Citation: Llapashtica, E (2019). Eye Movements & the Integrated Saccade Latency Test. (Unpublished Doctoral thesis, City, University of London)

Eye Movements

&

the Integrated Saccade

Latency Test

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December 2019

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Acknowledgements

Firstly, I would like to express my sincere appreciation to my first supervisor Prof. John Barbur for his continuous support and encouragement throughout this project. This study would not have been possible to produce without his immense knowledge.

I also would like to acknowledge Prof. Kenneth Grattan and Prof. Tong Sun who made possible the collaboration between both departments, helped secure the funding for the project and their continuous support.

My sincere thanks also go to Dr Gary Bargary for helping me to get established with MatLab and the eye-tracker. A further and special thank you also goes to Dr Mathias Fabian who supported me from day one. I simply could not imagine having a better mentor.

I would like to also extend my gratitude to all those who participated in my studies and made it possible to collect the valuable data that form the basis for my thesis.

Last, but not least, I would like to give a big thank you to my family: my husband Bujar for his endless love, support and encouragement. To my two beautiful daughters, Erina and Hana, for filling each day of my life with excitement and to my mother, who provided me with unconditional love throughout my life.

Abstract

A novel visual psychophysical technique has been developed and validated. The technique allowed the development of the 'EMAIL' (Eye Movement and Integrated Latency) test which has been optimised and used extensively in this thesis. This technique allows the measurement of eye movement response latencies and visual processing times, without the use of eye-tracking. The computed value produced by the test - labelled as ISL (Integrated Saccade Latency) - captures the overall time the subject requires to compute and generate an appropriate eye movement response and to process a specific stimulus attribute at the end of each saccade. In addition, the EMAIL test also measures the subject's decision response time (DRT). The latter is largely a measure of the motor response and indicates the time the subject needs to press the appropriate response button. To account for all the parameters that make up the ISL and to validate the EMAIL test as an effective visual psychophysical technique, three studies have been designed and carried out to answer the following questions:

1. Can a psychophysical test designed to measure the overall time subjects need to execute the eye movement and to perform a visual task at the end of each saccade be used as a viable testing procedure to assess saccadic response latencies and visual processing times?
2. Can the EMAIL test capture the known asymmetries that exist between the horizontal and vertical saccadic eye movements through ISLs?
3. Can the EMAIL test capture reliably the effects of aging associated with saccadic eye movements?

In the first study, the eye tracking equipment in conjugation with the EMAIL test, was used to determine the value of each component that makes up the ISL time. The latter also includes the post saccadic visual processing time (VPT). This set up makes it possible to test the hypothesis that VPT, when saccades are involved, are longer than those measured with identical stimuli in the absence of eye movements. The experiments carried out confirm this to be the case. I therefore proposed a second hypothesis to account for the extended VPTs. I hypothesise that the extended VPTs measured in this study can be attributed to instabilities of the eyeball or / and fixation errors. The experimental results confirm my hypothesis by demonstrating clearly that instabilities of the eyeball cause increased VPTs for small saccades as well as fixation errors which also contribute to the increased VPTs, particularly for large saccade amplitudes.

The second study aimed to test the hypothesis that the known vertical versus horizontal directional asymmetries in eye movement responses affect the measured ISL responses. By presenting the visual target along different meridians at specific locations in the visual field, the directional asymmetries in eye movement responses were investigated to test this hypothesis.

The results demonstrate clearly that ISL responses reveal the expected directional asymmetries with saccades along the horizontal meridian being faster than those measured along the vertical meridian.

The last study investigates the effects of age on oculomotor and decision response times. Since brain structures change significantly during both developmental and degenerative stages and such changes have been shown to translate into behavioural responses, it is reasonable to test the hypothesis that both ISL and in particular DRT, are also affected by age. The experimental findings show that the EMAIL test captures reliably the expected changes in both oculomotor and decision response times.
The results of the last study show that both ISL and DRT times increase non-linearly with age, a finding consistent with earlier reports from eye-movement and reaction time studies.

Glossary

4AFC Four alternative forced choice procedure
ADHD Attention deficit hyperactivity disorder
CEF Putative cingulate eye field
dlPFC Dorsolateral prefrontal cortex
DLPN Dorsolateral pontine nucleus NRTP -
DPI Dual Purkinje Image
DRT Decision response time
DV Cerebral dorsal vermis
EEG Electroencephalography
EOG Electrooculography
FEF Frontal eye field
ISL Integrated saccade latency
K-pathway Koniocellular cells
LGN Lateral Geniculate Nucleus
M-pathway Magnocellular cells
MST Medial superior temporal area
MT Middle temporal area (MT) which is also known as visual area V5
NRTP Nucleus reticularis tegmenti pontis
OPN Omnipause neurons
PEF Parietal eye field
P-pathway Parvocellular cells
PPRF Paramedian pontine reticular formation
PSO Post-saccadic oscillations
VPT Visual processing time
riMLF Medial longitudinal fasciculus
RT Reaction time
SC Superior Colliculus
SEF Supplementary eye field
SNr Pars reticulata reticular formation
STD Stimulus duration time
T0 Measurement variable δT
T1 Latency
T2 Saccade duration
T3 Post-saccadic visual integration time
V1 Striate cortex also known as visual cortex
δT Measurement variable of EMAIL test

1 Introduction and Literature Review

This chapter outlines the background literature related to studies presented in this thesis. First, the general background into the ways in which the brain processes visual information is given, followed by emphasis on saccadic eye movements including paradigms that are widely used to generate them under controlled conditions. The influence of physical properties of stimulus in saccade parameters and their effect particularly on its latency are also described. Finally, the brain mechanisms involved in saccade generation are outlined.

1.1 Processing of Visual Information

Since 1962 when David Hubel and Torsten Wiesel described in detail the response properties of neurons in the primary visual cortex, we have gained great understanding into the ways in which the brain processes incoming visual signals and transforms this information to inform our perception and behaviour. From studying how the retina organises visual information and how its neurons respond to spatial, temporal and spectral modulations in the retinal image, we gained significant insights into the processing of visual information in human vision. The first step of seeing begins in the retina where the photoreceptors, rods and cones convert the spatial modulations of intensity and spectral content in the retinal image into electrical signals that can then be used to code the information contained in the retinal image as needed for efficient transfer to the primary visual cortex. The visual information processing also begins in the retina, where neurons at each stage of the processing within the retina act as filters to compress the information by extracting key features such as colour, contrast and movement (Nassi and Callaway 2009). Compression of visual information is required due to limited number of axons in the optic nerve. While within the photoreceptor layer of the human retina there are approximately 5 million cones and 100 million rods that translate light into neuronal signal, there are only just over ~1 million axons of retinal ganglion cells that form the optic nerve in each eye, which connects the eye to the brain (Reichenbach and Bringmann 2013; Nassi and Callaway 2009). There is great regularity in the way axons distribute themselves.

As the axons leave the eye through optic nerve, the two optic nerves meet at the optic chiasma. There, the axons from ganglion cells of the nasal half of the retina cross at the optic chiasma where they join with axons from ganglion cells of the temporal half of the retina in the contralateral eye, before terminating in different visual areas (Figure 1). Each early-stage visual centre has a different role in visual processing and receives inputs from different types of ganglion cells (Wässle 2004). These include: Lateral Geniculate Nucleus - LGN (image forming pathways), Superior Colliculus - SC (plays a critical role in the neural control of saccadic eye movements - rapid shifts in eye position that redirect the fovea toward objects of interest so that they can be seen clearly), suprachiasmatic nucleus in hypothalamus (regulates circadian rhythm), and pretectum (adjusts the pupil size) (Reichenbach and Bringmann 2013).

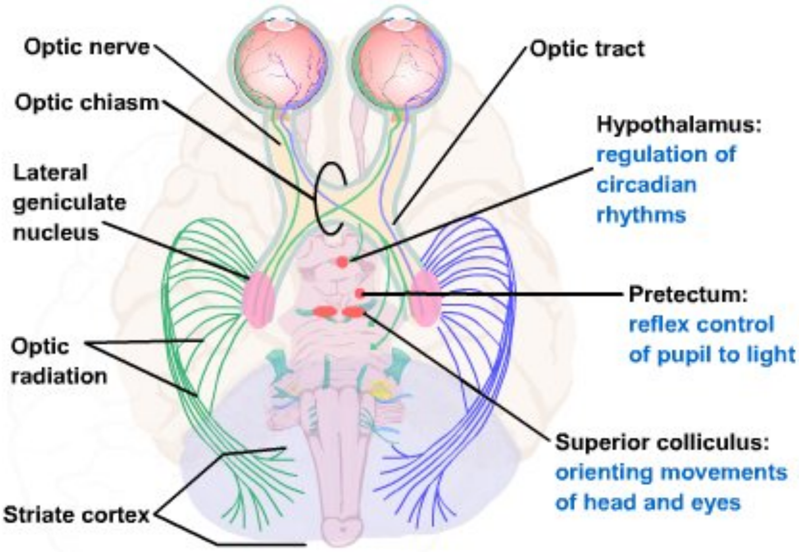


Figure 1. The visual pathway. The axons from the right half of the right retina terminate in LGN on the same side (right) and the axons from the right half of the left retina cross at the optic chiasm and terminate at the right LGN. It has been estimated that approximately 10% (V. H. Perry, A. Cowey, 1984) of the axons leave the optic tract and make connections with SC. (https://nba.uth.tmc.edu/neuroscience/m/s2/images/html5/s2_15_2.jpg)

The axons do not project directly to the striate cortex (V1), instead they are relayed to the cortex by neurons in the LGN through the optic radiation (Figure 1), known as the retina–geniculate–striate pathway. This pathway is retinotopically organised (Hubel 1995) to preserve the spatial arrangement of the visual image. Within this pathway, there are relatively independent streams.

In the primate retina, although there are at least 17 different types of ganglion cells, from those only three types are well characterised (Nassi and Callaway 2009) and form the three distinct pathways that are known as P (Parvocellular), M (Magnocellular) and K (Koniocellular). Each pathway is representative of a distinct population of ganglion cells. Midget ganglion cells are considered to be the origin of the P-pathway, and account for approximately 80% of the total population of cells that project to the LGN (Perry, Oehler, and Cowey 1984). These cells have small (ON-OFF) receptive fields, low contrast sensitivity and respond to changes in colour (Reichenbach and Bringmann 2013), whereas parasol ganglion cells are considered to be the origin of the M-pathway and account for 10% of the total population of cells that project to the LGN (Perry, Oehler, and Cowey 1984). These cells have large receptive fields, high contrast sensitivity and are responsible for orientation and movement detection (Perry, Oehler, and Cowey 1984; Nassi and Callaway 2009; Reichenbach and Bringmann 2013). Small and large bistratified ganglion cells are considered to be the origin of K-pathway and they account for approximately of 8% of the total population of cells that project to the LGN (Nassi and Callaway 2009; Reichenbach and Bringmann 2013). Bistratified ganglion cells have very large receptive fields, high contrast sensitivity and receive S-cone inputs also known as blue cones. The S-cones are responsive to short wavelengths between 380 and 500nm (Reichenbach and Bringmann, 2013; Nassi and Callaway, 2009).

Another interesting feature of the retina–geniculate–striate pathway is that visual space is not represented equally within the V1 (Hubel 1995).

The visual systems' spatial resolution varies systematically across the visual field because it is constrained by both spacing and the dendritic field size of the cells. Only the cells with high density and small dendritic fields (midget cells) can mediate high visual acuity (Reichenbach and Bringmann 2013).

It is well known that the very central region of the retina, called foveola, has only cone photoreceptors and no rods (Osterburg 1935). The spatial density of cones is very high in the fovea and decreases rapidly with eccentricity while the rod density peaks between 10° and 20° peripheral to the fovea (Osterburg 1935). Also, in central fovea the convergence from cones to ganglion cells is small (only 1 to 3, for which three midget ganglion cells are connected through three midget bipolar cells to one cone) while the convergence from rods to ganglion cells is much higher (Reichenbach and Bringmann 2013). This small convergence from cone to ganglion cells crates the basis for high spatial resolution that fovea provides. As the convergence of the photoreceptor cells to ganglion cells increases outside the fovea and the cone density decreases, so does the visual acuity.

Because the projection of visual signals to V1 maintains the topographic information, there is a much higher number of V1 cells that process visual signals from the fovea (Kiley, C. W., & Usrey 2016; Hubel 1995). As a result, the area in V1 dedicated to the fovea is very large when compared to the remaining visual field. Therefore, visual acuity decreases with increasing eccentricity.

The visual pathways (P, M and K) that began on the retina to LGN converge significantly within layers of V1. From there, two new segregated, but interacting, parallel pathways of information flow emerge: known as dorsal and ventral pathways (Mishkin, Ungerleider, and Macko 1983). The Ventral pathway (also known as the "what" stream) projecting from V1 to ventro-temporal regions is responsible for object recognition, whereas the dorsal pathway (also known as the "where" stream) projecting to the posterior parietal cortex is responsible for spatial information (Mishkin, Ungerleider, and Macko 1983; Milner and Goodale 2008; Goodale and Milner 1992). The over-representation of foveal vision is also seen in ventral stream. Ventral stream is associated with P-pathway and this comes as no surprise, since the role of the ventral stream is to construct detailed representation of our world, while the dorsal stream is associated with M-pathway. The representation of visual field is broader in this stream and the peripheral vision is well represented (Milner and Goodale 2008; Goodale and Milner 1992). In addition, Goodale and Milner defined these two streams not just by the kind of information they each process, but how this information is used. According to their interpretation, within the ventral stream the information is transformed to construct percept of the world through object recognition (vision-for-perception), whereas the dorsal stream processes visual information to guide our actions (vision-for-action).

Most of our perceptual experience is confined to central vision, therefore we continuously shift our gaze by generating saccadic eye movements, so that the very central foveal region fovea forms the point of regard.

The eye movements are a fundamental feature of vision. Our eyes move continuously even during the fixational pauses when the visual information is being taken in and integrated, to overcome the loss of vision due to constant stimulation of the retinal receptors (i.e. adaptation). It is well established that the cells' receptive fields respond vigorously only during changes to visual input, but rapidly lose their responses when the input is constant (Troncoso, Macknik, and Martinez-Conde 2008; Martinez-Conde, Macknik, and Hubel 2004; Martinez-Conde et al. 2009). As stated by Troncoso, X. G, 2008: “Our visual system has a built-in paradox: we must fixate our gaze in order to inspect the minute details of the world, yet if our eyes were perfectly still, all stationary objects would fade from view.” Thus, our natural vision is governed by a repertoire of gaze-shifting eye movements that guide our actions and behaviour. The next section examines different types of eye movements and their pivotal role in our everyday behaviour.

1.2 Eye Movements

The eye lies cushioned in fat in the bony orbit that is held in place by the six muscles that move it in any direction. Four of these muscles are the rectus muscles (the medial, lateral, superior and inferior), while the other two are labelled as the superior and the inferior oblique muscles.

These muscles are arranged in three opponent pairs, where the medial and lateral rectus move the eyes along the horizontal direction, the superior and inferior rectus control the up and down directions, and the superior and inferior oblique participate in torsion (Schiller and Tehovnik 2005). While these muscles can rotate the eye in any direction, the motor neurons that innervate the extraocular muscles are found in III (oculomotor), IV (trochlear) and VI (abducens) cranial nerve nuclei (Sparks 2002). These motor neurons are responsible not just for generating saccades, but for all types of eye movements (Ramat et al. 2007)

Before the eye starts to move, it must overcome the constrains imposed by orbital supporting tissues, such as viscous drag (due to connective tissues) and elastic restoring forces (due to muscle). For example, to produce rapid eye movements such as saccades, motoneurons must produce a burst of neural activity in ocular motor nuclei to overcome the viscous drag. In addition, as the eye reaches its new position at the end of the saccade, the eye must be held there against elastic restoring forces. This is achieved by sustained motoneuron firing that produces a steady contraction of extraocular muscles. These two components are known as pulse and step of innervation, where the pulse of innervation is produced to overcome the viscous drag of orbital tissues, whereas the step component is produced to overcome the elasticity of the orbital tissues (Ramat et al. 2007)

The tissues supporting the eyeball impose mechanical constraints on all types of eye movement, since all require pulse and step components (Robinson 1964; Optican 2010). Stabilising and aligning the retina with moving or stationary targets is essential for clear vision. As a result, humans have developed two main types of eye movements, one for gaze stabilisation and one for gaze shifting (Zee 1999).

1.2.1 Gaze Stabilisation System

As we move around our environment, we generate eye movements that counteract the effects that the head movements have on our vision. Without these eye movements, our ability to recognise and localise the objects of interest will be impaired, because each head movement will cause the retinal image to slip, resulting in blurred vision. Thus, the role of our gaze stabilisation system is to overcome the image blur by producing eye movements that compensate for self-motion caused by head movements (Hikosaka, Takikawa, and Kawagoe 2000). The gaze stabilisation mechanism is divided in to two categories: vestibular and optokinetic systems.

The vestibular system depends on the semicircular canal to calculate the rate at which the head is rotating (Kemp and Kirk 2014), whereas the optokinetic system gets its information from the photoreceptors, to calculate the speed and the direction at which the visual world moves across the retina (Zee 1999).

1.2.2 Gaze Shifting System

With the evolution of the primate fovea, it was necessary for the gaze shifting mechanism to evolve, so that when the new object of interest appears in the periphery, the fovea could be directed towards it.

The gaze shifting system can be divided into two main categories: the saccadic system that shifts the line of gaze from one point to another, and the smooth pursuit system that allows the fovea to follow a target as it moves across a stationary background.

While the smooth pursuit system is believed to have evolved from the optokinetic system, the saccadic system is thought to have evolved from behavioural mechanisms shared by both the optokinetic and vestibulo ocular systems (Hikosaka, Takikawa, and Kawagoe 2000).

With the development of frontal vision and binocularity, it became necessary to be able to point the fovea of both eyes simultaneously to one object of interest. When the eyes focus on an infinitely distant object, the lines of gaze projecting from the two foveas are parallel. However, as the object moves closer the lines of gaze converge. Consequently, each eye rotates in the opposite direction (disconjugates). Thus, vergence (disconjugate) movements move the eyes in opposite directions as we point the fovea of both eyes on a near object. While each of these systems have distinct neural entity they all share a common set of motor neurons and therefore share a common set of muscles.

In the next section, I will discuss the development stages of pursuit, fixation and saccadic systems.

1.2.3 The Pursuit System

The pursuit system is different from the saccadic system. Pursuit involves slow eye movements as well as compensatory saccadic movements, to achieve the speed of a moving target in order to keep the moving target on the fovea. While saccadic mechanisms are present since infancy, the smooth pursuit system it is not fully developed and continuously improves throughout childhood and may not reach maturity until adulthood (Luna, Velanova and Geier 2008). Cognitive processes such as attention, selection, learning and prediction exert a strong influence on the way the information is used to control the smooth pursuit eye movements (Barnes 2008). The pursuit accuracy is accomplished as the brain learns to monitor and generate predictive smooth pursuit movements to match the speed of the moving target. There is a wide brain circuitry involved in the pursuit system. These include a number of components, e.g. cerebellar dorsal vermis (DV), caudal fastigial nucleus, medial superior temporal area (MST), frontal eye field (FEF), supplementary eye field (SEF), dorsolateral pontine nucleus (DLPN), nucleus reticularis tegmenti pontis (NRTP) and middle temporal area (MT), which is also known as visual area V5 (Newsome, Wurtz, and Komatsu 1988). The formation of the mature pursuit system is believed to reflect the functional integration of this wide circuitry which continues to improve through adolescence (Ego et al. 2013).

1.2.4 The Fixational System

There are three different types of eye movements that occur during the fixation: tremor, drifts and microsaccades. Together, these eye movements help us keep the object of interest in the fovea, but also induce firing of neural responses to prevent visual fading, so that we are able to retain our vision during the fixation.

To be able to see the stationary object, the image must be held steadily on the fovea. The fixational eye movements not only keep the stationary object on the fovea, but also prevent visual fading and enhance visual perception (Troncoso, Macknik, and Martinez-Conde 2008; Susana Martinez-Conde et al. 2009; S Martinez-Conde, Macknik, and Hubel 2004).

Fading of vision occurs because the visual system habituates its responses to unchanging stimuli, therefore the fixational movements are necessary to prevent the loss of vision due to uniform stimulation of the photoreceptors (Martinez-Conde, Macknik, and Hubel 2004). The fixational eye movements enhance our visual perception by improving the discrimination of high spatial frequency stimuli. In addition, they also aid our vision when viewing natural scenes by sampling visual information by means of these movements (Rucci et al. 2007). Additionally, fixational eye movements play an important role in both maintaining focused attention and inhibiting inappropriate eye movements (Luna, Velanova and Geier 2008).

Although the ability to fixate is present in early life, our ability to hold the gaze steady is not well developed, and is acquired in the first few months of life (Luna, Velanova and Geier 2008). Fixation behaviour changes with time, in particular fixation stability continues to improve, with our ability to maintain the fixation (fixation duration) increases between the ages of 4–15 years-old (Aring et al. 2007), whereas our ability to inhibit inappropriate eye movements improves with age. Developmental limitations of visual fixations are due to higher order cognitive control processes and parallel the maturation of the brain system that continue to mature even during adolescence (Luna et al. 2004; Luna, Velanova and Geier 2008).

1.2.1 Saccadic System

Saccades are gaze shifting eye movements that are made to place the peripheral objects of interest in the foveal region. Saccades are key to our visual interaction with the world, because they move the high-resolution fovea from one part of the visual scene to the next, in order to direct fovea in succession towards the regions of interest within the visual field.

The saccadic system uses visual, somatosensory and auditory information to generate the eye movements that are necessary to direct the point of regard towards the peripheral target. Under natural viewing, we humans make several saccades per second. Our natural environment consists mainly of stationary targets and we generate a series of successive saccades to pursue them.

Each saccade is followed by fixation. It is during these fixational pauses that we acquire detailed spatial information. However, also during these fixational pauses we prepare and select the spatial location for the next fixation point using information gathered from our peripheral vision.

The sequence of the eye movements is not random, instead it depends largely on the nature of the observer’s task (Yarbus 1967). It is the ‘top-down’ control that allows the eyes to be directed to locations that are task relevant despite of their visual saliency (Hutton 2008). However, when a sudden visual target appears in the visual field, the eyes will move to that location regardless of the task being carried out.

In such cases, the afferent signal is sufficiently strong to overcome top-down modulations and goal-directed saccades become involuntary and the norm. Thus, the generation of saccades can involve different mechanisms to serve different functions. Saccades can be used to search for objects in the visual field, they can be triggered by the sudden appearance of new targets in the visual periphery, and they can also be influenced by other information such as the anticipated or remembered location of a visual target.

Trajectories of normal saccadic eye movements are remarkably stereotyped (Bahill, Clark, and Stark 1975). For a wide range of eccentricities saccade duration increases linearly with saccade amplitude, while peak velocity vs amplitude produces a nonlinear relationship (Bahill, Clark, and Stark 1975). In literature, the relationship between the saccadic peak velocity or duration as a function of amplitude is referred to as the main sequence.

Under controlled conditions, one can measure easily the mechanisms of saccade generation by precisely controlling the timing and location of the target that initiates the saccade. Figure 2 shows a typical saccadic eye movement trace recorded under laboratory conditions.

In addition, by manipulating the way the target is presented, one can create conditions that evoke different types of saccades, similar to those that occur under natural viewing.

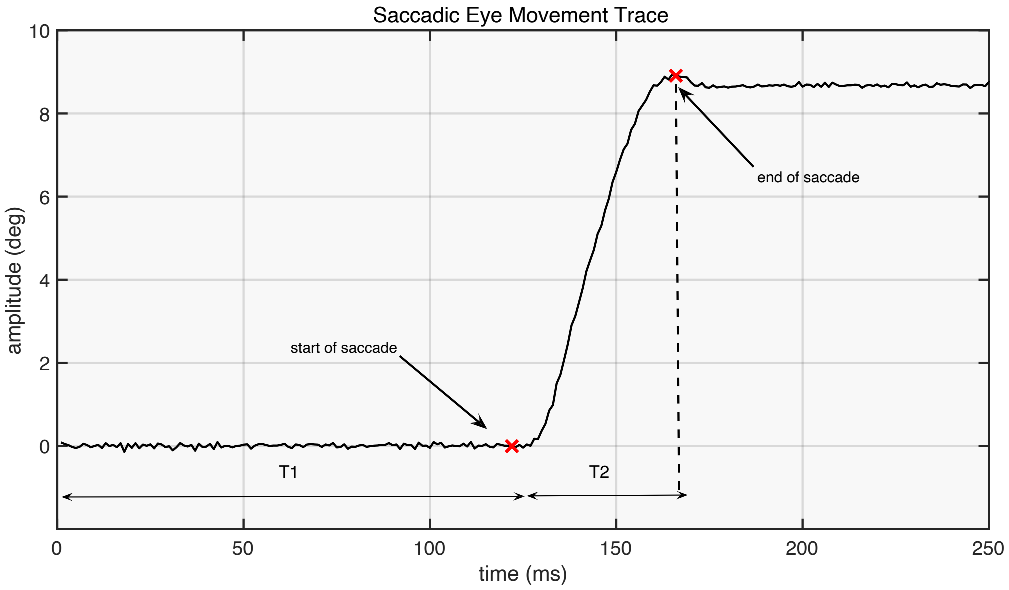


Figure 2. Saccadic eye movement trace of a single rightward saccade of approximately 9degree amplitude as recorded with EyeLink1000. Both, the start and end of saccade are indicated by red cross. T1 represents saccadic latency while T2 represents its duration.

It is well established that the saccade latency is strongly influenced by the physical properties of the stimulus; its size, direction of movement, luminance contrast, eccentricity, the presence of distractors, etc. (Walker et al. 1997; Bell, Everling, and

Munoz 2000; Bell et al. 2006; Kowler et al. 1995). These parameters can have a significant effect on the time course of saccades. Besides, saccade latencies show variations even under the conditions where task requirements are kept constant due to both within and inter-subject variability.

The nature of the task, arousal state and the age of the subject also effect saccade latencies (Corbetta and Shulman 2002; Munoz et al. 1998a; Walker et al. 1997; Fischer and Weber 1998).

The measurements of saccade latencies have attracted lots of attention in various fields, beyond the control of eye movement, because saccade latencies can reflect cognitive processes that take place during the decision to generate the saccade. Usually, saccades that occur automatically in response to the sudden appearance of a new visual stimulus require minimal cognitive control (Luna, Velanova and Geier 2008; Hutton 2008), and are called reflexive saccades (also known as reactive, prosaccades or targeting saccades). Whereas the saccades that are initiated on the basis of internal goals – such as during visual search, from memory, or as part of learned motor behaviour – are called voluntary saccades. Voluntary saccades are more complex and require higher level processes such as the ability to voluntarily suppress reflexive/automatic responses, in order to make a planned response (response inhibition), working memory (the ability to retain and manipulate information on-line in order to make a plan to direct a response), and attention switching (the ability to change attentional focus in a controlled fashion) (Miyake et al. 2000; Gaymard et al. 1998; Krauzlis 2005).

There are a number of different paradigms that have been designed to measure saccadic responses and each paradigm reflects different underlying mechanisms of saccade generation. In particular, the latencies (saccadic reaction times), are of interest because they reflect the time the brain takes to prepare a response, which must involve decision mechanisms. It is therefore not surprising that latency values are sensitive to different experimental paradigms. Moreover, the latency values also show variation from trial to trial, even if exactly the same experimental conditions are maintained.

When we explore our environment, we rely on two types of saccadic control: reflexive and voluntary. Different paradigms that are widely used to test different aspects of saccadic control are described below.

1.2.1.1 Reflexive Saccades

Sudden appearance of a visual target will trigger a saccade. Under laboratory conditions, one can measure reflexive saccades by instructing a subject to look at central fixation and generate a saccade towards a sudden onset of a peripheral target as quickly as possible. This condition generates reflexive saccades because of an unexpected change in the peripheral sensory environment. Reflexive saccades provide the means to assess sensorimotor aspects of eye movement systems since they are thought to exert minimal cognitive control (Luna, Velanova and Geier 2008; Hutton 2008). Normal subjects usually generate saccades within 180ms - 200ms. Distribution of saccadic latencies are not normal, instead they are skewed with more saccades having longer latencies (R. Carpenter 1981). There are three different experimental paradigms that are used widely to measure reflexive saccades (visually-guided saccades, pro-saccades) and are known as step, gap and overlap.

These three paradigms are distinguishable by the way they vary with the onset of the peripheral target. It is well established that the temporal relationship between the offset of central fixation and the onset of peripheral target also influences the saccade latency (Saslow 1967).

When the central fixation point is turned off at the same time as the onset of the peripheral target, a step response is generated. This paradigm creates the perception that the single stimulus is stepping from one point to another. While, during gap paradigm the fixation point is turned off just before the onset of peripheral target, whereas for overlap paradigm the fixation point remains on after the target onset. The overlap paradigm resembles the usual occurrence of new visual stimuli appearing in the visual periphery under natural viewing.

It is well established that saccadic latencies are shorter during gap when compared to overlap trials as reported in several studies (Saslow 1967; Gómez et al. 1996; Rohrer and Sparks 1993; Forbes and Klein 1996; Fischer, Gezeck, and Hartnegg 1997).

Different interpretations have been proposed to explain this reduction of saccade latencies in gap paradigm, however, the general agreement is that when the fixation point is present, the fixation system is activated and will suppress the saccades (Dorris and Munoz 1995). Whereas, when the fixation point is removed, the activity of fixation (omnipause) neurons will be decreased and the saccade-related neurons will show phasic target related responses. This phasic response of saccadic (burst) neurons provides evidence that there is an advance in motor preparation (Fischer and Weber 1998; Fischer, Biscaldi and Gezeck 1997; Forbes and Klein 1996). In addition, the removal of the fixation point is thought to act as a warning/readiness signal that is produced by advanced motor preparation.

Gap paradigm can produce saccades with very short latencies and their distribution is bimodal (distribution which produces two peaks i.e. two modes). These saccades are called express saccades and have very short latencies ~ 80ms –100ms. Besides, the express saccades are not exclusive to gap paradigm, they are also found to be triggered in overlap conditions (Fischer and Weber 1998). In our laboratory, we do measure consistently very short latencies with range 90ms–120ms during overlap paradigm. However, their distributions do not show bimodality (two peaks). This being the case, the express saccades deserve greater interest because a proper understanding of the distributed nature of pre-saccadic activities would provide us with an insight of how the cerebral cortex is able to register a transient cue, prepare sensory processing centres, and prepare the sub-cortical nuclei to enable the rapid response in such a short time.

1.2.1.2 Express Saccades

Express saccades are considered to be reflex-like orienting movements (Fischer and Weber 1998), mediated through the retino-cortical-tectal pathway. In monkeys, express saccades can be generated with lesions of frontal lobes, but not after lesions of the superior colliculus (Schiller, Sandell, and Maunsell 1987). In addition, a more recent finding from Hamm (2010), where an investigation of the gap effect on 15 human subjects using dense-array of electroencephalography (EEG), revealed that express saccade-related preparatory activities are only parietal, not frontal cortices. They found that at 80ms–110ms into gap period superior parietal cortex activity increased on trials preceding express saccades but not regular saccades (Hamm et al. 2010). This finding also confirms why in primates express saccades are eliminated with lesions of SC, but not with lesions of frontal lobe. It is still not clear that express saccades are a frequent occurrence during primate behaviour in the natural world, however children are found to make more express saccades than adults (Klein and Foerster 2001). It has been suggested that the express saccades are a laboratory phenomenon and may reflect preparatory processes that occur only under specific and artificial conditions. Carpenter (2001) suggested that this might be the result of the oculomotor system predicting target direction. As such, the saccades made towards the expected direction have shorter latency and the bimodality found in their distribution is not simply the result of a randomising process within the oculomotor system. Instead, it is a consequence of the way in which saccadic experiments are normally conducted (Carpenter 2001).

Furthermore, the express saccades are not evident during all gap trials, and unlike the gap effect (produces shorter latencies), their appearance seems to be highly dependent upon previous training (Fischer, Boch, and Ramsperger 1984; Rohrer and Sparks 1993; Dorris and Munoz 1995; Raquel and Edelman 2009). However, the proposition that the express saccades are produced due to prior knowledge about target location or upon predictability of the time of the target appearance due to learning effect was brought into question and instead hypothesis that the express saccades occur because of an early decision to generate saccades gained support (Rohrer and Sparks 1993). In addition, removal of a fixation point creates a temporal window, during which the active visual fixation system is disengaged and any visual target presented during the gap period will be acquired at faster rate and will influence the generation of express saccades (Dorris and Munoz 1995).

Neurophysiological studies of visual areas have shown that the physical properties of the stimulus (contrast, eccentricity, luminance etc.), have a strong influence on the response strength e.g. higher contrast stimuli will evoke neural activity with shorter onset times (Barbur, Wolf, and Lennie 1998).

Under laboratory conditions, visually-guided saccades are usually evoked in response to the appearance of an isolated target in the visual scene. Thus, the detectability of the target strongly depends on the physical properties of the stimulus. The studies on neural mechanisms underlying saccade generation in SC have provided a direct link between modulation in initial visual activity and saccadic reaction times (Bell et al. 2006). To address this issue, neural activities in the intermediate layers of the SC were measured, while monkeys generated saccades towards high and low-intensity visual stimuli during gap and delay paradigm (Bell et al. 2006). Findings in their study confirmed that earlier generation of saccades is attributable to reduced onset latency of visual responses in intermediate layers of SC caused by high-intensity visual stimulus. Moreover, because their study investigated the changes in neural activity to stimulus intensity and relation to saccadic reaction time, they found that stimulus intensity does not directly influence the motor processing stages. Instead, the shorter latency times observed for high-intensity visual stimulus correspond to reduced processing times along the visual pathway (higher intensity stimuli will evoke neural activity with shorter onset times). This observation leads to the interesting question of whether low-intensity stimuli are also capable of eliciting express saccades. Whereas, the distribution from high-intensity stimulus from both tasks (gap and delay) in their study produced bimodal distribution (distribution which has two peaks), this was not the case for low-intensity stimulus distribution. This absence of bimodality for low-intensity stimulus lead to neurophysiological approach that unveiled the evidence of some express saccades being produced during the low-intensity stimuli trials as well. Thus, the method which relies only on latency distribution is limited approach because does not reveal the occurrence of express saccades during the trails where the variability is higher due to the low intensity of visual stimulus and the distribution does not produce two distinct modes. This finding motivated the idea of questioning if express saccades can be considered as an independent saccade type at all.

As the ideas further developed, it became clear that the integration of both preparatory and visual signals within superior colliculus (SC) alter the pattern of subsequent saccades (Dorris, Olivier, and Munoz 2007). When visually-guided saccades are triggered, high-frequency bursts of action potentials related to visual target appearance and saccade onset can be observed as temporally separate events. Whereas, during express saccades these visual and motor responses merge together to produce a single higher frequency burst. Marino and colleagues (2015) confirmed the findings of Bell et al. (2006) that the likelihood of producing saccades are dependent on the physical properties of stimulus. In their study, they employed the gap paradigm to examine how target luminance levels affected timing and magnitude of visual responses within the SC. They found direct correlation between visual responses and build-up activity in intermediate layers of SC where both modulations in visual responses and build-up activity combined to influence express saccades and demonstrated clearly that express saccades occur toward both low-level and high-level luminance targets. In agreement with the previous study from Bell et al (2006), they too suggested that express saccades do not require presence of a bimodal distribution, since for low luminance/intensity stimulus bimodality that is normally observed in express saccades merges into a single mode. In addition, their study emphasised that express saccades can only be accurately dissociated from regular saccades when the exact timing of the visual response in the intermediate layers of SC is known. Thus, express saccades can be distinguishable from regular saccades only by investigating the neural mechanisms underlying the saccade generation.

Both studies discussed above have highlighted the effects that physical properties of stimulus have on the neural mechanisms underlying express saccade generation.

Also, have clearly demonstrated that bimodality is only evident during trials using high intensity/luminance visual stimulus while during low intensity stimulus, there will be an overlap of both sensory and motor-related discharges due to signal delay along the visual pathway that will hinder express saccades from regular ones. If express saccades can only be accurately dissociated from regular saccades when the exact timing of the visual responses in the intermediate layers of SC is known (because behaviourally they cannot be distinguished from regular saccades), then this leads to the question of whether express saccades are any different from reflexive saccades at all, or are they a consequence of the way in which saccadic experiments are normally conducted under laboratory conditions? Both express and reflexive saccades are controlled by parietal areas. Electroencephalography (EEG) recordings in human subjects have revealed that express saccade-related preparatory activities are only parietal, not frontal cortices. For reflexive saccades too, the cortical areas involved are only parietal. The parietal lobe integrates visuospatial information to generate a motor signal that is sent to the superior colliculus by a direct parieto-tectal pathway (Gaymard et al. 1998). Moreover, studies of patients with discrete cortical lesions have revealed that after lesions of FEF, reflexive saccades are only slightly affected, whereas after lesions of PEF, all contralateral reflexive saccades (i.e. saccades directed away from the lesion side) become inaccurate. If we consider regular reflexive saccades and their latency distribution, we find that individual latency values for a number of trails are not normally distributed, but are skewed with more saccades having higher latencies. Perhaps, the bimodality observed during some trials reflects the normal variability of latency distribution itself during reflexive saccades, by which a sudden appearance of the target will be directly transformed into saccadic motor command to move the eye towards it.

Express saccades are almost never observed during natural viewing, however they are seen in children. The fact that the express saccades are seen in children and cognitive processes that support visually-guided saccades continue to improve through developmental stages, give indication that express saccades are the primitive form of visually-guided saccades. They are the fastest and most direct sensory-to-motor transformation in the visual system. That being said, the extent to which they can be considered an independent saccade type remains debatable.

The studies discussed within this section have provided a good insight into the reflexive behaviour of the saccadic system. In the next section the range of behaviours that characterise voluntary saccades will be outlined.

1.2.1.3 Voluntary Saccades

Voluntary saccades are more complex and require higher-level processes, such as the ability to voluntarily suppress reflexive/automatic responses in order to make a planned response. They provide means to study the cognitive control of behaviour.

There are several paradigms that are used to investigate voluntary saccades. These include memory guided, delay and antisaccade paradigms.

In memory tasks, a visual target is presented in the periphery, and instead of looking toward the target, subjects hold central fixation and look toward the cued location only after the fixation is turned off. After the saccade is executed, the target is re-illuminated. Responses in this task are volitional, and provide means to investigate the ability to maintain a spatial location in mind over extended periods of time (Gaymard et al. 1998). Delay task is very similar to memory task. The difference between the two is that during delay task, the target remains visible but the subjects are instructed to maintain the fixation until the go signal is given. This task creates a condition to inhibit reflexive saccades. The antisaccade task also provides a measure of behavioural inhibition. In this task, subjects are instructed to look immediately away from, rather than toward, suddenly appearing visual targets.

Latencies of voluntary saccades are longer when compared to reflexive saccades. This is because voluntary saccades are more complex and require higher-level processes such as the ability to voluntarily suppress reflexive/automatic responses, in order to make a planned response (response inhibition), as well as working memory, the ability to retain and manipulate information on-line in order to make a plan to direct a response. In addition, the reflexive and voluntary saccades involve the activity of neurons in different cortical areas, of which parietal areas are considered to be more important for reflexive, and frontal areas for voluntary saccades (Müri and Nyffeler 2008; Gaymard et al. 1998; McDowell et al. 2008).

In summary, voluntary saccades are more intricate than reflexive saccades, their initiation requires involvement of wider cortical areas including the ability to be able to inhibit reflexive responses. In the next section, cortical areas involved in saccade generation are described.

1.3 Cortical Control of Saccades

The saccadic system has been extensively studied and a number of cortical areas – known as cortical eye fields – have been identified that are involved in the control of saccades. These include: parietal eye field (PEF), frontal eye field (FEF), supplementary eye field (SEF), putative cingulate eye field (CEF) and dorsolateral prefrontal cortex (dlPFC), (Pierrot-Deseilligny, Milea, and Müri 2004; Gaymard et al.

1998; Müri and Nyffeler 2008). Depending on the behavioural context in which the saccade is triggered, the brain recruits different cortical areas within this network (Gaymard et al. 1998).

PEF located in the posterior part of the intraparietal sulcus is crucial for reflexive saccade triggering and plays a role on visuospatial integration (Pierrot-Deseilligny, Milea, and Müri 2004; Gaymard et al. 1998). The PEF projects to both the FEF and the superior colliculus. For reflexive saccades, the parietal lobe integrates visuospatial information to generate a motor signal that is sent to the superior colliculus by a direct parieto-tectal pathway (Gaymard et al. 1998).

The FEF located in the precentral gyrus is involved in the preparation and the triggering of voluntary saccades (Gaymard et al. 1998; Pierrot-Deseilligny, Milea, and Müri 2004; Bruce et al. 1985). Within FEF, there are two types of neurons that are directly related to gaze: movement neurons that are active before and during saccades; and fixation neurons that are found to be active while gaze is held steady (Kirk G. Thompson, 2005). The FEF can influence saccade production through four descending pathways: (1) a projection to the ipsilateral superior colliculus; (2) a pathway through the basal ganglia via the ipsilateral striatum; (3) a projection to the cerebellum via the pontine nuclei; and (4) a projection to mesencephalic and pontine nuclei that make up the saccade generator circuit (Bruce et al. 1985).

The SEF located in the posterior-medial part of the superior frontal gyrus plays a less direct role in the control of saccades, but is important for movements that are guided by cognitive factors (Krauzlis 2005; Stuphorn, Taylor, and Schall 2000; Nachev, Kennard, and Husain 2008).

The CEF located in the anterior cingulate cortex appears to be involved in motivational modulation of voluntary saccades, whereas the dorsolateral prefrontal cortex (dlPFC) in the midfrontal gyrus plays an important role in reflexive saccade inhibition, visual short-term memory and decision processes (Pierrot-Deseilligny, Milea, and Müri 2004; Gaymard et al. 1998; Müri and Nyffeler 2008).

1.3.1 Superior Colliculus (SC)

The SC is a brain stem region and it is the key station for integrating and relaying commands from the cerebral cortex onto the saccade generating circuit in the brain stem (Leigh and Zee 1999; Sparks 2002; Hikosaka, Takikawa, and Kawagoe 2000). Besides, the neurons in SC respond to inputs from visual, auditory and tactile stimuli (Sparks 2002; Hikosaka, Takikawa, and Kawagoe 2000).

The SC consists of seven layers, of which the dorsal layers (layers I-III) are visual. These layers receive inputs directly from the retina and V1. The projections received from the retina are orderly, the visual field is mapped on its surface in topographical manner (Hikosaka, Takikawa, and Kawagoe 2000).

Dorsal layers project to pretectal nuclei, lateral geniculate nuclei, pulvinar and also connect with deeper layers IV-VII, known as ventral layers (Leigh and Zee 1999).

The ventral layers of SC have a sensorimotor role and receive information from auditory, tactile and motor systems. The FEF, SEF, PEF, dlPFC and CEF all project directly to ventral layers (Leigh and Zee 1999), or through basal ganglia via pars reticulata (SNr), part of substantia nigra (Hikosaka, Takikawa, and Kawagoe 2000).

Although the neurons from ventral layers project to the cortex via the thalamus, their primary output signals are to the structures in the brain stem that generate premotor commands for saccades (Leigh and Zee 1999). These projections are carried out through descending pathways known as the ipsilateral tectopontine and the contralateral tectoreticular pathways. It is through these descending pathways that the SC controls the sensory organs such as eye, ears, head and limbs that are moved during orientation responses.

Studies in awake monkeys (Robinson 1972), provided fundamental insights on how gaze shifts are controlled. These early studies demonstrated that the topographic map of the SC – referred to as a motor map – encodes the eye movements in the same manner as the visual area V1 encodes the visual stimuli with regard to their site of activation on the retina. The SC motor map produces the vectors for movements that direct gaze to a sensory stimulus of interest. These gaze shifts depend on the size of the movement needed and can be accomplished by saccadic eye movements alone, or by combined movements of eyes and head.

However, although the studies done in normal subjects have emphasised the pivotal role the SC plays in generating saccades, they have also shown that after the complete lesion of SC, monkeys learn again to generate saccades but with increased latency times and decreased velocity. Only when lesions of the SC and FEF are combined, the saccades can no longer be initiated (P H Schiller, True, and Conway 1980).

In addition, since cerebral lesions cause saccadic dysmetria (i.e. undershoot or overshoot with respect to the intended target), suggests that the SC alone cannot control saccade amplitude or direction and there must be a signal that emerges from different pathways that reaches the brainstem and cerebellum (Leigh and Zee 1999).

1.3.2 Brain Stem Saccadic Pulse and Step Generator

The commands for saccadic eye movements are generated in the brain stem. Two types of neurons play key roles for generating premotor commands. These are known as ‘burst’ (saccadic) and ‘omnipause’ (fixation) neurons (OPN). The commands for vertical and horizontal saccades arise from different regions in the brain stem. The saccades towards horizontal direction are produced by burst neurons within paramedian pontine reticular formation (PPRF), while the burst neurons in medial longitudinal fasciculus (riMLF) control the saccades towards the vertical direction as well as torsional rotations (Leigh and Zee 1999; Sparks 2002). The amplitude, duration and velocity of the saccades are closely correlated with the number of the spikes, burst duration and peak-firing rate of burst neurons in PPRF for horizontal saccades and riMLF for vertical saccades.

The OPNs lie in the midbrain very close to the midline near the rostral pole of the abducens nucleus, in the raphe interpositus nucleus (Büttner-Ennever et al. 1988). These neurons fire constantly during fixation and pause during saccades in all directions (Optican 2010). Thus, although the commands for horizontal and vertical/torsional movements originate from different regions of the brainstem, they do not work independently because the OPNs control the onsets of all components (Sparks 2002).

The aim of this chapter was to describe the background literature that would be relevant in understanding the concepts that will be useful when describing the EMAIL test techniques. However, while all the above mentioned studies have determined saccadic performance from eye movement recordings, the EMAIL technique allows the measurement of eye movement response latencies and visual processing times to be quantified without the use of any eye-tracking equipment. Therefore, to account for all the parameters that make up the ISL and to validate the EMAIL test as a valid visual psychophysical technique, three studies have been designed and carried out to answer the following questions:

1. Can a psychophysical test designed to measure the overall time subjects need to execute the eye movement and to perform a visual task at the end of each saccade be used as a viable testing procedure to assess saccadic response latencies and visual processing times?
2. Can the test capture the directional asymmetries that exist between the horizontal and vertical saccadic eye movements through ISLs?
3. Can the test capture reliably the effects of aging associated with saccadic eye movements?

In the next chapter (chapter 2), detailed information is provided to describe the EMAIL test procedure and experimental setup including the preparatory experiments needed to select appropriate stimulus parameters for the test. Chapter 3 describes series of studies aimed at testing the hypothesis that VPT, when saccades are involved, are longer than those measured with identical stimuli in the absence of eye movements. As part of these experiments, the eye movement recordings are used to describe the instabilities of the eyeball and account for the extended VPTs. While, chapter 4 tests the assumption that the vertical versus horizontal directional asymmetries in eye movement responses also affect the measured ISL responses. Chapter 5 addresses the hypothesis that both ISL and DRT measures are influenced by age, while chapter 6 summarises the findings presented in this thesis and relates them to other work, including limitations that have affected the outcome of the studies. Finally, the concluding remarks are also reported in this chapter.

2 EMAIL Test and Experimental Method

2.1 Introduction

This chapter explains the EMAIL test, experimental setup, equipment and data analysis employed in this thesis. The preparatory experiments needed to select appropriate stimulus parameters for the EMAIL test are also described in this chapter. Particular attention was paid to the selection of appropriate values for stimulus contrast and eccentricity.

2.2 The EMAIL (Eye Movements and Integrated Saccade Latency) Test

The EMAIL test is a novel psychophysical technique designed to measure saccadic eye movement responses without the need for any eye tracking equipment. Traditionally, under controlled conditions, the saccadic responses are measured by precisely controlling the timing and location of the target that initiates the saccade; the subject's performance is determined from eye movement recordings. Based on a similar principle, the EMAIL test also initiates the saccades, but its performance is determined from the variable δT, automatically computed by the test after the trial ends. The measured variable (δT), represents the time the subject needs to detect the peripheral target, generate an appropriate eye movement and process a specific stimulus attribute at the end of each saccade. The test also simultaneously measures the mean time the subject takes to generate a response. This measured variable has been labelled as decision response time (DRT). In addition, the EMAIL test can also be used to measure simple reaction times (RT). This variable describes the time the subject requires to detect the presence of the visual target and to generate a motor response.

The test runs in the Microsoft Windows operating system, while the stimuli for all experiments were displayed on a fully calibrated NEC Multisync P241W LCD monitor (NEC Display Solutions).

2.2.1 Subjects

All the data presented in this thesis were obtained at City, University of London. The method and testing procedures were approved by the university Research and Ethics Committee. In total, forty five healthy subjects were recruited to participate on the studies described on this thesis. Although neither phoria nor visual acuity was assessed, none of the subjects reported problems with either visual acuity or binocular vision. All experiments were carried out binocularly and each participant used their normal distance spectacle prescription during the tests, except for the few older subjects (see chapter 5) who wore their normal reading glasses. Small refractive errors or increased light scatter in the eye, particularly in the older subjects, are not likely to affect the results since the task required the detection of a 4 min arc gap in a Landolt ring (which is four times larger than the typical normal VA of 1 min arc). Prior to testing, all subjects gave written informed consent, were briefed on how to perform the test and after a period of practice, the testing procedure began.

2.2.2 Monitor calibration

Monitor calibration is essential to ensure that the stimuli presented on the visual display have the specified luminance, chromaticity and contrast. The luminance calibration program developed for the AVOT (Advanced Vision and Optometric Tests) system was used every six months to check the calibration of the display. The program measures the luminance of each primary colour over the whole dynamic range (i.e., 0 to 1023) and this takes ~ 15 minutes to complete.

A Gamma Scientific Telespectralradiometer (Model 2030-31) was used to measure the spectral power distribution of each of the three primary colours. The algorithms employed in the AVOT software use the calibration data to generate any luminance and chromaticity specification within the limits of the display. The results of the luminance calibration program are shown in Figure 3 for each of the primary display colours.

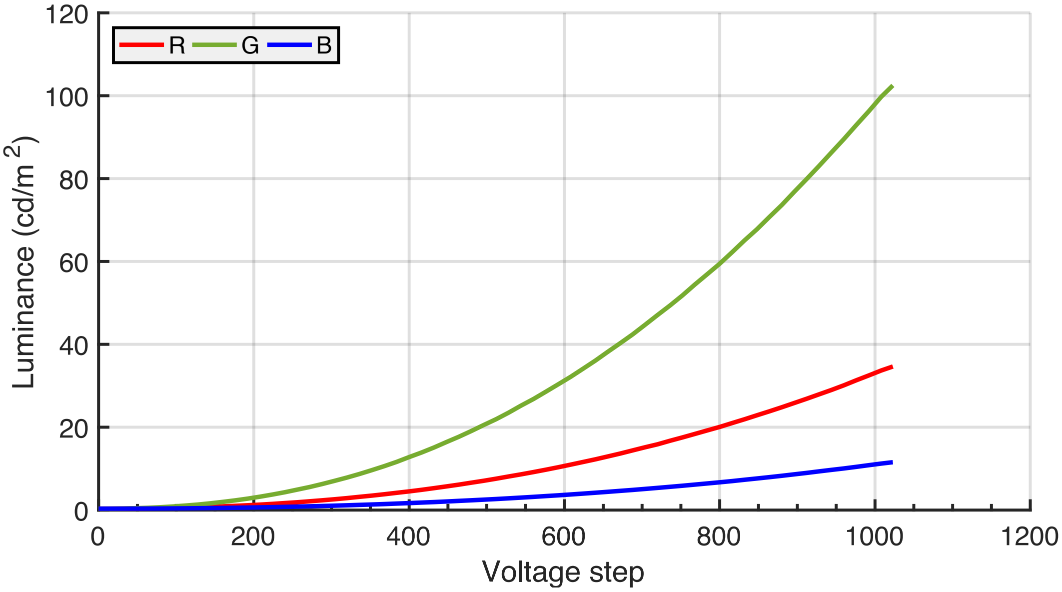


Figure 3. The measured luminance versus gun voltage value for the R, G and B primary colours of the NEC display.

2.2.3 **The Procedure**

The tests were carried out in a darkened room. The subject viewed the visual display from a distance of 80 cm, and a chin rest was employed to stabilise the subject's head position.

During testing, an overlap paradigm was employed, as fixation stimulus remained visible after target onset. Each trial began with the appearance of the central fixation target. The sudden appearance of the fixation target inevitably attracts the subject's point of regard.   This was followed by the onset of a peripheral target somewhere in the visual field. The subject's task was to saccade to the target and to register the gap orientation in a central Landolt ring, using a four-button response box (Figure 4). The test target was surrounded with four similar rings in order to generate sufficient visual crowding and ensure that the subject was unable to carry out the visual task using just the peripheral retina without saccading to the target. This is simply because visual crowding is very strong in the periphery, but less so or even absent at the point of regard.

A four-alternative, forced-choice (4AFC) staircase procedure is used to determine δT. The staircase employed varies the stimulus presentation time using a '2-down, 1-up' procedure. This requires two consecutive correct responses in order to decrease the stimulus presentation time and cause a staircase 'reversal', but only one incorrect response to trigger a corresponding increase in δT. The probability of getting a down response (i.e. two consecutive correct responses) on any given trial is equal to:

$[\mathrm{P(x)}]^2 = 0.5$, i.e. $\mathrm{P\ (X)} = \sqrt{0.5} = 0.707$ Equation 1. Response probability

Therefore, use of '2-down, 1-up' procedure yields a measure of a threshold response corresponding to 0.707% level on psychometric function (Levitt 1971) Thus, the δT measurement produced by the test corresponds to the threshold measurement of the subject's stimulus duration time needed for 71% of their responses to be correct.

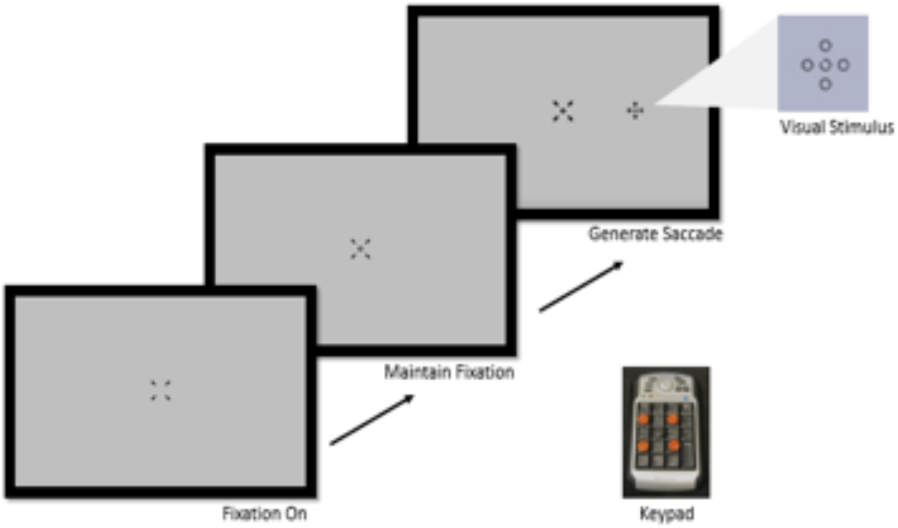


Figure 4. The stimulus sequence. First the subject fixates on the central mark, after some time the central cue appears in the middle of the cross, indicating to maintain the fixation. Once the target appears in the periphery, the subject is required to saccade towards the target, and to register the orientation of the gap in the central ring. The subject is then required to press one of four response buttons to indicate the perceived orientation of the gap, or to simply guess when unable to decide.

Since the measured variable (δT) reflects the time the subject needs to detect the peripheral target, generate an appropriate eye movement and register the orientation of the gap, δT also includes the post-saccadic visual integration time. In order to separate the latter from the remaining parameters that contribute to δT (i.e. saccade latency and duration), an eye tracker was integrated with the EMAIL test. Since the measurement of δT is subject-specific (i.e. it represents the stimulus duration the subject needs to achieve 71% correct response), δT = latency (T1) + saccade duration (T2) + post-saccadic visual integration time (T3). These parameters are indicated on the eye trace in Figure 5 below (where the measured time, δT is indicated as T(0)). For simplicity, δT was labelled as ISL (Integrated Saccade Latency) time throughout this study.

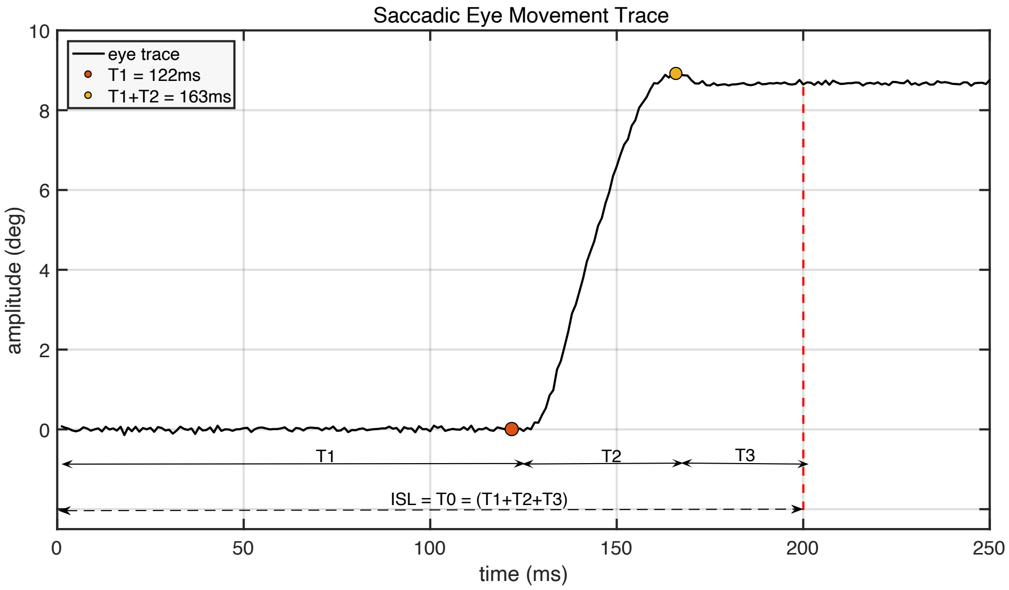


Figure 5. Representative record of a single rightward saccade as recorded with EyeLink1000. The signal depicts all saccade parameters where the latency is denoted as T1 = 122ms and corresponds to the time required to detect the stimulus and prepare the saccadic the saccadic eye movement. This is the time taken from the appearance of a stimulus at t = 0 to the beginning of a saccade when t = 122ms. Saccade duration is denoted by T2 and corresponds to the time interval t = 122ms (start of saccade) to t = 163ms (end of saccade). Whereas the T(3) represents post-saccadic visual integration time. The time interval denoted as T0 = ISL (i.e., the Integrated Saccade Latency time measured with the EMAIL test).

2.3 Eye Movement Measurements and the Testing Procedure

To determine the most suited target eccentricity to be employed in the EMAIL test, as well as separate post saccadic visual integration time, an SR EyeLink 1000 system with a sampling rate of 1000Hz was used. The EyeLink 1000 is a desktop mount that tracks the eye via an infrared mirror with accuracy of 0.25° - 0.5°. During recordings the eye tracker computes gaze position by monitoring the movement of the specular image of the light source with respect to the centre of the pupil (Collewet and Marchand 2011).

All eye movement recordings were conducted in a darkened room and the head position was stabilised with a chin rest at a viewing distance of 80 cm.

In order to calibrate the EyeLink system, a manual calibration was performed before each session, followed by a validation test to determine the gaze accuracy.

During the calibration process, a nine-point grid was presented on a stimulus display in sequence; the subject was instructed to fixate at the centre of black calibration target seen as a white dot. Since calibration target appears on both the host PC and the display monitor, fixations are accepted manually when the gaze is on the target. Once the first fixation was accepted, more targets appeared in sequence until the last target was presented. Each calibration was followed immediately by validation to confirm the accuracy of gaze position. If the errors exceeded 0.5 deg, adjustments were made to the head position and / or the illumination angle and the calibration process repeated. Only after the validation was accepted, the eye movements were recorded.

The experiments were performed binocularly, but the eye movement traces were measured only from the right eye.

The EMAIL test runs on a Windows 7 computer and employs a fully calibrated NEC Multisync P241W LCD monitor, as described in section 2.2. The eye tracker experiments also employed a custom-made photodiode attached to a corner of the display to capture the exact stimulus duration time. This arrangement made it possible to accurately measure the actual stimulus time on the display. The results show that on some occasions the stimulus presentation time varied by one display frame duration (i.e. 16.66ms). The hardware-based approach developed for these experiments to measure stimulus presentation time made it possible to measure this variable with ~ 1ms accuracy. The eye movement recordings were synchronised with the onset and offset of the visual stimulus, which allowed accurate estimates of eye movement parameters, as illustrated in Figure 5.

The eye tracker experiments employed a number of discrete stimulus presentation times selected to fall both above and below the subject’s ISL time. Each selected stimulus duration was presented at least 80 times in order to estimate accurately the time course of the saccade and the probability of a correct response. Three successive test runs were needed to complete one experiment. For the first run, the stimulus duration corresponded to the measured ISL time using the full EMAIL test, whereas during the second and third runs, stimulus durations were both above and below the measured ISL time (i.e. ISL ± 20ms as specified in the program).

The Weibull function was then fitted to the measured data in order to estimate the subject’s performance level with respect to stimulus duration times (ISL ± 20ms).

The general form of psychometric functions is given as:

$$\mathbf{P(x) = \gamma + (1 - \lambda - \gamma)F(x; \alpha, \beta)} \quad \text{Equation 1}$$

where $\mathrm{P(x)}$ is the probability of a correct response at stimulus level x, the function $\mathrm{F(x; \alpha, \beta)}$ in our case represents Weibull function, the γ and λ define the lower and upper asymptotes, whereas the shape of the curve is determined by α (position) and β (slope).

$$\mathbf{F(x; \alpha, \beta) = 1 - exp\left(-\left(\frac{x}{\alpha}\right)\beta\right)} \text{ Equation 2}$$

Prior to fitting the psychometric function, all the measurements for responses were transformed using the equation:

$$\mathbf{p(x) = \frac{P(x) - P(0)}{1 - P(0)}} \quad \text{Equation 3}$$

Where $\mathrm{P(x)}$ = number of correct responses prior transformation and $\mathrm{P(0)}$ is the chance probability of correct response. The measurements for T0 times corresponding to 71% correct responses for each subject were obtained from psychometric curves.

2.4 **Eye Tracking – EyeLink 1000**

All the data from the eye tracker (i.e. EDF output files), as well as the EMAIL test (i.e. XML output files), were analysed using custom written script in the Matlab program. The EDF files contain two sets of data: eye-position samples and events. The eye position samples produced by the EyeLink contained 1000 samples per second. Data set for events contained saccades, fixations, blinks, and synchronising events from the experimental setup (i.e. custom-made photodiode), which were marked clearly with a time stamp.

Three thresholds are usually used for saccade detection. These are:

1. Saccade velocity threshold
2. Saccade acceleration threshold
3. Saccade motion threshold

For our study, these thresholds were set according to the manufacturer's recommended settings for psychophysical research. This uses a threshold velocity of 22 °/sec, acceleration threshold = 4000°/sec^2, and 0 for saccade motion respectively. When these settings are selected for analysis, one can detect saccades with an amplitude as small as 1°.

For data analysis, a custom-made algorithm was used to extract the points of interest from the raw traces produced by the eye tracker. Figure 6 below shows a typical saccadic eye trace and its corresponding velocity profile, as produced by EyeLink 1000 during eye movement recordings.

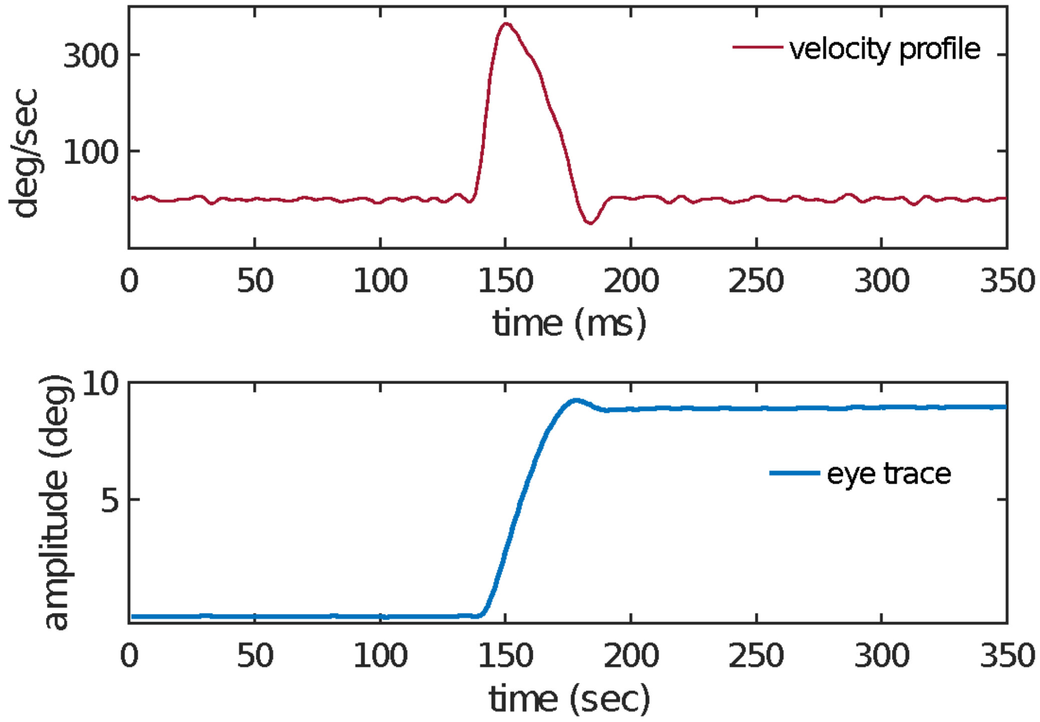


Figure 6. Saccade velocity profile and its corresponding eye trace. The change in x, y coordinate determines the eye position. The traces show a delay from the onset of the stimulus and the change in x, y coordinates in both velocity and eye trace profile. This time delay corresponds to saccade latency.

To achieve the experimental objectives, it was necessary to determine all saccade parameters, such as saccadic latency, amplitude, duration and peak velocity.

Before the parameters were determined, all trials that included blinks were removed. Also, saccades that occurred within 60ms from the stimulus onset were removed prior to the analysis. Figure 7 shows the eye traces obtained from a typical trial session. Plot (a) represents unfiltered eye traces, while plot (b) shows the remaining eye traces after filtering. In this example, 10 trials were excluded as a result of the filtering criteria.

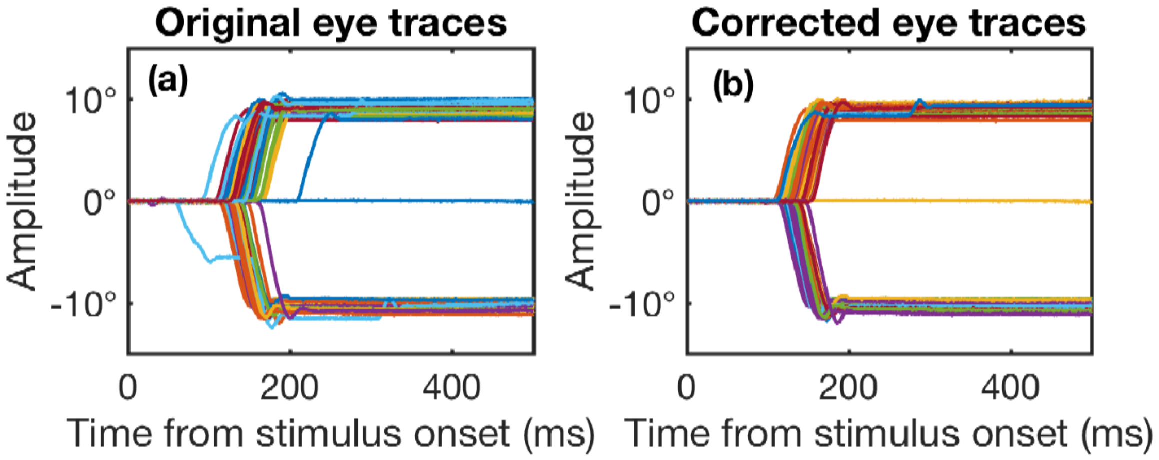


Figure 7. Unfiltered and filtered eye traces from a block consisting of 98 trials. The figure (a) represents 98 unfiltered eye traces of 10 ° horizontal saccades as recorded with EyeLink1000, whereas the figure (b) on the right is representative of corrected eye traces. In this block of trials only 10 traces were removed prior to analysis.

Data analysis also involved the use of upper and lower threshold ±2σ limits. In the example presented above, the mean saccade amplitude was 10°± 0.72° All traces outside the ±2σ limits were removed prior to the analysis. In this example, an upper threshold of 11.44° and a lower threshold of 8.56° was applied. Following initial analysis, it was decided that more relaxed limits of ±2.5σ were sufficient to eliminate outliers. The latency histogram is shown in Figure 8, together with the normal fit before and after the exclusion of the ±2.5σ threshold. Estimated parameters from the normal distribution are presented in Table 1. Applying threshold limits ensures that 'outliers' that are unlikely to be part of the normal distribution eliminated; on this occasion, while variance was reduced significantly, the sample mean did not change.

Table 1. Estimated parameters for mu and sigma from normal distribution fit.

Normal Distribution without exclusion rule		Parameter μ	Parameter σ
mean	128.43	128.4	14.8
variance	218.83		
Normal Distribution with exclusion rule of ± 2σ		Parameter μ	Parameter σ
mean	128.1	128.1	11.8
variance	139.1		

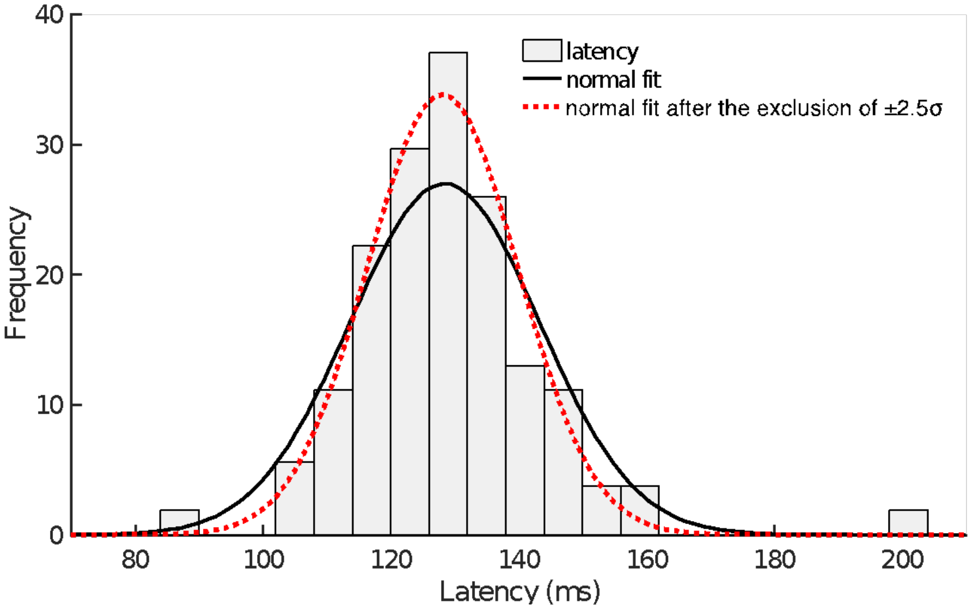


Figure 8. Latency frequency histogram and its corresponding normal fit. Solid line corresponds to latency data without filtering and dotted red line corresponds to best Gaussian fit after the exclusion of outliers outside ±2.5σ limits.

2.5 Visual Stimulus and its parameters

The visual stimulus, consisting of a Landolt C - flanked by four ring distractors of equal size (Figure 4), with a central ring consisting a gap size of 4 minutes of arc - was used for all experiments.

When the eye is presented with a cluttered scene, we can easily distinguish between objects and resolve fine spatial detail when these objects are viewed directly.

However, ‘visual crowding’ is much stronger in the periphery of the visual field. This makes it impossible to resolve the gap in the Landolt ring unless the target is fixated directly by the eye (Korte 1923).

‘Visual crowding’ occurs when objects are too close together, causing features from neighbouring objects to interfere with those of the target object during some stage of visual processing. This makes it more difficult to resolve fine detail, leading to a jumbled perception (Denis G. Pelli 2008; Denis G. Pelli and Tillman 2008; Levi 2008). Additionally, visual crowding depends on target flanker similarity, with crowding being most pronounced when the target and the flankers are similar in shape, size and contrast (Levi 2008). Critical spacing – which defines how separated the flankers should be from the target to allow unimpaired recognition of the target – is proportional to target eccentricity and does not depend on the object size (i.e. it is size invariant) (Denis G. Pelli and Tillman 2008; Maus, Fischer and Whitney 2011; Levi 2008). The critical spacing is large and can approach half the object eccentricity (Bouma 1970; 1973; D. G. Pelli, Palomares, and Majaj 2004).

Although crowding restricts our ability to recognise objects in peripheral vision, it does not affect our ability to detect the presence of the object. Once the target is detected, an appropriate saccade will be generated to place the object of interest on the centre area of the retina that corresponds to the point of regard.

The choice for the gap size of 4’ of arc in our test is four times larger than the average limit of resolution in a normal eye (usually measured with visual acuity tests). Given this choice of gap size, the subjects had no difficulty with the gap-orientation discrimination task at the end of each saccade. The experimental design ensures that although the subjects always detected the onset of the peripheral target, they were unable to carry out the task in the absence of a goal-directed saccade. Therefore, to be able to discriminate the gap orientation in the central ring, an appropriate saccade must be made to bring the point of regard onto the target.

2.6 **Target eccentricity**

This study has been designed to examine the effects of eccentricity on the three components that make up the ISL thresholds such as T1, T2, and T3. Because each component can be processed independently when the eye tracker is incorporated into the EMAIL test, the aim was to establish how stimulus eccentricity affects each component that makes up the ISL. This information can then be used to guide the choice of best target eccentricity to be employed on the EMAIL test.

Although visual search involves both saccades and head rotations, under controlled conditions, saccades as large as 80° degrees in magnitude ((Collewijn, Erkelens, and Steinman 1988b; 1988a), can be generated. Naturally occurring saccades are much smaller. It has been shown that under free viewing conditions, saccades larger than 15° are very rare. When they do occur, they are usually accompanied by head movements(A. T. Bahill, Adler, and Stark 1975). Trajectories of normal saccadic eye movements are remarkably stereotyped. Both duration and peak velocity obey stereotypical relation with respect to saccade amplitude, known as 'main sequence' (Bahill, Clark, and Stark 1975). For a wide range of eccentricities, saccade duration increases linearly with saccade amplitude, while peak velocity vs amplitude produces a nonlinear relationship. This is the result of a soft saturation beyond amplitudes of ~15°(A. T. Bahill, Adler, and Stark 1975). However, with increasing target eccentricity, saccade amplitudes have been shown to exhibit greater end point variability (Opstal and Gisbergen 1989; Beers 2007; Beers 2008; Abrams, Meyer, and Kornblum 1989;

Harris and Wolpert 2006). In recent years various theoretical models have been developed to explain the end point variability in saccade trajectories, and there is a general agreement that variability increase is a result of motor command noise occurring at the level of motor map (i.e. deeper layers) of superior colliculus (Opstal and Gisbergen 1989; Beers 2007; Beers 2008; Harris and Wolpert 2006) This noise has been shown to increase with higher activity levels that larger saccades demand, causing end point variability to increase as target eccentricity increases (Opstal and Gisbergen 1989; Beers 2007; Beers 2008; Harris and Wolpert 2006).

There is another important aspect of saccadic eye movement control that has received little attention in the past. It is well established that saccades do not exhibit perfect conjugacy (Zee, Fitzgibbon, and Optican 1992; Robinson 1964; Collewijn, Erkelens, and Steinman 1988a). Due to the eyes' horizontal separation, the temporal saccade of one eye is larger than the nasal saccade of the other eye. Because of these differences, these studies have demonstrated that saccades inherit transitory divergent binocular fixational error (i.e. image disparity between two eyes) which increases with increasing eccentricity. Although, this divergent fixational error is transitory and lasts only during the first part of saccade (i.e. until the saccade has ended), it has been shown that misalignment between the two eyes can still persist after the end of the saccade (Zee, Fitzgibbon, and Optican 1992; Robinson 1964; Collewijn, Erkelens, and Steinman 1988a). Despite this evidence, no study has so far been designed to measure if this causes any effect on post-saccadic processing of visual information. To my knowledge, this investigation is the first study to also include the measurement of post saccadic visual integration time when describing the effects of target eccentricity on the parameters of saccadic eye movements.

Another parameter of interest in this study is the latency of saccades. While the main sequence relationship describes how duration and peak velocity varies with the size of a saccade, in contrast, the effects of eccentricity on the latency of saccades vary depending on the nature of the task. Whereas during more complex tasks, such as visual search and discriminability tasks, latency is found to increase as target eccentricity increases (Hodgson 2002; Carrasco et al. 1995; Nazir, Heller, and Sussmann 1992) this is not the case for saccades that are triggered towards the sudden appearance of an isolated target (Kalesnykas and Hallett 1994; Hallett and Kalesnykas 1995; Hutton 2008; Wolfe, O'Neill, and Bennett 1998; Hodgson 2002; Dafoe, Armstrong, and Munoz 2007a). The effect of eccentricity is small on latencies of reflexive saccades, i.e. visually guided saccades. Its effects are absent when saccades are triggered towards an isolated target that appears within ~ 12° eccentricity. In fact, latency of reflexive saccades in relation to eccentricity can be described using a bowl-shaped function which has a central latency peak for a region smaller than 0.75°, no change from 0.75° to 12°, and from there a gradual increase towards the periphery (Kalesnykas and Hallett 1994; Hallett and Kalesnykas 1995). This is atypical behaviour for saccadic reaction times, given that the latency times are heavily dependent on other physical properties of the target as described in section 1.5. However, these studies made use of simple luminous points to trigger saccades. Although one would expect similar results, it is of interest to establish if use of a 'crowded' target, such as the one employed in our test, triggers an enhanced effect of eccentricity. This is because the central ring and its four ring distractors of our visual target are similar in size, shape and contrast. This arrangement, as described in section 2.3.2, generates a strong crowding effect. Therefore, when the target is presented in the periphery, its sudden simultaneous appearance is that of the cluster and not the centre, isolated target. So far, the reasons why eccentricity does not affect latency of reflexive saccades within this range are undefined, but it is possible that the amplitude and timing of triggering these saccades is determined only by target onset and that the saccade amplitude is computed on the basis of the ‘centre of gravity’ of the target (Gaymard et al. 1998). These saccades require minimal cognitive control, so the saccade is initiated once the target is presented.

Based on these findings in the literature, the decision was taken to employ three eccentricities: 4°, 8° and 12°. The use of three discrete values allows us to examine whether saccade amplitudes (of naturally occurring saccades < 15°) have any effect of latencies.

2.6.1 **Methods and procedure**

Subjects

Three male subjects took part in this experiment. They were between 26 and 40 years of age and had normal vision. As mentioned in section 2.2, all experimental procedures were approved by City, University of London, Research and Ethics Committee.

Stimuli and Display

The visual stimulus consisted of a Landolt C flanked by four ring distractors with a gap size of 4 arc min, with contrast level set at 75%. The measurements were taken for eccentricities of 4°, 8° and 12°. Each subject completed 3 blocks of measurements in succession for a given eccentricity. Each block ended after 32 reversals. For each eccentricity, the target was presented randomly on either side of the fixation point, along the horizontal meridian only.

Procedure

There are two parts to this experimental procedure: (1) measure the integrated saccade latency values (ISL) using EMAIL test program and (2) make use of these values in a modified version of the EMAIL test, while the eye movement recordings were taken. As explained earlier, in chapter 2, the measures of ISL are subject-specific and represent the shortest stimulus duration time – i.e. the minimum time required for the stimulus to remain on the display to yield 71% correct response. The difference between the two tests is that the first is used to measure the ISL values (i.e. subject specific) using a staircase procedure, whilst the latter makes use of these threshold values to present the visual stimulus at a number of discrete stimulus presentation times, selected to fall above and below the subject's ISL time.

Eye movements were recorded from the right eye using SR EyeLink 1000 Hz system. The participant's head was stabilised with chin and forehead rests at a distance of 80 cm in front of the stimulus display. Each trial began with an EyeLink, 9-point calibration and was followed by a validation check to evaluate the gaze accuracy as explained in section 2.3. Following satisfactory calibration, the testing session began, whereby each subject performed three successive blocks with stimulus presentation times corresponding to the subject's known ISL time, followed by two more fixed times set ±20ms with respect to the measured ISL time for each target eccentricity.

As explained earlier in this section, the photodiode attached to a corner of the screen makes it possible to measure accurately the stimulus presentation time. During each session two different stimulus presentation times were recorded, due to occasional one frame drop as shown on Figure 9. We labelled these timings as LONG and SHORT stimulus durations.

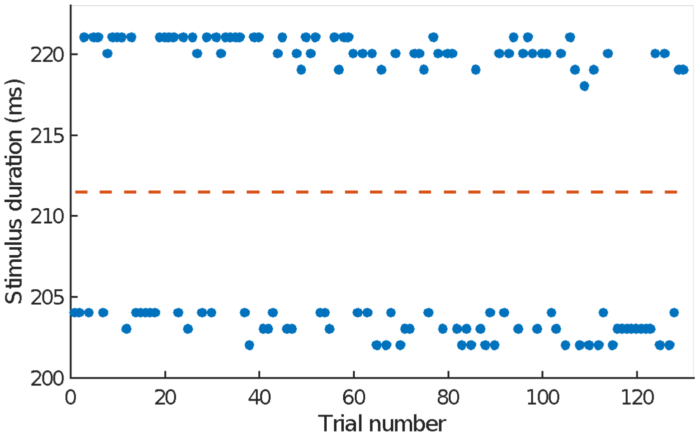


Figure 9. Actual stimulus durations as recorded with the photodiode system on the 60Hz visual display (with a screen refresh interval of 16.6ms). As the stimulus is presented on the screen, the photodiode and the associated electronics generate a signal that terminates on stimulus offset. This arrangement enables the measurement of the actual stimulus duration time.

2.6.2 Data Analysis

Saccades were detected automatically by the eye tracker. A customized MATLAB script was used to read eye tracker and EMAIL files (i.e. EDF and XML output files) as described earlier in section 2.3.1. Since ISL values are subject specific, the data were analysed on an individual basis. To measure the subjects' performance levels with respect to stimulus duration times (ISL ± 20ms), a Weibull function, as described in section 2.3, was used to fit the data, whereas the measurements from T1 and T2 were obtained from eye movement recordings. Only eye traces corresponding to correct responses were used for analysis. T1 and other main sequence parameters, i.e., amplitude, saccade duration and its peak velocity were extracted from eye traces. Parameter T3 was computed from the corresponding psychometric curve.

Results for latency (T1)

As explained earlier, the measurements were taken for 4°, 8° and 12° eccentricity where each subject completed 3 blocks of measurements in succession for a given eccentricity. Figure 10 below shows subject's latency histograms for each eccentricity tested. To determine the eccentricity effect on saccade latencies, repeated ANOVA measures were performed, with mean latency as the dependent variable. As with previous reports, T1 was found to be independent of eccentricity across the range tested. No significant effect was found between subject's latency means, F (2, 4) = 1.88, p>0.26, or within grouped means, F (2, 8) = 5.69, p>0.12. These results are in direct agreement with previous reports by other investigators, confirming that the eccentricity effect on latencies of reflexive saccades is absent when a visual target is presented within ±12° eccentricity (Kalesnykas and Hallett 1994; Hallett and Kalesnykas 1995; Hutton 2008; Wolfe, O'Neill, and Bennett 1998; Hodgson 2002; Dafoe, Armstrong, and Munoz 2007a).

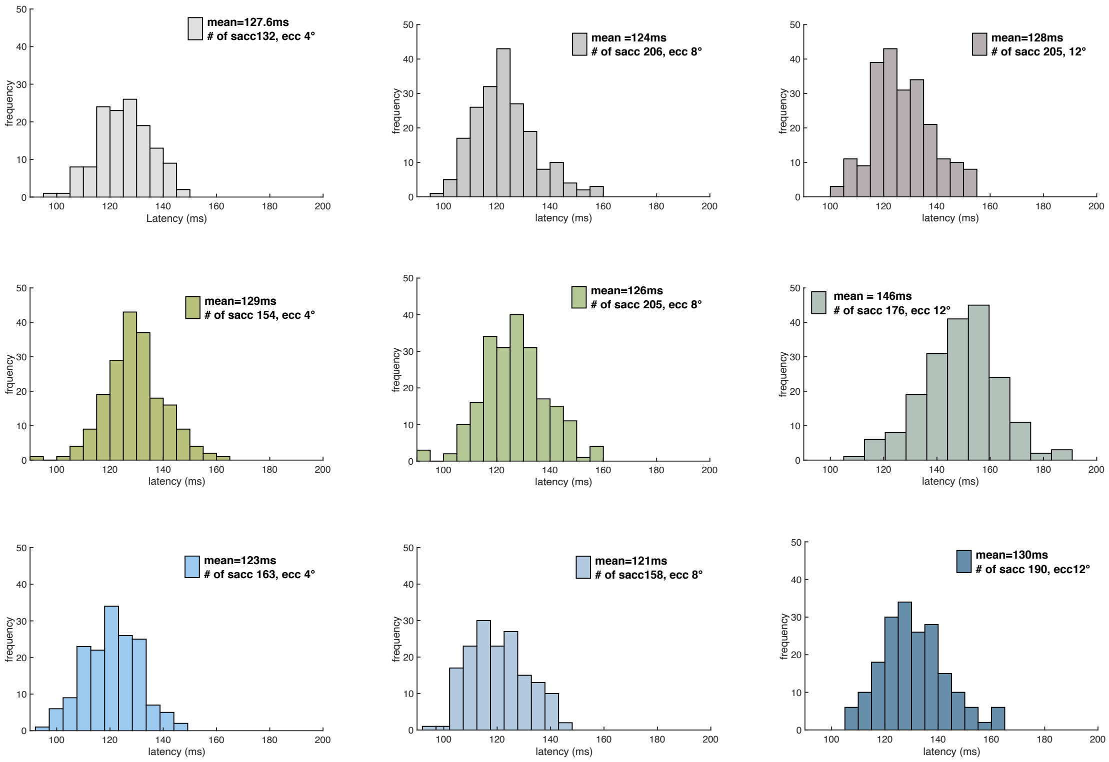


Figure 10. Latency histograms. Each row represents a subject's latency histograms for 4°, 8° and 12° eccentricity. The values for mean latency, number of trials and eccentricity are indicated on each plot.

Main Sequence Results

As mentioned earlier in the data analysis section, the parameters concerning main sequence involve saccade amplitude, duration and peak velocity. The approach taken to examine the main sequence parameters compliments the approach taken by previous investigators. First, the relationship between saccade duration with amplitude and saccade peak velocity with amplitude was determined from subjects overall mean. These data are shown in Table 2 below.

Table 2. Measurements of mean sequence parameters.

Mean amplitude (deg)	σ (deg)	Mean duration (ms)	σ (ms)	Mean peak velocity (°/sec)	σ(°/sec)
4.3	0.5	29.8	0.9	319.1	23.2
4.6	0.6	31.2	0.5	380.9	36.7
4.7	0.4	32.8	1.4	287.6	28.6
9.3	0.4	41.4	1.2	392.5	29.0
9.8	0.8	42.2	1.2	454.8	47.8
9.8	0.7	44.7	2.4	390.4	33.7
13.3	1.7	50.9	2.6	459.1	29.7
14.3	1.4	51.1	0.3	490.2	37.4
13.6	1.5	58.3	0.5	418.9	33.6

In agreement with previous research, all parameters measured were found to increase systematically with increasing eccentricity. The main sequence relationship for saccade duration and amplitude and saccade peak velocity versus amplitude is shown in Figure 11.

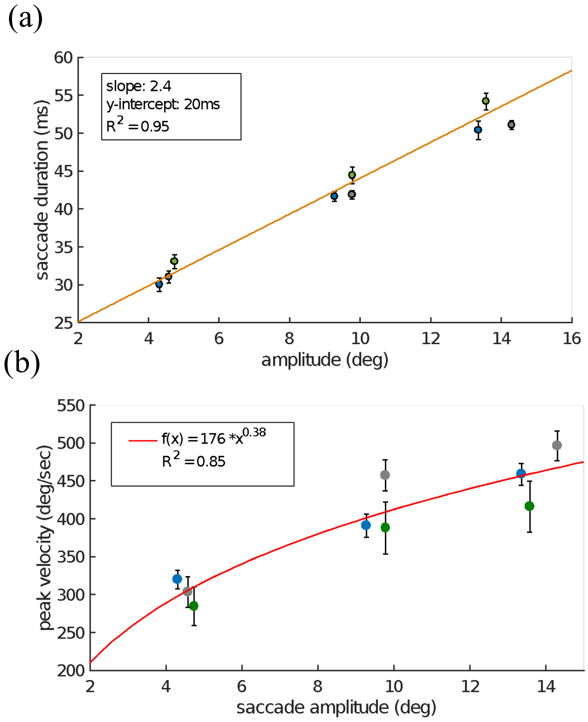


Figure 11. Main sequence relationship for saccade duration and peak velocity. Each filled circle plots a subject's overall mean for a given eccentricity. Vertical error bars represent ± 1 standard deviation from the mean. Line of best fit produced linear fit for duration vs amplitude whereas for peak velocity vs amplitude was nonlinear (shown as a solid read line). The slope, y-intercept and the R^2 obtained from each fit are as indicated on the plot.

As plot (a) shows, saccade duration increased linearly with saccade amplitude. The best line of fit for saccade duration produced a slope = 2.4ms and intercept = 20ms with R^2 = 0.95. This result, although obtained from a small range of eccentricities, agrees well with previous reports. Typically, the ranges for slope duration are within 2.1ms– 3ms, whereas the range for the interception is between 20ms - 25ms (Collewijn, Erkelens, and Steinman 1988a; Abrams, Meyer, and Kornblum 1989) Similarly, the nonlinear relationship found between peak velocity and amplitude, as shown in plot (b), is consistent with previous reports by other investigators (Bahill, Clark, and Stark 1975; A. T. Bahill, Adler, and Stark 1975; Collewijn, Erkelens, and Steinman 1988a). The best line of fit suggests that the relationship between peak velocity and amplitude is nonlinear. Peak velocity also increases with increasing amplitude, but the rate of increase decreases as saccade amplitude increases.

Not unexpectedly, saccade amplitudes also increased systematically with increasing eccentricity. The relationship between saccade amplitude and target eccentricity is plotted in Figure 12, where each filled grey circle represents the subject's mean amplitude, and error bars indicate ± 1σ (these data are shown in the first two columns of Table 2). The best line of fit (linear fit) for saccade amplitude vs eccentricity produced a slope = 1.1 and intercept = 0.1 with R^2 = 0.99 indicating overshoot. Usually, saccades are known to undershoot the target (Robinson 1964; Collewijn, Erkelens, and Steinman 1988a; Abrams, Meyer, and Kornblum 1989; Bahill, Clark, and Stark 1975). A possible reason for this is that, unlike most other studies, the target employed in our tests was not a conventional luminous spot. Instead, as described earlier, our target consisted of a crowded Landolt ring, while the subjects' task was to register and report the position of the gap in the centre ring. In this case, the subject may need to overshoot the target slightly to compensate for post saccadic oscillatory movement (see Figure 13) that occurs with each saccade before it comes to rest, as this is a high visual acuity task.

The observed saccade amplitudes also revealed that with increasing eccentricity there was a threefold increase in variability. An increase in amplitude variability with increasing eccentricity was consistent across three subjects tested and agrees well with previous investigators (Opstal and Gisbergen, 1989; Beers, 2007; Beers, 2007, 2008; H. G. Lemij and H. Collewijn, 1989)

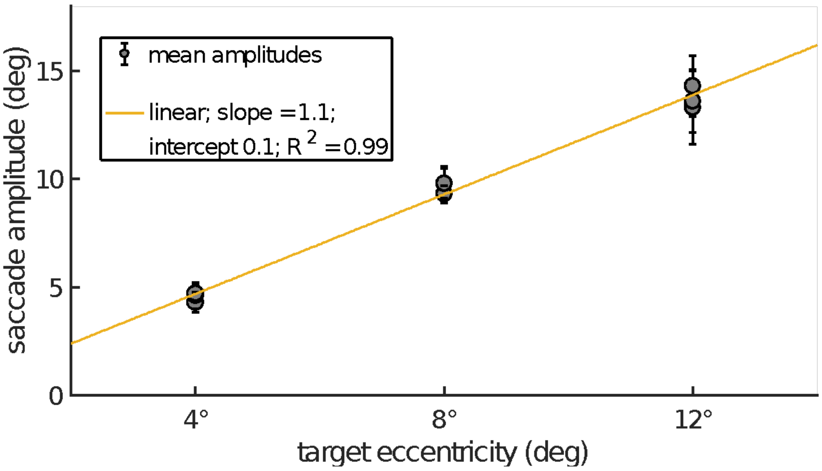


Figure 12. Mean amplitude versus target eccentricity. Each grey filled circle is representative of the subjects' mean amplitude for given eccentricity. Vertical error bars represent ± 1 standard deviation from the mean whereas the yellow line is a best fit line - linear fit. The Slope, y-intercept and the R^2 obtained from the fit are indicated on the plot.

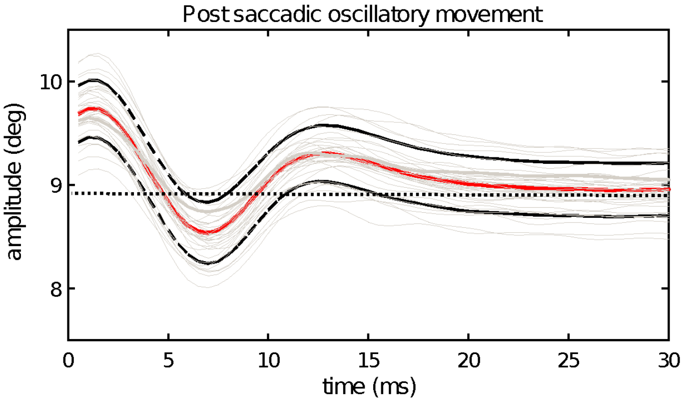


Figure 13. Post saccadic oscillatory movement. The red line represents the overall mean from post saccadic oscillatory trajectories that occur after the saccade has ended. Fine grey traces are actual traces from the eye movements whereas black lines above and below of the mean represent ± 1 standard deviation.

Results for post saccadic visual processing time - T3

As discussed earlier in the procedure section, to measure the subjects' performance levels with respect to stimulus duration times, a Weibull function was used to fit the data. In Figure 14, the subjects' psychometric curves are presented for each eccentricity tested. Psychometric fits demonstrate clearly that subjects' performance is dependent on the amount of time the target remains visible on the screen display (i.e. stimulus duration time). Also, each plot in Figure 14 shows that the stimulus duration threshold - the point along the abscissa where the subject achieves 71% correct response - increases with increasing target eccentricity. The rightward shift observed in psychometric curves with each target eccentricity tested was expected, given that T2 parameter (saccade durations) increases linearly with target eccentricity. Since stimulus duration thresholds obtained from each curve correspond to the subjects' ISL value for a given eccentricity (as explained in procedure section the ISL is equal to T1+T2+T3), it was possible to also determine T3 (i.e. T3 = ISL - (T1+T2). These values are shown in Table 3 below.

Table 2. Measurements of subjects' T1+T2 (latency + saccade duration i.e. end of saccade),stimulus duration thresholds (ISL) and post saccadic visual processing time T3 (ISL-T1+T2)

	Subject 1			Subject 2			Subject 3		
Eccentricity	4°	8°	12°	4°	8°	12°	4°	8°	12°
T1+T2 (ms)	152	163	180	159	166	179	162	168	207
ISL (ms)	193	209	237	203	220	238	207	212	270
T3 (ms)	40	46	57	44	54	59	45	44	63

Surprisingly, the T3 values were also found to increase with target eccentricity. The results revealed significant effect for T3 with target eccentricity, $F(2, 8) = 14.85$, $p < 0.005$. To inspect the small p-value found within grouped means, a post hoc test was performed using Tukey’s procedure. Post hoc analysis revealed that the grouped mean of T3 for 12° eccentricity is significantly different from both grouped means of 4° ($p<0.004$) and 8° ($p>0.02$), with no significant effect between the grouped means of 4° and 8° ($p>0.31$).

Significant increase in T3 with target eccentricity is an unexpected result since it seems reasonable to assume that once the target is foveated, the time required to process the parameters of the visual stimulus would not depend on target eccentricity. One possible explanation for this unexpected increase is that, with increasing eccentricity, there was an increase in variability of saccade landing positions (i.e. saccade amplitude).

Therefore, as a next step, it was important to determine if there was any correlation between T3 and variability found in saccade amplitude with increasing target eccentricity.

The result shows that there is a significant positive relationship between T3 and the variability in saccade amplitudes, $r(7) = 0.88$, $p < .003$. The relationship between T3 and variability in landing positions is shown in Figure 15. Also, from regression analysis, it can be seen that the linear trend produced $R^2 = 0.78$, indicating that 78% of the variation observed in T3 could be explained by the variability observed in saccade amplitudes with increasing eccentricity.

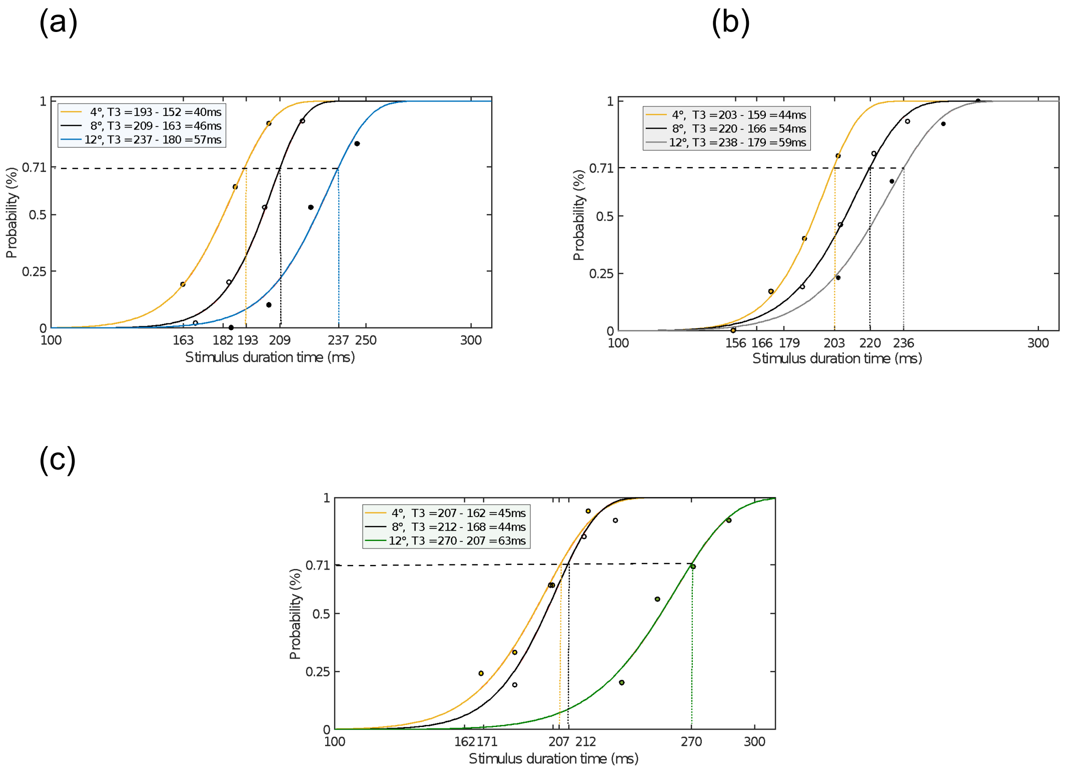


Figure 14. Subjects' performance with respect to stimulus duration time. Each plot shows subjects' superimposed psychometric curves for 4°, 8° and 12 ° eccentricity. Rightward shift on curves is consistent with increasing eccentricity. Subjects' values for ISL and T1+T2 are indicated in the plot.

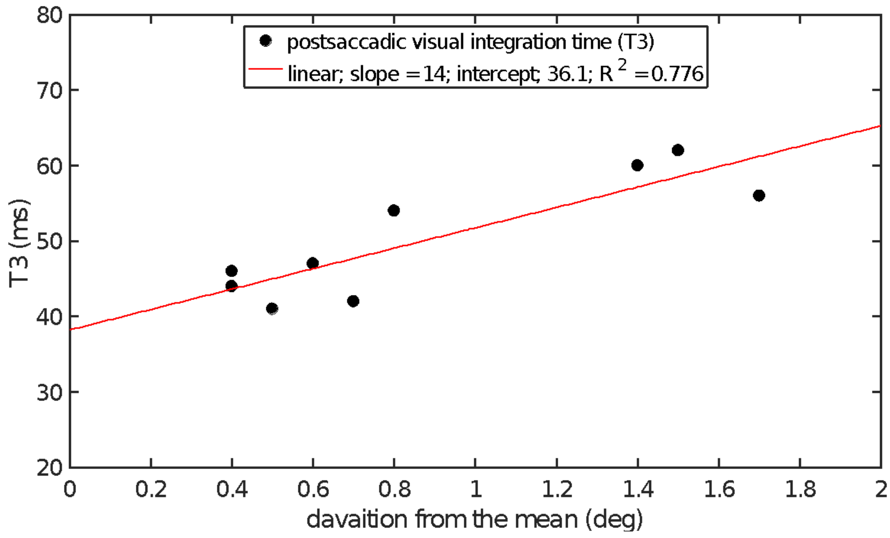


Figure 15. Relationship between T3 and observed variability in saccade amplitude. Each black dot represents the measured variability in saccade amplitude with the least-squares regression line shown in red.

Discussion

By aiming to gain a more complete view of the effects of eccentricity on each component that makes up the ISL, several important aspects of saccadic eye movement control have been revealed. These findings may be useful to help us understand perceptual processes. In this study, by making use of novel EMAIL test program, in conjunction with the photodiode device and the eye tracker, it was possible to account for all saccade parameters, including the minimum target fixation time needed to process the required visual information after each saccade has ended, i.e., the post saccadic visual processing time, T3. To my knowledge, this is the first study that has demonstrated how each parameter of saccadic eye movement varies with target eccentricity.

Effect of eccentricity on saccadic latency

Previous studies have demonstrated that eccentricity has very little effect on latencies when isolated targets are presented within ±12° eccentricity (Kalesnykas and Hallett 1994; Hallett and Kalesnykas 1995; Hutton 2008; Dafoe, Armstrong, and Munoz 2007a). In this study, similar results were also obtained during the discriminability task, when the target of interest cannot be resolved when in the periphery because of strong visual crowding. This is because when crowding occurs neighbouring objects interfere with each other and the peripheral object is perceived as a single cluster, rather than discrete elements. As a result, when the target appears in the periphery, the subject perceived an isolated target. This raises the question as to why the latencies of the reflexive saccades within this range are unaffected by target eccentricity. Although there is no clear explanation as to why eccentricity effect is absent within this range, one possible explanation is that these saccades require minimal cognitive control, since systematic latency increase found during more complex tasks has been attributed to a greater demand of attentional resources involved in target selection process (Wolfe, O'Neill, and Bennett 1998). In addition, it is well established that triggering reflexive saccades is performed via a separate neural pathway. These saccades are triggered only via the direct parieto-collicular pathway, where the neurons along this pathway have been shown to generate a signal that is used by the oculomotor system to initiate only reflexive saccades (Pierrot-Deseilligny et al. 1991; Gaymard et al. 1998; Pierrot-Deseilligny, Milea, and Müri 2004). Also, it has been shown that the latency responses and amplitudes of reflexive saccades are determined only by the onset of a visual target (Pierrot-Deseilligny et al. 1991; Gaymard et al. 1998; Pierrot-Deseilligny, Milea, and Müri 2004). This being the case, it might be that isolated targets that appear within this range of eccentricity generate visual onsets that are easily localised, resulting in target eccentricity playing little or no significant part in determining response latency. However, it is unclear whether altering stimulus parameters, such as its contrast or background adaptation level, will enhance the effect of eccentricity on the latency of reflexive saccades within this range. The stimulus contrast of 75% selected for use in this study was well above the detection threshold. Therefore, it would be of interest to establish in future studies if increasing the task difficulty by reducing the contrast level or the state of background adaptation can alter significantly the effects of eccentricity within this range.

Main sequence results

Although the measurements in this study employed only a small range of eccentricities, the results were found to be in direct agreement with previous reports by other investigators. Both duration and peak velocity increased systematically with increasing eccentricity, and were described by their stereotypical relation with respect to saccade amplitude known as main sequence (Bahill, Clark, and Stark 1975)
Also, large increases in variability of saccade amplitudes with increasing target eccentricity are in direct agreement with previous reports by other investigators (Opstal and Gisbergen 1989; Beers 2007; Beers 2008; Abrams, Meyer, and Kornblum 1989; Lemij and Collewijn 1989). Noisy variations occurring at the level of the motor map of superior colliculus have been suggested to cause an increase in endpoint variability (Opstal and Gisbergen 1989). However, binocular disparity can also contribute significantly to endpoint variability observed in saccade amplitudes. Usually, when saccades are made, the temporal saccade of one eye is larger than nasal saccade of the other eye (Collewijn, Erkelens, and Steinman 1988a; Robinson 1964). These studies also showed that divergent, binocular, fixation error increases with increasing eccentricity and can be as large as 3° in amplitude with saccades of 15° in magnitude. To confirm that this is the case, rightward and leftward saccades made with the right eye were examined separately. Results from the re-examined saccade amplitudes revealed that rightward and leftward saccades were indeed significantly different, $F(1,12) = 33.8$, $p < 0.005$. Figure 16 shows the means of subjects' leftward and rightward saccade amplitudes separately (worth noting again that the eye movement recordings were taken only from the right eye).

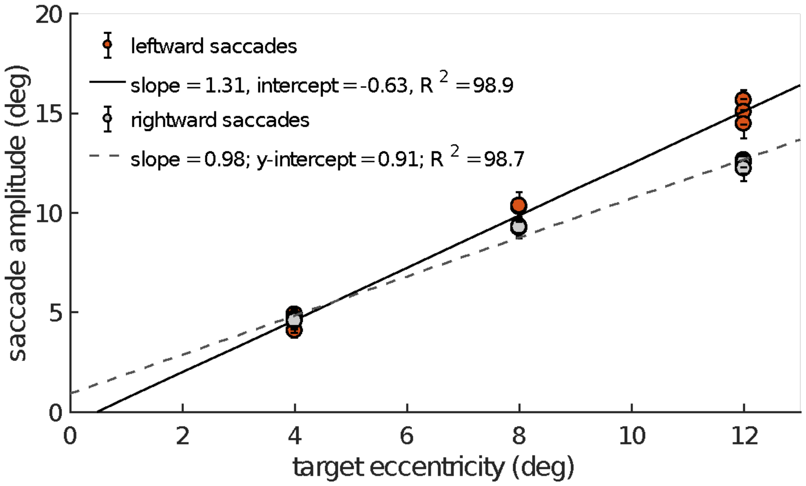


Figure 16. Amplitude of leftward and rightward saccades vs target eccentricity. Each filled red circle represents subject's overall leftward amplitude mean (black solid line is best fitting regression line). Similarly, grey filled circles represent subject's rightward amplitude mean for each target eccentricity (dotted black line is best fitting regression line). Whereas vertical error bars are representative of ±1

The results of a two way ANOVA test indicate an interaction between the target eccentricity and saccade amplitude ($p < 0.005$). Although both leftward and rightward amplitudes increase with increasing eccentricity, the effect of eccentricity is greater for leftward than rightward amplitudes. In addition, the magnitude of this difference varies with each target eccentricity, as shown in Figure 16. No significant effect was found between leftward and rightward durations $F(1, 12) = 0.15$; $p > 0.68$ or peak velocities $F(1, 12) = 1.65$; $p > 0.22$ clear indication that movements on both eyes are well synchronised despite leftward saccades made by the right eye having larger amplitudes ~3°. These results complement the assertions of (Yang and Kapoula 2003), “that binocular coordination of saccades is not built-in but is a process developing through visual experience and learning”. Under natural viewing, we have learned to avoid these large deviations that occur due to our eyes’ horizontal separation. Therefore, large saccades are rare, and are frequently accompanied by head movements.

Post saccadic visual processing time (T3)

The results for post saccadic visual processing time showed clearly that T3 also increases with target eccentricity. These increases were found to correlate significantly with increased variability in saccade amplitudes. While the increases in T3 for 4° and 8° eccentricity did not reach significance, T3 increased significantly with targets presented at 12° eccentricity. This trend mirrors the deviations between the amplitudes of leftward and rightward saccades as shown in Figure 16. It appears that the mechanisms of vergence that our visual system uses to minimise these divergent fixation errors become less accurate when saccade magnitude rises. Collewijn, Erkelens, and Steinman (1988a) have demonstrated clearly that misalignment between the two eyes can persist after the saccade has ended. They argued that binocular vision is not compromised, as this will be further corrected by a pre-programed post saccadic vergence drift that will occur 20ms after the saccade has ended. The reason as to why post saccadic vergence begins only after a short period saccade has ended remains unclear. It has been demonstrated that in these instances post saccadic vergence drift will cause the fovea from each eye to shift towards the target i.e. the eyes will converge, and the amount of this shift will be different for each eye (Collewijn, Erkelens, and Steinman 1988a)

The fact that during the instances when eyes are not properly aligned at the end of saccade, there is an ongoing movement as we attempt to bring (i.e. align) the point of interest to the fovea of each eye, could explain why T3 durations become longer with increases in fixation errors. In our case, the vergence signal was not available as the recordings were taken only from one eye (i.e., the right eye). Thus, one can only assume that post saccadic vergence drift followed to ensure alignment of the foveas of each eye at the end of each saccade.

In addition, there are other instabilities associated with each saccade that our visual system needs to overcome. Previous studies have provided confirmation that the eyeball is not a rigid body and does not rotate as a whole during saccades. Intraocular structures, such as the iris and the lens are not rigidly attached and can move independently of the eyeball. These effects can produce oscillatory movements that outlast the saccades by as long as 30 to 40 ms (Nyström, Hooge, and Holmqvist 2013; Hooge et al. 2015; Tabernero and Artal 2014; Kimmel, Mammo, and Newsome 2012; Deubel and Bridgeman 1995b; Nyström, Hooge, and Andersson 2016). Yet, it appears that pre-programmed post saccadic vergence drift relies on these instabilities, since to correct for any misalignment, the two eyes must first come to a rest. Our results for T3 were found to be subject specific and ranged between 40-45ms for 4°, 44-54ms for 8° and 57-63ms, for 12° eccentricity. Given that T3 durations for 12° eccentricity are considerably longer than the reported oscillatory durations, it is not unreasonable to assume that these increases are due to fixation disparities. If so, this is a significant finding, as it has been already shown that saccade conjugacy also depends on viewing distance (Yang and Kapoula 2003). Since, binocular coordination depends on viewing distance, it is implied that the speed at which processing of the visual information is acquired will also be affected as fixation errors increase. Yung & Kapoula (2003) have already demonstrated that young children (4.5 – 6 years) have very poor binocular coordination at near viewing distance (20cm), with average post saccadic errors of 2° in magnitude. Adjustment for viewing distance is essential for optimization of binocular coordination, although this may have implications for reading performance in very young children. Present results have demonstrated that target eccentricity, does indeed affect post saccadic visual processing time. Therefore, it would be of importance to establish in future studies how post saccadic visual processing time varies with viewing distance, since this effect may be important in visual ergonomics.

Conclusion

In this study, I have examined how each component that contributes to the measured ISL thresholds depends on target eccentricity. The results demonstrate that the variability in saccade end points is associated with lack of binocular coordination. As target eccentricity increases, variability in saccade amplitude (i.e., accuracy) also increases, resulting in fixation errors. These fixation errors can influence the time needed to process the visual stimulus and in the case of this study, to register the position of the gap. In order to minimise the errors expected for larger saccades, the effects of target eccentricity should be considered when designing future studies, particularly when head movements are restrained by using a chin rest. To minimize the errors associated with larger saccades, the decision was taken to use an eccentricity of 8 throughout the studies described in this thesis.

Additionally, post saccadic oscillatory movements can also influence the post saccadic visual processing time; this is the focus of the next chapter which describes the observed oscillatory movements in detail.

2.7 Stimulus contrast

When a visual target is presented on a uniform background field, its contrast is determined by the relative change in luminance against the background. Target contrast is an important variable in psychophysical studies as it strongly affects visual performance. Its effects are well established and understood. Neurophysiological recordings have provided clear evidence that signals generated in early visual areas, such as retina, LGN and V1, are strongly dependent on stimulus contrast and polarity (Oram 2010; Debecker and Zanen 1975). These studies have shown that their response latency increases as stimulus contrast decreases. Similar findings have also been reported for visual neurons in superior colliculus. As contrast can affect retinal transduction times (Barbur, Wolf, and Lennie 1998), this in turn can influence visual responses generated in the superior colliculus. Bell (2006) demonstrated clearly the relationship between changes in neural activity in the intermediate layers of superior colliculus and stimulus intensity. It was shown that with high-intensity stimulus, onset latency responses are reduced and the activity for saccade responses begins sooner, resulting in faster reaction times.

There is ample evidence from psychophysical experiments to show that higher intensity stimuli produce faster response times. In addition, studies have provided evidence that the accuracy of perceptual judgment relates closely to the intensity of visual stimuli (Reddi, Asrress, and Carpenter 2003; Palmer, Huk, and Shadlen 2005). In instances such as discriminability (Lupp, Hauske, and Wolf 1976; Hamerly, Quick, and Reichert 1977; Barbur, Wolf, and Lennie 1998), detection (Pins and Bonnet 2000) and visual search tasks (Näsänen, Ojanpää, and Kojo 2001; Verghese and Nakayama 1994), performance has been shown to improve significantly with stimulus contrast. In fact, the study by (Näsänen, Ojanpää, and Kojo 2001) demonstrated that during visual search tasks when subjects were asked to find a letter buried within an array of numerals, not only did performance related to response latency and number of fixations improved significantly, but fixation duration time also decreased with increasing contrast. In addition, these studies have also shown that at higher stimulus intensities performance becomes asymptotic, whereas at low intensity levels, as uncertainty in detection of the presence of stimulus increases, variability in response times also increases. Therefore, as stimulus contrast is an important variable in influencing subjects' performance, preliminary tests were conducted to inform on the effect of stimulus contrast on ISL and decision response times.

2.7.1 Experimental setup

Two experimental conditions were employed to aid selection of stimulus contrast. The first experiment was designed to measure the subjects' thresholds for simple reaction time (RT), while the second experiment investigated how stimulus contrast affects ISLs. The measurements were taken for a number of stimulus contrasts (i.e., 15, 25, 50, 75 and 100%). The decision to also measure RTs in conjunction with ISL measurements was made because both measures reveal how fast a response is initiated following the onset of a visual target. Both measurements were obtained using EMAIL test. To allow for a more direct comparison of the results, target arrangements (target size, background luminance, eccentricity and viewing distance) were kept unchanged for both experiments.

Subjects

Two female subjects completed five repeat measurements for Reaction Time (RT) and ISL for a number of stimulus contrasts. The stimuli had negative contrast polarity and contrasts were expressed as a Weber fraction (i.e., $C = L_t/L_b - 1$). The subjects were free from known medical conditions and had normal or corrected-to-normal visual acuity.

2.7.2 Method and procedure

Both measurements were obtained using EMAIL tests. The visual target employed on this round of the experiment consisted of crowded Landolt ring, as the one described in section 2.3.2. The subject viewed the display from a distance of 80 cm. Head movements were minimized using a chin rest. A uniform background with a luminance of 32 cd/m² and target eccentricity of ± 8° along a horizontal meridian were used throughout. Thresholds were measured with stimuli of 15, 25, 50, 75 and 100% contrast. The stimulus duration was controlled by 2-down-one up procedure, with an initial starting value of 300 ms. Each block ended after 64 reversals.

Each subject completed five repeat measurements for a given contrast for both RT and ISL. Whereas for ISL task the subject is required to generate eye movement towards the peripheral target (as described in section xx), in the RT task the subject is only required to give a response by pressing the central button of the bespoke numeric keypad (Figure 4) as soon as peripheral target in detected.

2.7.3 Results

Subjects’ mean threshold from five repeat measurements for each contrast level are shown in Table 4

Figure 17(a) shows subjects’ mean thresholds for RT and 17 (b) mean threshold for ISL. The best line of fit produced a nonlinear relationship for both measurements. The plots show clearly that both RT and ISL show an asymptotic behaviour with higher contrast levels, with little or no improvement above 50% contrast. The opposite is the case at low contrast levels when the both RTs and ISLs increase rapidly as the stimulus contrast is reduced below ~ 25% (see Figure 17).

Table 3. Threshold measurements for RT and ISL.

	Subject 1				Subject 2			
Contrast	RT	2*SE	ISL	2*SE	RT	2*SE	ISL	2*SE
15.0	403.1	9.8	297.8	8.3	380.0	8.3	348.0	7.7
25.0	313.9	4.4	241.0	4.4	327.9	4.9	249.8	5.9
50.0	304.4	5.2	198.1	4.7	294.9	4.8	218.6	3.6
75.0	299.4	3.9	186.2	2.9	288.4	4.5	213.9	4.9
100.0	287.4	4.4	172.0	4.3	293.3	4.7	192.1	5.4

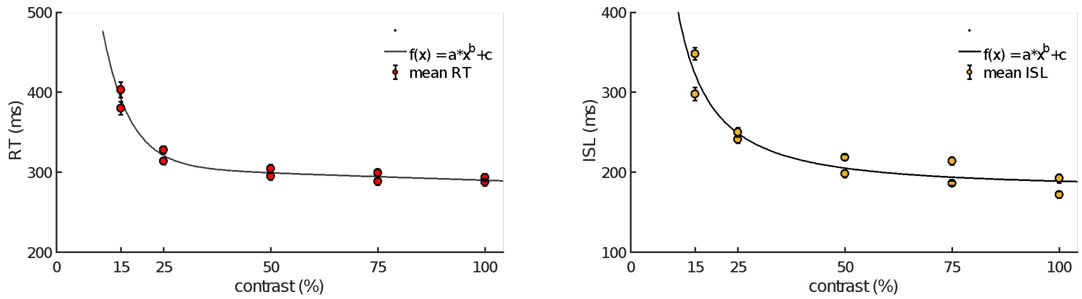


Figure 17. RT and ISL thresholds. Plot (a) shows subjects’ RTs with ±2SE. Similarly plot (b) shows subjects means for ISL thresholds. Best line fit (power regression) shows clearly that both RT and ISL thresholds start to increase rapidly when stimulus contrast decreases below 25%. Whereas above 50% reaches asymptotic level.

2.7.4 Discussion

These experimental findings demonstrate nonlinear relationships between stimulus contrast and the responses measured. Rapid increases found in response times for both RT and ISL at lower contrast levels, and the asymptotic behaviour with higher contrast levels (<50%), are in direct agreement with previous reports by other investigators. Present experiments also demonstrate that these two different behavioural responses are equally influenced by stimulus contrast, as shown in Figure 17. As both responses are triggered by the same visual input, i.e. onset of the peripheral target, this finding is consistent with suggestions that the relationship between the response and contrast level could reflect the receptor activities of visual system in relation to stimulation (Pins and Bonnet 2000).

ISL responses capture the fact that saccadic eye movements are the fastest oculomotor responses. Humans make 2-3 saccades every second, depending on these movements to guide our behaviour, as new visual information is acquired with each saccade.

Based on present results, the decision was taken to employ a stimulus contrast above the range at which asymptotic level emerged, which is at around 50% for both RT and ISL, as shown in Figure 17. A contrast value above which little or no improvement in RT and ISL times will ensure that within/or inter subject variability is minimised, To fulfil this requirement, a stimulus contrast of 75% was selected for use throughout this study.

3 The Effects of Post Saccadic Eyeball / Lens /Oscillations on Visual Processing Times

Abstract

The integration and processing of visual information takes a finite time, yet the acquiring of visual information appears to be so simple, seamless and effortless, something most of us take for granted. Our eyes are very mobile, moving continuously. Humans generate saccades up to three-times every second, searching our surrounding environment and acquiring new information. Each saccadic eye movement causes the light pattern to shift across the retina and owing to mechanisms of saccadic suppression the retinal signals generated do not immediately reach and trigger our awareness. During saccades our vision is largely suppressed and we can only see with high resolution when the object of interest in the visual scene is imaged and stationary on the very centre part of the foveal region. This is what is required in order to enable effective processing of the visual information to take place. In addition, it has been shown that with each saccadic eye movement - as the eye undergoes rapid acceleration - the eyeball does not move as a whole. Instead, different internal ocular structures such as the iris and the lens move relatively independently with respect to the optical axis. Also, as the eye stops abruptly at the end of each saccade, the mechanics of the system ensure that these internal structures sustain oscillatory movements that last well beyond the end of the saccade. It has been shown that sustained lens oscillatory movements produce retinal image shifts which can cause poor post-saccadic visual acuity. This being the case, post-saccadic visual integration times might well be affected by these oscillatory movements in addition to binocular

fixation errors that may occur due to the eyes horizontal separation. In this study, I present a novel method to quantify the post-saccadic visual integration times and investigate whether post-saccadic oscillatory movements detected, at least in part, with the video-based eye-tracking system employed in this study, can also account for the measured integrated saccade latency times.

3.1 **Introduction**

Given that only a very small region of the visual field that is imaged at the very centre of the retina and corresponds to the point of regard, can mediate high visual acuity, it follows that saccades are needed to bring the point of interest onto the central foveal region. Following each saccade, the retinal image is kept in focus by the crystalline lens which changes its shape appropriately through forces that are applied to it through the ciliary muscles. Nearly a quarter century has passed since Deubel and Bridgeman (Deubel and Bridgeman 1995a) used a fifth generation Dual Purkinje Image (DPI) eye-tracker, simultaneously with a scleral search coil technique. The results presented evidence to show that the eyeball is not a rigid body and does not rotate as a whole during saccades. Instead, each saccade produces large lens deviations which in turn, cause small changes in the optical axis of the eye. At the beginning of the saccade when the eye starts to accelerate, the lens lags behind, whereas when it reaches its final position (i.e. at the end of the saccade) it overshoots, at which point it is pulled back by passive elastic forces produced by zonule muscles (Deubel and Bridgeman 1995a). As a result, during each saccade a lens oscillatory movement is produced with magnitudes that are dependent on the elasticity of the zonule muscles and the lens. Deubel and Bridgeman also described the perceptual consequences of lens overshoot and proposed that for each degree of saccade~~,~~ there will be a retinal shift of 0.03° (Deubel and Bridgeman 1995b). Moreover, they also proposed that one of the functions of saccadic suppression is to prevent the perception of image shifts caused by movements of the lens.

Soon after, similar post-saccadic oscillatory movements were also detected using the pupil reflection method by Inhoff and Radach (1998), which proposed that similar elastic forces may also apply to pupil centre changes, whereby the fluid in the anterior chamber of the eye and pupil may lag behind at the onset of saccade, whereas at the end of the saccade when the eye stops, it will cause the pupil to move briefly towards the saccade direction, overshooting and oscillating around its final position before coming to rest.

These post-saccadic instabilities have captured the attention of the vision research community only recently, and are referred to as post-saccadic oscillations (PSOs).

The PSOs being a consequence of ocular instability due to the interocular structures i.e. iris and lens moving independently to the eyeball, have now been fully acknowledged (Nyström, Hooge, and Holmqvist 2013; Hooge et al. 2015; Nyström et al. 2015; Tabernero and Artal 2014; He et al. 2010; Hooge, Holmqvist, and Nyström 2016; Kimmel, Mammo, and Newsome 2012; Nyström, Hooge, and Andersson 2016; Deubel and Bridgeman 1995a). The recent experimental study done by Tabernero and Artal (2014), using a newly-designed device called the Dynamic Purkinje-meter have demonstrated clearly how the lens can indeed sustain inertial oscillatory movement with 9° saccades, that can last beyond 50ms. In their study they also estimated the retinal image displacement using a ray-tracing technique and reaffirmed the perceptual consequences of lens wobble already described by Deubel and Bridgeman (Deubel and Bridgeman 1995b). Their findings show that the lens decentration amplitude of only 0.3mm can generate retinal shift as large as 88 microns, which equates to 20 min arc in visual angle. During this short duration, the corresponding movements of the retinal image can produce very poor post-saccadic visual acuity of 0.05 decimal which is equivalent to 20/400.

The PSOs are also clearly captured with video-based eye-trackers such as the EyeLink 1000Hz (Nyström, Hooge, and Holmqvist 2013; Hooge et al. 2015; Kimmel, Mammo, and Newsome 2012; Nyström et al. 2015; Nyström, Hooge, and Andersson 2016), however as previously mentioned, these PSOs do not capture the lens wobble since video-based eye-trackers use the pupil centre and corneal reflections (i.e. pupil minus cornea) to estimate the gaze direction. Thus, these PSOs are the result of the displacement of pupil centre relative to the eyeball as well as the eyeball oscillations which affect the specular image generated by reflection from the cornea. As the eye undergoes rapid acceleration during the saccade, the iris trembles due to inertial oscillation of fluids in the anterior chamber allowing the pupil to move relative to the eyeball (Nyström, Hooge, and Andersson 2016; Kimmel, Mammo, and Newsome 2012; Inhoff and Radach 1998) in a similar manner to the lens.

While these studies attribute the PSOs to interocular structures of the eyeball, the studies that made use of search coil technique have also provided evidence that the eye does not come to a rest abruptly at the end of saccade. Robinson (1964) has recognised that saccades are indeed always associated with overshoots and ringing because the pulse force to initiate the movement is always larger than needed to overcome the viscosities of the eyes orbital tissues and the muscles. Accordingly, the study done by (Bahill, Clark, and Stark 1975) confirmed that overshoots have neural origin but more importantly, they also provided evidence that there is a close relationship between the eye velocity and the overshoot and have demonstrated that the post movement can be characterised based on velocity profiles. Usually overshoots produce return velocities by an order of 10 to 100deg/sec while post saccadic vergence drifts that are recognised to be small to compromise visual acuity (Optican and Miles 1985; Collewijn, Erkelens, and Steinman 1988a) have much smaller velocities by an order of 2 to 20deg/sec. It is surprising that these studies have made no remarks if the observed overshoots will cause any perceptual consequence given that it is well established that when the eye undergoes such high velocities small visual targets will be rendered invisible (Burr and Ross 1982).

As one can see, there is ample of evidence that there is an ongoing movement after the end of saccade and depending on a tracking technique being employed, they each describe the post saccade instabilities through different ocular structures i.e. scleral search coil - eyeball, EyeLink - pupil and DPI - lens. It is important to note that there are striking similarities between the coil and video based eye trackers when describing the movements observed at the end of saccades. Usually, when lens oscillatory movements are described, no directional asymmetries are mentioned whereas both the overshoots and PSOs are associated with directional asymmetries. The oscillatory movement of an abducting eye is consistently found to be smaller than that of the adducting in both coil and video techniques of tracking (Hooge et al. 2015; Bahill, Clark, and Stark 1975; Optican and Miles 1985). Importantly, there is an indication that PSOs are also closely related to the deceleration phase of saccades (Kimmel, Mammo, and Newsome 2012) which makes it possible that both PSOs and overshoots are the same, they only each represent different ocular structures pupil vs eyeball. Since video-based eye-trackers such as EyeLink 1000 are now widely used in laboratories, it is of great importance to have a method by which post-saccadic visual integration time can be quantified given that visual search heavily depends on eye movements. This could also provide us with the opportunity to examine the extent to which PSOs produced by video-based eye-trackers such as EyeLink 1000 can describe the perceptual consequences of retinal image movements caused by eyeball, pupil and lens oscillations and predict how visual search performance is affected.

3.2 **Method and Procedure**

All procedures were approved by Research Ethical Committee of City, University of London and all s gave their written informed consent and had normal or corrected to normal vision. Seven subjects ranging from 21 to 45 years took part in this experiment. All experiments were conducted in a darkened room and the head position stabilised with a chin rest at a viewing distance of 80cm.

As explained in chapter 2, (section 2.2.3) there are two parts to this experimental procedure: (1) measure the integrated saccade latency values (ISL) using EMAIL test program, and (2) make use of these values on a modified version of the EMAIL test~~,~~ while the eye movement recordings are taken. Whereby the stimulus presentation times were selected to fall above and below (± 20ms) of the subject premeasured ISL time. The testing was completed in one-session, during which time, each Subject completed three-trials in succession. For this round of experiments, the visual stimulus was presented peripherally at 8° eccentricity randomly on either side of a fixation point with contrast level set at 75%.

3.2.1 Data Analysis and Estimation of Post-saccadic oscillations

A custom made Matlab program (described in more detail in Chapter 2) was used for off-line analysis of data taken from the eye-tracker (i.e. EDF output files), as well as EMAIL test (i.e. XML output files). Because the ISL values are subject specific, the data were analysed on an individual basis. To measure the subjects' performance levels with respect to stimulus duration times (ISL ± 20ms), a Weibull function (as described in section 2.3) was used to fit the data, whereas the measurements from T1 and T2 were obtained from eye movement recordings. Only the saccades that corresponded to correct responses were used for analysis.

The approach taken in this study determines the PSO durations from incorporating subject's velocity data. There are two reasons for including velocity data on the PSO analysis. Firstly, the eye velocity will help determine the point at which the eyeball comes to a rest (i.e. end of PSO). Secondly, as noted in the introduction, it is the eye velocity that characterises the post movement (i.e. it can distinguish the post saccadic vergence drift movement from the overshoot). Before explaining the results, it is helpful to note the terminology used when considering the observed post movement in both saccade trajectories and velocity profiles. There are two distinguishable movements that occur with each post saccadic movement: the first is the fast oscillatory movement that has velocities of higher than 20deg/sec and the second is a slow moving post oscillatory drift with velocities bellow 20deg/sec. The velocity following the end of saccade will be referred to as the return velocity.

To estimate the durations when the eye comes to a rest after post saccadic oscillations, first the saccade and velocity mean profiles were extracted for each Subject. Normally, there is within-Subject variability for saccadic latency (i.e. the time between the onset of the stimulus and the start of the saccade) and as a result, saccade onset changes from trial to trial. To overcome this, the data from each trace were first aligned, so that the starting point of a saccade began 10ms earlier than saccade onset. By applying this alignment method, the mean for both saccadic and velocity trajectories were obtained for each Subject. Figure 18 shows individually aligned post-saccadic trajectories from rightward and leftward eye traces from one trial. As Figure 18 shows, the post movement is clearly reproducible with each trial and resembles the aspects of a damped oscillator. Also, as can be noted the oscillatory movement produced by leftward saccades is larger when compared to rightward saccades, and so too are their corresponding return velocities. This observation is found to be consistent across all Subjects tested and it confirmed previous reports made by other investigators that the PSO of the abducting eye is smaller than that of the adducting eye. The figure clearly shows that both PSOs and their corresponding return velocities (i.e. eye velocity after the end of saccade) are very reproducible and the shape of the mean trajectory in all plots is similar to the shapes of the thin grey lines. Rather than showing both leftward and rightward traces to explain the tight relation between the return velocity and PSO as well as in what way the end of PSO was defined, the example taken bellow presents the mean trajectories only from rightward saccades.

As Figure 19 shows, when the first zero crossing in the velocity profile occurs (plot b), this determines both the maximum displacement of the eyeball (i.e. saccade end point), as well as its duration. As it can be seen, when the first zero crossing occurs there is an ongoing movement, but in the opposite direction (i.e. start of the return velocity). Since the slope of the tangent at any point in the saccade trajectory will equal the velocity of the eyeball at that point, any change on the direction of the movement is clearly reflected on both plots. When max (black dots) or min (blue dots) peaks occur in saccade trajectory the tangent is a horizontal line, meaning $f'(x) = 0$, therefore the velocity at these points crosses zero. Also, both plots illustrate clearly that there is 90° phase difference between the eye position and velocity. When the eye position is at maximum, velocity is passing through zero and vice versa. Note that, when the maximum peak occurs in the saccade trajectory after the saccade has ended (plot a), this corresponds to a period of one-cycle that return velocities produce. Once the cycle is complete the eye approaches its mean position. During this phase the eye velocity retains vergence velocities (smaller than 20deg/sec) before terminating around zero crossing which also defines the end of post saccadic movement. This pattern of post movement is consistent across all Subjects tested. In addition, since the aim of the study is to determine if the observed PSOs with video based eye trackers can also provide account for perceptual consequences associated with lens oscillatory movements, in the results section only the post movement starting 10ms before the end of saccade will be presented.

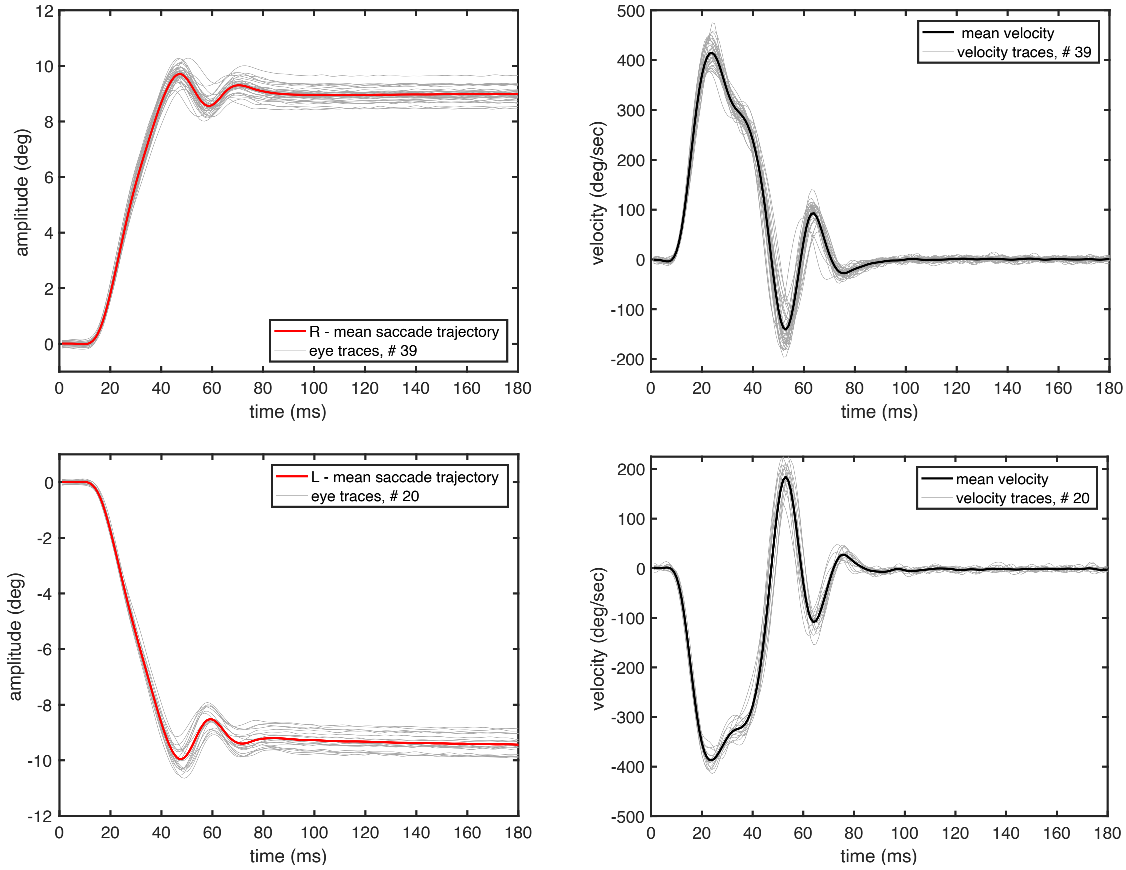


Figure 18. Aligned saccade and velocity trajectories. Data were aligned 10ms before saccade onset. Grey lines are individual eye and velocity traces. The red line in saccadic traces represents the mean of 39 rightward and 19 leftward saccade trajectories. Similarly, the black line in velocity plots represents the mean of 39 rightward velocity traces and 19 leftward velocity traces respectively.

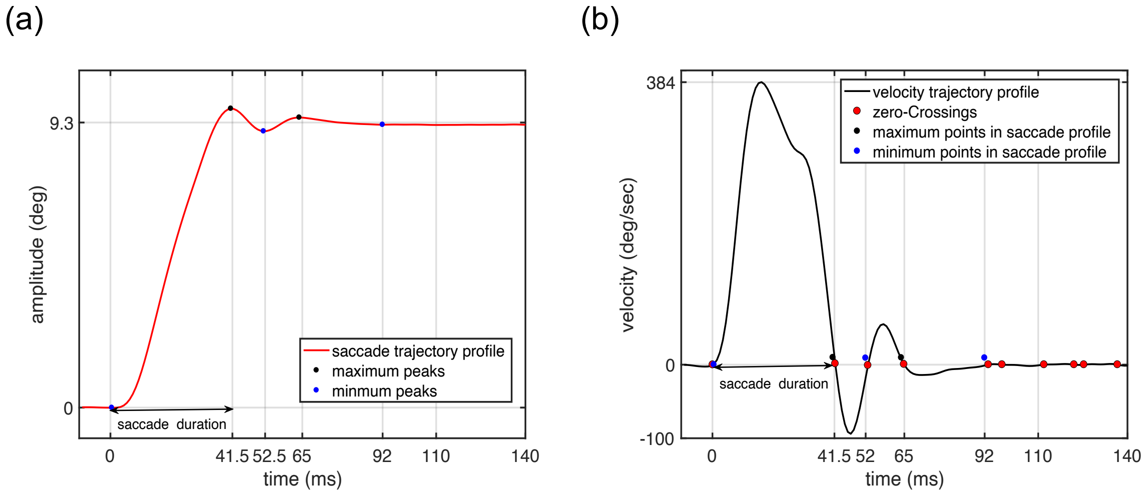


Figure 19. Mean saccade trajectory and velocity profile. The occurrences of max (black) and min (blue) peaks precisely coincide with zero crossings indicated by red dots. As one would expect there is a phase difference of $\frac{\pi}{2}$ between the saccade trajectory and velocity and zero when the eye comes to a rest.

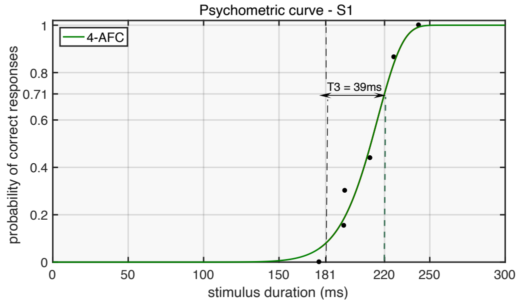
3.2.2 **Results**

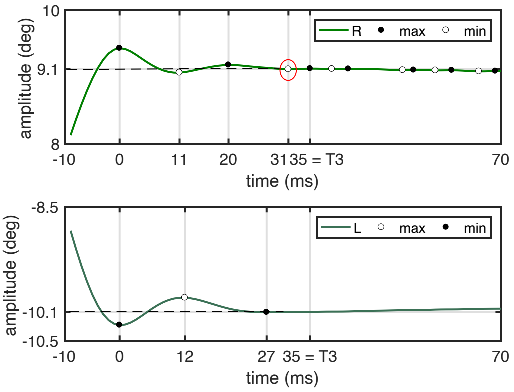
The measured parameters including T3 (post saccadic visual processing time = T3) values are shown on Table 4. Second column presents Subjects T0 measurements estimated from Subjects' psychometric curves. These values were found to be rather consistent and ranged between 209-220ms. The last two-columns in the table present Subjects estimated T3 values and PSO durations respectively. As indicated on the table, T3 values are Subject-specific with duration times ranging from 35-53ms (Table 14). Similarly, the PSO durations were also found to be Subject-specific with some Subjects having higher damping than others. Figure 20 shows Subjects leftward and rightward PSOs and their corresponding psychometric curves arranged depending on the length of the Subject's T3 durations - shortest to longest. As figure shows, T3 across all Subjects occurs following the end of PSO (indicated by red circle) and reveals that visual processing is accomplished only after the eye has reached its mean position (i.e. eye velocity is at 0). A significant positive correlation between these two variables $r(6)=0.91$, $p<0.005$, which provides clear indication that T3 is dependent on PSO duration. As it can be noted, the larger the PSO is, the longer it takes for the eye to reach its mean position.

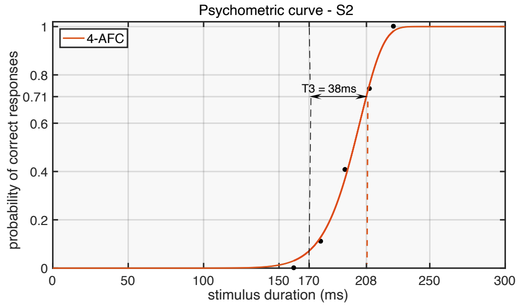
Also, across all subjects, leftward saccades produced larger oscillatory movement confirming previous accounts by other investigators that PSOs are not symmetrical in both directions. Importantly, as can be noted they also have longer phase durations when compared to rightward saccades which indicates that during PSOs there will also be asynchrony of action between the two eyes. This observation has been described before and the post saccadic movement is recognized to be monocular phenomenon (Robinson 1964; Optican and Miles 1985; Collewijn, Erkelens, and Steinman 1988a; Bahill, Clark, and Stark 1975). In addition, as was noted above (fig 18) during the oscillatory movement, the Subjects return velocities are also very high and from previous studies we have clear evidence that although visual sensitivity would be maintained at high velocities, the ability to resolve fine spatial details would be greatly affected (D C Burr, Morrone, and Ross 1994; David C. Burr and Ross 1982). These observations provide clear indication that PSOs could indeed bear perceptual consequences in particular since T3 succeeds only after the eye reaches its mean position i.e. eye velocity is within zero. To confirm that this is the case, a new set of experiments were employed to directly estimate the rate at which visual processing can be performed in the absence of the eye movements. Providing that PSOs do not delay processing of visual information, then one would expect T3 to be equal to the time needed to process visual information in the absence of the eye movements.

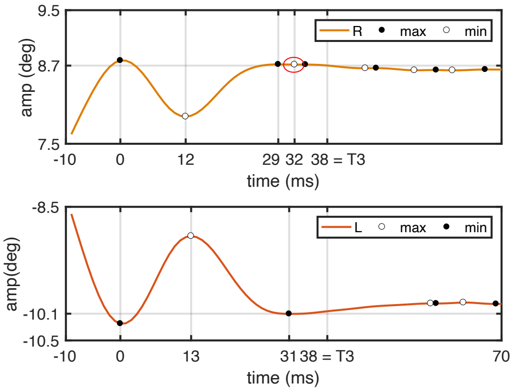
Table 4. Measurements of saccade parameters including ISL values and PSO durations. ISL values were derived from psychometric curve for 71% correct responses. The saccadic parameters; amplitude, T1 and T2 represent the mean values from eye movement recordings during three tests.

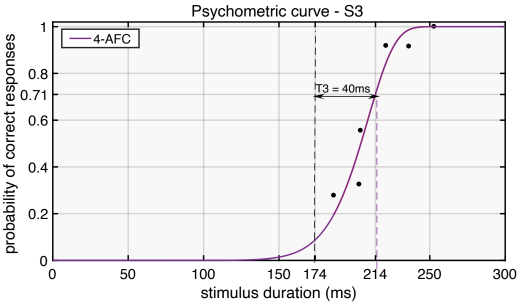
	ISL (T0)	Amplitude	Latency (T1)	Duration (T2)	T3 T0 - (T1+T2)	PSO
Subject 1	220 ms	9.8°±0.6°	140 ±9.6	44.9±0.6	35 ms	31 ms
Subject 2	209 ms	8.8°±0.7°	130±4.6	41.6±1.6	38 ms	31 ms
Subject 3	214 ms	8.9°±0.4°	130±4.8	44.8±0.5	40 ms	35 ms
Subject 4	211 ms	9.6°±0.6^0	126±3.2	41.0±1.2	44 ms	34 ms
Subject 5	214 ms	8.1°±0.5°	116 ±6.5	43.7±0.5	53 ms	45 ms
Subject 6	209 ms	9.3°±0.3°	120±3.5	41.0 ±0.7	48 ms	47 ms
Subject 7	214 ms	9.3°±0.6°	121±1.6	41.8±1.1	51 ms	45 ms

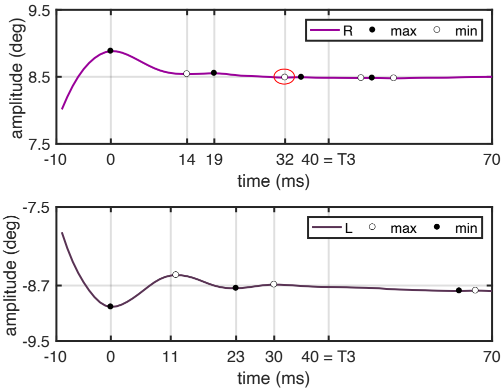


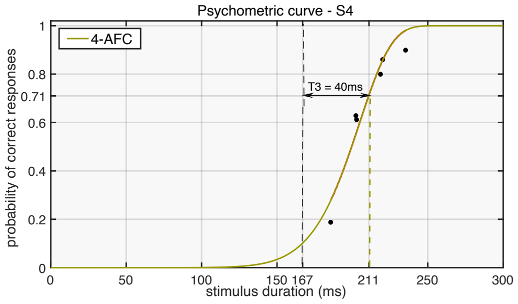







Psychometric curve - S3
4-AFC
T3 = 40ms
probability of correct responses
0
0.2
0.4
0.6
0.71
0.8
1
0
50
100
150
174
214
250
300
stimulus duration (ms)


R
max
min
amplitude (deg)
9.5
8.5
7.5
-10
0
14
19
32
40 = T3
70
time (ms)
L
max
min
amplitude (deg)
-7.5
-8.7
-9.5
-10
0
11
23
30
40 = T3
70
time (ms)


Psychometric curve - S4
4-AFC
T3 = 40ms
probability of correct responses
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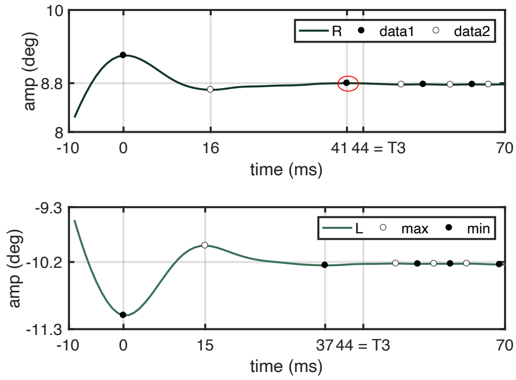
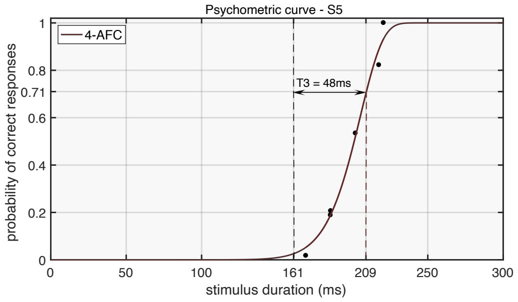
0.2
0.4
0.6
0.71
0.8
1
0
50
100
150
167
211
250
300
stimulus duration (ms)


R
data1
data2
amp (deg)
10
8.8
8
-10
0
16
41
44 = T3
70
time (ms)
L
max
min
amp (deg)
-9.3
-10.2
-11.3
-10
0
15
37
44 = T3
70
time (ms)


Psychometric curve - S5
4-AFC
T3 = 48ms
probability of correct responses
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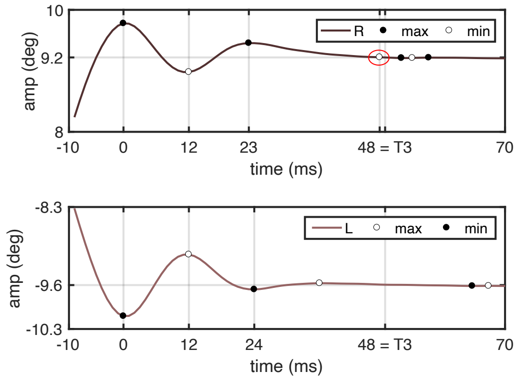
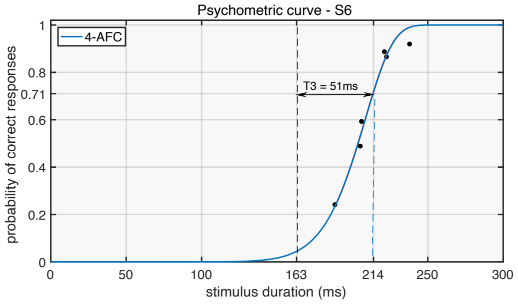
0.2
0.4
0.6
0.71
0.8
1
0
50
100
161
209
250
300
stimulus duration (ms)


R
max
min
amp (deg)
10
9.2
8
-10
0
12
23
48 = T3
70
time (ms)
L
max
min
amp (deg)
-8.3
-9.6
-10.3
-10
0
12
24
48 = T3
70
time (ms)


Psychometric curve - S6
4-AFC
T3 = 51ms
probability of correct responses
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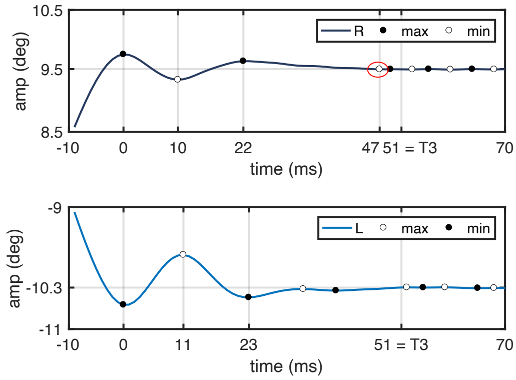
0.2
0.4
0.6
0.71
0.8
1
0
50
100
163
214
250
300
stimulus duration (ms)


R
max
min
amp (deg)
10.5
9.5
8.5
-10
0
10
22
47
51 = T3
70
time (ms)
L
max
min
amp (deg)
-9
-10.3
-11
-10
0
11
23
51 = T3
70
time (ms)

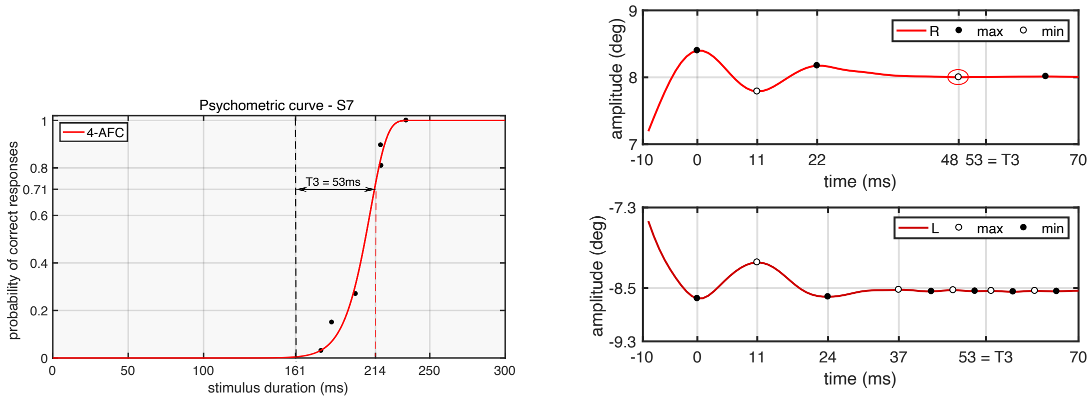


Figure 20. Psychometric curves and PSO profiles. Each plot on the left represents Subjects' psychometric curve and their corresponding left/rightward PSO profiles obtained from averaged saccades starting 10ms before the end of saccade are shown on the right. The dashed black line in psychometric curves indicates saccade offset duration whereas dashed coloured lines indicate durations for T0. Note, that stimulus durations across the Subjects are within the range of 208 to 220ms.

The y-axis on PSO plots is limited to 2 degrees so the post saccadic oscillations can be easily seen. The zero time on each plot corresponds to the end of saccade. The end of PSO in each plot is indicated by red ellipse. As can be noted T3 always occurs after end of PSO, i.e. the eye has approached its mean position. T3 values estimated from psychometric curves T0 - (T1+T2) are indicated in x-axis.

In the previous chapter it was acknowledged that visual response is a variable quantity and depends on physical properties of visual stimulus - i.e. higher contrast stimuli will evoke faster responses. With this in mind, a number of stimulus contrast levels: 15, 25, 50, 75, and 100% was employed under two-conditions. For the first-condition, the visual stimulus was presented centrally at 0° eccentricity to obtain the T0 values for each contrast level. For the second condition, the same measurements were repeated, but the visual stimulus was presented peripherally at ±8° eccentricity with respect to the central fixation point.

Although the experiment is attractive, the hardware employed in the EMAIL test limits the shortest stimulus time that can be presented to two frames (~25ms). This is simply because each frame lasts 16.66ms, but the display luminance decays in each frame within ~8ms. While this may seem like a short stimulus time, it has been shown that the visual system can process and extract the correct gist from a complex scene, with presentation times as short as 20ms (Thorpe, Fize, and Marlot 1996). However, as the time needed to gain enough information to process the visual stimulus increased above 25ms with lower contrast stimuli, it was possible to measure T0 values accurately in central vision for stimulus contrast level only at 15%. It was actually this observation that provided a direct measure of the effect of PSOs on visual processing time. This relatively simple measurement acts as a reference to identify the difference between the visual processing time when the eye movements are involved.

3.2.3 Results for 8° and 0° eccentricity

The measurements for each contrast level are shown in Table 5 and superimposed psychometric curves obtained from various stimulus contrast levels (i.e. 100, 75, 50, 25 and 15 %) are shown in Figure 21. As expected, higher contrast stimuli will evoke faster responses, thus produce shorter visual processing times, i.e. rightward shift with higher contrast stimuli. For each stimulus contrast employed, the Subject's performance level with respect to stimulus duration times was obtained from psychometric curves as indicated in Figure 22. As noted earlier, due to hardware limits T0 at 0° eccentricity was only measured for stimulus contrast at 15% and its corresponding psychometric curve is shown in Figure 23.

Table 5. Contrast measurements for latency, duration, post saccadic processing time and PSO duration

Contrast	**ISL (T0)**	**Latency (T1)**	**Duration (T2)**	**T3 T0 -(T1+T2)**	**PSO**
100%	209 ms	132 ±9.6	39 ±1.6	38 ms	31 ms
75%	209 ms	132±4.6	42 ± 0.6	38 ms	31 ms
50%	217 ms	135±4.8	41.5 ± 0.5	40 ms	31 ms
25%	241 ms	146±3.2	41.0±1.2	53.5 ms	31 ms
15%	273 ms	167 ±6.5	41.5±0.5	75 ms	31 ms

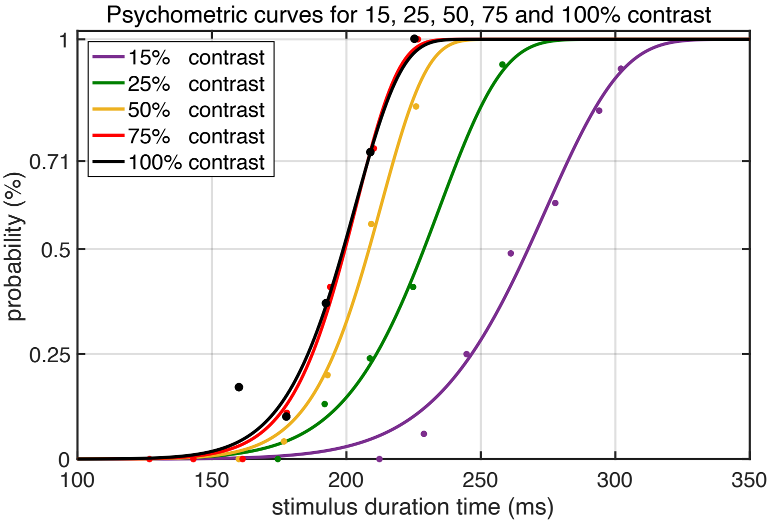


Figure 21. Superimposed psychometric curves for various stimulus contrast levels presented peripherally at ±8° eccentricity. The coloured curves show clearly how Subject's performance varies with stimulus contrast level. As the contrast level decreases, the time needed to achieve same performance level increases, which can be clearly seen as a rightward shift. Also, the figure clearly depicts that higher contrasts do not contribute to further improvement in the measured response times – i.e. the performance level for 100 and 75% – is identical.

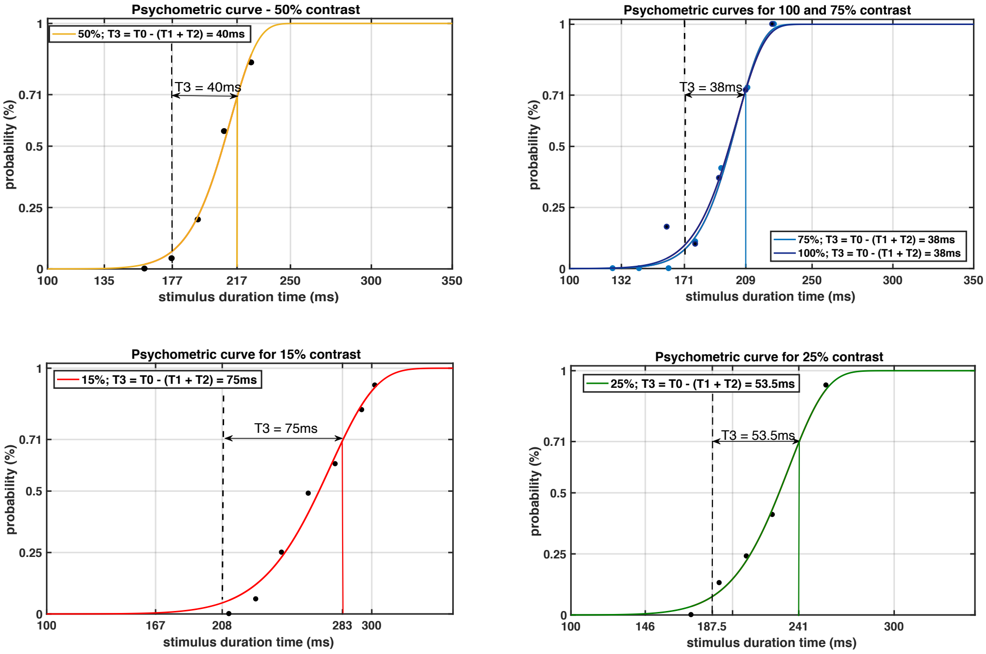


Figure 22. Subjects performance level for different contrasts. Each plot shows how measured parameters vary with stimulus contrast. Dashed line in each plot represents the end of saccade T1+T2 (latency + saccade duration). The time needed to achieve 71% correct responses T0 is represented by solid coloured line. Estimated values for T3 are indicated on top of the arrow.

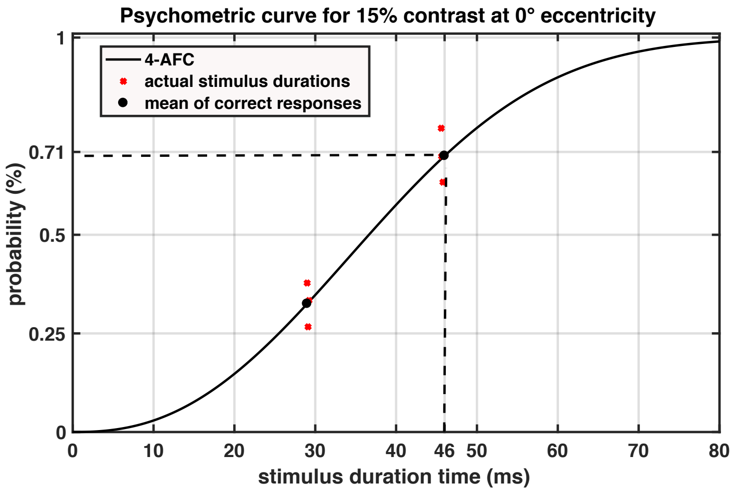


Figure 23. Psychometric curve for 15% stimulus contrast presented centrally at 0°. Red dots represent the actual stimulus durations. The time subject needed to achieve 71% correct responses is represented by dotted line. This time duration corresponds to 46ms.

Comparing T3 at 15 ° and T0 at 0° degrees, we see that time duration to preform visual analysis is 29ms longer when the eye movements are involved. This is what one would expect if the PSOs delay visual processing time. To understand how this time difference relates to the subject's post saccadic movement, it is useful to first examine the PSO profiles and their corresponding peak times. For demonstration purposes only three superimposed left/rightward PSO profiles and their corresponding velocity profiles for 75, 25 and 15 percent contrast are shown in Figure 24 (while the remaining are displayed in Appendix A).

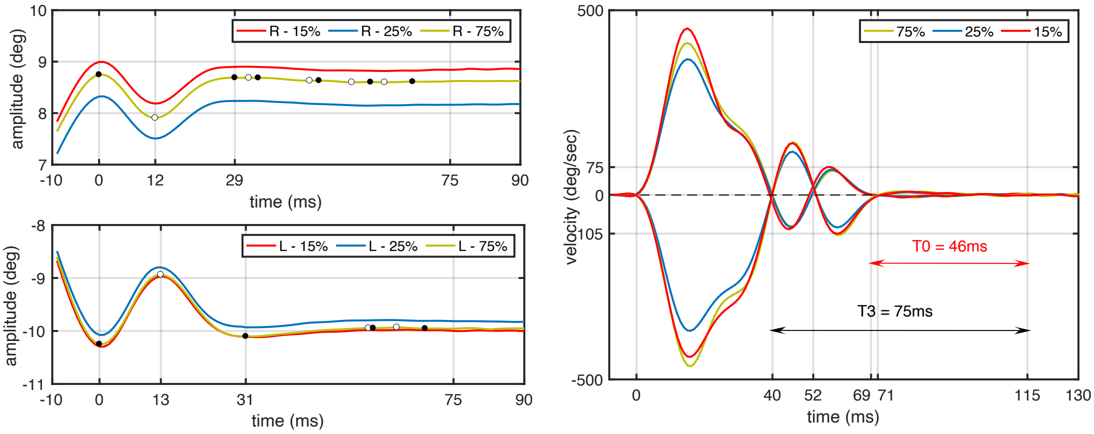


Figure 24. The PSO and velocity profiles for 75, 50 and 15 percent contrast. The traces show clearly that all three stimulus contrasts generate identical PSO profiles. Similarly, the velocity profiles are also identical and resemble the variability of PSOs. The figure on the left also depicts clearly that VIT for 0° is very close to T3 – PSO with only 2ms difference. This confirms that due to PSOs visual processing time is delayed.

Figure 24 demonstrates that the shape of waveforms for both PSO and velocity profiles does not change with contrast, except that due to within-subject variability there is slight variation in both PSO and velocity profiles. While there is a maximum difference of 0.6° between trials, the size of overshoot from its mean position remains unchanged. This is simply because the size of overshoot is proportional to return velocities. This behaviour should not be considered surprising and it is in fact what one would predict from main sequence relationship. Saccades of the same magnitude have stereotyped behaviour, therefore both saccade trajectories and velocity profiles will be consistent. Also, since the return velocities depend on saccade deceleration phase, they too will be consistent for a given eccentricity (Kimmel, Mammo, and Newsome 2012).

Importantly, as Figure 25 shows the time difference between T0 and T3, is equal to exact period of a cycle in velocity profile which also corresponds to the duration of PSO. In this occasion, as figure shows, subject return velocities reach peak velocities in excess of 100deg/sec which confirms previous measurements that only when the eye velocity falls within vergence velocity range (which is below 20 deg/sec) that visual analysis can be performed. This result provides a clear confirmation that PSOs observed with video based eye trackers can also account for perceptual consequences. In addition, since subjects PSO durations do not change with stimulus contrast, by subtracting 29ms from T3 for each stimulus contrast the values for T0 at 0° were estimated for 100, 75, 50 and 25% contrast. The relationship between VPT and stimulus contrast is shown in Figure 25 where the black line represents T3 at 8° and red line represents T0 at 0° obtained from estimated values. While the red dotted line represents the actual values for T0 at 0° that were generated by the test. Figure 25 shows that the relationship between VPT and stimulus contrast is nonlinear.

The most significant feature on this figure is that VPT time increases rapidly with lower contrast stimuli and shows asymptotic behaviour with higher contrast levels (<50%). This result reveals precisely what one would expect from visual responses in relation to contrast to reflect, because at very high contrast levels the sensitivity of the eye saturates. Also, from neurophysiological studies we know that superior colliculus receives projections directly from retina, and stimulus contrast influences visual responses generated in the superior colliculus in similar way that that neurons in early visual areas, such as retina, LGN and V1 are affected. Since latency values too can provide a direct measure as to how quickly the response is initiated in relation to the contrast, then one would expect there to be a close agreement between the responses for latency vs contrast and VPT vs contrast. Comparing the responses for latency and T3 for each stimulus contrast, we see that the difference in increase between each contrast level is equal in both measurements. The latency, T3 and T0 is plotted as a function of contrast in Figure 26. As figure shows, contrast affects all three parameters equally and verifies not only the estimated T0 values, but also confirms that PSO durations are constant. In addition, T3 – 29ms yields a value shorter than what could be presented by the test at 0° for higher contrast stimuli (Table 5) which reaffirms the fact that our visual system is indeed capable of processing visual information at a faster rate: ~10ms (DeValois, Spatial Vision January 2008) when no eye movements are involved.

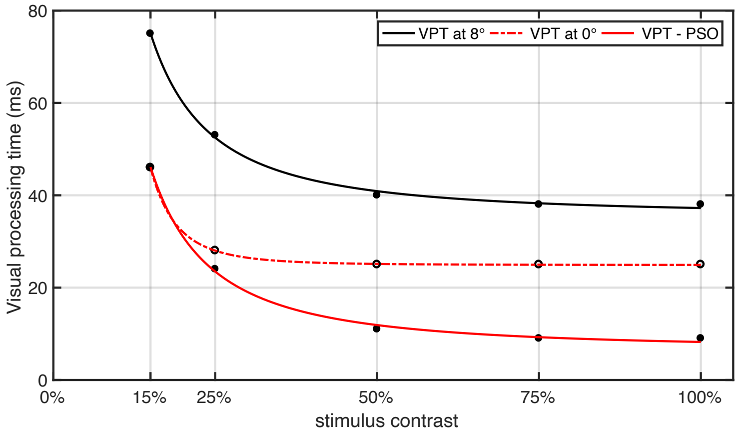


Figure 25. Visual processing time (VPT) is plotted as a function of contrast for stimulus presented at 0° (central fixation point) and ± 8° eccentricity across the horizontal meridian. The upper black solid line corresponds to T3 measurements at ±8° eccentricity and the dot-dash red line corresponds to actual VPT measurements at 0° eccentricity. Whereas the solid red line represents the predicted VPT where the values for 100, 75 and 50 and 25% contrast where estimated by subtracting T3-24ms. The data are fitted with two term power function curve $f(x) = ax^b+c$. The power function captures clearly how VPT’s vary with stimulus contrast $f(x) \rightarrow \infty$ as $x \rightarrow 0$.

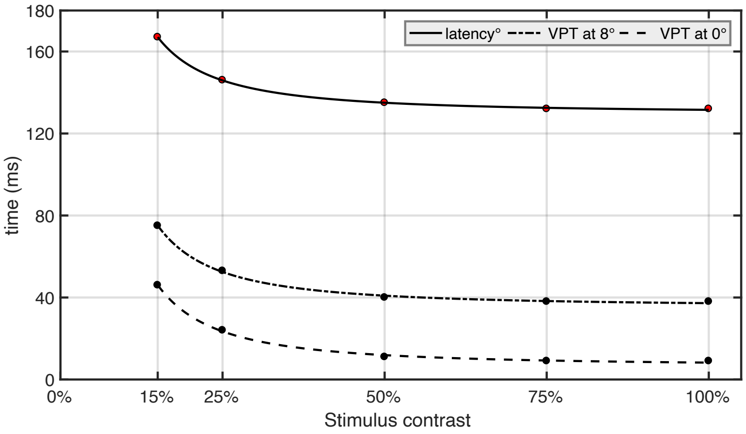


Figure 26. Latency, T3 and T0 versus stimulus contrast level. All three parameters response to changes in contrast equally. At higher contrast levels all parameters show asymptotic behaviour. Accordingly, all three parameters increase rapidly at low contrast levels. The line that best represented the relationship between the three parameters and contrast produced nonlinear relationship. Two term power function ($f(x) = ax^b+c$) was used to fit the data.

From the previous page described data, it appears clear that visual processing time is longer when the eye movements are involved due to PSOs. Also, a significant positive correlation exists between subjects observed PSOs and their T3 durations $r(6)=0.91$, $p<0.005$, which also provides indication that T3 is indeed dependent on PSO durations. As demonstrated for all subjects, T3 is only accomplished after the eye approaches its mean position (i.e. during fixation) which further verifies this result. However, the main issue confronting these results is that the PSO amplitudes decrease with increasing eccentricity (Bahill, Clark and Stark) while in the previous chapter it was shown that T3 durations get longer with increasing eccentricity. If the PSOs described in this study appear to be highly corelated with T3 duration, one might wonder then why the T3 durations increase with larger saccades when PSOs decrease. The reason why PSOs decrease with increasing eccentricity simply lies in deceleration phase of saccades. As was shown above, the subjects PSOs for a given eccentricity are consistent because saccades have stereotyped behaviour, therefore saccades of the same magnitude will produce similar return velocities resulting in equal size PSOs. However, while the acceleration phase of saccades remains consistent for approximately all saccade magnitudes, its deceleration phase changes with increasing saccade sizes. Saccades of small magnitudes have more symmetrical velocity profiles (i.e. their acceleration and deceleration phase is equal), whereas larger saccades have been shown to have shorter acceleration phases and longer deceleration phases (Baloh et al. 1975; Opstal and Gisbergen 1987). As a result of this, their corresponding velocities produce more skewed profiles, which in turn have smaller return velocities thus smaller PSOs.

As noted in the previous chapter, T3 is also subjected to fixation errors associated with larger eccentricities and it was acknowledged that the role of the post saccadic drift is functional and occurs to reduce the persisting fixation errors at the end of saccades. This being the case, one would expect longer drift durations to be observed although the PSOs have smaller amplitudes. To consider this further, the decision was made to inspect the PSOs from the data described in previous chapter for 4, 8 and 12 degrees eccentricity, since the testing procedure as well as the method employed was identical to this study.

3.2.4 **PSO results for 4, 8 and 12 degrees eccentricity**

Figure 27 presents subjects superimposed leftward and rightward velocity profiles for 4°, 8° and 12° degrees eccentricity where each column corresponds to a subject, whereas their corresponding PSOs are displayed in figure 28. As figure 27 shows, deceleration phase across all subjects changes depending on saccade magnitude. Accordingly, the subjects’ PSO waveforms also conform to these changes and produce different PSO magnitudes for each eccentricity level. This observation confirms that PSO amplitudes indeed depend on saccade deceleration phases. Across all subjects, the return velocities of leftward saccades are larger, thus their corresponding PSOs too are larger when compared to rightward saccades. Saccades of 8° in magnitude produced highest PSO amplitudes in all three subjects. Not surprising as these saccades have the steepest deceleration phase (note that the slope determines deceleration). In addition, the velocity profiles also capture clearly that the peak velocity does not increase linearly, but instead the rate at which increases, decreases with larger saccades. The difference in peak velocities (i.e. the highest peak in velocity profile) is smaller between 8° and 12° when compared to 4° and 8° saccades. Hence, 12° saccades have shorter acceleration phase and longer deceleration phase and are more skewed, therefore resulting in smaller PSO amplitudes. Whereas, velocity profiles for 4° saccades are more symmetrical, accordingly their acceleration and deceleration phase will be also symmetrical. The slope of these saccades is less steep when compared to 8° saccades, therefore slightly slower deceleration phase. These observations clearly demonstrate how PSOs are directly proportional to saccade deceleration phase, i.e. the steeper the slope of deceleration, the larger its overshoot will be and vice versa. However, despite the fact that the amplitude of the PSO changes depending on the deceleration phase, the observed PSOs show that the size of the overshoot has very little effect on influencing T3 as their durations remains fairly consistent. As figure shows, the PSO sizes for 12° saccades (bottom row) produce smallest overshoots, yet their corresponding T3 values have the longest durations as indicated in each plot. Notably, the observed drift size does not become larger with increasing eccentricity while the deviation between the rightward and leftward saccades clearly increases. While for 4° saccades the deviation between left/rightward PSO ranges are between 0.1°-0.3°, for 8° saccades it increases by almost a degree (between 0.4°-1.2°), whereas for 12° eccentricity the deviation is approximately 3° for each subject. This observation indicates that longer T3 durations are due to fixational disparities. Also, throughout this study it was demonstrated that the PSOs produce a predictable pattern; consisting of fast oscillatory movement followed by a slow moving drift. Although the PSO waveforms do not allow for complete unambiguous measure to conclude if drift follows to reduce the fixation error, the fact that its occurrence is consistent, makes it appear that its function is to offset the eyes position from the oscillatory movement rather than helping to reduce the fixation error. This assumption rests on these observations because if the function of drift occurrence was to reduce the fixation error, then the fixational disparities would have been reduced in size. Clearly, this is not what is being observed as with increasing eccentricity, fixational disparities increase so does T3, while the drift becomes smaller.

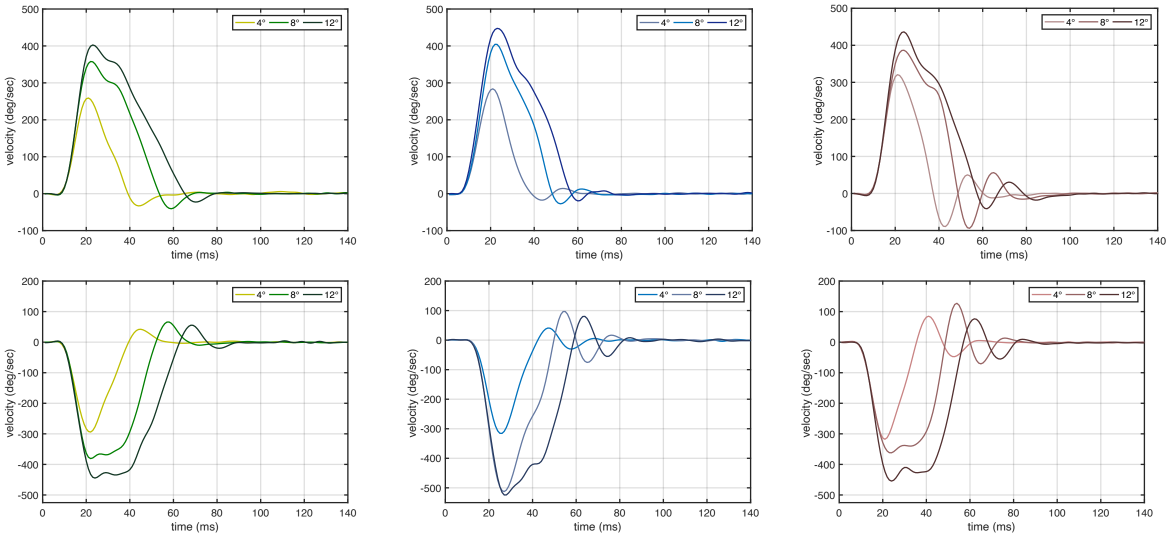


Figure 27. Superimposed velocity profiles as a function of time. Subjects' return velocities change depending on a slope of deceleration phase. Note that leftward velocity produce not only slightly higher peak velocities but also have less skewed profiles accordingly generate larger PSOs.

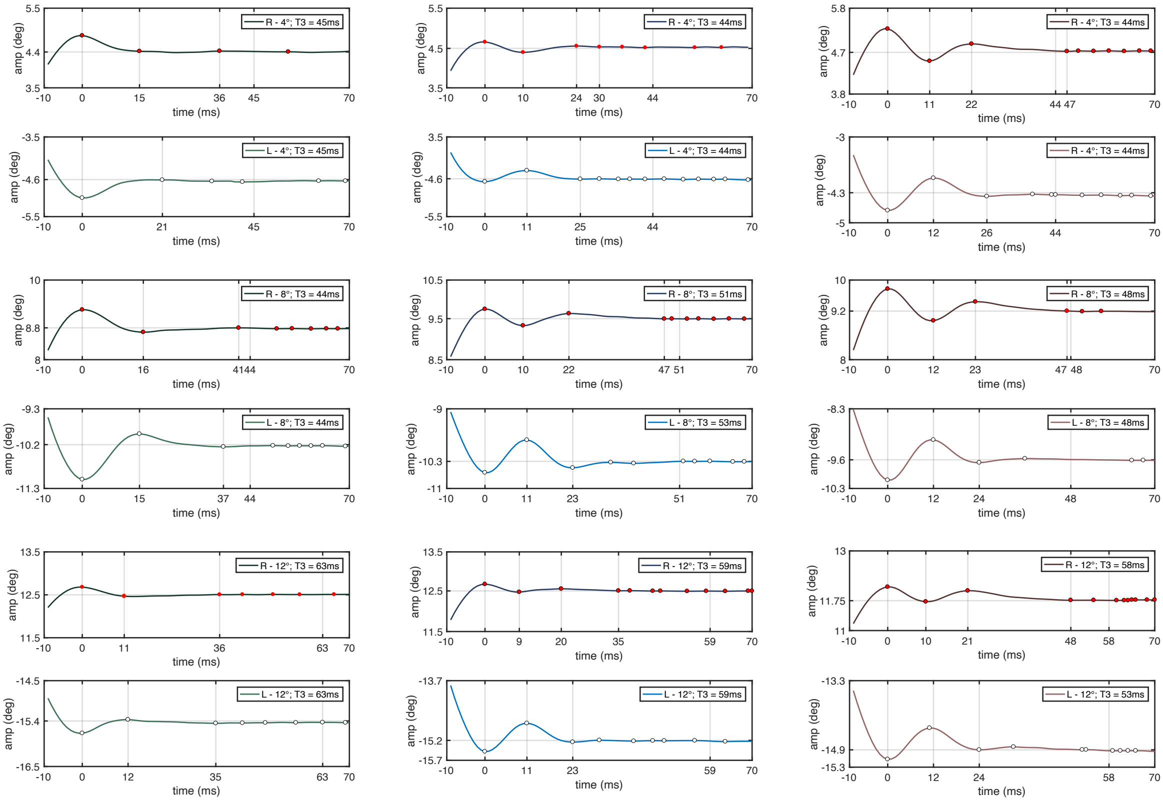


Figure 28. PSO profiles as a function of time. Size of PSO varies with saccade magnitude. Although the PSO waveforms are subject specific the pattern of movement is consistent across all subjects. After the oscillatory movement the eye drifts always towards it mean position. Note that with

increasing eccentricity the deviation between the leftward and rightward progresses thus, T3 also gets larger while PSO duration remains rather consistent.

3.3 Summary of results and discussion

This study was conducted in an attempt to verify a method by which post-saccadic visual processing time could be quantified and also to investigate if the PSOs measured with the EyeLink eye-tracker can describe the perceptual consequences of the non-rigid eye, particularly since the retinal image motion can be caused by both the lens and eyeball oscillations. The study was primarily focused on whether the PSO durations could also be accounted for in our integrated saccade latency measurements.

The observations made in this study suggest that the post-saccadic visual processing time is longer due to the eyes post oscillatory movement in addition to fixational disparities associated with larger saccades. This finding was further validated by comparing the rate at which the visual analysis can be performed when eye movements are not involved. This observation was taken as evidence to demonstrate that visual processing is indeed longer due to post saccadic oscillatory movements that corresponded to each subject’s PSO duration time. In addition, the findings have also demonstrated that the PSO durations are related to the deceleration phase of the saccade and do not change with stimulus contrast, thus yielding identical PSO durations (fig 24). This attribute of PSOs provided the means to estimate the visual processing times for higher contrast levels (25, 50, 75, and 100 percent). In addition, the results measured for different eccentricities revealed how PSO durations and amplitudes change with saccade size. Importantly, it was also observed that despite there being an increase in divergence, the drift did not increase. Instead, the drift movement became smaller as PSO amplitude decreased. It was this observation in addition to the subject's predictable, post movement pattern that inspired us to consider whether the drift proceeded to offset the eyes position from the oscillatory movement or to reduce the remaining fixation error. As demonstrated, the drift movement ended as soon as the eye approached its mean position defined when the eye velocity was at 0. Also, from previous studies we have evidence that changes in vergence are carried out by saccades and post-saccadic vergence drift is pre-programmed movement that is independent of a visual disparity (Collewijn, Erkelens, and Steinman 1988a; Optican and Miles 1985; Bahill, Clark, and Stark 1975). Since PSOs are so prevalent across all subjects, it seems that such motor output would have been necessary to evolve to overcome the eyes oscillatory movement. It has been previously hypothesised that the drift is an involuntary movement an animal learns to generate after every saccade (Optican and Miles 1985). This being the case then one can simply learn to generate the motor output that is a function of its PSO, which seems to be indeed what takes place based on these observations. One might wonder then why this has not been previously proposed. One of the main reasons for this could lie in the traditional recording technique – scleral search coil technique. We know that there are discrepancies between the coil and video based eye tracker measurements such as the one used in this study (EyeLink, SR research 1000). Although both techniques have very high spatial (<1°) and temporal accuracy (1ms), the discrepancies between the two techniques lie on the measurements of peak velocities and PSOs (Kimmel, Mammo, and Newsome 2012). Coil technique yields slightly smaller values for saccadic peak velocities and also the PSOs are considerably less pronounced in coil traces. If observed, the PSO will be limited to a single phase, while the PSOs observed with EyeLink are subject dependent with some subjects having more damping than others. However, this does not mean that video based PSOs are an artefact, as the return velocities are observed with both techniques. For example, when Collewijn, Erkelens, and Steinman (1988a), describe their approach for measuring post saccadic drift using coil technique they state that “This period started 20ms after the end of each saccade in order to avoid contamination by the dynamic overshoot frequently associated with a saccade.” Similarly, as was noted throughout this study, the oscillatory phase, depending on a subject, lasts between 19-29ms which was then followed by a drift. Also, once the drift occurred, the return velocities were within the range of vergence velocities known to be less than 20deg/sec. This pattern of occurring events based on the subjects return velocities rather than PSOs shows that there are striking similarities between these two techniques in addition to the above presented leftward rightward asymmetries.

Perhaps, more practical question then would be why overshoots observed with coil were not associated with perceptual consequences. It is unclear why the overshoots were not associated with perceptual consequences since there was a recognition for the existence of the post saccadic drift suppression (Optican and Miles 1985; Robinson and Optican 1981). This alone indicates clearly that the vision would have been suppressed during the drift resulting in longer post saccadic processing times. After all, it is well established fact that every saccade generates retinal motion and introspection shows that these signals never reach our awareness owing to the mechanisms of saccadic suppression (Robert H. Wurtz 2008). So too, it is a well-known fact that suppression outlasts the saccade. The fact that there is an ongoing movement well beyond the end of the saccade, perhaps it is not surprising that suppression will outlast the saccade since it is generated as a protective response to block out unwanted retinal image motion. Also, as PSOs were found to be subject specific and suppression is known to be selective only for M-pathway (D C Burr, Morrone, and Ross 1994; Ross et al. 2001) this would suggest that the suppression too is subject specific.

Consistent with studies that have described lens oscillatory movements, this study also confirms that other structures of the eye, in our case mainly the eyeball oscillations as reflected by the EyeLink 1000 can be used to quantify the perceptual consequences of the non-rigid eye since, the retinal image motion can be produced by both the lens and the eyeball oscillations.

To my knowledge, this is the first study to quantify the post-saccadic visual processing times and provide a detailed account that post-saccadic visual processing times are dependent on both the subject's PSO durations as well as fixational disparities occurring with larger saccades. Given that binocular coordination is dependent also on viewing distance, as the fixation errors increase significantly at near viewing distance, therefore, it would be of a great interest to establish if PSO waveforms too would differ as this will help examine further the exact function of post saccadic drift.

4 Directional Asymmetries Measured with the EMAIL Test

Abstract

It is well established that for a fixed eccentricity, eye movements along or close to the horizontal meridian produce significantly shorter times than equivalent close to or along the vertical meridian. In this study, the aim is to examine these directional asymmetries simply through measurements of ISL. As described already, the EMAIL test elicits saccades towards peripheral targets and measures the time the subject needs to detect the peripheral target, program and carry out the saccade and register correctly a specific stimulus attributes at the end of each saccade. The test also captures the subject's decision response time – DRT (i.e. the overall time from the onset of the stimulus until the response is given), this measurement could provide some indication as to whether the DRTs are also associated with the expected asymmetries between horizontal and vertical meridian.

4.1 Introduction

The role of the saccadic system is to prepare and generate an appropriate rotation of the eyeball to bring the subject's direction of gaze onto the peripheral stimulus. Saccades are key to our visual interaction with the world and are the most reoccurring behavioural response. We normally make two to three saccades every second. Our eyes are very mobile, they are moved around the orbit by contraction or relaxation of the six extraocular muscles. These muscles are arranged in three opponent pairs, where the medial and lateral rectus move the eyes along the horizontal direction, the superior and inferior rectus control the up and down directions, whereas the superior and inferior oblique contribute to torsion (Peter H. Schiller and Tehovnik 2005).

There are two types of neurons in the brainstem: burst and omnipause (OPNs) that are essential for generating premotor commands for saccades (Leigh and Zee 1999). The commands for vertical and horizontal saccades originate from different regions within the brainstem. The saccades towards the horizontal direction are produced by burst neurons within paramedian pontine reticular formation (PPRF), while the burst neurons in medial longitudinal fasciculus (riMLF) control the saccades towards the vertical direction (Sparks 2002; Ramat et al. 2007; Leigh and Zee 1999).These commands, although generated from different regions of the brainstem, do not work independently. The OPNs discharge constantly during the fixation, but stop firing during saccades, therefore they regulate the onsets of both horizontal and vertical directions (Sparks 2002).

It is well established that asymmetries exist between horizontal and vertical saccades. The performance of horizontal and vertical saccades was analysed systematically over the full oculomotor range (up to 80^{o} towards horizontal and up to 70^{o} along the vertical meridians) by (Collewijn, Erkelens, and Steinman 1988b; 1988a) using the scleral search coil technique and their results have demonstrated clear differences between horizontal and vertical saccade parameters. Their results have shown that the saccades made in the vertical direction are less accurate when compared to horizontal saccades, and are also slower (i.e. their durations are longer) and their maximum speed does not reach the asymptotic level for amplitudes larger than 40°. Instead, for vertical saccades the speed continues to increase with amplitude. In addition, while the horizontal saccades are found to be symmetrical across the meridian plane, the upward and downward saccades maintain symmetry only up to 30° (Collewijn, Erkelens, and Steinman 1988b; 1988a).

In addition, asymmetries have also been reported for saccade latencies in many other studies (Goldring and Fischer 1997; Vernet et al. 2009; H. Honda and Findlay 1992; Bonnet et al. 2013). Overall, there seems to be a general rule; saccade latencies towards targets located on or close to the horizontal meridian are shorter than equivalent saccades along the vertical meridian. There is also an additional asymmetry between upward and downward vertical saccades with shorter upwards saccades (Vernet et al. 2009; H. Honda and Findlay 1992; Goldring and Fischer 1997). The observed vertical and horizontal asymmetry for saccade latencies is consistent across all studies, but there are discrepancies between studies reporting left/right and / or up/down asymmetries.

It is well established that the saccadic reaction times depend very strongly on the paradigm being used to trigger the saccades and it appears that the reported directional asymmetries for left/right or up/down are also very dependent on the paradigm being used to trigger the saccades. While some studies found no latency asymmetries between leftward and rightward saccades (Dafoe, Armstrong, and Munoz 2007b; Goldring and Fischer 1997; Vernet et al. 2009) for gap, overlap and antisaccades, the study done by Weber and Fischer (1995) found that the trials during overlap, short (0ms) and long (400ms) gap durations produced very little or no directional asymmetry, whereas trials with short gap durations (100ms and 200ms) produced directional asymmetry (more express saccades towards the right). On the other hand, the study done by Honda (2002) on twelve subjects found that the left/right asymmetry was evident only in eight out of twelve subjects tested during both gap and overlap trials. Equally important, this study also found that the direction of asymmetry was not the same among all subjects. For six subjects, saccade latencies were found to be shorter when a target appeared in the right, while the other two subjects showed the reverse result and four other subjects did not reveal any effect at all.

Since the visuospatial attention system is known to affect the saccadic latency, the visuospatial attentional bias specific to individual subjects was claimed by Honda to be involved in generating this idiosyncratic left/right asymmetry of saccade latencies.

In addition, lack of consistency across studies is found between nasal and temporal saccades. However, a more recent study by Johannesson et al (2012) confirmed in various tasks that there are no nasal/temporal asymmetries for saccadic latency, consistent with an earlier study by Honda (2002).

Similar conflicting reports were also found for saccades made towards vertical direction, and reported findings for up/down asymmetry for latency have not proved to be consistent. The up/down asymmetry is most pronounced during gap trials, with upwards latencies being shorter (Vernet et al. 2009; Tzelepi, Yang, and Kapoula 2005; H. Honda and Findlay 1992; Goldring and Fischer 1997; Zhou and King 2002). However, this asymmetry appears to disappear during voluntary saccades, like saccades during delay (Tzelepi, Yang and Kapoula 2005; Zhou and King 2002), antisaccade (Goldring and Fischer 1997; Bonnet et al. 2013) and memory task (Abegg et al, 2015). Only two studies reported no asymmetries between up/down during overlap paradigm (Bonnet et al. 2013; Yang and Kapoula 2006).

The lack of consistency in these findings makes it difficult to draw plausible conclusions as to the mechanisms involved. However, from the experimental results, disengagement from the fixation point seems to be the only consistent factor producing the asymmetries.

The aim of the present study is to investigate these asymmetries through measures of ISL (integrated saccade latencies times) produced by the EMAIL test. The test also captures the subject's decision response time – DRT (i.e. the overall time from the onset of the stimulus until the response is given). This measurement may provide some indication as to whether the expected asymmetries also affect the subject's overall behaviour.

4.2 Method and procedure

Six healthy subjects with a normal or corrected-to-normal vision between 24 and 37 years participated in this study.

The tests were performed in a dark, quiet room with subjects having their head position stabilised with a chin rest facing the monitor at eye level and 80cm away from the subject's eye.

The tests were performed binocularly with measurements taken separately for horizontal (180°–0°) and vertical (90°–270°) directions. In addition, monocular testing was also performed on three subjects along the horizontal meridian (180°– 0°).

Each trial began with the appearance of the central fixation point. The subjects were required to view the fixation mark and to generate a saccade towards the 8^{o} peripheral target which could appear on either side of fixation along any meridian within ± 15° elevation (see Figure 29). Once on target, the subject's task was to register the orientation of the gap in the central Landolt ring and to report its position using a four-button response box with the keypad buttons placed to match the four possible gap locations. As described previously, the EMAIL test employs a Four Alternative Forced Choice – 4AFC Procedure to measure the time the subject needs to carry out this task.

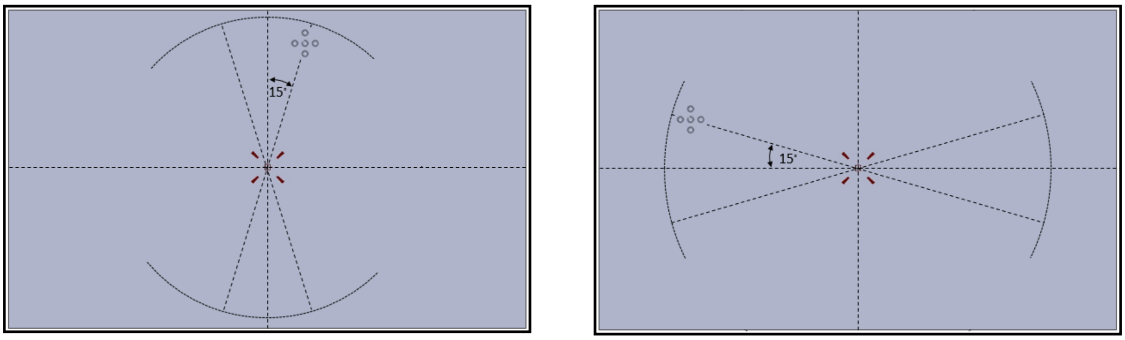


Figure 29. Schematic diagrams representing the visual stimulus employed in the EMAIL test. The section on the left shows the possible target locations for vertical saccades. The stimulus appeared randomly at 8° eccentricity either upward or downward from the fixation point within ± 15° range from the midline. Similarly, the section on the right shows the possible target locations for horizontal saccades. The stimulus appeared randomly at 8° eccentricity on either side of the fixation within ± 15° from the midline.

In each block of the experiment, there were two staircases interleaved that corresponded to left /right along the horizontal meridian or up/down along the vertical meridian. Initial stimulus duration time for all trials was set at 300ms, and the trials ended on completion of 16 reversals. Six repeat measurements were taken for each subject along the horizontal and vertical meridians. For monocular testing either the left or right eye was patched in alternating order during each trial. Similarly, six repeat measurements were taken for both left and right eye. Note that, as EMAIL test does not require any calibration, after each trial subjects were allowed to take a break if they wished to, and carry on with testing procedure when ready.

4.3 Data analysis and statistical test

After each trial, the EMAIL test program calculated two variables; decision response time (DRT) and integrated saccade latency time (ISL). The data collected from trials were analysed off-line using MatLab. The DRT captured the overall time the subject takes to detect the peripheral target, generate the eye movement and generate a response to indicate the correct orientation of the gap. The ISL, on the other hand, represents the minimum time the subject needs to detect the peripheral target, generate the eye movement and register the orientation of the gap at the end of each saccade. The mean values for both ISL and DRT for each subject were obtained from six repeat measurements. The mean values from repeated measures were classified with respect to each location 180°/left, 0°/right, 90°/up and 270°/down. The obtained mean values for ISL and DRT are shown in Table 6 and 7 respectively.

With the exception of monocular results, these dependent measures were analysed with one-way repeated measures of ANOVA. Mauchly's test for ISL (p = .07) and DRT (p = .15) as well as linearity, normality and homogeneity of the data, indicated that assumptions were met to perform one-way repeated measures of ANOVA. Post hoc analysis were performed using pairwise comparisons with Bonferroni corrections. Whereas, for monocular results, paired sample t-test were used. To meet the assumption that the differences between pairs are normally distributed, the Jarque-Bera (JB) test was performed. For all monocular data sets, the H value returned 0 indicating that the data have the skewness and kurtosis matching a normal distribution.

	Left	Right	Up	Down
Subject 1	198.1 ± 12.4	204.1 ± 7.1	238 ± 18.5	269 ± 22.4
Subject 2	168.4 ± 9.4	186.6 ± 8.1	209.2 ± 4.1	200 ± 5.7
Subject 3	164.8 ± 4.25	172.3 ± 4.3	198.5 ± 5.2	188.4 ± 4.4
Subject 4	192.3 ± 1.41	206.2 ± 2.6	230.0 ± 2.6	235.3 ± 2.3
Subject 5	172.02 ± 6.3	173.4 ± 7.6	182.8 ± 9.7	186.0 ± 5.8
Subject 6	180.4 ± 8.45	192.5 ± 11	206.7 ± 14.5	199.2 ± 10.1
Sample mean	179.34	190.52	210.87	209.65
SEM	13.46	16.47	20.31	32.6

Table 6. The subjects' mean ISL measurements for each direction. The ± sing indicates the standard error of the sample mean (SEM).

	Subject 1	Subject 2	Subject 3	Subject 4	Subject 5	Subject 6
Left	1001 ± 49	687 ±6.66	764± 11.4	734 ± 19	866± 31.8	852 ± 45
Right	933± 26.5	719±19.6	728± 28.5	741 ± 22	866.3± 31	821 ± 57
Up	1032± 80.4	718 ± 16	781± 26.5	782± 33.8	940 ± 53	823 ± 53
Down	1007 ± 47	734 ± 7.3	774± 33	800 ±20.1	953± 43.7	800 ± 62
Horizontal	967± 28.32	700 ± 11	745± 22.3	737 ±14	876± 21.4	836 ± 35
Vertical	1050 ±45	939± 8.85	778 ± 20	791± 19.4	947± 33	811 ± 39

Table 7. The DRT results for each direction; left, right, up and down. The data in the table show mean DRT values and the corresponding standard errors calculated from 6 repeat measurements.

4.3.1 Integrated saccade latency time – ISL results

The results from a repeated measures of ANOVA revealed that ISL values are dependent on target location, $F(3, 15) = 15.76, p<0.008, \eta^2= 0.755$ with post hoc comparisons results showing that ISL performance although it is symmetrical along both horizontal ($p > .45$) and vertical meridian ($p > .98$), significant differences exist between left vs up ($p<.001$), left vs down ($p<.001$), right vs up ($p<.02$) and right vs down ($p<.007$). Figure 30 displays average ISL values along with confidence intervals. As figure shows, the ISL responses are shorter (i.e. faster) along the horizontal when compared to vertical meridian with no significant differences between left vs right or up vs down.

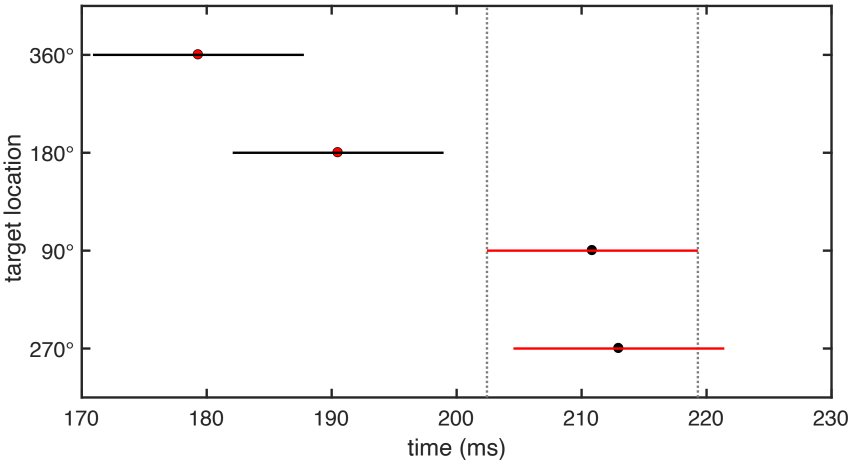


Figure 30. Pairwise comparison test using Bonferroni corrections. The difference between the sample means of horizontal and vertical direction is significant as indicated by dotted line. Confidence intervals, red line segments of upward and downward ISL sample means do not overlap with black CI segments of leftward and rightward sample means.

For demonstration purposes, the mean values of ISL for horizontal and vertical direction for each subject are also presented on the bar chart (Figure 31) where grey and blue bars represent horizontal and vertical ISL values respectively. Equally, this figure too shows that ISL values are shorter along horizontal direction across all subjects. This finding is consistent with previous reports done by other investigators and confirms that saccadic performance across a horizontal meridian is indeed faster than across a vertical meridian (Vernet et al. 2009; H. Honda and Findlay 1992; Goldring and Fischer 1997; Dafoe, Armstrong, and Munoz 2007b; Yang and Kapoula 2006).

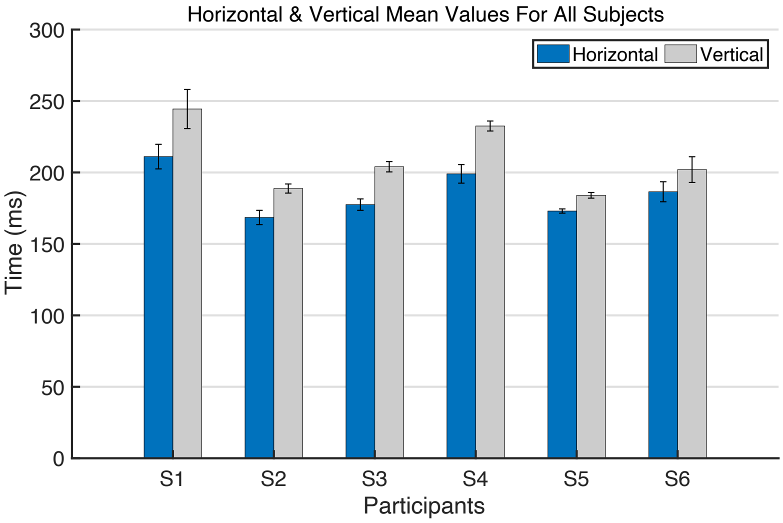


Figure 31. Mean ISL values for horizontal and vertical directions for all six subjects (the subjects were ranked in alphabetical order). Each bar represents collapsed data along horizontal and vertical direction with error bars representing the standard error of the sample mean. The mean ISL values for saccades along the vertical meridian are on average 15ms longer.

4.3.2 The decision response time – DRT results

The DRT measurements were also analysed using repeated measures ANOVA. However, in contrast to ISL findings, the DRT analysis did not reveal any directional asymmetry $F(3, 15) = 4.39, p<0.089, \eta^2= 0.47$. The mean DRT values are presented on the bar chart (Figure 32) with error bars representing 95% confidence intervals. As figure shows, the CIs overlap which further verifies that DRT responses are independent from target location. These results indicate that the asymmetries found on ISL measurements have minimal effect on overall response time, as these differences are no longer present in DRT measurements.

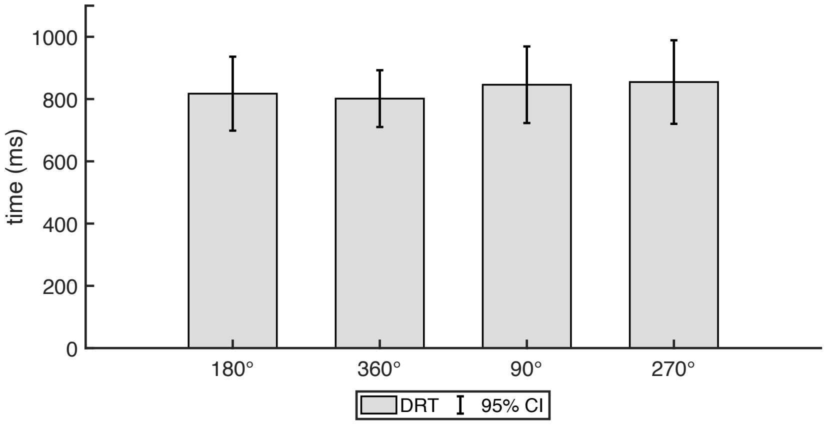


Figure 32. Mean DRT values for each direction with error bars representing 95% CIs (confidence intervals). As shown, CIs overlap, confirming that no significant differences exist in DRT responses.

4.3.3 The monocular results

The paired sample t-test for monocular results too, revealed that no significant differences exist between nasal(left)/temporal(right) for the right eye or nasal(right)/temporal(left) for the left eye, for the three subjects tested. The paired sample t-test results are displayed on Table 8. Since no significant differences were found between nasal vs temporal direction on each eye, additional paired sample t-tests were also performed to compare the mean differences between the left and right eye. Similarly, no significant differences were found between the left and right eye (p=0.12; p=0.45; p=0.73). Figure 33 displays the compared sample means. As figure shows, the differences between the left and right eye are small across all three subjects. These results agree well with previous reports by other investigators as saccades along horizontal meridian are usually symmetrical (Dafoe, Armstrong, and Munoz 2007b; Vernet et al. 2009; a H. Bell, Everling, and Munoz 2000; Vergilino-Perez et al. 2012) with no significant differences also being present between nasal and temporal saccades (Hitoshi Honda 2002; Jóhannesson, Ásgeirsson, and Kristjánsson 2012).

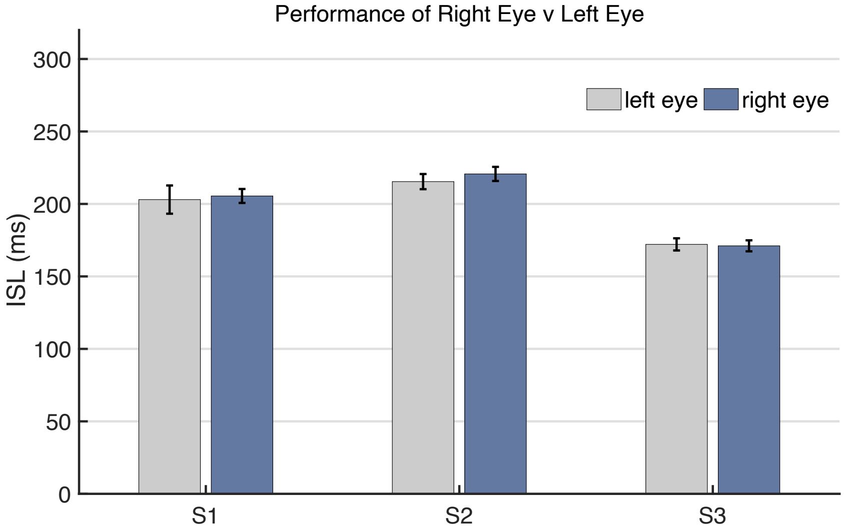


Figure 33. Monocular ISL measurements for the right and the left eye. Each paired bar is representative of the subject's mean ISL obtained from 12 trials (i.e. 6 repeat measurements for each of the two directions) for the right and the left eye. The purple bars represent the right eye, while the blue bars represent the left eye with error bars at ± 1SEM respectively.

	PDM	STD	SEM	95% CI of the Difference		t	df	P(T<=t) two-tail
				Lower	Upper			
S_1 L-N/T	-8.07	15.35	6.27	-24.18	8.04	-1.29	5	0.254
S_1 R-N/T	-0.15	19.52	7.97	-20.63	20.33	-0.02	5	0.986
S_2 L-N/T	5.27	11.82	4.83	-7.14	17.67	1.09	5	0.325
S_2 R-N/T	-3.28	18.54	7.57	-22.74	16.17	-0.43	5	0.683
S_3 R-N/T	-1.37	27.56	11.25	-30.29	27.56	-0.12	5	0.908
S_3 R-N/T	1.10	41.75	17.04	-42.71	44.91	0.07	5	0.951

Table 8. The analysis of monocular testing. No significant differences exist between the sample means of nasal vs temporal for the left or right eye. As indicated on the table two-tailed p-value is larger than .05

4.3.3.1 Summary of the Results

The main findings were as follows:

(a) Significant asymmetries were found between horizontal and vertical directions,

(b) No asymmetries were found along horizontal direction for both left/right or nasal/temporal,

(c) The absence of asymmetries was also found for vertical direction (up/down), and

(d) The measurements of decision response time (DRT) did not reveal any directional asymmetry.

4.4 Discussion

This study is the first to explore these asymmetries through measurements of ISL. While the previous studies have used eye-tracking equipment to measure the dependence of saccade parameters (i.e. latency, accuracy, duration and its peak velocity) on target location, in this study, the minimum stimulus duration time (ISL) needed to achieve 71% correct response was used. As the ISL value is made up of three components i.e. latency + duration + visual processing time, the directional asymmetries found on the ISL measurements reflect the directional asymmetries found in saccade parameters under similar conditions.

The studies that compared the performance of saccadic eye movements along horizontal and vertical direction have provided evidence that both saccadic latency (Vernet et al. 2009; H. Honda and Findlay 1992; Goldring and Fischer 1997; Dafoe, Armstrong, and Munoz 2007b; Yang and Kapoula 2006) as well as saccade duration time (Collewijn, Erkelens, and Steinman 1988a; 1988b) are shorter for saccades made towards the horizontal rather than the vertical meridian. In this study too, the ISL responses along horizontal meridian were found to be faster across all 6 subjects. The results from repeated measures of ANOVA have indicated clearly that significant differences exist between the horizontal and vertical ISL responses confirming well recognised asymmetries between horizontal and vertical eye movements.

However, while horizontal saccades are typically found to be symmetrical (Dafoe, Armstrong, and Munoz 2007b; Vernet et al. 2009; a H. Bell, Everling, and Munoz

2000; Vergilino-Perez et al. 2012), this is not always the case for vertical direction, owing largely to changes in saccadic latency.

There is a latency bias found for visually-guided vertical saccades, with upward saccades having shorter latencies when compared to downward saccades (Goldring and Fischer 1997; Dafoe, Armstrong, and Munoz 2007b; Vernet et al. 2009; a H. Bell, Everling, and Munoz 2000; Tzelepi, Yang, and Kapoula 2005; Zhou and King 2002; Abegg et al, 2015). This asymmetry was not captured through measurements of ISL where both upward and downward ISL times were found to be statistically insignificant. It is known that the up/down latency asymmetries are always found to be absent during paradigms that elicit voluntary saccades (Goldring and Fischer 1997; Tzelepi, Yang, and Kapoula 2005; Zhou and King 2002; Dafoe, Armstrong, and Munoz 2007; Yang and Kapoula 2006). This being the case, it suggests that these asymmetries may depend on the testing procedure undertaken.

Although the EMAIL test employs overlap paradigm to trigger visually-guided saccades, the procedure is very different from conventional testing. While the bottom-up component of saccadic latency is influenced by stimulus duration time which is controlled by 2-down, 1-up procedure, the top-down component is manipulated by the target location ± 15° from the midline as well as the gap orientation from the crowded central ring (i.e. 4AFC procedure). Also, it is well established that both the top–down and bottom-up factors have an effect on saccadic reaction times (Hutton 2008)

Besides, it has been demonstrated that the response of frontal eye field neurons can be modulated by the behavioural significance of a visual stimulus (R H Wurtz and Mohler 1976). This being the case, it could explain the lack of any directional bias for upward saccades in this study.

The monocular results were also found to be symmetrical for all three subjects. Perhaps, this is not a surprising result, as these tests were restricted only along horizontal meridian. As was noted above, the saccades along horizontal meridian are usually symmetrical (Dafoe, Armstrong, and Munoz 2007b; Vernet et al. 2009; a H. Bell, Everling, and Munoz 2000; Vergilino-Perez et al. 2012), and so too, are nasal/temporal saccades (Hitoshi Honda 2002; Jóhannesson, Ásgeirsson, and Kristjánsson 2012), therefore these differences are independent of the paradigm being used and have significantly changed the measured ISL values, which indicates clearly that the visual stimulus presented along the horizontal meridian is processed faster (i.e. shorter stimulus duration time). After all the visual system has evolved to meet the needs of environmental demands and shorter ISL values along the horizontal direction may reflect the importance of horizontal tasks such as reading. Our visual environment is intrinsically more concentrated along the horizontal line and this may account for the improvement in response parameters for horizontal saccades.

Decision Response Time performance: The measured DRT values did not reveal any directional asymmetry. This finding indicates that the asymmetries found in saccadic eye movements are subtle and may not cause significant changes in overall behaviour. After all the measurements of DRTs were found to range between 700ms up to 1,000ms and the differences found between horizontal and vertical ISL rarely exceed 20ms.

4.5 Conclusion

This study presented a new method to measure the identified asymmetries in saccadic responses latencies and durations, and the corresponding visual processing time at the end of each saccade. The EMAIL test does not require any eye-tracking equipment and this can be of great advantage. Asymmetries that are often found in saccadic eye movements were also captured reliably without a need for eye tracking equipment instead these differences were simply measured through ISL measurements generated by EMAIL test. Given that asymmetries exist is saccadic performance, all studies involving assessment of the saccadic eye movements must consider these directional asymmetries.

5 Age Effects on Measures of Integrated Saccade Latencies and Decision Response Times

Abstract

One of the most pervasive effects of age is that it slows one down with deleterious effects over all behaviour. The brain volume shrinks with increasing age and these changes (due to atrophy) are also known to reduce the efficiency of cognitive function, in particular processing speed, working memory and ability to inhibit attentional and behavioural responses, as well as slowing of movement. Even the simplest behavioural measures, such as reaction times, reveal that older adults need more time to respond (Salthouse 1996; Verhaeghen and Salthouse 1997). While there is an ample of evidence that oculomotor responses are too effected by normal aging, the conventional techniques used to investigate the eye movement responses rely on eye tracking equipment. In this study, the aim is to demonstrate that visual psychophysical techniques can also be relevant when investigating age effects on oculomotor responses. The results produced by EMAIL test show that both ISL and DRT measures progress nonlinearly with normal ageing, presenting a broad agreement with previous research.

5.1 Introduction

One of the most prominent effects of ageing is that the speed of processing information decreases gradually with direct consequences on many aspects of performance. Even the simplest behavioural measures, such as reaction times, reveal that older adults need more time to respond (Salthouse 1996; Verhaeghen and Salthouse 1997). The measures of reaction time (RT) although simple and easy to perform, nonetheless provide a measure of three processing stages: detection, the decision-making process and the time needed for execution of a motor response (Botwinick and Thompson 1966).

Longer RTs in older subjects were found in several studies (Fozard et al. 1994; Salthouse 1996) with reaction times increasing linearly with age. It is also well established that ageing causes changes to the brain size, vasculature and cognition (Peters 2006).

The saccadic system has been shown to provide a useful approach in examining the relationship between brain and behaviour. The cortical areas involved in saccade generation are well characterised and these include frontal eye field (FEF), supplementary eye field (SEF), dorsolateral prefrontal cortex (DLPFC), posterior parietal cortex (PPC), anterior cingulate cortex (ACC), basal ganglia, thalamus, and superior colliculus (Pierrot-Deseilligny, Milea, and Müri 2004; Hikosaka, Takikawa, and Kawagoe 2000; Luna, Velanova, and Geier 2008; Leigh R.J and Zee D.S 1999). In addition, their characteristics are well understood. Every SEM produces a similar pattern and for normal saccades the relationship between duration/magnitude and magnitude/peak velocity follows a main sequence (Bahill, Clark, and Stark 1975). Besides, abnormalities of saccadic responses can be characterised accurately and often point to disorders of specific mechanisms (Leigh R.J and Zee D.S1999).

SEMs can be manipulated behaviourally in the laboratory using a number of different experimental paradigms (i.e. gap, overlap, antisaccade and memory guided saccadic tasks), where each paradigm has been designed to evoke different types of saccades and to probe into different behavioural and cognitive processes. Many studies that have investigated the effects of age on saccadic performance using different paradigms (Peltsch et al. 2011; Munoz et al. 1998b; Yang and Kapoula 2006; Noiret et al. 2017; Luna et al. 2001; 2001) have shown that these changes can be interpreted within neurological framework.

Saccadic performance is assessed through its parameters and these include; latency, amplitude, peak velocity, variability and overall accuracy. Saccadic latency, which represents the time interval between the onset of the stimulus and the eye rotation is known to reflect many core cognitive functions (Leigh R.J and Zee D.S 1999). There is a general agreement across studies that investigated SEMs, which found that latency parallels the changes on the brain during both developmental and normal degenerative stages (Peltsch et al. 2011; Munoz et al. 1998b; Noiret et al. 2017; Fischer, Biscaldi, and Gezeck 1997; Luna, Velanova, and Geier 2008; Luna et al. 2001). It has been shown that while latency decreases exponentially during developmental stages, from birth up to approximately 15 years of age (Fischer, Biscaldi, and Gezeck 1997; Luna, Velanova, and Geier 2008; Luna B and Sweeney J.A 2004; Munoz et al. 1998b). Above this age, the response latency starts to increase again. The relationship between latency and age has been shown to be curvilinear (Munoz et al. 1998b; Fischer, Biscaldi, and Gezeck 1997) and mirrors the structural brain changes that take place during both developmental and degenerative stages (Giorgio et al. 2010; Whitford et al. 2007; Giedd et al. 1999).

On the other hand, age does not seem to have significant effect on other saccade parameters, such as peak velocity and accuracy. It has been shown that both parameters stabilise during childhood (Luna et al. 2004; Munoz et al. 1998b) with no effects as we age (Luna et al. 2001; Yang and Kapoula 2006; Bonnet et al. 2013; Munoz et al. 1998b).

The purpose of this study is twofold: 1) to introduce a new method to test oculomotor parameters; and 2) to investigate age-related changes on decision response times (DRT) and integrated saccade latency times (ISL).

5.2 Experimental Procedure

This study was approved by the Research Ethics Board of City, University of London. Thirty-two healthy subjects ranging between 10–79 years-old were recruited for this study. Subjects were divided into five age groups as shown below (Table 9). All but one subject had normal trichromatic colour vision. The one subject with severe deutan deficiency, as measured on the CAD test, was also included in the study. As described on section 2.2.1 although neither phoria nor visual acuity was assessed, none of the subjects reported problems with their visual acuity or binocular vision. All experiments were carried out binocularly and each participant used their normal distance spectacle prescription during the tests, except for the few older subjects who wore their normal reading glasses.

Table 9 Composition of age-related groups

Age Group	Age Range	Mean age group ± σ	Number of subjects	Female	Male
Children	10-12	11 ± 1.4	2	2	0
Young Adults	20-34	25 ± 4.4	13	7	6
Middle-aged	35-49	40 ± 4	7	3	4
Old Adults	50-64	56.7 ± 6.4	3	0	3
Seniors	65-80	73 ± 4	7	4	3
Total			32	16	16

Prior to testing session, all subjects were briefed on how to perform the test and after a period of practice, the testing procedure began. This step was taken to ensure that a subject is capable of using the response pad and understands the testing procedure. Experiments were conducted in a darkened room where subjects were seated 80cms away from the visual display. A forehead / chin-rest was used for comfort and to minimise head movements. Each subject completed three trials in a single session, which involved approximately 70 to 90 stimulus presentations per trial. After each trial subjects were allowed to take a break if they wished to, and carry on with testing procedure when ready. Each trial began with the appearance of central fixation point, which remained illuminated (overlap paradigm), while a peripheral visual stimulus appeared randomly 8° to the left or right along the horizontal meridian within ± 5° elevation. Visual stimulus was generated and presented on the monitor by the EMAIL test program (EMAIL test and procedure is explained in detail in Chapter 2).

Following each trial, the EMAIL test program computed and generated the threshold values for decision response times (DRT), and the integrated saccade latency times (ISL). The DRT captures the overall time interval between when the stimulus is presented and response is generated. In contrast, the ISL time captures the time interval the subject needs to detect the peripheral target, generate the eye movement and register the stimulus attribute of interest at the end of each saccade. Thus, the DRT captures ISL time as well as the time required to generate the motor response.

This arrangement allowed us to investigate the age effects on both oculomotor responses (stimulus driven responses) and decision responses (internally driven responses).

5.3 Results

The data were analysed offline using Matlab. The mean values for both ISL and DRT for each subject were obtained from their three measured threshold values produced by the EMAIL test. To analyse age effects, the subjects were separated into five age groups: children (10-12yrs), young adults (20-34yrs), middle age (35-49yrs), older adults (50-64yrs) and seniors (65-80yrs) (see Table 10).

Table 10. The mean values of age-related groups for all measured parameters.

Age range	Mean age group ± σ	Number of subjects	DRT ± σ	ISL ± σ
10-12	11 ± 0.7	2	884.8 ±20.5	209.3±5
20-34	25 ± 4.4	13	721.2±68	178.4±14
35-49	40 ± 4	7	816.4±120.7	190±14
50-64	56.7 ± 6.4	3	925.3±110	207±8
64-80	73 ± 4	7	1059.1±137.2	278±29
Total		32		

One way ANOVA was applied to assess the differences between the age groups for both ISL and DRT. The ANOVA results show significant effect on ISL [$F = 35.1$, $p < 0.001$] with post hoc (Tukey's HSD) analysis indicating clearly that the seniors group (65-80yrs) is significantly different from all other age groups (Figure 34). Although no statistically significant difference ($p > 0.05$) was found between the other groups (10-12yrs, 20-34yrs, 35-49yrs and 50-64yrs), the best performing age group were found to be young adults (20-34yrs) closely followed by the middle age group (35-49yrs). The ANOVA findings are displayed graphically as multiple comparison plots in Figure 34, where the group mean is represented by the circle, whereas the extended line from the circle is representative of confidence intervals. Due to small sample sizes for children and older adults, the confidence intervals are very large for those two groups when compared to the remaining groups.

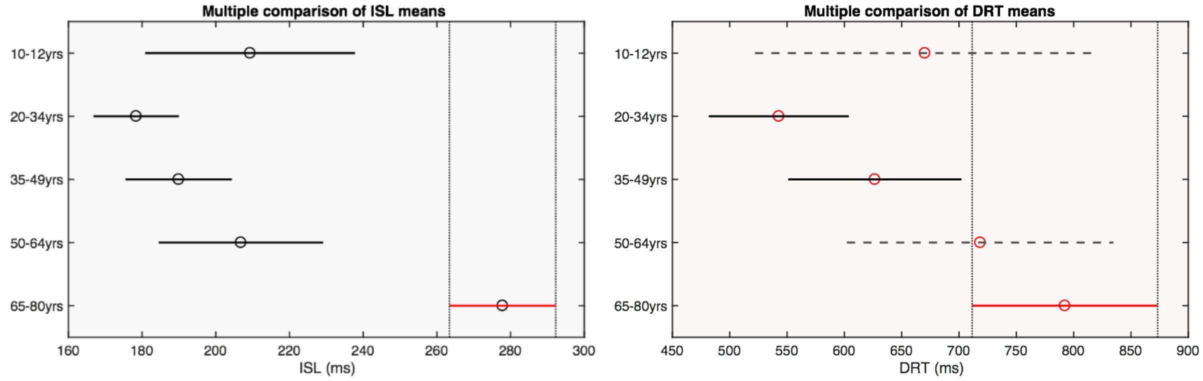


Figure 34. Multiple comparison of ISL and DRT means. The figure on the left represents ANOVA analysis for ISL measurements. A multiple comparison test shows clearly that the ISL mean of seniors (65-80) represented by red bar is significantly different from all other age groups shown by black bars where the group mean is the circle and the extended horizontal line represents confidence interval. Similarly, the figure on the right represents ANOVA analysis for DRT measurements. The mean DRT of senior age group (65-80) represented by the red bar is significantly different from both younger adults (20-34yrs) and middle-aged groups (35-49yrs), represented by black bars. The children (10-12yrs) and older adults (50-64yrs) are shown by dashed grey lines. These two age groups were not found to be statistically different from any age group. As can be seen, the extended lines (i.e. confidence intervals) are very large due to very small sample sizes for those two groups.

Same analysis was performed on DRT measurements. The ANOVA results showed significant effects on DRT results [F = 13.36, p < 0.0002], however the post hoc analysis (Figure 34) revealed that only the senior age group (65-80yrs) were significantly different from two other age groups: younger adults (20-34yrs) and middle-aged (35-49yrs). The full ANOVA analysis are shown in Table 11.

The scatter plots for both ISL and DRT values are shown on Figure 35 and 36 respectively. The plots reveal that the relationship with age for both ISL and DRT is nonlinear. The two-term exponential fits clearly demonstrate that both ISL and DRT performance changes during two different stages (for comparison of linear and nonlinear fit see Figure 37). While during childhood our performance improves – i.e. decreases exponentially – as we age, we start to slow down. The fitted curve on the scatter plot explains convincingly the relationship between age and ISL with r-squared equal to 0.82. As expected, the fitted line predicts that changes occur at a much faster rate during developmental stages, the time where rapid improvements on overall behaviour take place. With developmental changes in the prefrontal cortex still continuing into adulthood (A. Diamond, 2002), it is not surprising that the best performance predicted from the fitted line is ~ 25years of age. Similarly, as other structures on the brain change with age, so does the performance of ISL. Also, the DRT fit with r-squared found to be 0.66 also depicts that decision responses during developmental stages decrease rapidly until ~17 years of age, at which point the trend reverses. The curve shows that the increase from 20yrs onwards is gradual and increases at constant rate of 7.4ms every year. In line with previous studies, these results confirm that the reaction times increase linearly with age.

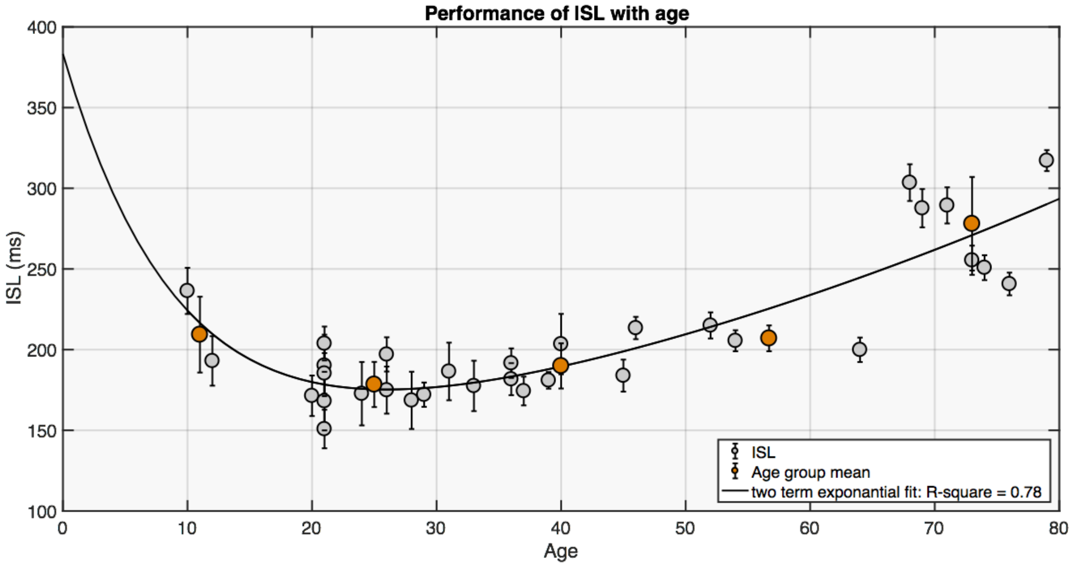


Figure 35. Performance of ISL with age. Each grey point represents the threshold values of ISL obtained from EMAIL test. The orange circles correspond to the mean values of ISL for each specific age group (10-12, 20-34, 35-49, 50-64 and 65-70). Two term exponential fit $266e^{-0.1x} + 118e^{-0.01x}$depicts clearly behavioural changes that occur during developmental and degenerative stages with changes taking place at much faster rate during developmental stages.

Figure 36. Performance of DRT with age. Each grey point represents the threshold values of DRT obtained from EMAIL test. The yellow circles correspond to the mean values of DRT for each specific age group (10-12, 20-34, 35-49, 50-64 and 65-70). Similarly, two term exponential fit $6785e^{-0.32x} + 600e^{-0.008x}$shows clear behavioural changes during developmental and degenerative stages with rapid changes occurring up to 17 yrs of age (at which point trend reverts and starts to increase.

Additional information regarding the best line of fit

To ensure that the nonlinear fit describes best the relationship between ISL and age, linear regression was also performed. Figure 37, which also includes residual plots shows clearly that, while 82% of variation in ISL with respect to age is described with nonliar relationship, only 62% of variation can be described by linear relationship; as indicated on each plot r-squared was found to be R^2 =.82 for nonlinear fit while for linear fit R^2=.62 which confirms nonlinearity for ISL vs age.

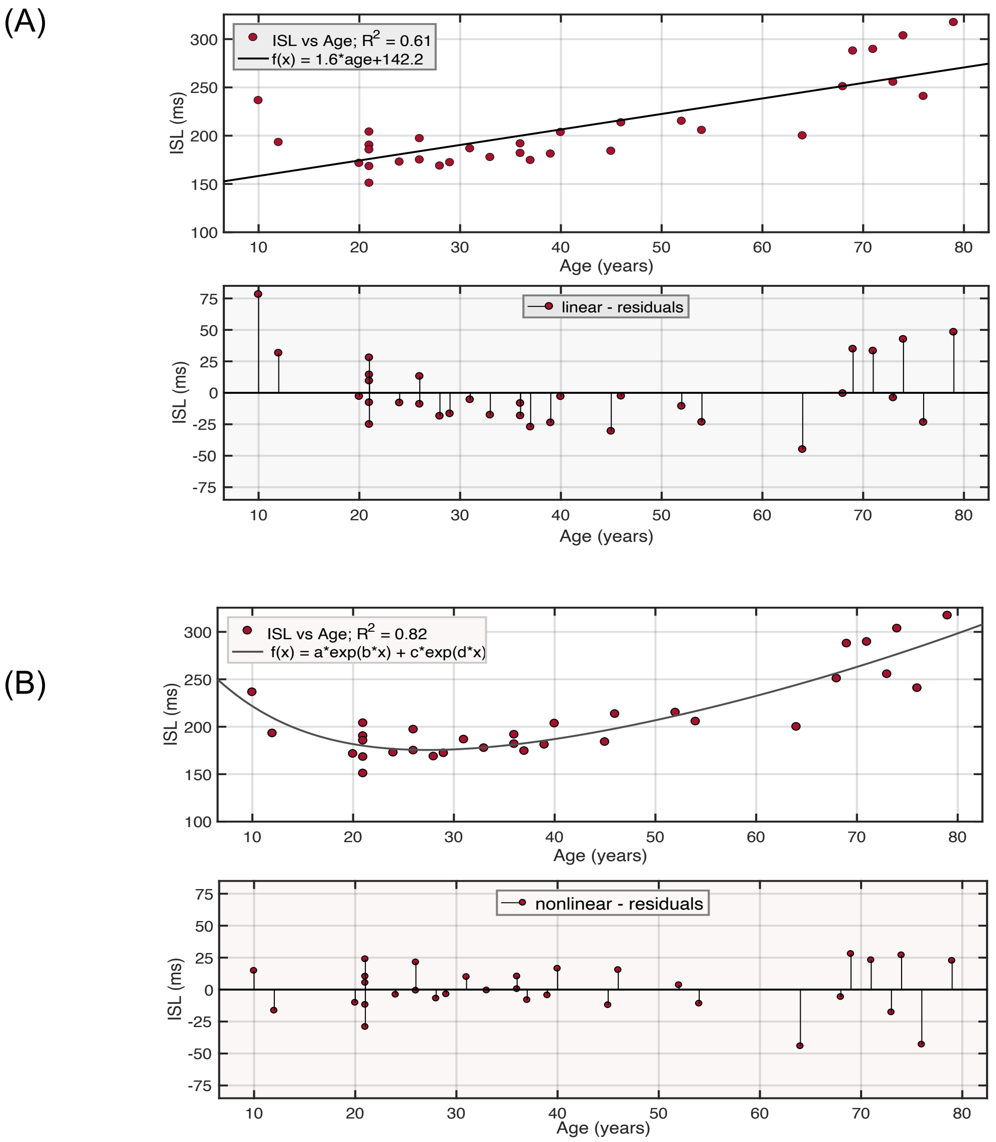


Figure 37. Linear and nonlinear regression analysis for ISL versus Age . In Plot (A) a linear fit is used to describe the relationship between ISL and age, whereas in plot (B) a nonlinear fit is used. Their corresponding residual plots are presented underneath. As shown, variation of ISL with age is better described with a nonlinear relationship as R^2 = .82 as a result the nonlinear residuals are smaller too when compared to linear residuals.

Table 11. The ANOVA and post hoc analysis results for DRT and ISL.

One way ANOVA - DRT	Source'	SS'	df'	MS'	F'	Prob>F'
	Groups'	555179	4.0	13879	13.36	0.000
	Error'	28044	27	10386		
	Total'	83561	31			
DRT- Post-hoc analysis	Age groups	Age groups				
	11-12	20-34	-60	165.7	392	0.23
	11-12	35-49	-170	68.4	307	0.91
	11-12	50-65	-312	-40.5	231	0.99
	11-12	65-80	-413	-174.3	64.4	0.23
	20-34	35-49	-237	-97.4	42.2	0.27
	20-34	50-65	-397	-206	-15.6	0.02
	20-34	65-80	-480	-340	-200.5	0.000
	35-49	50-65	-314	-109	96.6	0.54
	35-49	65-80	402	-243	-83.5	0.0012
	50-65	65-80	-339	-134	71.6	0.34
One way ANOVA - ISL	Source'	SS'	df'	MS'	F'	Prob>F'
	Groups'	47805	4.0	11951	35.1	0.000
	Error'	9202	27	340.8		
	Total'	57008	31			
ISL Post-hoc analysis	Age groups	Age groups				
	11-12	20-34	-10	30.92	72	0.2
	11-12	35-49	-24	19.4	63	0.68
	11-12	50-65	-46	2.5	52	0.99
	11-12	65-80	-112	-68	-25	0.0007
	20-34	35-49	36.8	-11.5	-13.7	0.67
	20-34	50-65	-63	-28	6.1	0.14
	20-34	65-80	-124.7	-99	-74	0.0000
	35-49	50-65	-54.1	-17	20	0.67
	35-49	65-80	-116.7	-88	-59	0.000
	50-65	65-80	-108.2	-71	-34	0.0001

5.4 Discussion

The aim of this experiment was to investigate age-related changes and to validate the EMAIL test as a novel way for measuring both oculomotor and decision response times.

The results demonstrate clearly that the ISL measured using the EMAIL test is affected by age-related changes in response parameters. The test provides a new method to investigate both oculomotor ISLs and DRTs, independently and without a need for eye tracking equipment.

Before discussing the experimental findings from this study, it is worth emphasising the fact that all previous studies that investigated saccade parameters have used eye movement recording techniques such as magnetic search coil, electrooculography (EOG) or video-based systems. None of these studies measured visual processing times. In this study, the combined oculomotor response latencies were captured without any eye movement recording techniques, using only the EMAIL test which relies entirely on visual psychophysics (as described in the methods and procedure section).

5.4.1 Integrated Saccade Latencies

The results demonstrate clearly that ISL values parallel the changes in the brain that are expected during both developmental and normal degenerative stages, and are in agreement with many previous studies that have investigated the effects of age on SEM performance (Munoz et al. 1998b; Peltsch et al. 2011; Noiret et al. 2017; Yang and Kapoula 2006; Fischer, Biscaldi, and Gezeck 1997; J. Sweeney 2001). Since normal aging does not affect significantly either the amplitudes or the peak eye movement velocities (Bonnet et al. 2013; Munoz et al. 1998b; Fischer, Biscaldi, and Gezeck 1997; Yang and Kapoula 2006), the differences found in ISL values are therefore likely to reflect changes in saccade latency.

Because SEMs follow very closely the age-related changes in brain structure, the principal discussion will focus upon these two stages.

It is well established that our ability to voluntarily initiate and suppress behaviour is influenced by the maturation of integrated functions between the cerebral cortex, striatum, thalamus and cerebellum due to myelination and synaptic pruning that take place during childhood and remain active even during adolescence (Sowell et al. 2003; 1999; Luna et al. 2001; Luna, Velanova and Geier 2008). Additionally, brain structures also change as synaptic pruning takes place. There is a reduction in the grey matter (GM), whereas during myelination white matter (WM) increases (Sowell et al,. 1998, 1999; A. Gorgio et al,. 2010; J.N. Girl et al,. 1999; T.J. Whitford et al,. 2007). This continuous synaptic pruning and myelination enable neuronal computations and the functional integration of widely-distributed cortical areas to became more efficient, which results in improved control over behaviour (Luna et al. 2001; 2004; Luna, Velanova and Geier 2008; Giedd et al. 1999; Sowell et al. 1999; 2003). These improvements in basic cognitive functions, such as our abilities to respond appropriately, maintain focus and process information faster (due to myelination) appear to translate also to the saccadic behaviour which is found to improve as these changes take place.

The results from this study show that ISL performance continues to improve until the second decade reaching its peak at ~23 years of age. It remains unchanged during the second decade and well into the third decade, from where it starts to increase gradually up to the beginning of the sixth decade, at which point it starts to deteriorate significantly. These results are in direct agreement with findings of Fischer et al (1997) and Munoz et al. (1998b), who investigated the saccadic performance on a large number of subjects (286 between 8-70yrs and 168 between 5-79yrs) and found a slight increase from just after 30 years of age, with the largest increase for those aged 60 and above.

While continued improvements happen during normal development stages, as we age our brain starts to deteriorate. It is known that during the normal ageing process, the brain structures show volumetric decrease and that the number of dopaminergic receptors declines (Park and Reuter-Lorenz 2009; R. Peters 2006). In fact, these changes in the brain become evident as early as the fourth decade, with actual rate of decline increasing even more around the seventh decade. The relationship between total WM and age is also found to be curvilinear, it increases in volume during developmental stages well into adulthood reaching its peak on the fourth decade at which point it starts to decrease (Sowell et al. 2003; Giorgio et al. 2010; Raz 2000; Raz et al. 2005). It is clear that the saccadic system follows very closely these changes. ISL changes measured in this study show similar behaviour, although there is a slight increase for 20-34yrs and 35-49yrs, these changes do not reach significance until after the sixth decade with the seniors age group (65-80yrs). The latter corresponds to the rate of rapid decline which occurs at the end of sixth decade (see ANOVA table).

5.4.2 Decision Response Time

Measurements of decision response times capture both oculomotor responses as well as the motor response time. Similarly, to ISL measurements, DRT results too, capture both developmental and degenerative stages, as illustrated by the two rapidly changing regions of the fitted curve. These results are in direct agreement with previous studies that have measured reaction times and have shown that the duration of the responses increases linearly (Verhaeghen and Salthouse 1997; Salthouse 1996; Bleecker et al. 1988). Our findings also reveal that the age-related effects and the corresponding changes in DRT times appear earlier than changes in ISL take place. The older age group (50-65yrs) did not show any significant difference when compared to seniors (65-80yrs). It has been suggested that besides the reduction on the performance being due to age-related decrements in brain connectivity, the increase in decision response times may also be due to older adults being more cautious while they generate responses. The tendency to acquire more information would normally result in longer DRTs (Smith and Brewer 1995; Forstmann et al. 2011). This strategy – believed to be adopted by older adults due to having bias for accuracy over speed – is known as the speed-accuracy trade-off (Starns and Ratcliff 2010; Salthouse 1996; Forstmann et al. 2011; Smith and Brewer 1995) and recently, the link between the elderly being more risk averse and the neurobiological basis for this behaviour has been established. A recent study conducted on a large cohort (n = 25,189), aged 18-69 years, to evaluate the extent to which ageing affects decision processes, found that attraction to potential reward also declines with age, suggesting that decline in dopamine levels may explain why older people are less likely to seek rewards (Rutledge et al. 2016). Perhaps this decline in potential reward is reflected by a more conservative strategy that is used by the elderly and a more cautious attitude before making a decision, thus resulting in longer response times. While during adolescence when the dopamine levels are much higher, this age period is recognised as a period of rapid cognitive development as well as increased risk-taking

(Wahlstrom et al. 2010; Wahlstrom, White, and Luciana 2010; Li, Lindenberger, and Sikström 2001; Bäckman et al. 2010). As a result, the response times are much faster and this is clearly depicted on the DRT curve. In addition, DRT changes take place at a much faster rate when compared to ISL, the parameter b, is larger than the corresponding parameter that affects the ISL curve. Also, DRT when compared to ISL, reaches the peak performance much earlier.

Besides, the decline in cognitive and motor performance due to ageing has already been associated with decline in the number of neurotransmitters such as dopamine and serotonin (Li, Lindenberger, and Sikström 2001). The dopamine levels start to decline by 10% per decade from adulthood and there is an indication that the number of neural projections that rely on dopamine levels between the frontal cortex and the striatum also declines with increasing age (Raz 2000; Raz et al. 2005; R, Peters 2006).

It is well known that striatum is a major target of midbrain dopaminergic projections (Schultz 1998) and its role for facilitating voluntary movements, suppressing involuntary movements as well as evaluating the consequences of past choices, is well established (Kim et al. 2009; Hikosaka, Takikawa, and Kawagoe 2000). If dopaminergic receptors are integral to cognition because they play an important role in regulating attention and in modulating response to contextual stimuli (Park and Reuter-Lorenz 2009), then it is likely that the linearity observed in DRT with increasing age is due to the linear changes of dopamine levels across the adult life span.

5.4.3 Conclusion

The findings from this study demonstrate that the EMAIL test provides a new method for measuring both oculomotor responses and decision response times without the use of eye-tracking equipment. The measured parameters capture well the changes that take place during the brain’s developing and degenerative stages due to normal ageing.

This being the case, the EMAIL test provides a novel and easy method to investigate a wide range of degenerative disorders. The test may be of value in studies of Parkinson’s, Alzheimer’s and Huntington’s disease (Anderson and MacAskill 2013), as well as in cases of mental disorders such as schizophrenia, attention deficit hyperactivity disorder (ADHD) and autism that are believed to have neurodevelopmental basis (Luna B and Sweeney J.A 2001; Sweeney et al. 2004; Kliemann et al. 2010).

6 Summary of findings and conclusion

The work presented in preceding chapters introduced a novel visual psychophysical technique that can be used to measure the eye movement responses without eye tracking equipment. Since the ISL value measured by the test captures the sum of three events, i.e. (latency)T1+(duration)T2+(processing)T3, the addition of full eye-tracking to the EMAIL test, makes it possible to determine accurately the time course of each event. To my knowledge, this is the first experimental study to show that the duration of post saccadic visual processing time is a variable quantity, dependent on subjects' PSO characteristics and the target eccentricity. In this chapter, I summarise the main findings and describe future experiments that can enhance the current findings and explore other potential applications of the EMAIL test.

6.1 Summary of findings

Previous research has provided evidence that saccades do not exhibit perfect conjugacy resulting in an increase in misalignment between the two eyes with increasing saccade magnitude. Also, as the eye stops abruptly at the end of each saccade, the mechanics of the system ensure that the eyeball as well as the internal structures sustain oscillatory movements that last well beyond the end of the saccade.

From the preparatory experiments described in chapter 2, and the subsequent results obtained from chapter 3, it has been demonstrated that the post-saccadic visual processing time is longer due to the eyes post oscillatory movement in addition to fixational disparities associated with larger saccades. This finding was ratified by comparing the rate at which the visual analysis can be performed when eye movements are not involved. While previous studies have provided indication that post saccadic drift removes the fixational errors caused by misalignment between the two eyes (Optican and Miles 1985; Lemij and Collewijn 1989; Robinson and Optican 1981), in contrast the observations made in this study showed that the drift decreases as size of the PSO decreases while divergence between the two eyes increases. It was this observation in addition to subjects' PSO waveform generating predictable pattern that lead to the proposition that the drift movement could be a learned response that follows to offset the eyes' oscillatory movement rather than reduce the remaining fixation error. However, this assumption requires further investigation as currently there is not sufficient data to confirm this. Future studies should consider investigating the PSOs by varying viewing distance as binocular coordination is also subject to viewing distance. In particular there is an evidence that in near viewing, the fixation errors can be as large as 2° (Yang and Kapoula 2003). This could provide us with better understanding of the mechanisms that the visual system employs to avoid the perceptual consequences that can arise due to the misalignment between the two eyes.

The findings from this study also suggest that saccadic suppression might be subject-specific, in line with the measured PSOs, and so too, the T3 durations. This inference has been drawn from the suggestion made by previous investigators that suppression is selective only for M-pathway (D C Burr, Morrone, and Ross 1994).

Consistent with studies that have described lens oscillatory movements, this study also confirms that other structures of the eye, in our case mainly the eyeball oscillations as revealed in the EyeLink 1000 recordings, can be used to quantify the perceptual consequences of the non-rigid eye, since the retinal image motion can be produced by both the lens and the eyeball oscillations. As presented, significant positive correlation exists between the PSO and T3 durations indicating clearly that T3 is dependent on PSO.

In the study detailed in chapter 4, it was demonstrated that the EMAIL test can measure the directional asymmetries between horizontal and vertical saccades. The findings from this study are in a strong agreement with the published literature and confirm that performance along the horizontal meridian is faster when compared to vertical direction. No directional asymmetries were found within horizontal (left/right) and vertical (up/down) directions. Similarly, in agreement with previous studies, no asymmetry was found between nasal and temporal saccades. Given the fact that asymmetries between horizontal and vertical saccades exist, future studies must consider these asymmetries while investigating the ISL performance.

The last study investigated the effects of age on ISL performance. The preliminary results from this study show that the EMAIL test provides a valid method to investigate the age effects. The results obtained so far are in direct agreement with the literature and capture clearly the behavioural changes of the saccadic system during both developmental and degenerative stages, demonstrating the potential usefulness of the EMAIL test. Future studies can make use of the test as a reliable method to create normative data from a healthy population for age-related changes on saccadic performance, which could be used to distinguish and gain better understanding of various mental and degenerative disorders.

There are three principal advantages to using this test:

1) Testing procedure is short and completely non-invasive

2) Testing can be performed easily by both young and elderly subjects.

3) The ISL captures changes in a number of different parameters, including visual processing time as well as changes in DRT’s.

However, there are a number of technical limitations that have affected the outcome of the three studies reported here. The equipment running the EMAIL test was not fully integrated with the eye-tracking apparatus. Although the additional hardware constructed for this study ensured accurate synchronisation of the stimulus onset with the eye movement trace, the 60 Hz frame rate of the visual display employed in the EMAIL test limits the accuracy of the estimated ISL. This is particularly evident when the visual processing times are measured in the absence of eye movements. A display rate as high as 500 Hz would have improved the accuracy of these measurements. Also, it would have been of great interest to measure and compare ISLs for other visual attributes such as colour, motion and rapid flicker. This was unfortunately not possible because of the extensive programming required and the limited time available for the study.

Equally important, the potential application of the email test to study how ISLs are affected in mental disorders such as schizophrenia, autism and traumatic brain injury patients. Such studies were again not possible because of limited resources and time involved.

The present studies do, however, demonstrate the potential usefulness of the EMAIL test in patients with mental health disorders, or the effectiveness of treatments in such patients. Future studies are needed to examine the potential clinical applications of the EMAIL test.

6.2 Conclusion

The findings from this study add useful new knowledge to the body of research. The novel visual psychophysical technique developed to measure integrated saccade latencies has been validated and shown to yield useful oculomotor responses without having to record eye movements. Equally important, the method employed to measure post saccadic visual processing times, has been validated and used to describe the perceptual consequences of a non-rigid eye and the variability in binocular coordination. This can help our understanding of perceptual processes, such as how do we exactly re-establish binocular fusion in the instances when fixation errors are large? Could it be that on these instances we rely on monocular information to increase visual efficiency? Or, do the increases in T3 occur as a result of matching information between the optic arrays? This kind of analysis may provide better understanding of the mechanisms the visual system employs to prevent us from sensing the perceptual consequences that arise due to these impediments. These findings may also influence future research and the design of experiments needed to establish how the subject's PSO relate to the drift movements of the eyes at the end of a saccade.

7 Appendices

Appendix A: Velocity and PSO profiles for subject S1, S3 and S7.

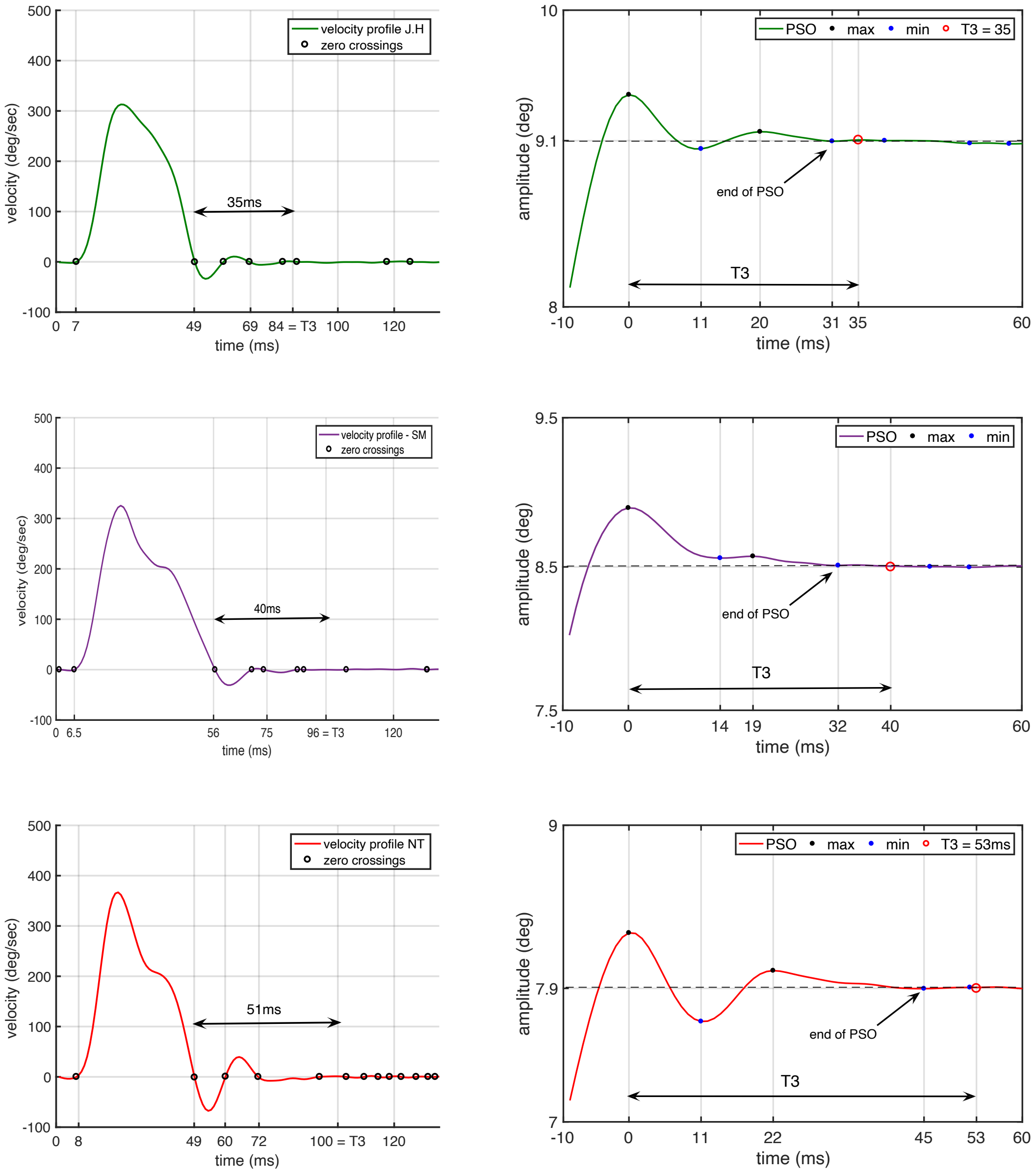


Figure 38. Velocity and PSO profiles for rightward saccades. The occurrences of max (black) and min (blue) peaks precisely coincide with zero crossings indicated by black dots in velocity profiles.

Appendix B: PSO profiles for various contrast levels.

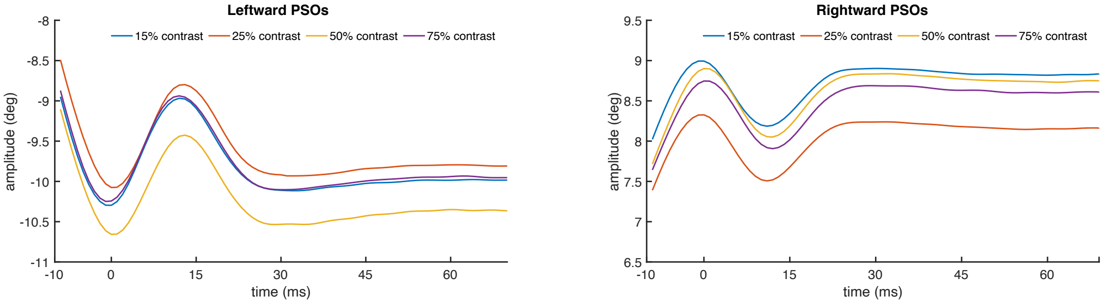


Figure 39. PSO profiles of 8° saccade magnitude for various contrast levels.

Figure 39 demostrates clearly that the amplitude of PSOs is contrast invariant. This is simply becasue the size of PSO depends on decceleration phases of saccade (chapter 3, section 3.2.1).

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