.

6.2.3.2 Low load condition

In the low load condition, as explained the target letter because of the iso-feature suppression effect becomes more salient than the surrounding O's. In addition, the spatial top-down interactions about the circular area according to the task's instructions will further amplify the target's neural activity. This will result to strong inhibition from the target letter towards the surrounding O's yet much smaller combined inhibition from all the stimuli in the circular area towards the distracting flanker

than in the high load condition. The reason for the smaller combined inhibition is mainly because of the reduced activation levels of the distracting stimuli in the circular area at the low load condition compared with the high load condition. Again the consequences of these interactions in the first stage of processing are reflected on the output results. More specifically the reaction time of the target's response is significantly lower than in the high load condition because of its stronger activations during the whole process. More importantly however, in this condition there is a significant difference in the reaction time between the compatible and incompatible case. This observation results due to the fact that the flanker's neural activity was only slightly diminished in the first stage of processing and thus it continued in the second stage of processing with sufficient levels of activations. Thus it was able to persuade the analogous interactions in the incompatible case (Figure 6-16).

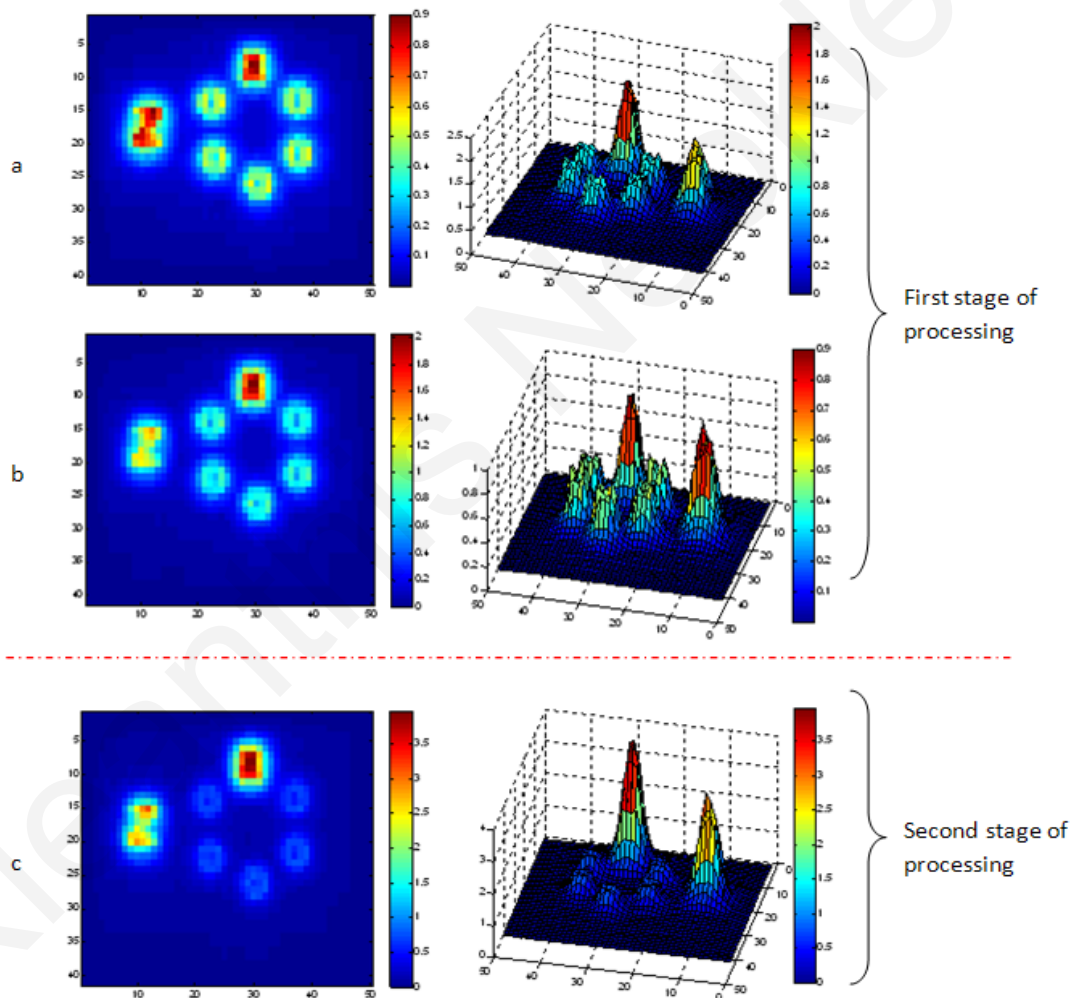


Figure 6-16 a) shows the level of activations of the neurons that correspond to each stimulus in the low load condition as these are calculated according to the saliency map without taking into consideration the spatial attention interactions and b) with the spatial top down signal interactions. c) Shows the level of neural activity after the semantics top down interactions in the second stage of processing

In Figure 6-17 the neural activations that correspond to the target and the flanker when measured from the second layer of the first stage of processing (FS_2) and the second layer of the second stage of processing (SL_2) in the low load condition are presented. From Figure 6-17 one can see that there are significant neural activations that correspond to the flanker in the second stage of processing, therefore it is possible for semantic interferences to interact with the progression and processing of the target's neural activity in the working memory layer.

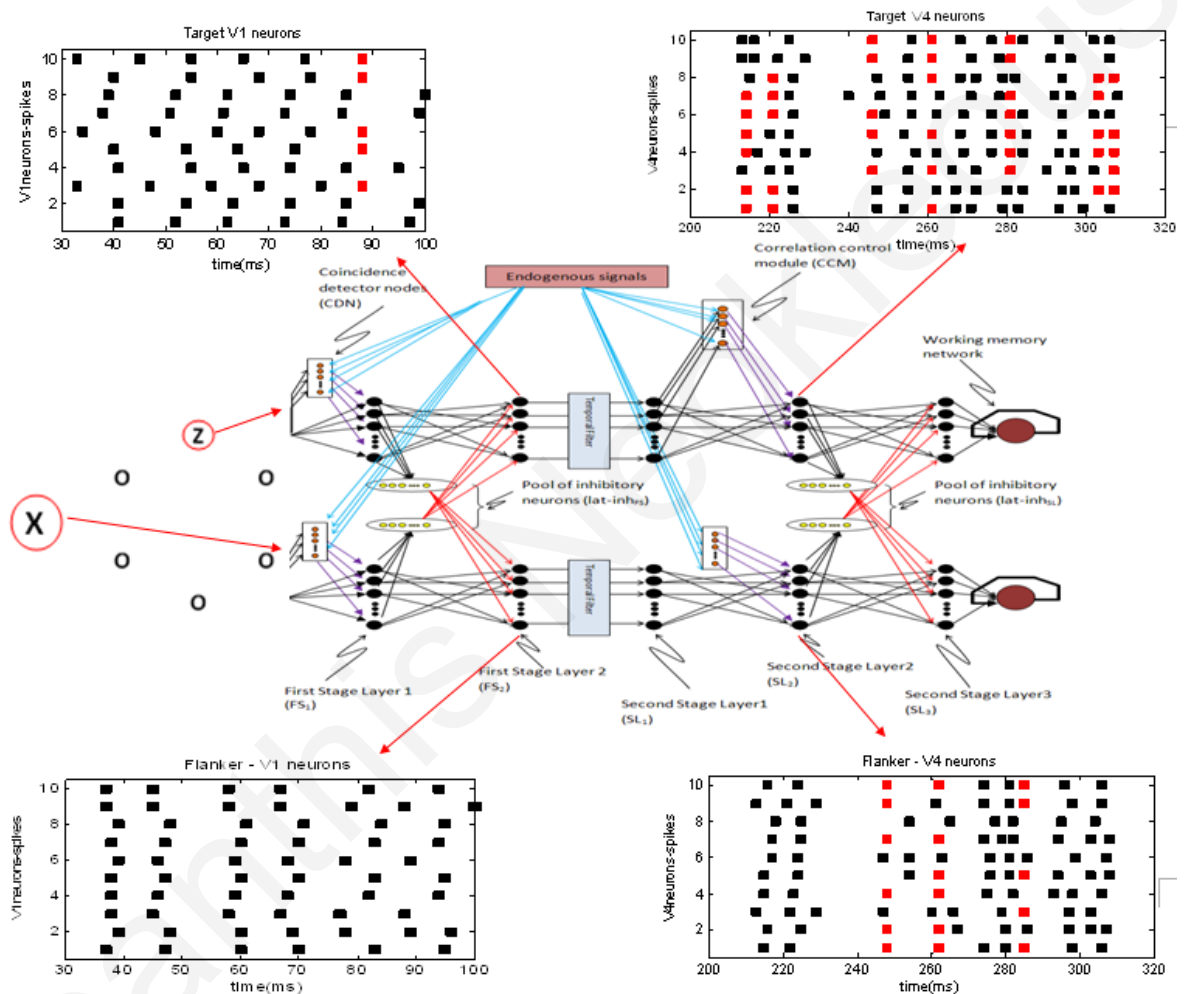


Figure 6-17 The neural activations that correspond to the target and the flanker when measured from the second layer of the first stage of processing (FS_2) and the second layer of the second stage of processing (SL_2) in the low load condition.

6.2.3.3 Cued conditions

In the cued conditions, the specific spatial attention top down signals raise the neural activity of the preceding stimulus in to very high levels. As a consequence, this will result for the specific stimulus to strongly inhibit the neural activations of all the other surrounding distracters and eventually to produce the simulation output results of Figures 6-10 and 6-11.

6.2.4 A comment on the simulation results

As a concluding remark based on the simulations of the specific behavioural experiment what can be pointed out is that the proposed computational model offers an explicit and concrete account for perceptual load effects. Importantly, the model does not rely on any definition of what constitutes high or low load. Instead, whether a task is susceptible to distractor interference is determined by the relative saliency of the stimuli in the visual field as well as the current goals of the person. Thus, the model is compatible with the claims by Eltiti et al. (2005) that saliency is an important determinant of perceptual load effects. The model is also compatible with the theorizing of Torralbo and Beck (2008) who argued that the neural basis of perceptual load is the competitive interactions in the visual cortex and the biasing mechanisms needed to resolve the competitions in favor of the target. Indeed, on one hand, the model includes continuous inhibitory interactions among the stimuli in the visual field with relative saliency determining the strength of the inhibitions that are exerted while on the other hand, top-down signals can bias this competition by amplifying the activity of neurons representing stimuli that match the spatial and semantic goals.

6.3 A behavioral experiment regarding the relation between attention and consciousness by Naccache, Blandin and Dehaene, (2002)

Even though the role of attention as a control system is ubiquitous, to fully understand the functioning of this mechanism one must closely examine its relation with other psychological constructs such as working memory, learning and consciousness. However, perhaps the most interesting, albeit controversial, issue concerns the relationship between selective attention and consciousness. Although psychologists and neuroscientists accept that selective attention and consciousness are related constructs, the exact nature of this relation remains unclear. Some researchers emphasize this close relation and argue that attention is necessary and sufficient for consciousness (e.g. Posner, 1994; Jackendoff, 1996; O'Regan & Noe, 2001), while others posit that since the two constructs are subserved by separate neural processes, they must be regarded as distinct mechanisms (Lamme, 2003; Bachmann 2006; Koch & Tsuchiya, 2006). The claims that selective attention and consciousness are very similar constructs or even the same, is reinforced by the plethora of evidence showing that a person becomes consciously aware of a stimulus when s/he focuses attention on it (Mack and Rock, 1994). In fact, many inattentional blindness studies have shown that a stimulus easily evades conscious awareness when no attention is directed at it (Simons and Rensick, 2005). Alternatively, evidence from studies using dual task paradigms demonstrates that it is possible to perceive stimuli presented in the peripheral visual field even when spatial attention is endogenously focused on a central task (Sperling & Doshier, 1986; Braun & Jules, 1998). Also, both forward and backward masking has been shown to interfere with the visual awareness of a stimulus as is the AB paradigm.

Therefore, the proposed model was used to simulate the findings of a behavioural experiment conducted by Naccache et al., (2002) which have sparked a debate on the possible links between attention and consciousness in the attempt to contribute in this scientific research area. The simulations along with the corresponding results were published on Neokleous et al., (2010).

6.3.1 Method and experimental results of the Naccache, Blandin and Dehaene, (2002) task

In the specific study by Naccache et al., (2002) participants were presented with a number-comparison task in which they were asked to indicate if a presented numeric stimulus (a number between 1 and 9 but excluding 5) was greater or smaller than 5. Shortly before the appearance of the target stimulus, a prime was presented that could be either congruent with the target (both the prime and target are greater or smaller than 5) or incongruent (the prime is greater than 5 but the target smaller or vice versa).

The prime was presented among masking stimuli for only 29ms and as confirmed by the study, participants were not aware of its presence. In addition to the basic task, a temporal cue was presented in some trials. The cue did not reveal any information about the identity of the target but allowed the participants to anticipate when the target would be presented (Figure 6-18).

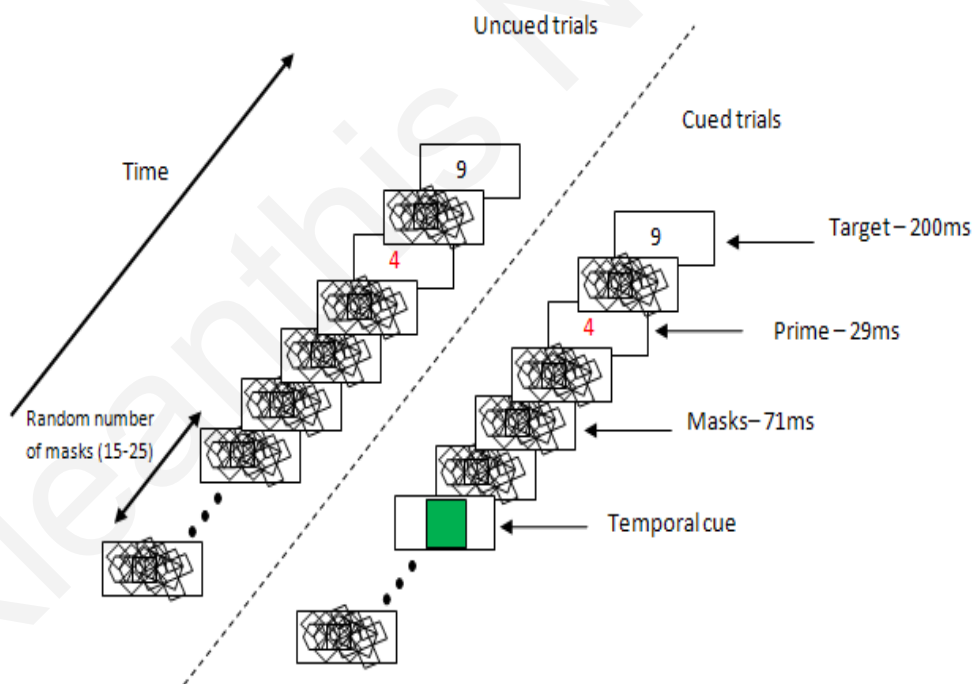


Figure 6-18 The experimental setup by Naccache et al., (2002)

Results from the study revealed an interaction between cueing condition and target compatibility. Participants were faster responding to a congruent than an incongruent target but only when a temporal cue was provided. When no temporal cue was present, response times for congruent and

incongruent targets were equal. Overall, the temporal cue enhanced performance as response times were faster for cued than non cued trials. The basic pattern of the findings by Naccache et al. (2002) is presented in Figure 6-19.

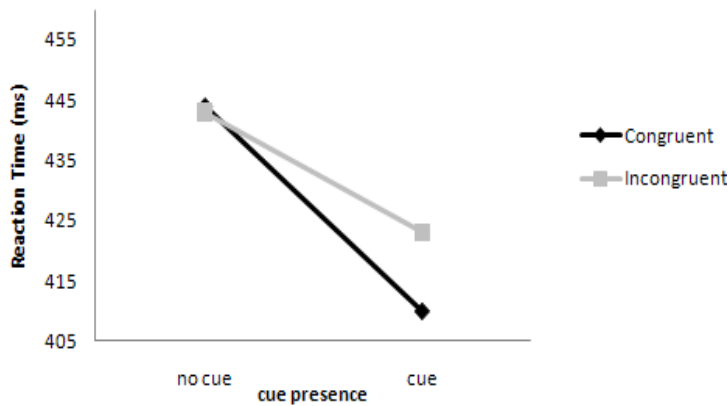


Figure 6-19 Basic pattern of findings from Naccache et al., (2002)

6.3.2 Simulation results of the Naccache, Blandin and Dehaene, (2002) task.

The model was used under four conditions to provide simulation data for each combination of cueing and compatibility. The simulations were run 50 times for each of the four conditions and reaction time was recorded. Reaction time in the simulations was operationalized as the interval between the encoding of the probe (i.e., firing of the first spike in the first stage of the model) and the firing of the working memory node to denote that a decision was made.

Median reaction times (RT's) from the simulations are presented in Figure 6-20. However, comparing these findings with those from the experiment of Naccache et al (2002) one can verify that, although the model is overall slower in responding, it does replicate the pattern of behavioural findings.

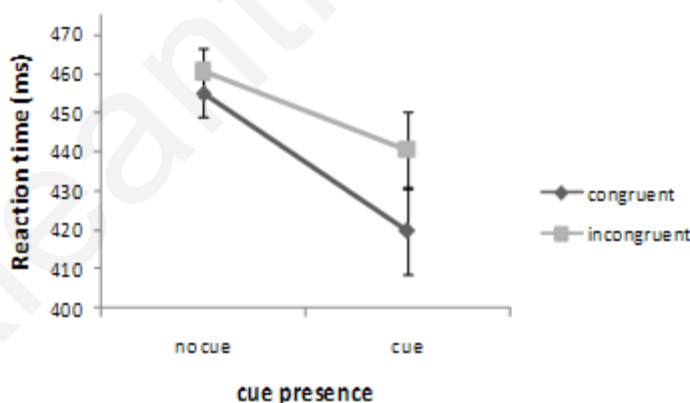


Figure 6-20 Median reaction times from the simulations, (error bars represent standard errors).

6.3.3 How the model reproduces the experimental data

This pattern of latencies produced by the model is a consequence of the competitive interactions of neural activity in the first stage of the model and the semantic modulation of activity by top-down

signals in the second stage of the model. In the uncued conditions, the input neurons that correspond to the prime generate spike trains for 29ms (i.e., the duration of the prime) with a mean firing rate that is based on its saliency. This neural activity when interacted from backward and forward masking is not adequate to advance strongly in the neural pathway of the computational model. In fact, in most of the cases it is completely suppressed before it even reaches the second stage of processing. Therefore, even though the prime contains semantic information, its interference is diminished, and as a consequence the processing of the target is not influenced. A more comprehensive demonstration of the latter can be seen in Figure 6-21 where the neural activity that corresponds to the prime is presented when measured in the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing (SL₂).

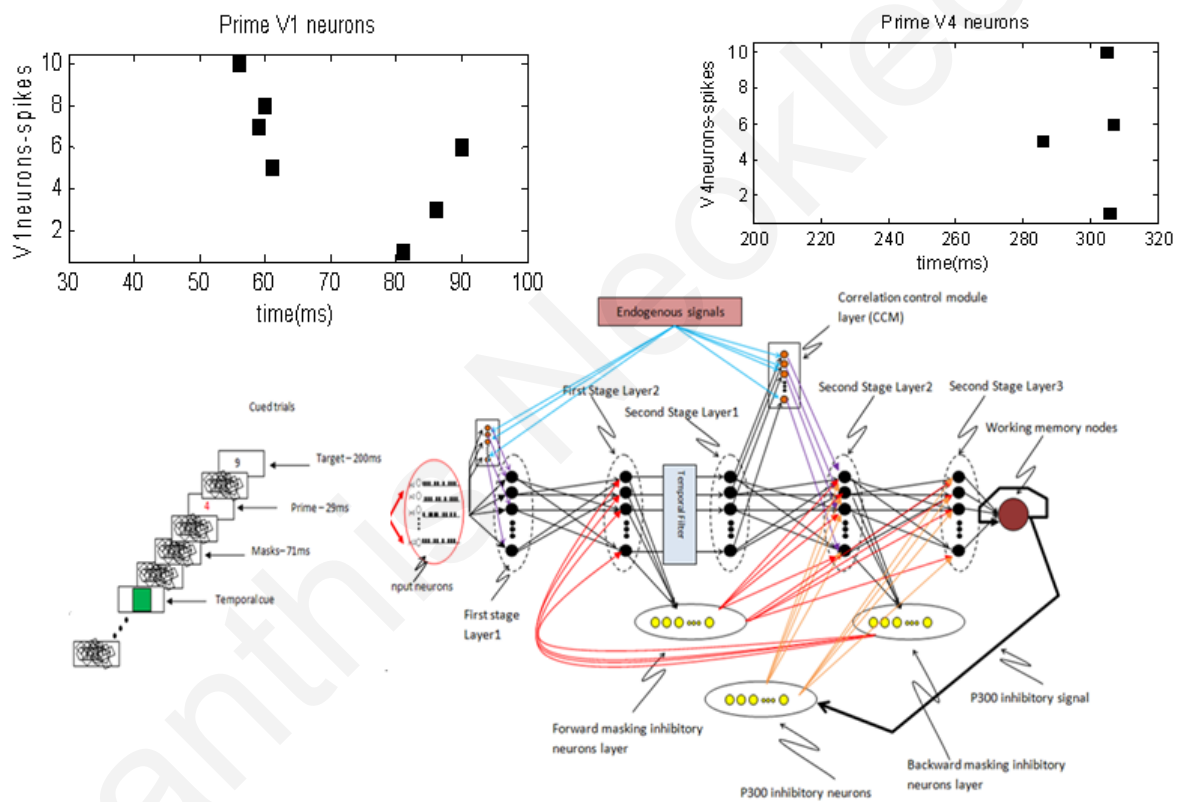


Figure 6-21 The neural activations that correspond to the prime when measured from the second layer of the first stage of processing (FS₂) and the second layer of the second stage of processing (SL₂).

In the cued conditions, top down signals initiated by the presence of the cue interfere with the processing of the prime and the target. These top-down signals that are represented in the model by a series of spike trains begin to excite the input neurons very shortly after the appearance of the cue. This interaction results into an increase of the initial firing rate of any stimuli that appear within this temporal window. In the present experiment both the prime and the target are presented in this interval. It should be pointed out that the firing rate of the prime is still not strong enough to enter working memory and thus to be consciously perceived. Nevertheless, it is critically sufficient to

“push” the neural activity of the prime in the second stage of processing and therefore to exert semantic interference to the processing of the target. This can be seen more clearly in Figure 6-22 that presents the activations of the prime in the cued condition (measured in FS₁ and SL₂). More specifically from the activations in SL₂ one can see that there is sufficient neural activity to induce even at the minimum level some semantic interference.

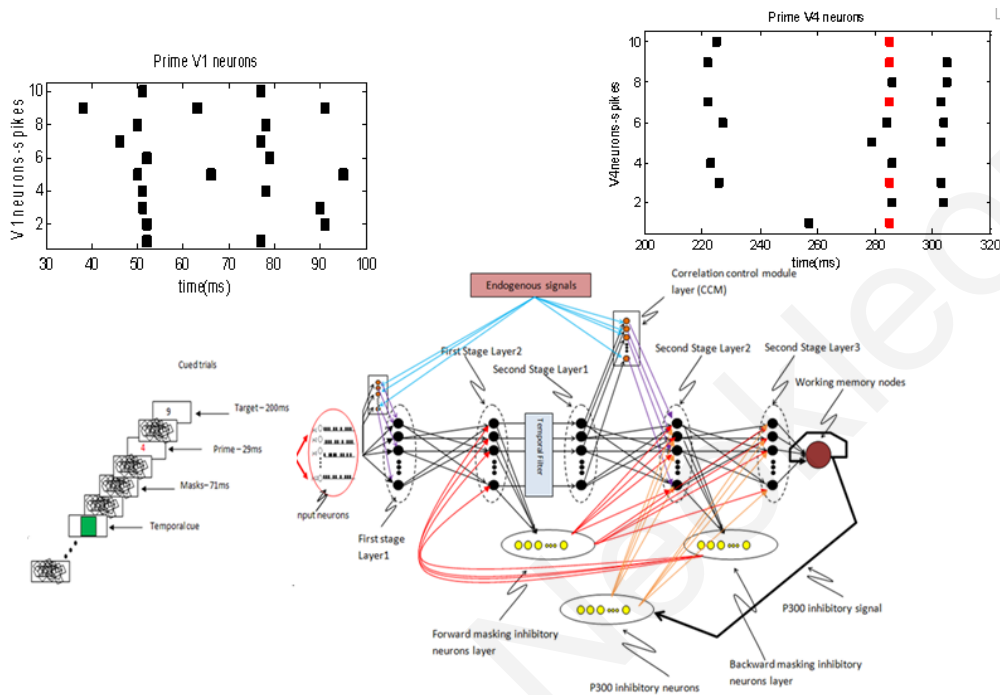


Figure 6-22 The neural activations that correspond to the prime in the cued conditions, when measured from FS₂ and SL₂.

6.3.4 A comment on the simulation results

The combination of backward and forward masking in this task makes the prime non-accessible for conscious report but it can nevertheless affect performance in the task. Koch and Tsuchiya, (2006) suggested that the visual masking technique in this task allows for an independent manipulation of attention and consciousness. They claimed that in order to obtain the priming effect it is necessary to allocate top-down attention to a perceptually invisible stimulus; this suggests, in their opinion, that two distinct processes are involved. In contrast Mole, (2008) posits that it is possible to visually process some of the attributes of an item and manipulate them with attentional mechanisms, even if the item has not been consciously experienced. Therefore, the proposition that attention and consciousness are two distinct processes is according to Mole not sufficient to explain the behavioural results.

The interpretation put forward by Dehaene and colleagues (2006) is based on the assumption that every stimulus causes a different level of processing depending on its strength. They argued that every stimulus can trigger subliminal, preconscious or conscious processing. Subliminal processing is defined as a condition in which the information is inaccessible due to insufficient bottom-up

activation. Preconscious processing causes enough activation to achieve conscious access, but the stimulus remains in a nonconscious state because of a lack of top-down attentional amplification. Conscious processing involves the interaction of top-down attention with the neural activity of a stimulus, in such a way that the activity exceeds the “threshold” of conscious access. Based on the logic of Dehaene et al., (2008), the strength of the prime in the cued condition is sufficient to reach the level of preconscious processing and therefore to semantically interfere with the processing of the target, but it is not adequate to reach the level of conscious processing.

This threefold distinction of stimulus processing is based on the global workspace hypothesis implemented in the model of Dehaene et al. (2003) as well as on neuroscience findings regarding the relation between attention and consciousness. For example, many studies have shown that neural activity is observed in extrastriate visual areas even if the participants deny seeing any stimulus (Dehaene & Naccache, 2001; Moutoussis & Zeki, 2002; Marois, & Chun, 2004). Moreover, in a study by Sergent et al. (2005), similar occipito-temporal event-related potentials were evoked by a visible word and by a word that was rendered invisible through masking. This finding is consistent with the hypothesis of different levels of processing proposed by Dehaene et al. (2006) as it documents that intense occipito-temporal activation is present in the cortex along with lack of conscious awareness of the stimulus that initiated it. However, these findings can also be interpreted as supporting the claim that attention and consciousness are two distinct, albeit interacting, processes. Perhaps then the crucial difference between the claims of Dehaene et al., (2008) and Koch and Tsuchiya (2006) is that according to the former top-down attention is regarded as necessary for conscious awareness of a stimulus while for the latter consciousness can occur without top-down attention.

My opinion related with this interesting topic around attention and consciousness is shaped by the simulation results and the underlying mechanisms of the proposed model. In the implementation, the hypothesis that the primary processing of visual information is performed in a feed-forward manner within the visual cortex is adapted. This hypothesis is based on evidence from the literature suggesting that complex visual processing can be reflected in the human cortex within 130–150 msec, (VanRullen & Koch, 2003). For visual information to become conscious however, the model follows the theory by Lamme (2003) who argued that sustained neural activity is required, possibly through global feedback from frontal regions of the cortex to visual areas and back. This reverberatory activity can gradually build up until it is sufficient to propagate in parietal and prefrontal regions that are believed to support short-term memory and other processes that relate to consciousness. This neural process has also been adopted by other scientists as a possible explanation for the creation of consciousness. For instance, Dehaene et al. (2006) suggested that if a stimulus is strong enough, then it can access a global network with long range axons that communicate with different cortical areas, and therefore it can initiate loops of neural activity. As a

consequence, a self-amplifying system will gradually push the corresponding stimulus into conscious awareness. Furthermore, in a slightly different interpretation, Taylor (2007) suggested that these loops of neural activity are possible candidates for the signals that generate the experience of ownership, that is, the experience one has of being aware of an external or internal stimulus. In a recent report on the CODAM model, Taylor (2007) regards this activity as a copy of the attention control signal denoted as the corollary discharge of the attention movement control signal. The copy of the attention signal was originally proposed in the CODAM model as a component used to make attention more effective and at the same time, it was suggested as a candidate signal for the creation of the “inner self”.

In the proposed computational model, this reverberatory activity is incorporated through forward and feedback interactions between the first and second stage of processing as explained in previous sections. However, conscious report of a certain stimulus in the model requires activation of the corresponding working memory nodes which are connected to the output layer of the second stage of processing. Therefore, the experience of being perceptually aware of a stimulus can be achieved only if a stimulus sufficiently activates working memory.

Therefore, I would suggest that the relation between attention and consciousness can become more obvious if top-down and bottom-up attentional mechanisms are seen as two distinct processes. The neural path following the two stages of processing in the proposed model can be seen as an independent attentional system that relies first on bottom-up information but subsequently on top-down signals as well. As a result, each stimulus that enters the visual field initiates neural activity that will progress in the visual cortex according to the “constructive rules” that underlie bottom-up attention combined with any interaction that might arise from a separate system that maintains endogenous goals. Furthermore, all stimuli that appear within the same temporal window compete with each other to win a place in working memory. Depending on the “strength” of each stimulus, which is reflected in the firing rate of its neurons, inhibition takes place and influences the neural progression of any other competitive stimuli. This inhibitory interaction can be negligible or significant and more importantly, it can influence the neural progression through the corresponding areas of the visual cortex of a certain stimulus, regardless of whether the stimulus that initiated the inhibition eventually accesses working memory or not. Therefore, although at the very initial stages of visual processing the route to consciousness coincides with processes involved in bottom-up attention, according to the model’s simulations one can suggest that top-down attention may play a key role on whether a stimulus reaches conscious awareness.

Summarizing, the three behavioral experiments presented in this Chapter have been deeply analyzed through extensive computational simulations. The corresponding investigations resulted into some interesting conclusions regarding the neural interactions that might produce their

corresponding behavioral data, which in their turn have offered a possible solution on the relevant scientific disagreements that these experiments have produced. Indeed, a general summary about the conclusions and contributions as well as on the future scientific paths that can be effectively linked with this thesis is given in Chapter 7.

Kleanthis Neokleous

7. Conclusions, contributions and future work

In this chapter the general conclusions of the research work are summarized. Also, the chapter identifies and explains the original contributions that have been derived during the different levels of the research.

It has been previously pointed that the research work is multidisciplinary, spreading in the fields of neuroscience, cognitive psychology and computer science, as they are related to visual selective attention. More specifically, the goals of the research work were to collect relevant information regarding the neurophysiology and cognitive behavior of the attentional process and integrate it into a new and plausible computational model, using elements of neural system dynamics, computational intelligence, and mathematical simulations. The multitude of facts and relevant data that have been accumulated from many scientific studies from different disciplines however, many times bring confusion since they can overwhelm our understanding. Computational sciences, have the ability to synthesize distinct facts, to simulate and measure them, and thus to create coherent testable hypotheses. Indeed, the visual attentional model that has been proposed in the thesis had been focused on the identification of candidate operating principles that may underlie the machinery of the attentional system through various simulations of important behavioral experiments.

More specifically, the combination of low level neural interactions and the more abstract psychological concepts as implemented in the model has given the opportunity to contribute in the theoretical explanation of the corresponding debatable behavioral experiments from a new perspective, and thus offering an alternative and novel approach from what has been presented in the relevant literature so far.

7.1 Contributions of the research work

The important contributions of the thesis are listed below.

- A generic model of visual selective attention has been designed and used for simulating three debatable psychological experiments in the relevant literature. These are the **attentional blink phenomenon** (Raymont et al., 1992), the behavioral experiment that inspired the **perceptual load theory** (Lavie, 1995) and the experiment that initiated a controversial debate on the **relation between attention and consciousness** (Naccache et al., 2002). The strategy followed, was to initially verify its credibility by comparing the simulation results with the

experimental data, and afterwards to give some potential explanations for their behavioural responses, based on low level neural interactions, something that has not been clearly presented in the literature so far. It is important to note that the model was indeed able to reproduce, with high accuracy, the data derived from these three behavioral experiments (Neokleous et al., 2009a; Neokleous et al., 2009b, Neokleous et al., 2010) and therefore, was considered as a very good tool for evaluating the explanatory theories behind their behavioral results.

- The combination of low level neural interactions and the more abstract psychological concepts as implemented in the model has provided the power to run simulations of behavioral phenomena, and at the same time to stay within the narrow limits of coupling interactions as these arise from the plethora of neurophysiologic evidence. The proposed method is a novel approach since it offers the opportunity to contribute from a new perspective in the field of cognitive science.
- To my best of knowledge, the proposed model is the first model that provides a solid explanation of the perceptual load theory (PLT) supported by computational simulations, on the basis of simple neural interactions combined with the stimuli saliency. The only other attempt to explain the perceptual load theory found in the literature is by Dayan (2009), however by using a different approach, on the basis of simple Bayesian inference for incorporating the existence of small and large receptive fields that contribute analogously in the process, depending on the condition of the task (high or low). As noted in section 6.2, the PLT offered an appealing account for how selection of information can either occur early or late. Therefore the corresponding computational simulations are of significant importance taking into account that they provided a possible explanation on how these results were obtained, especially since contradictions have been observed in the recent scientific literature regarding the validity of the theory.
- With regards to the behavioral experiment by Naccache et al. (2002), to the best of my knowledge, there is no other computational model in the literature that simulates the corresponding data. This task has sparked an interesting debate among distinct scientists regarding the relation between attention and consciousness with some researchers to support that these are two distinct processes and others that selective attention and consciousness are very similar constructs or even the same. The computational simulations as presented in section 6.3 resolve this contradiction by suggesting that the distinction is not between attention and consciousness but inside the attentional process itself and specifically among the two main mechanisms that result from bottom up and top down interactions. It is suggested that these two attentional mechanisms can work in accordance and separate and thus giving interesting results as the ones obtained from the specific experiment.

- Another important contribution of the work is that it has initiated a very promising collaboration between the departments of Cognitive Psychology and Computer Science of the University of Cyprus and thus opened the road towards a number of new PhD and postdoc studies. More specifically, in order to investigate several predictions by the model, as well as to refine some of its properties, four undergraduate and two postgraduate students partly under my supervision have dedicated their thesis on the design and execution of new and relevant behavioral experiments. Furthermore, more students have expressed their interest to be involved and continue their graduate studies in the path that the thesis has created as well as on several future applications that can be effectively linked to the current study, as these are analyzed in more detail in the next section.

7.2 Future work

Computational analysis in neurosciences can draw strengths from two sources: the scientific aim of understanding the brain, and the engineering goal of building simulations that imitate those mechanisms, once they are understood. In future work, related to this thesis, it is therefore desired to be driven towards both of these ideas. More realistic implementations could be incorporated in the model, based on new collaborations from laboratories performing single cell recordings, with the objective to combine more detailed low level mechanisms with behavioral responses.

More importantly, future work could be directed towards the design and implementation of novel computational intelligence algorithms that could be used in several applications such as robotics, security systems, computer networks, and diagnostic systems. Even more, straight forward applications could be driven towards studies that concentrate on the expansion of these modeling concepts on the social and medical fields. For example, it is possible to investigate the effects of several parameters such as the strength of inhibitory signals or the level of arousal in important medical conditions such as attention deficit hyperactivity disorder and schizophrenia. Furthermore, collaborations with governmental institutions could be initiated with the emphasis on the social implications of attention and how these could influence our everyday life, or into specialized research concerning tests and training tasks for airtraffic control engineers, pilots, police officers etc.

7.3 Concluding remarks

Although the model follows guiding lines from neurophysiologic studies concerning its operating principles, it is still not an entirely biologically realistic implementation. Several studies have been presented in the literature that explain and suggest candidate neural mechanisms for the attentional process with more realistic implementations. These results however, are usually compared with neurophysiologic studies that measure neural activity at the single neuron level. Conversely, given

that the proposed model is concentrated on the theoretical interpretations of behavioral experiments, a more abstract implementation is necessary. Still, the design of the model does not escape from the borderlines placed by neuroscience, and thus keeps its credibility and capability of predicting new findings. Also, the collaborations with the Experimental Psychology Lab (EPL) of the University of Cyprus, has offered the facilities to design and perform new variations of the existing behavioral experiments, and also to design and develop new experiments based on the computational analysis derived from the model. Therefore, the decision to work at this level of modeling concurs with the availability of experimental research within the project's collaboration group, for the proper evaluation of the model's behavior and the near optimum exploitation of the derived data.

Finally, concerning the discussion regarding the neurophysiologic guidance followed in the implementation and especially about the mechanism of selection as this had been expanded in section 5.5, it is pointed that although the idea to incorporate both mechanisms (manipulation of the firing rate and neural synchronization) was influenced by a number of discussions with distinct scientists and published studies, the final decision was based on my personal understanding and logical interpretation on how the human brain can manipulate and process the incoming visual information under the attentional mechanism .

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Kleanthis Neokleous

Appendix A

MATLAB files (.m)

```

% Kleanthis Neokleous
% Department of Computer Science - University of Cyprus
% November 18th 2010
% Computational model for visual selective attention

%main simulation %%%%%%%%%%
clear all
close all

initializations

% Firing rate calculated according to the saliency map toolbox

Firing_Rate = 0.35;
Firing_Rate_flanker=0.4;

%%%%%%%%%%%%%%
% % high load condition %%%
% %
%%%%%%%%%%%%%%
Firing_Rate_distractor=0.35;

%%%%%%%%%%%%%%
% % low load condition %%%
% %
%%%%%%%%%%%%%%

% Firing_Rate_distractor=0.25;

for i=1:iteration

    T1(i,1)=i-1;
    F1(i,1)=i-1;
    E1(i,1)=i-1;
    E2(i,1)=i-1;

    D1(i,1,:)=i-1;
    S1(i,1)=i-1;

    SpT(i,1)=i-1;
    SpF(i,1)=i-1;
    SpD(i,1,:)=i-1;

```

```

    i=i+1;

end;

for k=1:number_of_trials

[T]=target_spiketrains(Number_of_trains,Firing_Rate,Number_of_Spikepositions);
[F]=flanker_spiketrains(Number_of_trains,Firing_Rate_flanker,Number_of_Spikepositions);
[D]=distractor_spiketrains(Number_of_distractors,Number_of_trains,Firing_Rate_distractor,Number_of_Spikepositions);
[SpT1]=target_spiketrains(Number_of_trains,Spatial_prob_T,Number_of_Sp_Spikepositions);
[SpF1]=target_spiketrains(Number_of_trains,Spatial_prob_F,Number_of_Sp_Spikepositions);
[SpD1]=distractor_spiketrains(Number_of_distractors,Number_of_trains,Spatial_prob_dis,Number_of_Sp_Spikepositions);

T1(1:Number_of_Spikepositions,2:Number_of_trains+1)=T;
F1(1:Number_of_Spikepositions,2:Number_of_trains+1)=F;
D1(1:Number_of_Spikepositions,2:Number_of_trains+1,:)=D;

SpT(1:Number_of_Sp_Spikepositions,2:Number_of_trains+1)=SpT1;
SpF(1:Number_of_Sp_Spikepositions,2:Number_of_trains+1)=SpF1;
SpD(1:Number_of_Sp_Spikepositions,2:Number_of_trains+1,:)=SpD1;

Dis1=D1(:, :, 1);
Dis2=D1(:, :, 2);
Dis3=D1(:, :, 3);
Dis4=D1(:, :, 4);
Dis5=D1(:, :, 5);

SpDis1=SpD(:, :, 1);
SpDis2=SpD(:, :, 2);
SpDis3=SpD(:, :, 3);
SpDis4=SpD(:, :, 4);
SpDis5=SpD(:, :, 5);

sim('attention_model');

k=k+1;
end;

```

```

initializations.m

% Kleanthis Neokleous
% Department of Computer Science - University of Cyprus
% November 18th 2010
%Computational model for visual selective attention

Neuron_gainV1 = 20;
Neuron_gainV2 =20;
Neuron_gainV4 = 30;
time_const = 0.03;
coincidence_detector_threshold = 2;

iteration = 301;
Number_of_trains = 12;
Number_of_correlated_trains = 7;
Number_of_Spikepositions = 100;
Number_of_Sp_Spikepositions = 100;
number_of_trials = 50;
Number_of_distractors=5;

% Probabilities to initialize the spike trains of the spatial top down
% signals

Spatial_prob_T=0.25;
Spatial_prob_F = 0.1;
Spatial_prob_dis=0.25;

% adaptive gain - based on spatial prob and firing rate of each stimulus.

sp_inhibition_gain_flanker =
(0.8+(Spatial_prob_T*(4*Firing_Rate_distractor+Firing_Rate)));
sp_inhibition_gain_circle =
(0.8+(Spatial_prob_F*(4*Firing_Rate_distractor+Firing_Rate_flanker)));

% Inhibition gain - first stage of processing

inh_c = -1.5;
inh_f = -1.5;

% Degree of correlation between the letters X or Z with the endogenous
% signals
Degree_of_correlation = 0.8;

% Inhibition gain - second stage of processing

End_inh = -0.025;
End_gain=0.5;
Endogenous_corr_gain = 1;

% Working memory node threshold

Thresh_WM = 9000;

```

```
% Initialization of the input spike trains for target , flanker and  
% distractors  
  
T1=zeros(iteration,Number_of_trains+1);  
F1=zeros(iteration,Number_of_trains+1);  
S1=zeros(iteration,2);  
E1=zeros(iteration,2);  
E2=zeros(iteration,2);  
D1=zeros(iteration,Number_of_trains+1,Number_of_distractors);  
SpT=zeros(iteration,Number_of_trains+1);  
SpF=zeros(iteration,Number_of_trains+1);  
SpD=zeros(iteration,Number_of_trains+1,Number_of_distractors);
```

The function below initializes the target spike trains. A similar function is used for the flanker/distractors and the endogenous signals.

```

Target_initialization.m

% Kleanthis Neokleous
% Department of Computer Science - University of Cyprus
% November 18th 2010
%Computational model for visual selective attention

function [T] = target_spiketrains(NofT,FR,NofS)

% generation of random matrix A and Target matrix T

number_of_trains =NofT;

number_of_spikes=NofS;

A= rand(number_of_spikes,number_of_trains);

T=zeros(number_of_spikes,number_of_trains);

for i=1:number_of_trains

    for j=1:number_of_spikes

        if A(j,i)<FR
            T(j,i)= 1;
        else
            T(j,i)= 0;
        end
    else
        T(j,i)= 0;
    end
    j=j+1;
end

    i=i+1;
end

```

The file below calculates the degree of synchronization (Q) in the V2 and V4 layers

```

Calculate_Q.m

% Kleanthis Neokleous
% Department of Computer Science - University of Cyprus
% November 18th 2010
%Computational model for visual selective attention

function [Q_total, v_global] = calc_Q(V2)

[a,b] = size (V2);
mu=sum(V2);
kle=0;

for i = 1:b

eval(['v_' num2str(i) '=V2(:,i);']);

kle=kle+i;

i=i+1;

end

count=0;
v_global=zeros(a,kle-b);
mu_global=zeros(1,kle-b);

for i =1:(b)

    for j = i+1:b
eval(['v_' num2str(i) num2str(j) '=v_' num2str(i) '+v_' num2str(j)
';']);
eval(['mu_' num2str(i) num2str(j) '=(mu(i)*mu(j))^0.5;']);

count=count+1;
v_global(:,count)=(eval(['v_' num2str(i) num2str(j)]));

% [r,e]=size(find(eval(['v_' num2str(i) num2str(j)])>1));
%
% C1(count)=r;
%
%
mu_global(:,count)=(eval(['mu_' num2str(i) num2str(j)]));

j=j+1;

    end

    i=i+1;
end
    
```

```
[f,h]=size(v_global);

for i=1:h
    count1=0;
    for j=1:f

        if v_global(j,i)==2
            count1= count1+1;
        end
        j=j+1;
    end

    for j=1:f-1
        if v_global(j,i)==1 andand v_global(j+1,i)
            count1= count1+1;
            v_global(j,i)=2;
        end
        j=j+1;
    end

    end
C2(i)=count1;

i=i+1;
end

Q = (C2)./mu_global;

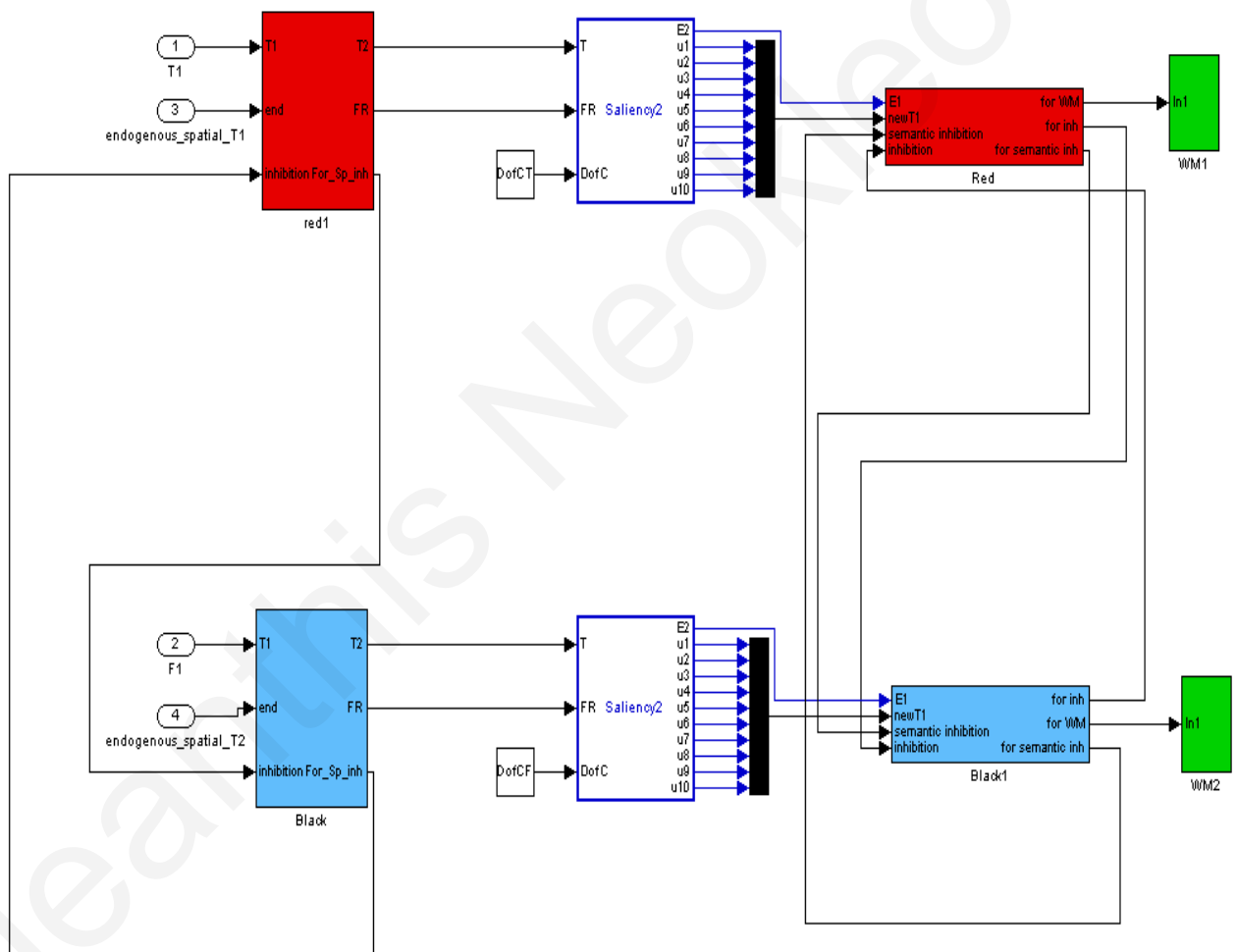
Q_total= sum(Q)/(kle-b);
```

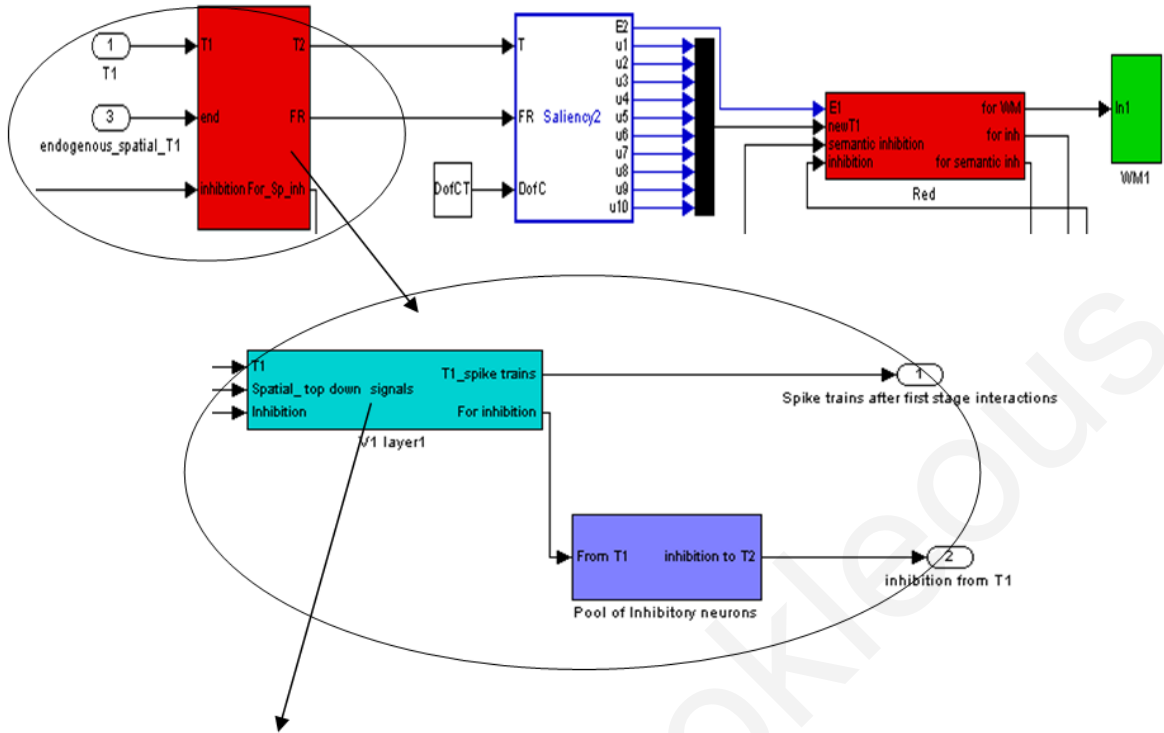

Appendix B

MATLAB SIMULINK models (.mdl)

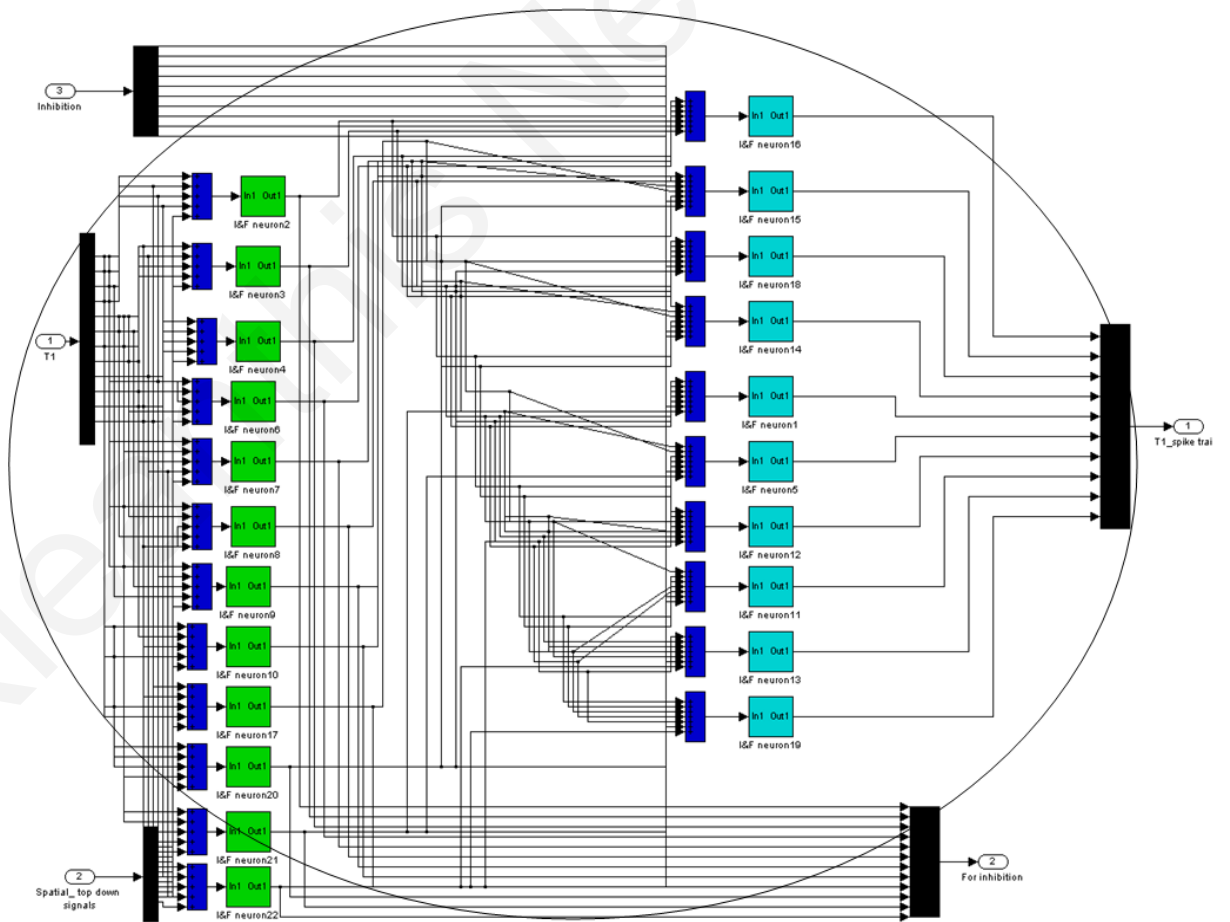
For the SIMULINK models, a simple implementation is presented according to a straightforward example in which two competitive stimuli appear simultaneously in the visual field.

The details and operations performed inside every block in the implementation are presented separately below.

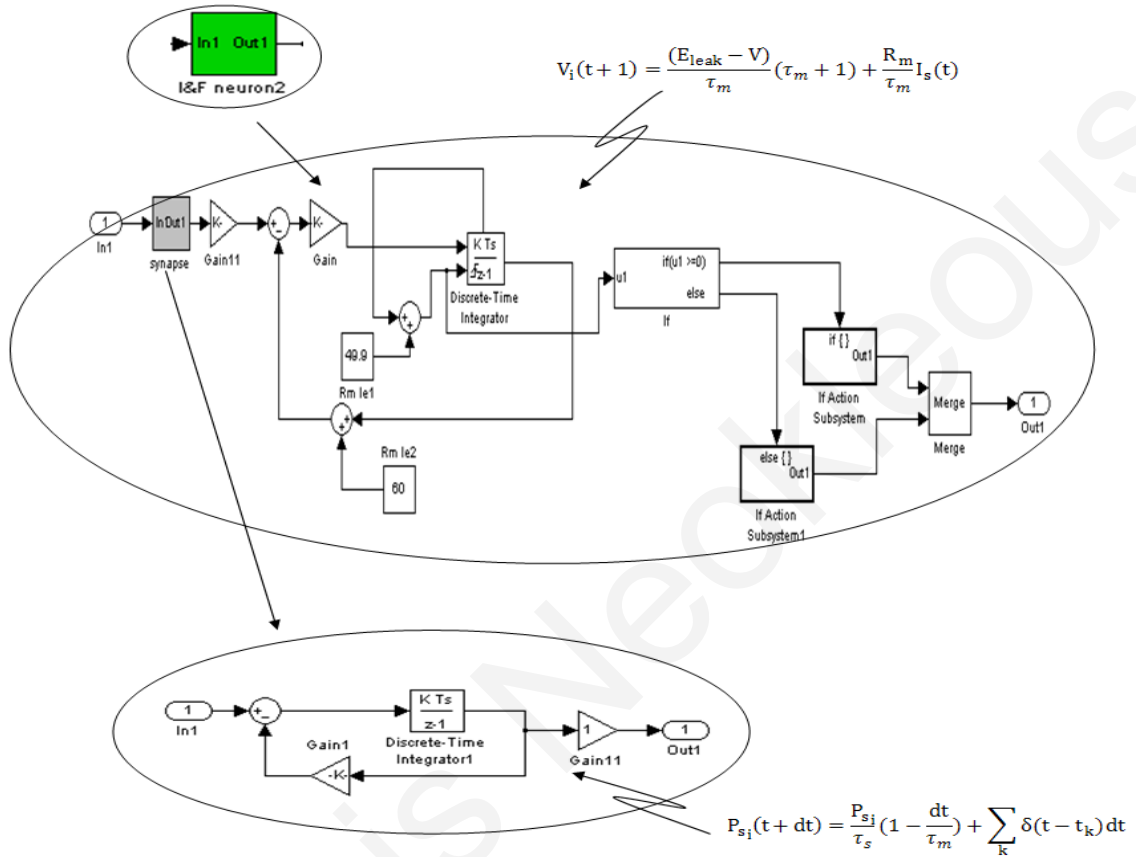




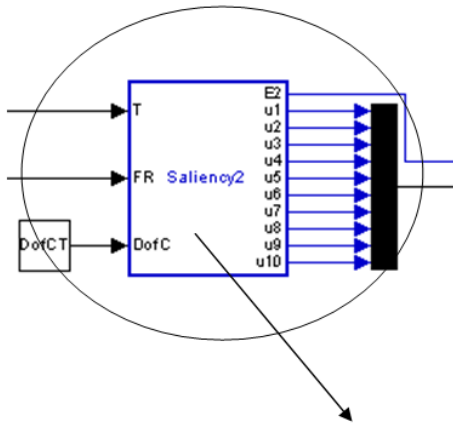
Every green block represents a discrete I&F model of neuron.



The grey blocks simulate the synaptic input which is shown below.



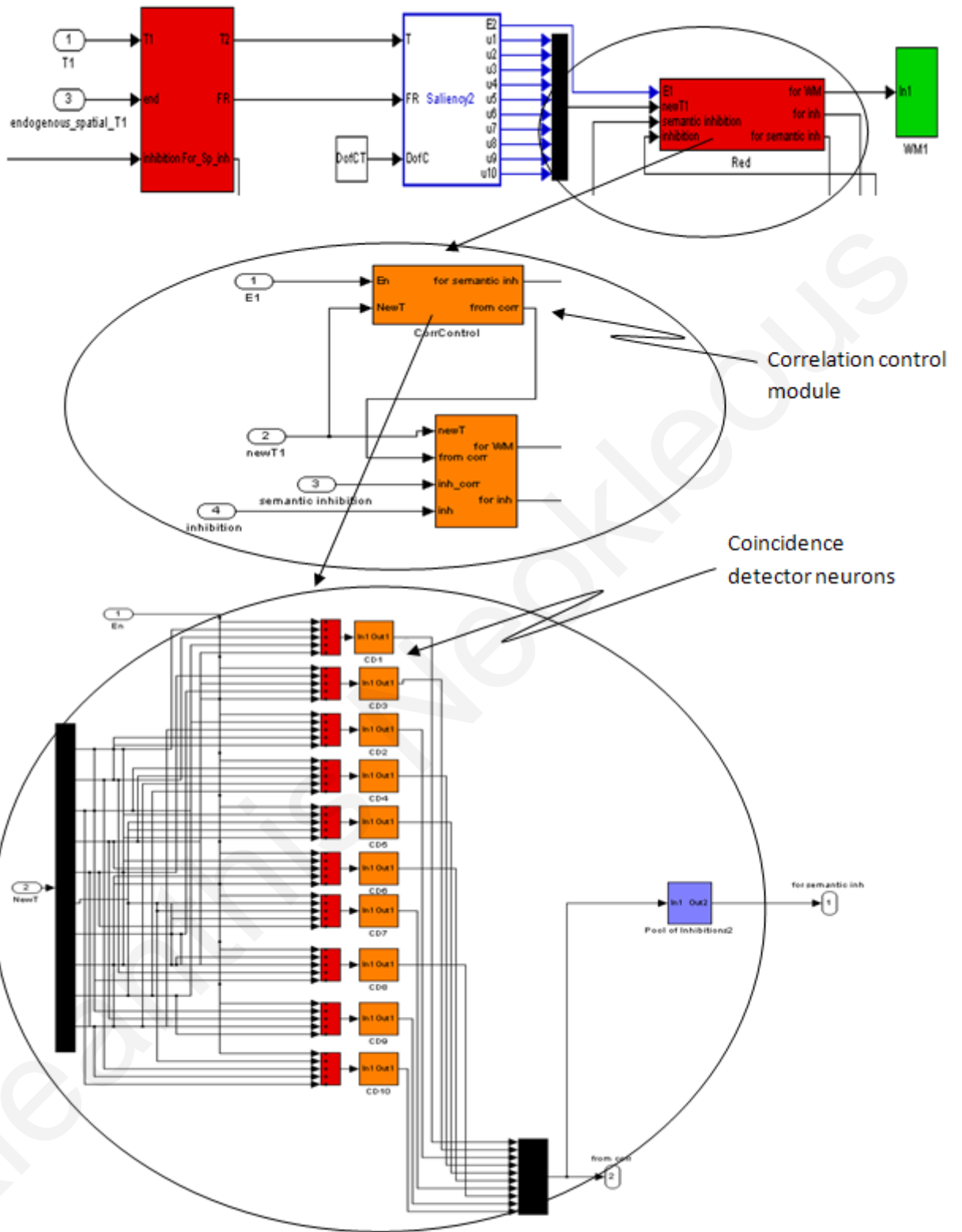
The temporal filter mechanism

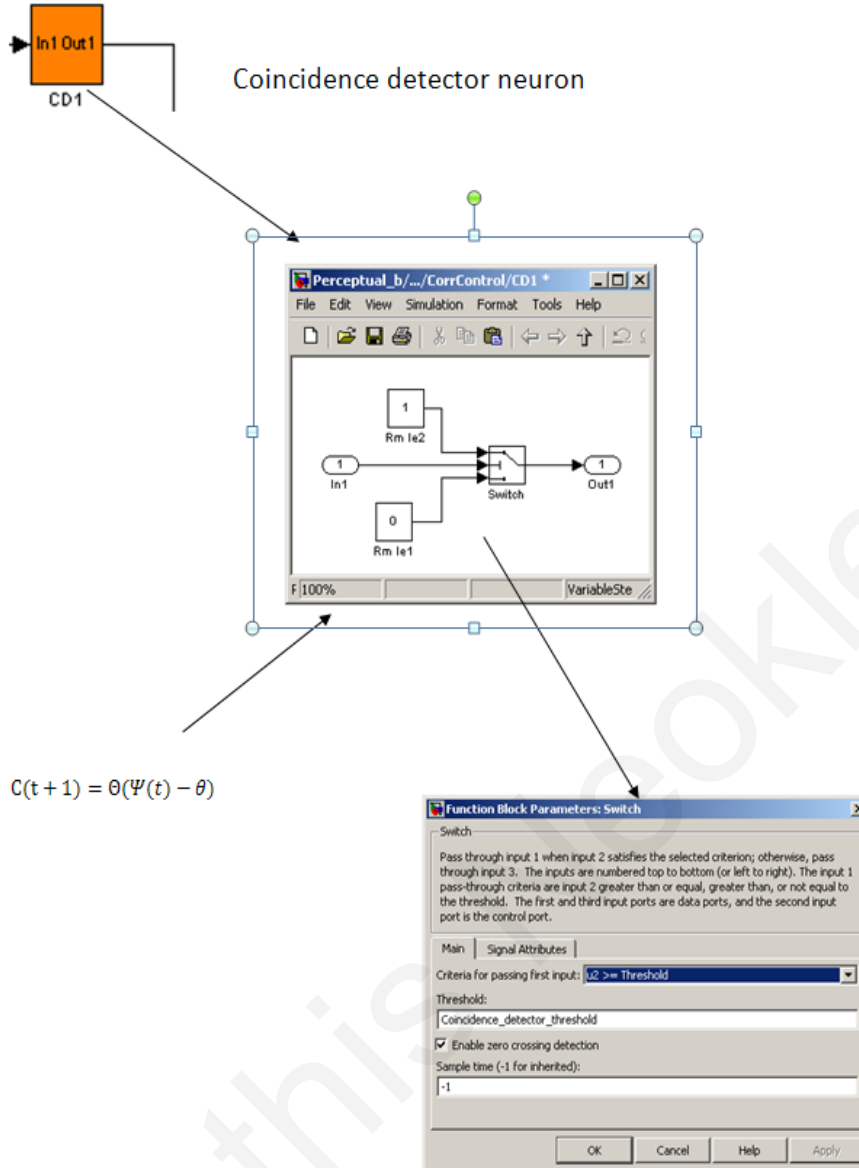


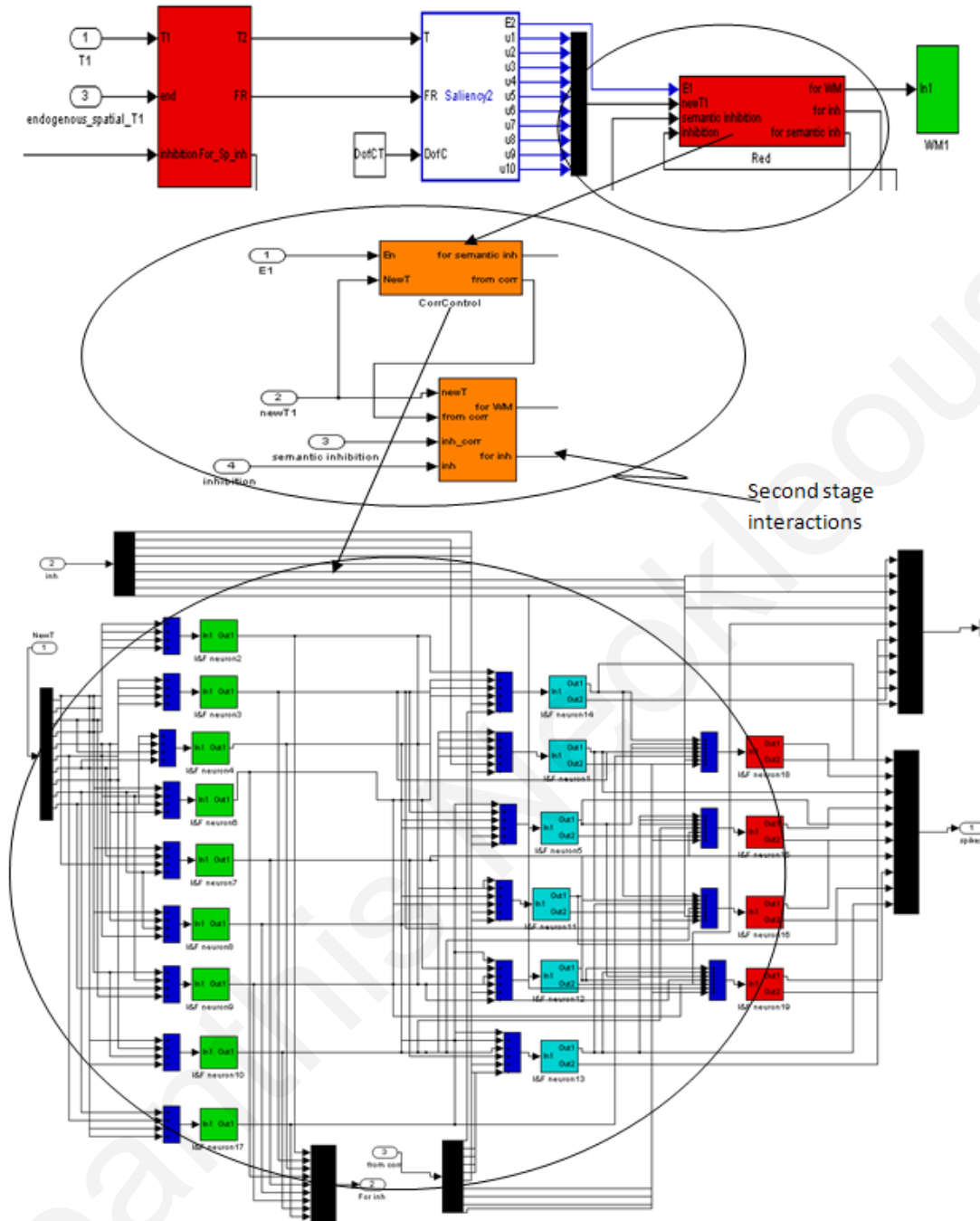
```

Embedded MATLAB Editor - Block: Perceptual_b/Embedded MATLAB Function*
File Edit Text Debug Tools Window Help
[Icons]
1  % Temporal filter algorithm
2  % the filter takes as inputs the incoming spike trains along with their
3  % calculated firing rate and the degree of correlation that corresponds
4  % to the specific stimulus.
5  % The output of the algorithm is a new spike train with the same firing
6  % rate, yet with adjusted the exact spike time appearance.
7
8  function [E2,u1,u2,u3,u4,u5,u6,u7,u8,u9,u10] = Saliency2(T,FR,DofC)
9
10 - u1=T(1,:);u2=T(2,:);u3=T(3,:);u4=T(4,:);u5=T(5,:);
11 - u6=T(6,:);u7=T(7,:);u8=T(8,:);u9=T(9,:);u10=T(10,:);
12
13 - A=rand(1);
14 - B=rand(1);
15
16
17 - if A<FR
18 -     E2=1;
19 - else
20 -     E2=0;
21 - end
22
23 - if B<DofC
24 -     u1= E2;
25 - else
26 -     u1=u1;
27 - end
28
29 - C=rand(1);
30 - if C<DofC
31 -     u2= E2;
32 - else
33 -     u2=u2;
34 - end
35
36 - D=rand(1);
37 - if D<DofC
38 -     u3= E2;

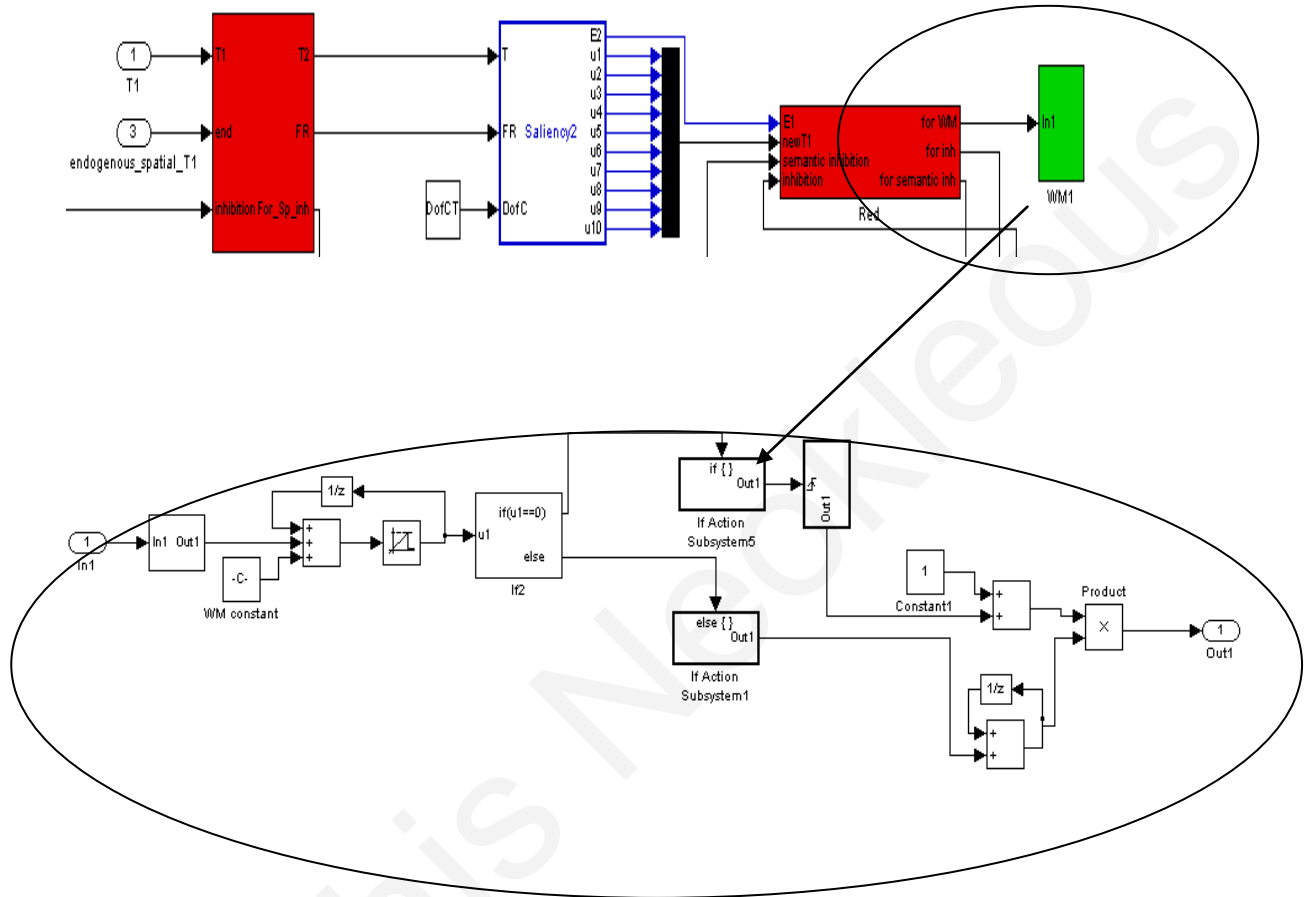
```







A recursive attractor simulating working memory nodes



Appendix C

Undergraduate and graduate theses relevant with this PhD thesis

AΔE/2009/Master thesis by Katia Nicolaidou

Title: An information system for an experimental study on visual selective attention

Abstract

This study is part of a larger project aiming at the neural network computational modeling of visual selective attention. The main goal of this thesis is to exploit experimentally specific aspects of visual selective attention. More specifically the focus of this work is to study how selective attention filter's out the irrelevant information by designing a behavioral experiment similar with the one presented in Lavie (1995), yet with specific variations to investigate deeper the effect of perceptual load in the overall processing. The experimental results are expected to bring some clear conclusions regarding the role of perceptual load in the process of filtering the irrelevant information contained in the distracting flanker and more generally in the visual selective attention. A deeper analysis is presented regarding possible explanations on the experimental results based on computational simulations and a future work linked to this thesis is explained.

AΔE/2010/Master thesis by Christiana Christou

Title: Computational modeling of perceptual load and selective attention

Abstract

A great number of scientists is involved in the understanding of human cognition with the ultimate target to design systems of artificial intelligence. The research is mostly focused on the identification of the primary factors that contribute in the creation of human behavior. Similarly we aim in contributing in this important area of computer science by studying and modeling the functionality of visual selective attention. More specifically, this study is concentrated in the creation of two behavioral experiment that will feed with new data and guiding observations the attempt to implement a neural network model of visual selective attention. Both of the experiments are new modifications of the perceptual load experiment by Lavie (1995) and are a logical progress of the master thesis by Katia Nicolaidou (**AΔE/2009**). The first experiment examines the role of visual saliency in the overall processing while the second experiment concentrates on the effect that a go, no-go instruction before the execution of the main task has on the output results. Visual saliency is examined by manipulating the boldness of the distracting letters in the main task while a go no-go instruction that indicates to the subject whether will proceed and respond to the immediately preceding task or not, examines the working memory interactions.

AΔE/2009/ Bachelor thesis by Evi Procopiou

Title: An information system of auditory and visual attention

Abstract

The main target of this thesis is to present the work done in order to effectively study some important issues that concern auditory and visual attention. In the first chapter a general introduction on human attention is presented and how it can be studied using computational intelligence methodologies and techniques. In the second chapter a literature review on previous studies that examine visual and auditory attention separately and together is presented and in the third chapter explains the experiment that I have programmed and examines this relation under the attentional process. In this chapter I present a detail description of the purpose that this experiment was designed, the results and a possible explanation on how these results were obtained. In the final chapter, I comment on the experimental results and explain how these could be incorporated in a computational model. Furthermore, I analyze some possible ideas on how this work could be effectively linked to new studies.

AΔE/2009/ Bachelor thesis by Athina Mouxouri

Title: An information model of visual attention.

Abstract

To simulate the human responses with an information system is a very important research topic and therefore my goal is to contribute through my experimental results and conclusions in the understanding of the fundamental processes that constitute visual selective attention. More specifically, by studying some reports of important impact in the literature, I understood the way that the human brain interacts according to one or more external stimulations within visual space. Therefore, according to the conclusions and ideas I had on the previous studies I created an experiment to measure the reaction times of a number of subjects based on some specific instructions of the given task. In my experiment, a number of visual stimulations are presented in the computer screen and one of those is the target that the subjects are instructed to respond accordingly while another is a distracting stimulus that shares similar semantics with the target. The main objective is to investigate how the attentional mechanism deals with this conflict and to provide some possible theoretical interpretation on the obtained experimental results. These instructions will be used for guidance in the implementation of a neural network computational model for visual selective attention.

ΔΕ/2010/ Bachelor thesis by Nicoletta Christou

Title: Study of the saliency of stimuli through experimental studies.

Abstract

Modeling the visual attention system using computational algorithms is a very important and interesting subject of study. Through various experimental studies in the past, it is known that during the process in which it is asked to focus attention in one specific target, the observer is influenced also from stimulations that are never being consciously perceived. The purpose of this study is to study through the design and implementation of a behavioral experiment if the saliency of unconscious stimuli is analogous to the interaction they will exert on the processing of a target. The main question that we attempted to address was whether we could increase the effect that unconscious stimuli have in the processing of information by increasing their saliency. Initially several experiments that examine the controversial connection between attention and consciousness have been studied in order to increase my understanding on the subject and to design a different variation task.

In the experiment that I have implemented a sequence of random masking images are presented and in the end a number-target between 1-9 (excluding 5) appears. The participants are asked to respond as fast as possible with the left key if the number was lower than 5 or with the right key if the number was higher than 5. Without knowing however, before the target number appears a prime is presented among the masking distracters for a very short time that does not allow for the human brain to consciously perceive it. Yet, even though that the participants are not aware of the existence of the prime, it can still influence their reaction time. Therefore by manipulating the prime's saliency we can measure the variations in the subject's response.