Visual perception and oculomotor control during pursuit eye movements

Viktor V. Nedelchev

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Supervisors: Dr Lee Mcilreavy, Dr Fergal Ennis

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Abstract

Smooth pursuit is a gaze shifting eye movement that attempts to place the fovea on, or close to, a slowly moving target. Until recently it was presumed that there is negligible position error between the eye and the target during pursuit, and where this did occur, it was eliminated by recruiting saccades (catch-up or backup saccades).

Experiments were conducted to determine how the positional error between the eye and the target varies as a function of target velocity and direction. Results indicated that positional error increased as a function of target velocity, but not direction. Further analyses were performed to examine the proximity of the eye from the target when saccades were initiated. Similar to the previous findings, the positional error corresponding to saccade initiation increased as a function of target velocity but not direction. Furthermore, most saccades made during pursuit were catch-up, rather than back-up saccades.

The properties of saccades are well established, however these relate to potentially unnatural viewing conditions, and might not relate to saccades made during pursuit. Experiments showed that the targeting accuracy and precision of saccades during pursuit decreased as a function of target velocity, but not direction.

Finally, I have undertaken experiments to determine whether a novel fixation target that recruits optokinetic reflexes can result in a self-stabilising fixation target. Experiments showed that such a target results in improved accuracy but not precision compared to currently adopted fixation targets.

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Chapter 1. Introduction

1.1. Smooth pursuit

Smooth pursuit is a class of eye movements that are gaze shifting (Carpenter 1988). Their role is to move the eye to keep pace with a moving target so that the target is (continuously) imaged on the fovea. In the human eye, the highest density area of photoreceptors can be found in the fovea, located in the middle of the retina, hence the highest visual acuity in healthy individuals.

Smooth pursuit eye movements have a delay of about 100ms (Terry Bahill and McDonald 1983) after the initial movement of the target and/or any subsequent change in direction. This is the amount of time the visual system needs to process the change/environment and return an appropriate response to facilitate the tracking. Therefore, if a target changes its direction suddenly, and/or in an unpredictable manner, that processing time can increase, and a substantial positional error can occur. Furthermore, the velocity of smooth eye movements peaks around 90°/s (Meyer et al. 1985). Smooth pursuit eye movements will try their best to keep the moving image stable on the fovea and reduce the positional and/or velocity error.

However, the smooth pursuit system has limitations, and other strategies need to be used. One of those strategies is to predict the target movement and plan the smooth pursuit based on that prediction (Barnes and Asselman 1991). This process is dependent on the target having a consistent predictable trajectory. Otherwise, if the target has random unpredictable direction, this strategy would be insufficient. An example of predictable motion would be a car driving along a road. In this case, the car has a relatively consistent velocity and trajectory (i.e. cars in a lane will generally only travel in one direction and at the speed limit). Thus, the visual system can extrapolate that data and make an accurate predictable pursuit. On the other hand, a curve ball in baseball, which makes an unpredictable turn on its trajectory, will be outside of the capabilities of smooth pursuit, and thus represent an unpredictable motion. Therefore, the smooth pursuit system needs consistent and manageable stimulus velocities to operate efficiently.

Pursuit eye movements can generally only be elicited by a visual stimulus and not at will (Rashbass 1961). Most people require a moving target in order to initiate smooth pursuit movements. However, even in the presence of such a target, a person could still choose not to initiate pursuit (i.e. it is voluntary). Smooth pursuit is most commonly defined as a closed loop system with negative feedback of eye velocity (Wyatt and Pola 1983). However, in the first 100ms of smooth pursuit, further information about the stimulus would not have had time to be processed. Therefore, at this initial period, a moving target just initiates the pursuit in an open loop system. Afterwards, when enough information about the stimulus and the retinal slip has been processed, the loop closes, and the parameters of the pursuit are defined. The initial stage of smooth pursuit is dedicated to get the eye moving (Lisberger, 1987).

Recently, the accuracy (but not precision) of eye position during smooth pursuit has been demonstrated (Shanidze et al. 2016b). Moreover, the authors of the paper have investigated whether the visual system foveates the target in its centre of mass during pursuit for maximum visual acuity. Their results are intriguing and indicate that during smooth pursuit the strategy was not to foveate the target, but rather the gaze was placed away from the target centre. This is opposite of what they found for saccades to a stationary object. However, the researchers were limited by their apparatus and technology used. Therefore, in Chapter 3, I investigate how this can be improved and attempt to test fixational stability as a function of target velocity and direction.

Pursuit performance is traditionally calculated using gain (Meyer et al. 1985). Gain is defined as the ratio of eye velocity to target velocity. Gain values of 1 indicate that (on average) eye velocity was equal to the target, whereas gain values of more or less than 1 indicate that (on average) eye velocity was faster or slower

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than the target, respectively. One study (Meyer et al. 1985) showed that there is an approximately linear increase in eye velocity as target velocity increases (i.e. gain is constant) up to approximately 90°/s, after which eye velocity saturates. Indeed, the study showed that typical pursuit gain values range between 0.8 and 1.0 (Meyer et al. 1985) over a range of target velocities. Comparing eye velocity to target velocity is just one method of determining how well an individual can pursue a target. There is a possibility that even if eye and target velocity match, the eye might not be on the target. Therefore, I felt a more appropriate measure for my experiments would be a newer technique (Mcilreavy et al. 2019) which measures accuracy and precision of eye position during pursuit. What is more, it also considers target relative eye positions. This technique virtually (but not practically) renders the target motionless for the analysis and takes only the error of the eye positions. Exploring the accuracy (how far away the eye positions are from the target) and precision (the area over which the eye positions occurred) in 2D presents us with an elaborate combined measure of accuracy and precision. Ultimately, the visual system attempts to keep the fovea on the target, and therefore, the difference between the eye positions and the target positions should be an appropriate way of analysing the data.

1.2. Saccades

Saccades are ballistic eye movements, with all of their parameters being seemingly predetermined before the initiation phase (Ross et al. 2001). Saccades are used to redirect the position of the fovea to various objects of interest. Unlike smooth pursuit, saccades are fast and brief eye movements. Typical saccades can reach a peak velocity of around 500°/s and be approximately 30 – 100ms in duration (Leigh and Zee 2015). Typically, they are defined by their main sequence, which is composed of three properties – peak velocity, duration, and amplitude (Bahill et al. 1975c). As the amplitude of a saccade is directly positively proportional to all other components, it is one of the more popular ways of

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defining saccades. In general, saccades tend to undershoot their targets by approximately 10%, with a small corrective saccade used to place the eye on target (Becker and Fuchs 1969).

Smooth pursuit is not perfect, with typical gain values less than 1 (Meyer et al. 1985). Therefore, to supplement pursuit, the visual system utilises saccades (known as catch-up saccades). The role of catch-up saccades has been thought to eliminate the position error between the eye and the target. Previous work on saccadic eye movements has been limited to stationary targets and the eye moving between them (i.e. not during pursuit). However, it is questionable as to whether these findings can be extrapolated to saccades made during pursuit.

Objects can appear to move for two reasons: a moving object and a stationary observer, or a stationary object and a moving observer (or perhaps some combination of the two). To date, saccades to moving objects during pursuit have largely been unexplored. For example, one of the biggest differences between 'regular' saccades and saccades made during smooth pursuit is that the latter need to shift the fovea from one place to another taking in to account eye velocity and target velocity (De Brouwer et al. 2001).

In Chapter 4 I examine the positional error between the eye and the target at which saccades are initiated during pursuit, while Chapter 5 looks at whether these saccades eliminate the positional error during pursuit.

1.3. Fixation

Despite our best efforts, gaze is never truly stable when we try to fixate a stationary target. The eyes move and continuously change the line of sight due to a combination of drifts, which carry the eye away from the target, and microsaccades, that redirect the eye back on to the target. Furthermore, superimposed on drifts, is a high frequency tremor. What is currently known about

fixational eye movements has been heavily criticised since the literature is predominantly based on a small number of highly motivated individuals, who would generally have a research background and/or previous experience. These studies examine the area of fixation and report a small/tight distributions of fixational eye movements (Rattle 1969; Skavenski and Steinman 1970; Sansbury et al. 1973). A study of naïve individuals found that fixation performance in untrained observers was inferior compared to trained observers and deteriorated with the progression of time (Cherici et al. 2012).

While it may seem that these eye movements are intrusive, it has been shown that they may enhance certain aspects of vision (Intoy and Rucci 2020). In addition, these fixational eye movements play an important role in visual perception. Without them, a loss of vision would be experienced due to neural adaptation. Thus, the use of fixational eye movements keeps everything visible (Ditchburn B L Ginsborg 1951), and the visual system is required to produce those movements to constantly keep new information flowing to the retina, thus preventing adaptation (Martinez-Conde et al. 2004).

In the clinic, steady fixation is important for several clinical tests (e.g. visual field testing). However, these instruments employ very simple fixation stimuli (typically a dim LED). Therefore, in Chapter 6, a more 'favourable' fixation target is proposed. It is important to mention that attention plays a highly important role in overall fixation stability (Steinman et al. 2016). In recent years, there has been an interest in the most appropriate target for maintaining stable fixation (Bellmann et al. 2004b). The latest evidence suggests that a 'bull's eye and crosshair' target produced superior fixational stability compared to a range of other commonly used fixational targets (Thaler et al. 2013). However, these studies may well also be influenced by an observer's attention.

The optokinetic response or nystagmus (OKR/N) is a reflexive movement composed of series of initially slow-phase eye movements (smooth pursuit)

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following the direction of the target accompanied afterwards by fast-phase eye movements (saccades) that return the gaze to the initial starting position. This type of eye movements is generally seen when an individual is looking through the window of a moving train. While the moving scene is being tracked (smooth pursuit) and it eventually passes the boundaries of the visual field, the eye moves back (saccade) to the start position where the object was first observed. Through OKR, the visual system tracks objects in motion while the head/body is generally stationary. It is usually induced by full visual field stimuli on the retina (Furman 2014), however it has been shown that foveal stimuli could also elicit OKN as well (Miyoshi 1985).

In Chapter 6 I investigate the use of a novel fixation stimulus that utilises OKR. Since OKR is a reflexive eye movement, this type of stimulus may result in a selfstabilising fixation target, potentially improving fixation performance and circumventing poor attention.

Chapter 2. General methods

In this chapter, the experimental apparatus will be discussed as well as the methods used for the processing and analysis of eye movement data and their experimental validation.

2.1. Ethics statement

These studies were carried out in accordance with the tenets of the Declaration of Helsinki. Informed consent was obtained from all observers after they received an explanation of the nature and possible consequences of the study. Ethical approval was granted by the Research Ethics and Audit Committee of the School of Optometry and Vision Sciences, Cardiff University (Chapter 8).

2.2. Apparatus

a) Choice of eye tracker

Scleral search coils have been recognised as the "gold standard" method for eye tracking for a few decades. However, this older technology has several drawbacks. First, they are only adequate for short study durations, as they are invasive and associated with an acute reduction in visual acuity (from 6/4.5 to 6/15 Snellen in some instances (Irving et al. 2003). Second, they provide analogue rather than digital outputs and are difficult to integrate with modern programming environments (e.g., Psychtoolbox/MATLAB), to ensure appropriate time stamping of stimuli with responses. For these reasons, modern video-based eye trackers such as the EyeLink 1000 are preferred. While the quality of video-based eye trackers may vary, some can perform as well as scleral search coils in tracking eye movements (Houben et al. 2006). In particular, the EyeLink 1000 has been specifically validated against scleral search coils, with similar performance characteristics for the two systems (Kimmel et al. 2012; McCamy et al. 2015).

b) Choice of EyeLink 1000 mount

The EyeLink 1000 eye tracker has a range of mounting options, however the two options available for this project were the desktop mount and the tower mount. A comparison of these two mounting options is provided in Table 1.

EyeLink 1000	Tower Mount	Desktop Mount	
Average accuracy	0.25° - 0.05°	0.25° - 0.05°	
Gaze tracking range	±30° horizontally,	±16° horizontally,	
	±20° vertically	±12.5° vertically	
Optimal camera – eye	~38 cm (fixed above	40 – 70 cm in front of the	
distance	the forehead / chin	in head (e.g., table, desk)	
	rest)		
Latency	mean < 1.8 msec, mean < 1.8 msec,		
SD < 0.6 ms,		SD < 0.6 ms,	
	1000 Hz	1000 Hz	
Spatial resolution	< 0.01° RMS, 1000 Hz	< 0.01° RMS, 1000 Hz	

 Table 1 A comparison of the tower mount and the desktop mount (SR Research Ltd., Mississauga, Ontario 2009).

The EyeLink 1000 tower mount (Figure 1) was chosen over the desktop mount for several reasons. Both the tower and desktop mounts can record at 1000 Hz (1 ms sample intervals), however the desktop mount also allows binocular recording at 500 Hz per eye (2 ms sample intervals). In this research, the contralateral eye will be occluded, and the binocular aspect of pursuit is not the subject of interest. Thus, the data from one eye will be sufficient. Furthermore, the monocular option has twice the temporal resolution. While this is more than sufficient to allow accurate identification of the onset and offset (i.e. temporal resolution) of the fastest eye movements (saccades), which require a minimum sampling rate of 200 Hz (Juhola et al. 1985), it will also allow more data to be collected in the same time interval. Neither of the two mounting options allows for significant head movements, as both will need to be used with a chin and forehead rest.



Figure 1 Images to show the lab set up and the equipment used. a) The EyeLink 1000 tower mounted eye tracker. b) The Display++ monitor.

The tower and desktop mounts have different infra-red illuminator options. The tower mount has an infrared LED array in the invisible spectrum (910 nm) as opposed to the desktop mount which is in the somewhat visible range (890 nm), with a dim red glow. This could create a distraction and/or interference for the participant, diverting their gaze away from the stimuli, especially if the experiment is being conducted in a dark room. The tower mount also provides an unobstructed field of view, as it is mounted above the head. On the other hand, the desktop mount must be in front of the participant at 40–70 cm, potentially obstructing the lower field of view. Finally, the tower mount affords a larger trackable range compared to the desktop mount. This will be particularly important for pursuit-based experiments where the peak-to-peak amplitude of the pursuit target motion may be as large as $\pm 20^{\circ}$ horizontally and vertically.

c) Choice of stimulus display

Stimuli will be presented on a calibrated display that has been custom designed for vision science (Display++; Cambridge Research Systems Ltd, Rochester UK) (Figure 1). This display was chosen over conventional LCD monitors due to its large field of view (32" at 1920×1080), fast refresh rate (120 Hz) and quick response time (5 ms grey-to-grey). In addition, the display has an integrated sensor for real time luminance calibration and real time spatial uniformity correction, thus ensuring consistent luminance across the screen. Indeed, several studies have utilised this display for pursuit-related experiments (Braun et al. 2017). One study has compared the Display++ to CRT and other LCD counterparts for the purposes of vision research (Ghodrati et al. 2015). A summary of the differences is provided in Table 2. This analysis concluded that the Display++ is a respectable successor of CRT monitors, especially because it has real time spatial uniformity correction, and thus, accurate light output. Furthermore, for my pursuit experiments, I will require the display to have a large visual angle, which the Display++ provides over CRTs. Thus, it allows for displaying and assessing a larger field of view and larger amplitude pursuit.

	Display++	Conventional LCD (Iiyama ProLite B2283HS-B3)	CRT (Sony GDM F520)
Refresh rate	120 Hz	75 Hz	85 Hz
Resolution	1920×1080	1920×1080	1920×1440
Aspect ratio	16:9	16:9	4:3
Brightness	350 (cd/m²)	250 (cd/m ²)	208 (cd/m ²)
Contrast	1400:1	1000:1	315:1
Size	32"	21.5"	21"

Table 2 Comparison of different display technologies for vision science.

d) Programming environment and stimulus rendering

Experiments were written in MATLAB (version 2016b; Mathworks, Natick, USA) and used routines from the psychophysics toolbox (Brainard 1997; Pelli 1997; Kleiner et al. 2007). Stimuli were displayed using a GeForce GTX 1070 graphics card (NVIDIA; Santa Clara, California, USA) at a frame rate of 120Hz with a resolution of 1920×1080 pixels on the Display++.

2.3. Stimuli

For pursuit experiments I used a small dot stimulus (0.4°). This stimulus has been used previously in typical individuals (Mcilreavy et al. 2019), and those with infantile nystagmus (Mcilreavy et al. 2020a), an eye oscillation associated with reduced visual acuity. This size would appear to be small enough to evoke highgain pursuit, but still be large enough to be seen by a wide range of individuals, including those with a visual impairment.

2.4. Viewing distance

I chose a viewing distance of 57 cm for all experiments. Indeed, this is a common viewing distance for vision science since at this distance, 1° of visual angle corresponds to 1cm on screen. The visual angle subtended by the monitor at this distance would provide appropriate amplitudes for pursuit (e.g., a range of $\pm 16^{\circ}$) in all orientations (horizontal, vertical, and oblique). However, I have decided not to exceed $\pm 16^{\circ}$ for pursuit amplitude since the inherent non-linear tangent error of a flat screen will introduce potentially significant errors in position, timing, and speed of the pursuit stimulus. For example, an eccentricity of 1° will correspond to a distance of 0.99 cm from the centre of the screen, whereas an eccentricity of 16° corresponds to a distance of 16.34 cm from the centre of the screen (i.e. the rule of 1° of visual angle corresponds to 1 cm on screen does not hold for large angles).

2.5. Pursuit velocity calculation

Velocities were calculated in °/s using a constant pixel shift per frame refresh. The 'on screen' amplitude (cm) of pursuit was calculated from the viewing distance (cm) and the desired visual angle (°) in the following way:

Amplitude = (tan (Visual angle) * Viewing distance)

Afterwards, the pixels/cm value was calculated from the screen dimensions (70 cm = 1920 pixels) over half of the pursuit amplitude (i.e. $\pm 8^{\circ}$). This gave the value of 27.4286 pixels per cm.

2.6. Eye movement recording and data processing

a) Eye movement calibration

Prior to each use, the EyeLink 1000 requires calibration. Eye movements were calibrated against a 3×3 grid of calibration points that spanned 95% of the area of the screen. Each calibration point was shown separately and in a random order. The calibration at each point was then accepted by the experimenter by a keyboard press. The EyeLink 1000 validation procedure was also used to confirm the 'quality' of the calibration. This validation procedure requires the observer to refixate the same calibration points, and the mean error for each point is calculated. The EyeLink grades the calibration as 'good', 'fair' and 'poor'. Only those calibrations which were graded as 'good' were accepted, and the rest were repeated.

b) Eye movement data processing

Data files (.edf files) were imported into the EyeLink Data Viewer software (v. 3.2.48) and data 'reparsed' into saccades, blinks etc with the correct pixel-perdegree resolution (27.47 pixels-per-degree at 57 cm). Saccades were detected using the pre-defined 'psychophysical' setting within the software (velocity threshold of 22°/s; acceleration threshold of 3800°/s²). Separate comma separated values files (.csv) were then exported for eye positions, saccades, target positions, and message events. These data files were then imported, processed, and analysed in MATLAB.

2.7. Analysis of eye movement performance: accuracy and precision

a) Accuracy and precision

When quantifying eye movement performance, I measured both accuracy and precision. I will now explain these terms using a normal distribution as an analogy. Normally distributed data can be described using descriptive statistics, such as the mean and standard deviation. The mean represents accuracy (the proximity of the

mean measured value to the reference value), whereas standard deviation represents precision (the spread of the measured values).



Figure 2: A one-dimensional schematic of the concepts of accuracy and precision. This diagram shows a hypothetical normal distribution (e.g. horizontal eye positions), the area under which sums to unity (i.e. 1). Accuracy represents the proximity of the mean measured value (e.g. the distance of the measured value from the reference value) while precision represents the spread of measured values).

b) Bivariate contour ellipse area (BCEA)

In eye movement research, it has become customary to measure the bivariate contour ellipse area (BCEA) as a two-dimensional measure of accuracy and precision of fixation (Crossland and Rubin 2002a; Bellmann et al. 2004a; Castet and Crossland 2012; Cherici et al. 2012). This measure is based on a contour that encompasses 68% of the highest density data (see Figure 4). To compute a BCEA, eye movement data first needs to be expressed *relative* to a target. As an example, target relative eye positions can be obtained by subtracting the target position from all eye positions. This operation is performed in both the horizontal and vertical planes. Thus, accuracy (the proximity of the BCEA centroid of the contour to the target) and precision (area of the BCEA contour) metrics can then be

computed. In this case, accuracy represents the proximity of the contour centroid to the target position (target relative distributions), whereas precision is the total area of the contour (see Figure 3). Despite the popularity of BCEA, it does assume that eye movements are normally distributed (i.e. parametric), similar to calculating the mean and standard deviation. This assumption has been shown to be flawed (Whittaker et al. 1988).



Figure 3 Performance metrics that can be calculated from either BCEA or bPDF. The shaded contour encompasses 68% of the highest probability density. Accuracy is represented by the distance of the centroid (i.e. centre of mass) of the contour from the origin of the target relative distribution. The greater the distance between the target and the centroid, the lower the accuracy. Precision is then represented by the area of the contour. The larger the area, the lower the precision as there will be a greater spread of the data. Line A (red solid line) is the major axis of the contour, representing the axis with the lowest precision. Line B (red dashed line) is the minor axis, representing the axis with the greatest precision.

c) Bivariate probability density function (bPDF)

A more suitable alternative that does not rely on the underlying assumption of normality (i.e. non-parametric) is the bivariate probability density function (bPDF) (Whittaker et al. 1988; Castet and Crossland 2012; Cherici et al. 2012; Mcilreavy et al. 2019; Mcilreavy et al. 2020b). As with BCEA, this measure is also based on a contour that encompasses 68% of the highest density data (see Figure 4), with accuracy and precision calculated in a similar fashion to BCEA. However, the BCEA

does not consider if the data are non-parametric. As shown in Figure 4, even though there are two modes (i.e. 'peaks') to this distribution, there is a single BCEA produced (indicated by the thin dashed line). Therefore, using this method would be inappropriate because the contour would greatly miscalculate the actual underlying distribution of eye positions. In this project, the bPDFs will be calculated using the method of (Mcilreavy et al. 2019; Mcilreavy et al. 2020b). In contrast to BCEA, the benefit of bPDFs can be appreciated from examining actual eye position data (see Figure 4), where the isolines outline separate clusters of data all coming from the total area that encompasses 68% of the full dataset. The accuracy and precision are then derived from the sum of these areas.



Figure 4 An example of both a BCEA and bPDF (Castet and Crossland 2012). The figure on the left shows a cluster of data points with two 'peaks'. A single BCEA (ellipse with 'thin' dashed line) has been fitted to that data. In addition, a bPDF has been fitted (contour with 'thick' dashed line). The bPDF considers that the underlying data is formed from two peaks (non-parametric), whereas the BCEA treats these data as being normally distributed along the x and y planes (parametric).



Figure 5 An example of a bivariate probability density function (bPDF) (Mcilreavy et al. 2019). In the upper figure the bPDF has been computed on the underlying data (grey data points). The 68% isocontour is indicated by the black contour. In the lower figure, the same 68% contour has been isolated for further analysis. The metrics calculated are identical to those depicted in Figure 4.

2.8. Research population

By the time my experiments had been devised, programmed, and tested, the UK had entered a national lockdown (March 2020). I was therefore unable to obtain full ethical approval for my studies until May 2021 for my revised experiments. It had been my intention to make comparisons of pursuit eye movements between typical individuals and those with a condition that results in a continuous

horizontal eye oscillation (infantile nystagmus). However, I was only permitted to recruit staff and students at the University (i.e. only typical individuals), and human research that involved members of public was not permitted. Despite this, recruitment was difficult due to the time-consuming nature of the experiments and the time restrictions of using a shared laboratory (sessions were limited to 4 hours maximum). However, the sample population in the revised experiments involved young healthy adults and investigated normal pursuit eye movements. It could be argued that this sample population would be more homogeneous compared to a condition like infantile nystagmus, and although the sample size was small, would still be representative of the adult population.

Chapter 3. Accuracy and precision of eye position during pursuit

3.1. Introduction

Smooth pursuit is a class of gaze-shifting eye movements that are regarded as maintaining the retinal image of a pursuit target on, or in close proximity to the fovea (Purves and Williams 2001). This definition seems to be commonly accepted and was investigated in a recent study (Shanidze et al. 2016b) where the author examined the extent to which pursuit stimuli were foveated (i.e. the positional lag between the eye and target). By examining pursuit along horizontal (0° - 180°), vertical (90° - 270°) and oblique directions (45° - 225° & 135° - 315°), the authors found that the gaze was displaced from the target (see Figure 6). Typically, this positional error was of 1° or less but could be as much as 3° - 4°, with the magnitude of the displacement increasing with the size of the target. In summary, this study demonstrated that pursuit targets are not directly or continuously foveated during pursuit. Despite their interesting findings, there are several study limitations that affect the broader applicability of their findings to smooth pursuit.



Figure 6 Results from Shanidze et al. (2016b). Data shows the mean distance (i.e. positional error) between the eye and the centre of the target during smooth pursuit. Blue bars indicate small pursuit target size (0.6°) and orange bars indicate large pursuit target size (1.7°). Data shows that most participants had a positional error of approximately 1° or less irrespective of the target size, although for some participants it could be as much as 3-4°.

3.2. Limitation of eye tracking

The authors used a confocal scanning laser ophthalmoscope (SLO) to track the eye movements. The sampling rate of the SLO was limited to 60 Hz (16.67 ms sample intervals). As previously discussed, this sampling frequency does not have the temporal resolution for high velocity eye movements (i.e. a minimum of 200 Hz is necessary for saccades (Juhola et al. 1985; Gibaldi et al. 2017), but would be able to sufficiently record low velocity eye movements (i.e. pursuit). In general, higher sampling frequencies should be preferred, as more detailed information can be extracted. However, the temporal resolution is quite low (1 sample/16.67ms) in comparison to many video-based eye trackers. A higher sampling rate (e.g. 1000 Hz) would not only provide more samples in the same time frame, but the better temporal resolution (1 sample/ms) would enable saccade onsets and offsets to be better defined.

3.3. Limitation of pursuit parameters

The authors' chosen pursuit parameters would be considered as small amplitude (i.e. $\pm 6^{\circ}$) and low velocity (5°/s and 6°/s). Thus, it is unclear as to whether these parameters would reflect the speeds and amplitudes of motion typically encountered in the natural world (e.g. motion of balls during sport, cars moving along roads etc.). Furthermore, it is well recognised that pursuit performance declines with increasing target velocity (Collewijn and Tamminga 1984; Kolarik et al. 2010; Skinner et al. 2019). However, it would be beneficial to address whether the identified positional lag increases as a function of velocity.

3.4. Limitation of analyses

Pursuit sweeps in the study took approximately 2 seconds to perform (e.g. 6°/s along an amplitude of 12°). However, not the entire 2 seconds of pursuit eye movements were analysed. Instead, the authors restricted their analysis to a brief epoch within the 2 seconds of pursuit. More specifically, this was:

"the longest continuous period of smooth pursuit where velocity was within ± 0.2 of the median velocity after pursuit onset".

This approach is likely to avoid catch-up/back-up saccades, ignoring the fact that involuntary eye movements act in tandem with pursuit to place the retinal image of the target on or closer to the fovea. For instance, immediately following a catchup saccade, the fovea will be in close proximity to the target, whereas just before a catch-up saccade, the fovea will not be in close proximity to the target. Thus, the results may not represent typical positional lag during pursuit. Finally, the authors only analysed eye position data relative to the target using BCEA. Given so little data (a combination of a small sample of eye position within the 2 seconds of pursuit, coupled with the low sampling rate), it is unclear whether there was sufficient data to compute an appropriate BCEA. More importantly, as discussed in the general methods (Chapter 2), there are potentially unsuitable assumptions underlying the use of BCEA. These have been shown to be flawed when used for eye position during fixation (Whittaker et al. 1988), but it is unclear whether there are valid for pursuit eye movements.

3.5. Effect of target direction

A number of previous studies have clearly demonstrated that typical individuals have higher pursuit gain performance when following horizontally moving targets compared to vertically moving targets (Rottach et al. 1996; Skinner et al. 2019). Although Shanidze et al. (2016b) have observed pursuit performance in different directions (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°), the authors did not analyse their data by pursuit direction. Therefore, it is possible that, like the differences observed in velocity, the positional error between the eye and target may vary with target direction.

3.6. Effect of target velocity

There is a well-documented reduction in pursuit performance with increasing target velocity (Collewijn and Tamminga 1984; Kolarik et al. 2010; Mcilreavy et al.

2019; Skinner et al. 2019). However, the study by Shanidze et al. (2016b) used a limited range of target velocities. Therefore, it remains unclear how the positional error between the eye and the target varies as a function of target velocity.

3.7. Summary

The results of Shanidze et al. (2016b) are interesting and question the foveal nature of pursuit. However, several limitations involving the eye tracking hardware, study design and analyses limit whether the results are generalisable.

3.8. Aims

The aim of this study is to investigate the accuracy and precision of the positional lag during pursuit as a function of target direction and target velocity.

3.9. Hypotheses

The hypotheses under test are as follows:

- The positional error for horizontal pursuit will be less than for vertical pursuit (Mcilreavy et al. 2019), and the positional error for oblique directions falling between that of horizontal and vertical pursuit.
- The positional error between the eye and the target will increase as a function of target velocity.
- 3.10. Methods
- a) Participants

Informed consent was obtained from all observers after they received a description of the nature and possible consequences of the study. Ethical approval (study number 1556) was granted by the Research Ethics and Audit Committee of the School of Optometry and Vision Sciences, Cardiff University (see Chapter 8). Participants were excluded from the study if they had any self-reported eye condition (e.g. amblyopia, cataract, age-related macular degeneration). There was no upper age limit for this study. Eleven observers were recruited, and six were excluded either due to poor data quality, or failure to complete all trials in the

same single session. All of the remaining five observers (mean age 31 years ± standard deviation 5.56 years; range 26-38 years; 2 males and 3 females) all had normal vision of 0.0 logMAR or better uncorrected (i.e. emmetropic).

b) Apparatus

The experimental apparatus is as described in Chapter 2. Observers were seated 57 cm from the display with their head supported by a chin and head rest in an otherwise dark room. Each observer performed a calibration routine on the eye tracker before commencing the experiment. The calibration routine was a 3×3 grid of calibration targets that covered 95% of the screen. Calibration was accepted if the on-board software rated the calibration as 'GOOD', otherwise the calibration was repeated until an acceptable result was obtained.

c) Stimuli

The pursuit stimulus was a 0.4° dot that moved through a linear peak-to-peak amplitude of 32° with a constant velocity of either 8°/s, 16°/s, or 32°/s. The pursuit target moved in 8 different directions: 0° (rightward), 45° (oblique), 90° (upward), 135° (oblique), 180° (leftward), 225° (oblique), 270° (downward) and 315° (oblique), (see Figure 7).



Figure 7 Diagram demonstrating the different meridia that pursuit took place along.

d) Procedure

The experiment was divided into 12 blocks (3 velocities × 4 pairs of orientations). The order of the conditions was randomised for each participant. Each pursuit trial was self-paced and required a button press on a wireless keyboard. Observers were asked to "follow the moving target to the best of their ability". Each trial began with a central fixation target. On pressing a keyboard button to start the trial, the target stepped by half of the pursuit amplitude along the plane of pursuit, in the opposite direction to the target motion. For example, on an 8°/s velocity × 0° trial, the target would step left by 16° from the centre of the screen before moving rightwards at 8°/s through a total amplitude of 32°. To avoid observers anticipating the onset of the target motion, the target onset had a random delay of 1.5 - 3.0 seconds. Each trial contained two sweeps of the target direction. Each participant performed 32 seconds of pursuit so that the total duration of pursuit data for each condition was equal.

e) Analyses

Eye movements were processed in the manner outlined in Chapter 2. The bivariate probability density function of eye position (minus any saccades and blinks) was computed, and the individual metrics (accuracy and precision) were examined as a function of target velocity and direction. All statistical testing was performed in JASP (JASP 0.15.0.0). Repeated measures ANOVA was performed to examine the main effect of target velocity and target direction. In brief, when performing a repeated measures ANOVA, all data are 'pooled' to investigate main effects, e.g. to investigate a main effect of velocity, data from all target directions are pooled by velocity. If the assumption of sphericity was violated (the requirement that variances of the differences between all combinations of related groups must be equal), a Greenhouse-Geisser correction was used to adjust the degrees of freedom and the level of significance. Since all participants were young (pre-presbyopes aged 18 to 38), I did not examine the effect of age on any of the results (i.e. age as a co-variable). Post-hoc analyses were only performed when
there was a significant main effect. The post hoc analyses were pairwise comparisons that used a Bonferroni correction to adjust the level of significance based on the number of pairwise comparisons.

3.11. Results

Typical eye movement traces for pursuit along each of the directions are presented in Figure 8 - Figure 11.



Figure 8 Eye position traces from a typical horizontal pursuit trial (0° and 180° orientations). These data represent a single trial from a single participant (Participant 05). Blue lines – horizontal eye positions. Yellow lines – vertical eye positions. Orange lines – horizontal target positions. Purple lines – vertical target positions. The graph shows the target trajectory and where the gaze was in relation to it. The gaps in the eye traces are removed blinks and saccades. Data shown are for Participant 05.



Figure 9 Eye position traces from a typical oblique pursuit trial (45° and 225° orientations). Blue lines – horizontal eye positions. Yellow lines – vertical eye positions. Orange lines – horizontal target positions. Purple lines – vertical target positions. In this case the horizontal and vertical target positions are superimposed because of the oblique trajectory. The graph shows the target trajectory and where the gaze was in relation to it. The gaps in the eye traces are removed blinks and saccades. Data shown are from Participant 05.



Figure 10 Eye position traces from a typical vertical pursuit trial (90° and 270° orientations). Blue lines – horizontal eye positions. Yellow lines – vertical eye positions. Orange lines – horizontal target positions. Purple lines – vertical target positions. The graph shows the target trajectory and where the gaze was in relation to it. The gaps in the eye traces are removed blinks and saccades. Data shown are from Participant 05.



Figure 11 Eye position traces from a typical oblique pursuit trial (135° and 315° orientations). Blue lines – horizontal eye positions. Yellow lines – vertical eye positions. Orange lines – horizontal target positions. Purple lines – vertical target positions. The graph shows the target trajectory and where the gaze was in relation to it. The gaps in the eye traces are removed blinks and saccades. Data shown are for Participant 05.



Typical Isocontour of the 68% encompassing area for pursuit along each of the directions are presented in Figure 12 - Figure 14.

Figure 12 Typical 68% isocontours of eye positions for horizontal pursuit (0° and 180 °directions) for a single trial. The blue line encompasses 68% of the highest density of datapoints. The blue asterisk indicates the centre of mass of the isocontour, whereas the red circle indicates the target position. The distance between the centre of mass and the target position refers to the accuracy and the area of the isocontour to the precision. Data shown are for Participant 05.



Figure 13 Typical 68% isocontours of eye positions from a participant for oblique pursuit (45° and 225° directions). The blue line encompasses 68% of the highest density of datapoints. The blue asterisk indicates the centre of mass of the isocontour, whereas the red circle indicates the target position. The distance between the centre of mass and the target position refers to the accuracy and the area of the isocontour to the precision. Data shown are for Participant 05.



Figure 13 Typical 68% isocontours of eye positions from a participant for vertical pursuit (90° and 270° directions). The blue line encompasses 68% of the highest density of datapoints. The blue asterisk indicates the centre of mass of the isocontour, whereas the red circle indicates the target position. position. The distance between the centre of mass and the target position refers to the accuracy and the area of the isocontour to the precision. Data shown are for Participant 05.



Figure 14 Typical 68% isocontours of eye positions from a participant for vertical pursuit (135° and 315° directions). The blue line encompasses 68% of the highest density of datapoints. The blue asterisk indicates the centre of mass of the isocontour, whereas the red circle indicates the target position. The distance between the centre of mass and the target position refers to the accuracy and the area of the isocontour to the precision. Data shown are for Participant 05.

a) Effect of target direction

In this study, a repeated measures ANOVA showed that that there was no main effect of target direction on the accuracy [F(7, 28) = 1.824, p = 0.122, $\eta 2 = 0.122$] or precision [F(7, 28) = 0.433, p = 0.873, $\eta 2 = 0.013$] of eye positions (Figure 15).



Figure 15 Eye position precision and accuracy as a function of target direction. Error bars indicate ±95% confidence intervals. The left-hand side if the graph shows the precision of eye position as a function of target direction. Larger values for precision indicate a larger spread of eye movements. The graph indicates that the precision values were similar across all target directions. The right-hand side of the graph shows the accuracy of eye position as a function of target direction. Larger values for accuracy indicate that eye positions were farther from the target. The graph indicates that while there was some variation in accuracy across the target directions, it was broadly similar.

On the left-hand side of Figure 15, are data relating to the precision of eye position. As precision increases, there is greater spread in eye position. These data indicate that the mean precision in eye position is similar across all target directions. On the right-hand side of Figure 15 are data relating to the accuracy of eye position. As accuracy increases, the eye positions are farther from the pursuit target. These data indicate that while there is some variation in the mean accuracy, it is broadly similar across all target directions.

b) Effect of target velocity

In this study, a repeated measures ANOVA showed that there was a significant main effect of velocity on accuracy [F(2,8) = 7.209, p = 0.016, $\eta^2 = 0.2$] and precision [F(2, 8) = 20.164, p = <.001, $\eta^2 = 0.583$] on eye positions (Figure 16). Post hoc comparisons are shown in Table 3 (precision) and Table 4 (accuracy).



Figure 16 Eye position precision and accuracy as a function of target velocity. Error bars indicate ±95% confidence intervals. The left-hand side of the graph shows precision of eye position as a function of target direction. Larger values for precision indicate a larger spread of eye movements. The graph shows that precision values are increased with target velocity, hence eye positions became more variable. The right-hand side of the graph shows accuracy of eye position as a function of target direction. Larger values for accuracy indicate that eye positions were farther from the target. The graph shows the magnitude of accuracy increased with target velocity, hence eye positions were farther from the target.

As mentioned in the previous section, the precision is the spread of eye positions and accuracy is the proximity of the eye positions to the target. In Figure 16 both the accuracy and precision increase with increased target velocity. This means that eye positions during pursuit are farther from the target and spread over a larger area, as target velocity increases.

Since it was the change in velocity (and not direction) that was significant. it would be interesting to explore how velocities (8°, 16°, 32°) relate to each other. We see

that velocity has a significant effect. However, it would be of interest to know which velocities produce the significant effect.

Post Hoc Comparisons - Velocity									
			95% CI fo Differe						
		Mean Difference	Lower	Upper	SE	t	p bonf		
8	16	-0.594	-2.599	1.411	0.665	-0.893	1.000		
	32	-3.917	-5.922	-1.912	0.665	-5.892	0.001		
16	32	-3.323	-5.328	-1.318	0.665	-4.998	0.003		

Note. P-value and confidence intervals adjusted for comparing a family of 3 estimates (confidence intervals corrected using the Bonferroni method). *Note.* Results are averaged over the levels of: Direction

Table 3 Results of the post-hoc analysis of target velocity on the precision of pursuit positions.

In Table 3 Results of the post-hoc analysis of target velocity on the precision of pursuit positions. Table 3 (precision) and Table 4 (accuracy) the post-hoc results are presented. These data are pairwise comparisons for every combination of velocity. From these tables, we see that there is a significant difference between 8°/s and 32°/s as well as between 16°/s and 32°/s. Therefore, there was a significant effect on precision between those velocities. As for accuracy, there was only a significant difference between 8°/s and 32°/s.

Post Hoc Comparisons - Velocity									
			95% CI for Mean Difference						
		Mean Difference	Lower	Upper	SE	t	Cohen's d	p bonf	
8	16	-0.117	-0.611	0.377	0.164	-0.715	-0.320	1.000	
	32	-0.587	-1.081	-0.094	0.164	-3.587	-1.604	0.021	
16	32	-0.470	-0.964	0.024	0.164	-2.872	-1.284	0.062	
<i>Note.</i> Cohen's d does not correct for multiple comparisons.									
<i>Note.</i> P-value and confidence intervals adjusted for comparing a family of 3									
estimates (confidence intervals corrected using the Bonferroni method).									
No	<i>Note.</i> Results are averaged over the levels of: Direction								
abla	able 4 Desults of the next has analysis of target value its on the assured of nursuit positions								

Table 4 Results of the post-hoc analysis of target velocity on the accuracy of pursuit positions.

c) Eye position error: lagging vs leading the target

So far, I have established that as target velocity increases, the positional error between the eye and the target also increases. However, it is important to determine the direction of the inaccuracy (i.e. does the eye lag or lead the target?). To address this question, all pursuit trials were rotated so that they represent the target moving rightwards. Next, the orientation of the centroid of the isocontour relative to the target was plotted as a polar graph. If the eye was lagging the target, then the mean orientation of the distribution would be approximately 180° (i.e. leftwards of the target). However, if the eye was leading the target, then the mean orientation would be approximately 180° (i.e. rightwards of the target). The results of this analysis are presented in Figure 17.



Figure 17 Polar distribution of the orientation of the 68% isocontours centroid relative to the target (blue circle).

In order to investigate the effect of velocity, all trials were rotated so that the target was moving rightward (i.e. along 0°) by subtracting the relevant angle. For example, pursuit along 90° required subtracting 90° from all orientation data, and pursuit along 180° required subtracting 180° from all orientation data. Each plot contains data grouped by the respective velocity (i.e. all 8°/s velocity trials were

put together irrespective of their direction). The mean vector (green line) length (r) in each plot ranges from 0 to 1 and shows both the mean orientation and indicates how clustered the data are around the mean angle (Θ). Important note: how clustered the data are on the polar plot. The greater the magnitude (i.e. length of the mean vector, the more clustered the data). These plots indicate that while the mean orientations (Θ) for each velocity were similar, the data became more clustered as velocity increased. To determine if the distributions have a significant mean orientation for the given velocity (in °) the Kuiper's V test (V α , α – degrees for comparison) was used. For all velocities used there appears to be a significant mean orientation. Also, the higher the velocity the stronger the effect.

The data show that there is a tendency for observers to lag behind the target at all three velocities (i.e. all three velocities have similar mean angles of approximately 180°), and that this bias becomes stronger as function of target velocity (i.e. the magnitude of the resultant vector r increases). The faster the target moves, the greater the likelihood of eye positions to lag behind the target. This result contrasts with Shanidize et al (2016):

"We rotated all trials so that the target was at the origin moving leftwards and found a broad distribution of eye placements for both target sizes (Figure 5B, C). In particular, there is no systematic trend for the eyes to lag the target (to be on the right of the target)."

In their study, Shanidze et al. (2016b) have not quantified their pursuit data using circular statistics, but instead have only made a *qualitative* judgement of the distributions (see Figure 18). Therefore, it remains possible that the data of Shanidze et al. (2016b) do demonstrate an unexplored tendency to for the eye to lag behind the target.



Figure 18 Data from Shanidze et al. (2016b). The data show the distribution of average eye positions relative to the target during smooth pursuit for 0.6° (B) and 1.7° (C) targets. A notable finding is the lack of any tendency to lag or lead the target.

A possible explanation of that would be the velocities (5°/s or 6°/s) used for the experiment were just too slow for any bias to be qualitatively observed. I have found there is a trend for the eye to lag less with decreasing/lower velocities and the lowest velocity we have used was 8°/s. Therefore, if the magnitude of the mean vectors (r) from Shanidze et al. (2016b). were plotted against the corresponding target velocity, it should be possible to estimate the amount of positional lag in the study by Shanidze et al. (2016b). Extrapolating the line of best fit would indicate that a 5°/s target would have a small but noticeable lag, with an r value of 0.1601 (see Figure 19). However, it is important to note that those are conclusions based on only 3 data points. Results for more velocity combinations and with a wider pool of participants might show a different trend as a better fit would be available. Thus, the current data should only be considered as indicative.



Figure 19 Line of best fit the for mean vector magnitude plotted against target velocities.

The black circles indicate the data from our experiment (at 8°/s, 16°/s, and 32°/s). Also, they represent the mean vector magnitude for each target velocity (from Figure 20). Red asterisk represents the hypothetical mean vector magnitude for data of Shanidze et al. (2016b). There is a positive trend indicating that faster targets have higher mean vectors. This suggests that in the study by Shanidze et al. (2016b), there should be a small but measurable bias towards the eye position lagging behind the target. The line of best fit is given by f(x) = 0.01578*x + 0.0812 and has an R-square of 0.9903.

3.12. Discussion

The aim of this study was to determine how the positional error between the eye and the target varies as a function of the target direction and velocity. The main findings of the study are discussed below.

a) Position error is independent of target direction

In contrast to previously reported results relating to pursuit gain, it was found that the positional error between the eye and target does not differ with target direction. While the two-dimensional distribution of eye positions with respect to the target were considered, it was not possible to determine the temporal relationships within the distribution (i.e. change of eye position over time), hence velocity. In theory, it is entirely possible to have the same distribution of eye positions arising from very different eye velocities. Thus, my results do not exclude the possibility of different gains with direction.

b) Position error is dependent on target velocity

It was found that the positional error between the eye and target increases as a function of target velocity. In addition, it was found that the variability in the positional error also increases as a function of target velocity (i.e. lower precision). This indicates that fast moving targets are not imaged on the fovea, but rather on the parafoveal retina (i.e. low accuracy). Furthermore, the retinal image of targets is not stable but undergoes considerable amount of 'jitter' (i.e. low precision).

c) Eye position lags target position

The results indicated that the eye tends to lag behind the target position. This is true most of the time, but not all of the time. However, this tendency is positively correlated to the target velocity. This finding is consistent with typical gain values being lower than 1.0. Indeed, the gain values are known to decrease as a function of target velocity (Meyer et al. 1985).

d) Limitations of the study

While careful consideration was given to designing the study, there are key limitations that may have implications regarding the generalisability of the results. These are as follows:

• Target velocity was constant

The target speed along a particular direction did not change during the trial. This makes the target motion highly predictable. It has been previously demonstrated that predictability and knowledge about the target can greatly increase the accuracy of the pursuit (Terry Bahill and McDonald 1983). Despite this, highly significant differences as a function of target velocity were still observed. This suggests that while such stimuli may be predictable, and potentially 'easier' to follow, the visual system remains unable to track the target foveally. Given this finding, it is expected that the positional error would likely increase if less predictable stimuli were used. Nonetheless, the current results indicate the best possible performance of the visual system under what could be considered 'ideal' conditions of constant velocity and path of the target.

• Inclusion of all pursuit data (minus saccades and blinks)

It is well known that saccades are used to supplement pursuit. If the eye is lagging the target, then a catch-up saccade is used to bring the eye back onto the target. Similarly, if the eye is leading the target, then a back-up saccade is used to bring the eye back onto the target. The data used in this study will therefore have included eye positions immediately before and after saccades. However, it is not possible to determine how saccadic changes in position during pursuit will have altered the results. It is possible that the number of saccades would increase with target velocity (and hence lower gain). Therefore, more saccades would be expected in the 32°/s velocity than the 16°/s or 8°/s velocity, and more in the 16°/s velocity than the 8°/s velocity. Thus, it is possible that the errors observed with increasing velocity are the minimum errors. In other words, a portion of eye movement data immediately after catch-up saccades were removed, this would potentially increase the positional error. Nonetheless, given that all pursuit data have been included, it could be argued that the results of this study are representative of typical pursuit performance.

• Calibration

The calibration of the eye tracker is critical to the findings of this study since any error in the calibration could give rise to position errors between the eye and the target. However, prior to each block of trials, participants underwent a drift correction to eliminate any potential positional error. Since drift errors accumulate over time, to observe an effect of positional error with target velocity, slower trials would have to be run before faster trials. However, this was not the case since the order of the trials was randomised in this study. Thus, there is a high level of confidence that the effects observed were genuine and not due to an order effect.

3.13. Conclusions

This study has demonstrated that:

- There is no difference in the accuracy and precision of eye positions during pursuit along different directions.
- Eye positions during pursuit become less accurate and less precise as a function of target velocity.
- The eye positions tend to lag the target position during pursuit and that this tendency increases as a function of target velocity.

Chapter 4. Positional error of saccade initiation during pursuit

4.1. Introduction

When following a target, the eyes perform a combination of smooth pursuit movements and supplementary saccades. Both eye movements are used to minimise the positional error and the retinal slip (i.e. velocity error) between the object of interest and centre of the eye. It has generally been shown that the smooth pursuit and saccadic systems have significantly more in common than was previously believed. The position error and velocity error affect both types of eye movements (De Brouwer et al. 2002). For example, if I consider a catch-up saccade made to a moving target and assume only the position error has been accounted for, then that saccade would presumably land approximately at the position of where the target was originally sampled. Saccades have a latency of approximately 200 ms (Purves 2001), however it has been demonstrated that catch-up saccades account for the underlying eye velocity during pursuit as they tend to be fairly accurate (Rashbass 1961; Gellman and Carl 1991). A variety of velocity error and position error combinations have been previously examined during smooth pursuit (De Brouwer et al. 2002), and demonstrated that the best predictor of whether to utilise a catch-up saccade or continue pursuit is based upon on how long it will take for the eye to intersect the target with its current velocity. To be exact, they have found that eye intersecting time for pursuit to be sustained is approximately between 40 - 180 ms. If the eye intersecting time is \leq 40 ms and \geq 180 ms, the visual system would generally prefer to initiate a saccade.

So far, we have observed previous experiments where the stimulus parameters are subject to change while pursuit is ongoing (i.e. a velocity and position step during pursuit). The present study is concerned with how the visual system behaves when presented with an uninterrupted predictable target motion which

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stays constant throughout the trial. This would allow us to evaluate whether velocity itself influences the start position of catch-up saccades, rather than the change in velocity and/or position. Catch-up saccades during sustained pursuit with stimulus velocities up to 32°/s were considered, which are well within the capabilities of the human pursuit system (Meyer et al. 1985).

As a consequence, a central question that remains unanswered in the literature is whether different, but constant, pursuit velocities influence the accuracy and precision relative to the target of the catch-up saccade initiation during pursuit. In this study, the data from Chapter 3 are retrospectively examined to determine the position error at which saccades were evoked during pursuit.

The distributions of eye position in the previous chapter can be considered as being bound to the start and end positions of saccades. As the previous chapter examined 'pure' pursuit eye movements, all the saccades were excluded from the data. Consider the diagram in Figure 21. The magenta region on the left-hand side of the isocontour can be considered the region where potential catch-up saccades could be initiated. This is because it is the most distal portion of the isocontour. Given that the contour increased in distance from the target position (i.e. lower accuracy) and the contour had a larger area (i.e. lower precision) as target velocity increased, it would follow that the starting position of saccades made during pursuit will also be related to target velocity, but not target direction.



Figure 21 A hypothetical 68% isocontour for rightward pursuit. Since the eye positions lagged the target positions, the isocontour is depicted to the left of the target. Thus, the magenta region to the left-hand side of the isocontour represents the potential region where the eye would be when initiating a catch-up saccade. Since the distance of the isocontour centroid from the target (i.e. accuracy) increased as well as the total area (i.e. precision) of the isocontour increased as a function of velocity (see Chapter 3 results), this leads to the hypothesis that the distribution of eye positions from where saccades are initiated will also show lower accuracy and precision as a function of target velocity. Furthermore, this would also suggest no relationship with target direction.

4.2. Aims

The aim of this study is to explore the accuracy and precision of those eye position when a saccade is initiated during smooth pursuit, across 3 different stimulus velocities (8°/s, 16°/s, and 32°/s). As well as, determining whether the saccades are predominantly catch-up.

4.3. Hypotheses

The hypotheses under test are as follows:

 The difference in eye position between the eye and the target when saccades are initiated varies as a function of target velocity, but not target direction. Most saccades during pursuit are catch-up saccades rather than back-up saccades.

4.4. Methods

This is a retrospective analysis of the eye movement data that were collected as part of the study in Chapter 3. The same methods are applicable here as well.

4.5. Analysis

Eye movement data were processed and analysed as described in Chapter 2. Saccades were identified in the EyeLink Data Viewer using predefined criteria ('psychophysical' setting; velocity criterion of 22°/s and acceleration criterion of 3800°/s²). The start positions of the saccades that were initiated during the final 85% of the target sweep, and that ended before the end of the target sweep, were included in the analysis. All other saccades were excluded. A bivariate probability density function of the start positions of the saccades was then computed and the 68% isocontour was selected for further analysis.

a) Statistics

A repeated measures ANOVA was performed to determine the effect of target direction and target velocity. All repeated measures ANOVA analyses were performed in JASP (0.15.0.0). A brief overview of a repeated measures ANOVA is provided in Chapter 3. Angular data were analysed using the circular statistics toolbox for MATLAB (Berens 2009; Berens and Valesco 2009).

4.6. Results

Typical isocontour plots for horizontal pursuit (towards 0° and towards 180°) are shown in Figure 22. Only these pursuit trials are shown as there was no significant main effect of target direction on the accuracy or precision of the saccade start position (see 'Effect of target direction' in results section).



Figure 22 Typical 68% isocontours of saccades start positions from a participant during horizontal pursuit (0° and 180° directions). The blue line encompasses 68% of the highest density of datapoints. The blue asterisk indicates the centre of mass of the isocontour, whereas the red circle indicates the target position. The distance between the centre of mass and the target position refers to the accuracy and the area of the isocontour to the precision. Data shown are from Participant 05.

a) Effect of target direction

In this study, a repeated measures ANOVA showed that there was no main effect of target direction on the precision [F(7, 28) = 1.01, $p = 0.446 \eta^2 = 0.014$] or accuracy [F(7, 28) = 1.302, p = 0.286, $\eta^2 = 0.028$] of saccade start positions (see Figure 23).



Figure 23 The effect of target direction on the precision and accuracy of the saccade start positions. Error bars indicate ±95% confidence intervals. The left-hand side if the graph shows the precision of eye position, at the point of saccade initiation, as a function of target direction. Larger values for precision indicate a larger spread of eye movements. The graph indicates that the precision values were similar across all target directions, so the area over which saccades were initiated was similar for all target directions. The right-hand side of the graph shows the accuracy of eye position, at the point of saccade initiation, as a function of target direction. Larger values for accuracy indicate that eye positions were farther from the target. The graph indicates that while there was some variation in accuracy across the target directions, it was broadly similar, so saccades were initiated from similar distances from the target for all target directions.

As mentioned in the previous section, the precision is the spread of eye positions and accuracy is the proximity of the eye positions to the target. The data presented in Figure 23 results indicate that the distance of the eye from the target (accuracy) and the area over which saccades are initiated is unaffected by target direction.

b) Effect of target velocity

In this study, a repeated measures ANOVA showed that there was main effect of target velocity on the precision [*F*(2, 8) = 37.386, p = < .001, $\eta^2 = 0.695$] and



accuracy [F(2, 8) = 263.143, p = <.001, $\eta^2 = 0.795$] of saccade start positions (see Figure 24).

Figure 24 The effect of target velocity on the precision and accuracy of the saccade initiation positions. Error bars indicate ±95% confidence intervals. The left-hand side of the graph shows precision of eye position, at the point of saccade initiation, as a function of target direction. Larger values for precision indicate a larger spread of eye movements. The graph shows that precision values are increased with target velocity, hence the area over which saccades were initiated became more variable with increased velocity. The right-hand side of the graph shows accuracy of eye position, at the point of saccade initiation, as a function of target direction. Larger values for accuracy indicate that eye positions were farther from the target. The graph shows the magnitude of accuracy increased with target velocity, hence saccades were initiated farther from the target with increased velocity.

The data presented in Figure 24 indicate the difference in position between the eye and the target when initiating saccades during pursuit is affected by target velocity (i.e. positively associated). The results of the post hoc analyses are provided in Table 5 (precision) and Table 6 (accuracy).

Post Hoc Comparisons - Velocity								
			95% CI for Mean Difference					
		Mean Difference	Lower	Upper	SE	t	Cohen's d	p bonf
8	16	-0.798	-2.605	1.009	0.599	-1.331	-0.595	0.659
	32	-4.833	-6.640	-3.025	0.599	-8.065	-3.607	<.001
16	32	-4.035	-5.842	-2.228	0.599	-6.734	-3.011	<.001
<i>Note.</i> Cohen's d does not correct for multiple comparisons.								

Note. P-value and confidence intervals adjusted for comparing a family of 3 estimates (confidence intervals corrected using the Bonferroni method). *Note.* Results are averaged over the levels of: Direction

Table 5 Results of the post-hoc analysis of target velocity on the precision of saccade start positions.

In study it was observed that there was a significant difference between the target velocities of 8°/s and 32°/s as well as between 16°/s and 32°/s on the precision of saccade start positions.

Post Hoc Comparisons - Velocity									
			95% CI for Mean Difference						
		Mean Difference	Lower	Upper	SE	t	Cohen's d	p bonf	
8	16	-0.267	-0.654	0.119	0.128	-2.087	-0.933	0.211	
	32	-2.668	-3.054	-2.281	0.128	-20.828	-9.315	<.001	
16	32	-2.400	-2.787	-2.014	0.128	-18.742	-8.381	<.001	
<i>Note.</i> Cohen's d does not correct for multiple comparisons.									

Note. P-value and confidence intervals adjusted for comparing a family

estimates (confidence intervals corrected using the Bonferroni method).

Note. Results are averaged over the levels of: Direction

Table 6 Results of the post-hoc analysis of target velocity on the accuracy of saccade start positions.

In study it was observed that there was a significant difference between the target velocities of 8°/s and 32°/s as well as between 16°/s and 32°/s on the accuracy of saccade start positions.

c) Saccade direction

It has not yet been established whether the saccades made during pursuit are catch-up (made towards the target because the eye is lagging the target) or backup (made towards the target because the eye is leading the target) saccades. To determine this, a similar process to the one described in Chapter 3 was employed. Each saccade direction was computed as the orientation of the saccade end position from the start position. Then all of the data were rotated so that they were based on a rightward pursuit (i.e. target was moving towards 0°). All saccade directions were then analysed using circular statistics (Figure 25). If participants made mostly catch-up saccades, then the mean saccade direction would be oriented rightwards (a mean orientation of approximately 0°). However, if participants made mostly back-up saccades, then the mean saccade direction would be oriented leftwards (a mean orientation of approximately 180°).



Figure 25: Polar distribution of the start positions of the saccades relative to the target (blue circles). In order to investigate the effect of velocity all direction were converted to rightward saccades (i.e. along 0°) by subtracting the relevant angle. For example, saccades along 90° required subtract 90° from all

orientation data, and saccades along 180° required subtracting 180° from all orientation data. Each plot contains data grouped by the respective velocity (i.e. all 8°/s velocity trials were put together irrespective of their direction). The mean vector (green line) length (r) in each plot ranges from 0 to 1 and shows both the mean orientation and indicates how clustered the data are around the mean angle (Θ). The greater the magnitude (i.e. length of the mean vector, the more clustered the data). These plots indicate that while the mean orientations (Θ) for each velocity were similar, the data became more clustered as velocity increased. To determine if the distributions have a significant mean orientation for the given velocity (in °) the Kuiper's V test (V α , α – degrees for comparison) was used. For all velocities used there appears to be a significant mean orientation. Also, the higher the velocity the stronger the effect.

The results of this analysis are presented in Figure 25. The three polar plots indicate that the majority of saccades were catch-up saccades, since the mean direction of the saccades were oriented towards 0° (the target). Furthermore, it can be observed that as the target velocity increased, the proportion of catch-up saccades increased, since the magnitude of the mean vector (r), increased as a function of target velocity. An increase in the mean vector indicates that more of the data is clustered at the mean orientation.



Figure 26 Mean vector magnitudes as a function of target velocity. The closer to 1 (y axis) the more clustered the data are. Black circles indicate the data from my experiment (at 8°/s, 16°/s, and 32°/s). Each black circle represents the mean orientation vector magnitude containing data grouped by the respective velocity (i.e. all 8°/s velocity trials were put together irrespective of their direction). The linear fit is given by f(x) = 0.005617*x + 0.7926 with an R-square of 1. This unusual result suggests a highly linear relationship between the proportion of catch-up saccades and pursuit target velocity.

A plot of the magnitude of the mean vectors for each target velocity is shown in Figure 26. The relationship between the magnitude of the mean vector and target velocity is highly linear. Extrapolating this trend indicates that for all target velocities (i.e. greater than 0° /s) the visual system makes predominantly catch-up

saccades. However, it is important to note that those are conclusions based on only 3 data points. Results for more velocity combinations and with a wider pool of participants might show a different trend as a better fit would be available. Thus, the current data should only be considered as indicative.

d) Saccade start positions

It is important to note that so far it is known only that the majority of saccades made during pursuit (across all stimulus velocities) are generally catch-up. However, it is not known whether saccade start positions occur behind (lagging) or in front (leading) of the target. To determine this, a similar technique to the one described in Chapter 3 was used. To address this question, all pursuit trials were rotated so that they represent the target moving rightwards. Next, the orientation of the centroid of the isocontour of the saccade start positions, relative to the target was plotted as a polar graph. If the eye was lagging the target at that instance, then the mean orientation of the distribution would be approximately 180° (i.e. leftwards of the target). However, if the eye was leading the target, then the mean orientation of the distribution would be approximately 0° (i.e. rightwards of the target). The results of this analysis are presented in Figure 27.



Figure 27 Polar distributions of the saccade start positions relative to the target (blue circle). In order to investigate the effect of velocity all directions were converted to rightward saccades (i.e. along 0°) by subtracting the relevant angle. For example, saccades along 90° required subtract 90° from all orientation data, and saccades along 180° required subtracting 180° from all orientation data. Each plot contains data grouped by the respective velocity (i.e. all 8°/s velocity trials were put together irrespective of their direction). The mean vector (green line) length (r) in each plot ranges from 0 to 1 and shows both the mean orientation and indicates how clustered the data are around the mean angle (Θ). The greater the magnitude (i.e. length of the mean vector, the more clustered the data). These plots indicate that while the mean orientations (Θ) for each velocity were similar, the data became more clustered as velocity increased. To determine if the distributions have a significant mean orientation for the given velocity (in °) the Kuiper's V test (V α , α – degrees for comparison) was used. For all velocities used there, appears to be a significant mean orientation. Also, the higher the velocity the stronger the effect,

As observed in Figure 27 the start positions of the saccades appear to be a function of the velocity of the pursuit stimulus. The faster the target moved, the greater the number of start positions originated behind the target (lagging). This trend is similar to the trend that was observed for pursuit in Chapter 3.



Figure 28 Mean vector magnitudes as a function of target velocity. The closer to 1 (y axis) the more clustered the data are. Black circles indicate the data from my experiment (at 8°/s, 16°/s, and 32°/s). Each black circle represents the mean orientation vector magnitude containing data grouped by the respective velocity (i.e. all 8°/s velocity trials were put together irrespective of their direction). The linear fit is given by $f(x) = 0.02577^*x + 0.1458$ with an R-square of 0.988. This unusual result suggests a highly linear relationship between the proportion of saccade start positions in relation to the target and pursuit target velocity.

The plot of the magnitude of the mean vectors for each target velocity about the start positions of the saccades is shown in Figure 28. The relationship between the magnitude of the mean vector and target velocity is highly linear. Extrapolating this trend indicates that for all target velocities (i.e. greater than 0°/s) the visual system predominantly lags with the start position of the saccades. However, it is important to note that those are conclusions based on only 3 data points. Results for more velocity combinations and with a wider pool of participants might show a different trend as a better fit would be available. Thus, the current data should only be considered as indicative.

4.7. Discussion

The aim of this study was to explore the difference in accuracy and precision of eye positions between the eye and the target when a saccade is made during smooth pursuit. The main findings of the study are discussed below.

a) Accuracy and precision of saccade start positions are independent of target direction

This finding is based on the results from Chapter 3, which showed that target orientation did not play a role on the accuracy and precision of smooth pursuit. As hypothesised, the target direction made no difference to the position difference between the eye and the target required to evoke a catch-up saccade as well.

b) Accuracy and precision of saccade start positions are dependent on target velocity

The distance (accuracy) and area (precision) over saccades were initiated increased as a function of target velocity, in line with what was hypothesised. This means that for faster targets, the retinal image can move further away from the fovea before a saccade is made.

c) Most saccades made during pursuit are catch-up saccades

For all three target velocities, most saccades made were catch-up saccades (i.e. the saccades were made towards the target). While occasional back-up saccades were observed, the proportion of back-up saccades decreased as a function of target velocity, with an increasing proportion of catch-up saccades.

d) Limitations of the study

As this is a retrospective analysis of data already collected in Chapter 3, many of the limitations discussed in that chapter, are also applicable to these results. These are as follows:

• Target velocity was constant

As previously mentioned, typical pursuit gain is less than 1.0. This means that eye velocity will lag target velocity and hence it would be expected for most saccades made during pursuit to be catch-up rather than back-up. However, this may not be the case with a less predictable stimulus, where there would likely be a greater proportion of back-up saccades. In terms of the real world, there will be a mixture of targets with approximately constant velocity (e.g. cars driving past, people walking), as well as more dynamic targets (e.g. a fly). Arguably, very different patterns of saccade behaviour would occur in these two situations.

• Time to initiate pursuit

When initiating pursuit, a saccade is often used to place the eye initially on the target. It is important to exclude these initial targeting saccades, where possible. If they were included, the distance travelled by the pursuit target before the initial saccade will increase with velocity, since most saccades will have a latency of around 200 ms (Purves 2001). Thus, this would lead to an increase in the position difference between eye and target for when a saccade is evoked. Therefore, analyses were limited to the final 85% of the target sweep in order to eliminate the inclusion of initial saccades to the target as much as possible. Thus, the results should represent saccade start positions *during* pursuit rather than the *initiation* of pursuit.

• Duration of pursuit and number of saccades

As mentioned above, the first and 15% of the pursuit trial was not analysed. For the 32°/s condition, that represents a total of 850 ms of pursuit per trial, as the total amplitude was 32° in size. A possible limitation would be the short amount of time the stimulus was on screen, and that it might not be as representative of natural conditions as the other velocities (i.e. 16°/s and 8°/s). To minimise this effect, the total time of pursuit was equated between conditions. For example, the 32°/s had twice as many trials as the 16°/s condition, and four times as many trials compared to the 8°/s. As a result, the total duration of data collected was the same for each condition, fixed at 32 s.

4.8. Conclusions

This study has demonstrated that:

- There was no main effect of target direction on the accuracy and precision of saccadic start positions. Therefore, the position difference between the eye and the target required to make a saccade does not depend on target direction.
- 2) There was a main effect of target velocity on the accuracy and precision of saccadic start positions. Therefore, the position difference between the eye and the target required to make a saccade increases with target velocity.
- Most saccades made during pursuit were catch-up saccades. As target velocity increased, a greater proportion of saccades were catch-up saccades.
- Tentative results indicate that for all pursuit velocities, most saccades made during pursuit are catch-up saccades.
Chapter 5. Targeting accuracy and precision of saccades during pursuit

5.1. Introduction

When a catch-up or back-up saccade is initiated, the aim is to close the position error between the eye and the target in an attempt to bring the fovea closer to the target for (presumably) greater visual acuity. A good measure of saccadic performance is to examine their accuracy (their distance from the target when they land) and precision (the area in which the end position is in) (Mcilreavy et al. 2019). However, it is worth investigating whether the accuracy and precision of these saccades are affected by the stimulus parameters. Extensive examination of the literature reveals that the *two-dimensional* targeting accuracy or precision of saccades made during typical smooth pursuit, whether catch-up or back-up, has not yet been examined.

However, although somewhat different to 'regular' saccades, the accuracy and precision of microsaccades has been measured. What has been found is that the accuracy and precision of microsaccades (14'-20') (Poletti et al. 2020) are comparable to those of regular ones, which is to be expected, considering that both are, in practicality, types of ballistic eye movements. What is more, it has been found that the larger the amplitude of the microsaccade, the less accurate and precise it tends to be (Poletti et al. 2020). It would be reasonable to assume that the same pattern will exist for regular saccades. As was suggested in Chapter 3, the higher the velocity of the stimulus, the less precise and accurate the smooth pursuit. Consequently, the faster the stimulus, the farther away from the centre of the eye it is pursued. Therefore, if a catch-up saccade is to be made, it will need to cover a greater amplitude. Greater saccadic amplitudes are known to result in increased peak velocity and duration (Bahill et al. 1975b), which might result in larger errors due to the increased distance from centre of the eye.

It has been found that saccadic eye movements tend to undershoot the target by approximately 10% of the saccadic amplitude (Becker and Fuchs 1969), with smaller correcting saccades (10° or less) attempting to eliminate the remaining positional error. Furthermore, research indicated that these corrective saccades also tend to undershoot the target (Henson 1979). However, this study used large eye movements in the order of 40°. Generally, the majority of naturally occurring saccades tend to have amplitudes of approximately less than 15° (Bahill et al. 1975a). A subsequent study (Kowler and Blaser 1995) examined the onedimensional accuracy and precision of saccades (i.e. saccadic gain) for small (3.8° to 4.2°) saccades, and found approximately 1% undershoot rather than the typical 10%. Thus, it could be argued that as the eccentricity of the target increases, so does the pursuit undershoot. More recently Shanidze et al. (2016b) investigated the targeting accuracy of saccades as a function of target size (0.6° and 1.7°). In general, the researchers found that the majority of saccades were hypometric and there was no difference in the precision and accuracy for the different target sizes (i.e. undershooting the target) (Shanidze et al. 2016b) (see Figure 29).



Figure 29 Published data relating to the accuracy of pursuit saccades. Each figure depicts all trials, and the data have been rotated so that the saccade target lies at the centre. Since most of the data are to the left of the plot, this indicates an undershoot (Shanidze et al. 2016).

While all research mentioned so far in this chapter indicates that saccades generally undershoot the target, it is unclear how these data will relate to the accuracy and precision of saccades made during pursuit. This is because there are several key differences, summarised in Table 7. Thus, in this study, the targeting accuracy and precision of saccades made during smooth pursuit will be investigated to gain insight into whether the properties of the catch-up saccades are different to 'conventional' or 'regular' saccades.

Saccadic Property	'Conventional' saccade	Saccade during pursuit		
Volition	Voluntary	Involuntary		
Amplitude	Large (e.g. 40°)*	Very small (~1.5°)***		
	Small (e.g. 3.8°)**	saccades		
	saccades	Varied (~0-10°)*****		
	Microsaccades (14'-	saccades		
	20')****			
Eye velocity at saccade	Approximately equal to	Approximately equal to		
initiation	zero (assuming steady	the pursuit target		
	fixation)	(assuming high gain		
		pursuit)		
		Non-constant		
Saccade target velocity	Zero	Non-zero		

Table 7 Summary of the key differences between 'conventional' saccades and saccades made during pursuit (i.e. catch-up and back-up). *Becker and Fuchs (1969); ** Kowler and Blaser (1995); *** Mcilreavy et al. (2019); *****(Poletti et al. 2020); *****(de Brouwer et al. 2002).

To examine what might occur during pursuit, Figure 30 will be considered. The magenta region on the right-hand side of the isocontour can be considered as the region where potential saccades could terminate. This is because it is the most proximal portion of the isocontour. Given that the contour increases in distance from the target position (lower accuracy) and the contour has a larger area (lower precision) as target velocity increases, it would follow that the end position of saccades made during pursuit will also be related to target velocity, but not target direction.



Figure 30 A hypothetical 68% isocontour for rightward pursuit. Since the eye positions lagged the target positions, the isocontour is depicted to the left of the target. Thus, the magenta region to the right-hand side of the isocontour represents the potential region where the eye would be when completing a catchup saccade. Since the distance of the isocontour centroid from the target (i.e. accuracy) increased as a function of velocity as well as the total area (i.e. precision) of the isocontour (see Chapter 3 results), this leads to the hypothesis that the distribution of eye positions following a saccade will also show lower accuracy and precision as a function of target velocity. Furthermore, this would also suggest no relationship with target direction.

5.2. Aims

The aim of this study is to determine the accuracy and precision of saccades end points made during smooth pursuit.

5.3. Hypotheses

The hypothesis under test are as follows:

 Saccades made during pursuit will undershoot the target rather than eliminate the position error between the eye and the target. In addition, the precision and accuracy of undershoot will be a function of stimulus velocity – i.e. the faster the target goes the less accurate and precise the saccades will be. Saccadic undershoot will be affected by pursuit target velocity but not target direction. This is based on the finding that target direction was shown to be of an insignificant effect in Chapter 3 and Chapter 4.

5.4. Methods

This is a retrospective analysis of the eye movement data that were collected as part of the study in Chapter 3.

5.5. Analysis

Eye movement data were processed and analysed as described in Chapter 2. Saccades were identified in the EyeLink Data Viewer using predefined criteria ('psychophysical' setting; velocity criterion of 22°/s and acceleration criterion of 3800°/s²). The end position of the saccades that were initiated during the final 85% of the target sweep and that ended before the end of the target sweep were included in the analysis. All other saccades were excluded. A bivariate probability density function of the end positions of the saccades was then computed and the 68% isocontour was selected for further analysis.

a) Statistics

A repeated measures ANOVA was performed to determine the effect of target direction and target velocity. All repeated measures ANOVAs were performed in JASP (0.15.0.0). A brief overview of a repeated measures ANOVA is provided in Chapter 3. Angular data were analysed using the circular statistics toolbox for MATLAB (Berens 2009; Berens and Valesco 2009).

5.6. Results

a) Examples of typical isocontour data

Typical isocontour plots for horizontal pursuit (towards 0° and towards 180°) are shown in Figure 31. Those are the only pursuit trials shown, as there was no significant main effect of target direction (see 'Effect of target direction in the results section') on the accuracy or precision of saccade end position.



Figure 31 Typical 68% isocontours of saccade end positions from a participant during horizontal pursuit (0° and 180° directions). The blue line encompasses 68% of the highest density of datapoints. The blue asterisk indicates the centre of mass of the isocontour, whereas the red circle indicates the target position. The distance between the centre of mass and the target position refers to the accuracy and the area of the isocontour to the precision. Data shown are from Participant 05.

b) Effect of target direction

In this study, a repeated measures ANOVA showed that there was no main effect of target direction on the precision [F(7, 28) = 0.425, p = 0.878, $\eta 2 = 0.01$] and accuracy [F(7, 28) = 1.461, p = 0.222, $\eta 2 = 0.077$] of saccade end positions (see Figure 32). These results indicate that the accuracy and precision of the saccade end positions are unaffected by target direction.



Figure 32 The effect of target direction on the precision and accuracy of the saccade end positions. Error bars indicate ±95% confidence intervals. The left-hand side if the graph shows the precision of eye position, at the point of saccade termination, as a function of target direction. Larger values for precision indicate a larger spread of eye movements. The graph indicates that the precision values were similar across all target directions, so the area over which saccades terminated was similar for all target directions. The right-hand side of the graph shows the accuracy of eye position, at the point of saccade termination, as a function of target direction. Larger values for accuracy indicate that eye positions were farther from the target. The graph indicates that while there was some variation in accuracy across the target directions, it was broadly similar, so saccades terminated at similar distances from the target for all target directions.

c) Effect of target velocity

In this study, a repeated measures ANOVA showed that there was main effect of target velocity on the precision [F(2, 8) = 9.956, p = 0.007, $\eta 2 = 0.482$] and accuracy [F(2, 8) = 10.292, p = 0.006, $\eta 2 = 0.235$] of saccade end positions (see Figure 33).



Figure 33 The effect of target velocity on the precision and accuracy of the saccade end positions. Error bars indicate ±95% confidence intervals. The left-hand side of the graph shows precision of eye position, at the point of saccade termination, as a function of target direction. Larger values for precision indicate a larger spread of eye movements. The graph shows that precision values are increased with target velocity, hence the area over which saccades terminated became more variable with increased velocity. The right-hand side of the graph shows accuracy of eye position, at the point of saccade termination, as a function of target direction. Larger values for a function of target direction. Larger values for accuracy indicate that eye positions were farther from the target. The graph shows the magnitude of accuracy increased with target velocity, hence saccades terminated farther from the target with increased velocity.

The data presented in Figure 33 indicate that the difference in position between the eye and the end point of the saccade during pursuit is affected by target velocity. These data suggest that as the velocity increases, then saccades will terminate at a greater distance from the target (lower accuracy) and over a larger area (lower precision). The results of the post hoc analyses are provided in Table 8 (precision) and Table 9 (accuracy).

Post Hoc Comparisons - Velocity								
			95% CI for Mean Difference					
		Mean Difference	Lower	Upper	SE	t	Cohen's d	p bonf
8	16	-0.669	-3.285	1.947	0.867	-0.772	-0.345	1.000
	32	-3.636	-6.252	-1.020	0.867	-4.192	-1.875	0.009
16	32	-2.967	-5.582	-0.351	0.867	-3.420	-1.530	0.027
<i>Note.</i> Cohen's d does not correct for multiple comparisons.								

Note. P-value and confidence intervals adjusted for comparing a family of 3 estimates (confidence intervals corrected using the Bonferroni method). *Note.* Results are averaged over the levels of: Direction

Table 8 Results of the post-hoc analysis of target velocity on the precision of saccade end positions.

In study it was observed that there was a significant difference between the target velocities of 8°/s and 32°/s as well as between 16°/s and 32°/s on the precision of saccade end positions.

Post Hoc Comparisons - Velocity									
			95% CI for Mean Difference						
		Mean Difference	Lower	Upper	SE	t	Cohen's d	p bonf	
8	16	-0.083	-0.478	0.312	0.131	-0.632	-0.283	1.000	
	32	-0.551	-0.946	-0.156	0.131	-4.207	-1.881	0.009	
16	32	-0.468	-0.863	-0.073	0.131	-3.575	-1.599	0.022	

Note. Cohen's d does not correct for multiple comparisons. *Note.* P-value and confidence intervals adjusted for comparing a family of 3 estimates (confidence intervals corrected using the Bonferroni method). *Note.* Results are averaged over the levels of: Direction

Table 9 Results of the post-hoc analysis of target velocity on the accuracy of saccade end positions.

In study it was observed that there was a significant difference between the target velocities of 8°/s and 32°/s as well as between 16°/s and 32°/s on the accuracy of saccade end positions.

d) Saccadic undershoot vs overshoot

To determine whether saccades were undershooting or overshooting the target, the orientation of the isocontour centroid relative to the target was examined. To do this, all pursuit directions were rotated so that the target was moving rightwards. Thus, if the saccades were undershooting the target, the isocontour centroid would lie to the left of the target (i.e. left of the origin of the plot), whereas if the saccades were overshooting the target, the isocontour would lie to the right of the target (i.e. right of the origin of the plot). The results of the analysis are shown in Figure 34. indicating that saccades tend to generally undershoot only for the highest velocity $(32^{\circ}/s)$, since the mean orientation of the isocontour is

oriented at approximately 180°. For 8°/s and 16°/s, the relative end points are distributed all around the target, which would indicate that no general undershoot is present.



Figure 34: Polar distribution of the end positions of saccades relative to the target (blue circles). In order to investigate the effect of velocity all directions were converted to rightward saccades (i.e. along 0°) by subtracting the relevant angle. For example, saccades along 90° required subtract 90° from all orientation data, and saccades along 180° required subtracting 180° from all orientation data. Each plot contains data grouped by the respective velocity (i.e. all 8°/s velocity trials were put together irrespective of their direction). The mean vector (green line) length (r) in each plot ranges from 0 to 1 and shows both the mean orientation and indicates how clustered the data are around the mean angle (Θ). The greater the magnitude

(i.e. length of the mean vector, the more clustered the data). To determine if the distributions have a significant mean orientation for the given velocity (in °) the Kuiper's V test (V α , α – degrees for comparison) was used. These plots indicate that for 8°/s and 16°/s there is no significant mean orientation (Θ) for the saccade end positions relative to the target. However, with 32°/s there is a significant mean orientation.



Figure 35: Mean vector magnitudes as a function of target velocity. The closer to 1 (y axis) the more clustered the data are. Black circles indicate the data from my experiment (at 8°/s, 16°/s, and 32°/s). Each black circle represents the mean orientation vector magnitude containing data grouped by the respective velocity (i.e. all 8°/s velocity trials were put together irrespective of their direction). The linear fit is given by $f(x) = 0.0125^*x - 0.04321$ with an R-square of 0.3773. This result suggests a weak linear relationship between the proportion of saccades end positions in relation to the target and pursuit target velocity.

Building upon this, given the data at hand, if the mean orientation angle (Θ) is greater than 90° and less than 270° (or on the left side of the polar plot) (Figure 34), this would indicate that the end points of the saccades undershoot the target (i.e. on the left). Hence, the vector value r (from the polar plot) is given a negative sign. Conversely, if the mean orientation (Θ) is greater than 270° or less than 90° (i.e. on the right) the vector r (from the polar plot) would be overshooting the target and assigned a positive sign.

Applying this analysis would yield a correlation of the likelihood of a saccade to undershoot or overshoot the target based on the target velocity. Thus, negative r value would indicate a preference for undershooting the target, a value of 0 – no preference for undershooting/overshooting, positive value – overshooting. By doing this, theoretically the stimulus velocity which will exhibit no bias for undershooting/overshooting the target can be interpolated. The correlation is shown below (Figure 36). However, it is important to note that those are conclusions based on only 3 data points. Results from more velocity combinations and with a wider pool of participants might show a different trend as a better fit would be available. Thus, the current data should only be considered as indicative.



Figure 36: Mean vector magnitudes as a function of target velocity and mean orientation angle (Θ). The closer to 0 (y axis) the less bias is there for the saccade ends to undershoot or overshoot the pursuit target. Black dots indicate the data from my experiment (at 8°/s, 16°/s, and 32°/s). Each black dot represents the mean orientation vector magnitude (r) containing data grouped by the respective velocity (i.e. all 8°/s velocity trials were put together irrespective of their direction). Adjusted for the rule set above, if the mean orientation is between 90° - 270° (negative value) and 270° - 90° (positive value). The linear fit is given by f(x) = -0.02282*x - 0.3524 with an R-square of 0.9452. This result suggests a strong linear relationship between the saccade tendencies and the pursuit target velocity. Red star marks a hypothetical target velocity where the saccade end points would have no bias of undershooting or overshooting the target (i.e. without a mean orientation preference). Thus, using the linear fit equation and solving for the R magnitude (y axis) of 0 = -0.02282 * x + 0.3524 (x axis – stimulus velocity) the stimulus velocity where they should be no bias is 15.4426°/s.

5.7. Discussion

The aim of this chapter is to consider the performance of saccades made during smooth pursuit. Specifically, the accuracy and precision of the saccade end positions relative to the target were investigated. The main results of from this study are as follows:

a) Saccades made during smooth pursuit undershoot the target

The literature indicates that saccades made from one stationary target to another stationary target are consistently undershot by approximately 1 to 10% depending

on the saccade amplitude (Becker and Fuchs 1969), usually followed by a smaller corrective saccade (Henson 1979). However, it is unclear how these findings relate to those saccades made during smooth pursuit, which are not performed in a stable fixation environment. Thus, it can be hypothesised that there would be no effect of target direction or velocity (i.e. all saccades should undershoot irrespective of the pursuit parameters). One possible explanation for this would be the idea that, by undershooting the target, the saccadic flight time is minimised (Toyomura and Omori 2004). This would suggest a benefit for the visual system by decreasing the time until clear vision is available again after the saccade. The utilisation of undershoots attempts to minimise the saccadic amplitude rather than the positional error. It was found that the highest gains observed (0.93 – 0.97) were when the saccadic amplitude was approximately 10% shorter of the target distance (Harris 1995). Other explanations of the undershooting trend have been suggested, they might be a strategy for the visual system to decrease instability (de Bie et al. 1987), or a strategy from ecological standpoint to conserve energy and time (Becker 1989).

Nevertheless, the current experiment shows that target velocity does influence the accuracy and precision of saccade end point positions. The faster the target moves, the less accurate and less precise they become. However, for the 8°/s and 16°/s conditions there was no general trend for the majority of saccades to be catch-up. A possible explanation of this might be distance between the eye and the target during pursuit. Shorter/smaller eccentricities for saccades have been demonstrated to be fairly accurate and precise (Kowler and Blaser 1995; Poletti et al. 2020). On the other hand, the majority of saccades in the 32°/s condition tend to undershoot the target. That is in line with what is usually reported in the literature. What is more, the majority of experiments generally discovered an undershoot (Becker and Fuchs 1969; Henson 1979; Deubel et al. 1982). Upon further investigation, it appears that the undershoot might be a deliberate action of the saccadic system. In experiments where the positional error was corrected

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artificially (i.e. target step, contact lens), the saccadic system adjusted for this correction until an undershoot of around 10% was achieved (McLaughlin 1967; Henson 1978). Therefore, the current results relating to pursuit saccades are novel but in line with literature reports.

b) Limitations

As this is a retrospective analysis of data already collected in Chapter 3, many of the limitations discussed in that chapter, are also applicable to these results. These are as follows:

• Constant velocity target

In this study the targets moved with constant velocity. Therefore, it could be argued that the target motion was to some degree, highly predictable. It is unclear how saccade performance would be affected by a more unpredictable pursuit motion, such as targets that change velocity (for example a 'sinusoid' target waveform), or targets that change both direction and velocity (for example a 'sum of sinusoid' waveform). Nonetheless, as constant velocity targets are highly predictable, the results could be considered as representative of the best possible saccade performance, with more complex patterns of target movement resulting in lower accuracy and lower precision.

• Pursuit initiation time

When initiating pursuit, a saccade is often used to place the eye initially on the target. It is important to exclude these initial targeting saccades, where possible. If they were included, the distance travelled by the pursuit target before the initial saccade will increase with velocity, since most saccades will have a latency of around 200 ms (Purves 2001). Thus, this would lead to an increase in the position difference between eye and target for when a saccade is evoked. Analyses were limited to the final 85% of the target sweep in order to eliminate the inclusion of initial saccades to the target as much as possible. Therefore, the results should

represent saccade end positions *during* pursuit rather than the *initiation* of pursuit.

• Time on screen for each sweep

As mentioned above, the first and 15% of the pursuit trial was not analysed. For the 32°/s condition, that represents a total of 850 ms of pursuit per trial, as the total amplitude was 32° in size. A possible limitation would be the short amount of time the stimulus was on screen, and that it might not be as representative of natural conditions as the other velocities (i.e. 16°/s and 8°/s). To minimise this effect, the total time of pursuit was equated between conditions. For example, the 32°/s had twice as many trials as the 16°/s condition, and four times as many trials compared to the 8°/s. However, the total duration of data collected was the same for each condition at 32 s.

5.8. Conclusions

In summary, this study found that saccades made during pursuit tend to undershoot the pursuit target, and that the level of undershoot increases with increased target velocity. In addition, for target direction, as the study consisted of 5 participants, there was no effect found in this experiment on the accuracy or precision of the saccade end points, whereas target velocity did. As the target velocity increased, the accuracy of the saccades decreased (i.e. they terminated further away from the target) and the precision decreased (the area over which they terminated increased). These results are, to the best of my knowledge, the first study to examine the two-dimensional targeting performance of saccades made during pursuit.

Chapter 6. Dynamic fixation targets to improve fixation stability

6.1. Introduction

Currently, fixation stimuli are composed of simple shapes (e.g. a dot (Tarita-Nistor et al. 2006) or a cross (Crossland and Rubin 2002b)) of various sizes. There has been ongoing interest as to whether one fixation stimulus is better (i.e. improved fixation stability) when compared to others. Recently, it has been proposed that a 'bull's eye and crosshair' target provided the most stable fixation (Thaler et al. 2013). Improved fixational stability would also imply that the fixational stimulus can seemingly minimise the natural movements of the eye, as it is never perfectly stationary. Yet the uncontrolled movements such as microsaccades, drifts, and tremors are constantly present and inevitable (Barlow 1952).

Furthermore, previous studies have found that stimulus specifications such as contrast, luminance, colour, shape, target size, etc., have little to no effect on the fixational stability (Steinman 1965; Boyce 1967). Furthermore, stimulus blur and contrast also seem to play little to no effect on fixational performance (Ukwade and Bedell 1993). All of this would suggest that the range of different target variations has a marginal effect on fixational stability. Having this in mind, I could turn to other aspects of the experimental design in an attempt to improve the stability.

It has been shown that in fixation tasks trained individuals would show far superior performance than naïve ones. For example, the fixational stability between healthy controls and elite shooters was tested. Both groups were instructed to fix their gaze with the presence of a fixational stimulus (a cross inside of a white circle, 0.3°) for a minute, and a similar task but with distractors (Di Russo et al. 2003). For the trained individuals, time seemed not to influence their fixational stability, since they performed far better even when distractors were introduced. Both types of temporal and selective attention proved to be superior in the group with

prior experience. Relating this to the clinical environment, people without previous experience or training would not perform as well on fixation tasks. This could be especially detrimental in visual field testing (for example as part of a glaucoma screening), which on average requires long periods of fixation while the visual fields are mapped (Advanced et al. 1994; Membrey et al. 2000). However, if the patient moves their eyes, whether voluntarily or involuntarily, that might produce incorrect mapping of retinal sensitivity. Therefore, as healthy untrained individuals showed fixational deterioration with time, it would be of use if fixation stability could be improved through involuntary responses of the visual system.

As mentioned, attention plays significant role in fixation. It has been found that, based on different instructions, different fixation stabilities have been measured. Specifically, the authors were able to improve fixational stability purely by giving different instructions on how to perform the experiment (Steinman et al. 2016). A further example of the role of attention comes from another experiment (Denison et al. 2019), where the authors explored the predictability of stimulus onset and microsaccades. Whenever the subjects were cued and anticipated the stimulus, their fixation improved. This would show that attention plays a role in fixational stability. Therefore, if there's a possibility to have a target which increases fixational stability based on a reflexive mechanism, which is not affected by instruction, or which cannot be deliberately ignored, it would create a situation where fixational stability would be less affected by external factors.

What all of these previous studies have in common is that they use stationary (static) stimuli, and the observer is required to hold their gaze steady while viewing them. In contrast, it is interesting to know whether a dynamic stimulus would improve fixation stability. Indeed, a dynamic pursuit stimulus that morphed from one simple animal into another was found to yield higher pursuit gains in young adults, suggesting that dynamic stimuli are better (Vinuela-Navarro et al. 2017). To that end, in this chapter, I examined the use of the optokinetic response (OKN), a reflexive eye movement that is used to stabilise gaze (e.g. those eye

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movements evoked when looking out of a train window), to generate a dynamic stimulus. Typically, studies that investigate OKN use large drifting black and white sine wave gratings, and the eye reflexively follows this drifting patten with high gain (Honrubia et al. 1968). Furthermore, in this experiment, the authors had two groups which received specific instructions on how to perform the task. One of the groups was told to follow the OKN grating and the other to fixate their gaze and not follow the stimulus. Even when actively trying to ignore the stimulus, the optokinetic reflex persisted. Therefore, this is a reflexive function of the visual system on which it seems that we do not have full control. Also, by adjusting different parameters of the stimulus (i.e. amplitude, velocity, direction), they were able to predict the quality of the OKN reflex. Having that in mind, it could be said that the OKN response is fairly predictable and the parameters to modulate and control it are also well established.

Considering the above, the current study seeks to utilise these reflexive OKN eye movements. If in a way the human aspect (attention, volition) could be removed, even to a degree, we would be left with a reflexive action which is unaffected by the participants motivation or concentration, thus ensuring greater fixational stability in experiments where having one's gaze on the target is of importance. By utilising that reflexive action with a radial sine wave that either drifts inwards (contracts), or outwards (expands), reflexive eye movements can be generated that would cause gaze to be moved towards (contracting) or away from (expanding) the intended fixation location.

6.2. Aims

The aim of this chapter is to determine how fixation is affected by using a dynamic fixation target.

6.3. Hypotheses

The hypotheses under test are that:

- A radial sine wave grating drifting inward (i.e. contracts) will promote a more stable fixation (precision and accuracy) than a 'traditional' target, since the slow phase component of the OKN eye movements will be directed *towards* the centre of the target.
- A radial sine wave grating drifting outward (i.e. expands) will promote a less stable fixation (precision and accuracy) than a 'typical' target, since the slow phase component of the OKN eye movements will be directed *away from* the centre of the target.
- A stationary radial sine grating (i.e. no motion) will yield fixation that is less stable than the Inward and more stable that the Outward conditions. No OKN is to be expected from this target as it is stationary. This is a control condition.

Previous research (Thaler et al. 2013) has shown that a conventional fixational stimulus ('bull's eye and crosshair') yields the highest fixational performance. This would be used here as another control condition.

6.4. Methods

a) Participants

Informed consent was obtained from all observers after they received an explanation of the nature and possible consequences of the study. Ethical approval (study number 1558) was granted by the Research Ethics and Audit Committee of the School of Optometry and Vision Sciences, Cardiff University (see Chapter 8). Participants were excluded from the study if they had any self-reported eye condition (e.g. amblyopia, cataract, age-related macular degeneration). There was no upper age limit for this study. Eleven observers were recruited, and six were excluded either due to poor data quality, or failure to complete all trials in the same single session. All of the remaining five observers (mean age 31 years ± standard deviation 5.56 years; range 26-38 years; 2 males

and 3 females) all had normal vision of 0.0 logMAR or better uncorrected (i.e. emmetropic).

b) Apparatus

The experimental apparatus is as described in Chapter 2. In brief, observers were seated 57 cm from the display with their head supported by a chin and head rest in an otherwise dark room. Each observer performed a calibration routine on the eye tracker before beginning the experiment. The calibration routine was a 3×3 grid of calibration targets that covered 95% of the screen. Calibration was accepted if the on-board software rated the calibration as 'GOOD', otherwise the calibration was repeated. Prior to beginning each experiment all participants performed a drift correction.

c) Stimuli

This experiment used four different stimuli. Three of the stimuli were radial sine wave gratings. Two of the gratings drifted, either inwards or outwards, while the third was stationary. The stationary radial sine wave represented a control condition. To compare with conventional fixation stimuli, a fourth stimulus known as a 'bull's eye and crosshair' target (Thaler et al. 2013) was also used. This 'bull's eye and crosshair' target stimulus has been shown to offer superior fixation when compared to other typical fixation stimuli such as a dot or a cross.

Each radial sine wave was 3° in diameter and had a spatial frequency of 1 cycle per degree. It drifted with a temporal frequency of 2 Hz for the inward and outward conditions. The 'bull's eye and crosshair' stimulus replicated the dimensions used by (Thaler et al. 2013). It had an outer diameter of 0.6° and an inner diameter of 0.2° and was black in colour. All stimuli were presented against a grey (mean luminance) background.

a) Procedure

Observers were instructed to fixate each stimulus to the best of their ability and started each trial by pressing a button on a wireless keyboard. Each trial contained

one of the four different fixation stimuli, which was displayed for a total of 90 seconds. All participants viewed the stimuli binocularly, and eye movements were recorded monocularly.



Figure 37 Examples of the two types of fixation stimuli. (a) This image depicts the radial sine wave that was used as a fixation target. The radial sine wave was made to either drift inward (contract), outward (expand), or remain stationary. (b) This image depicts the "bull's eye and crosshair target" that was used as a fixation target. *Note that neither fixation target is shown to scale.*

6.5. Analysis

Eye movement data were processed and analysed as described in Chapter 2. Saccades were identified in the EyeLink Data Viewer using predefined criteria ('psychophysical' setting; velocity criterion of 22°/s and acceleration criterion of 3800°/s²). All eye movement data (position samples, timestamps, saccades, blinks etc) were then exported as a CSV (comma-separated values) file for further analysis in MATLAB (version 2016b; Mathworks, Natick, USA). The eye position data were then analysed by computing a bivariate probability density function from the two-dimensional distribution of target relative eye positions. The 68% isocontour of the bPDF was then analysed in terms of accuracy and precision.

6.6. Statistics

All statistical testing was performed in JASP (JASP 0.15.0.0). Repeated measures ANOVA was performed to examine the main effect of target velocity and target

direction. A brief overview of a repeated measures ANOVA is provided in Chapter 3.

6.7. Results

Aspects of this work were presented at the annual meeting for the Association for Research in Vision and Ophthalmology, May 2022 (see 9.1).

a) Eye movement recordings

Typical recordings eye position traces for each of the stimuli are shown in Figure 38 whereas typical isocontour plots for each of the stimuli are shown in Figure 39.



Figure 38 Target relative eye positions traces from a typical trial. Blue lines indicate horizontal eye positions and orange lines indicate vertical eye positions. Data shown are from Participant 05.



Figure 39 Typical 68% isocontours of eye positions from a participant for each stimulus type. The blue line encompasses 68% of the highest datapoints. The blue asterisk indicates the centre of mass of the isocontour, whereas the red circle indicates the target position. In all cases this participant displayed a leftward gaze bias (i.e. the centre of mass of the contour was to the left of the target). Data shown are from Participant 05.

The drifting stimulus evoked a reflexive optokinetic nystagmus (OKN) in all the participants. However, the proportion of the trial containing OKN eye movements varied from participant to participant.

b) Stimulus type

In this study, a repeated measures ANOVA showed that there was a significant main effect of stimulus type on the accuracy of eye positions [F(3,12) = 5.979, p = 0.010, $\eta^2 = 0.599$]. A post hoc comparison showed that the contracting stimulus resulted in a significantly more accurate fixation than the conventional target ($p_{bonf} = 0.009$) (Table 10). There were no other significant differences among the

different stimuli for fixation accuracy (Figure 40). As a reminder, a greater value for accuracy indicates that the eye is farther away from the target.



Figure 40 Eye position accuracy between the different stimulus types. Error bars indicate ±95% confidence intervals. As a reminder, larger values for accuracy indicate that eye positions were farther from the target. The graph shows that expanding and contracting stimuli had better accuracy (i.e. lower values and hence closer to the target) than static or contracting stimuli.

Post Hoc Comparisons - Stimulus type								
			95% CI for Mean Difference					
		Mean Difference	Lower	Upper	SE	t	Cohen's d	p bonf
Expanding	Contracting	0.123	-0.105	0.350	0.072	1.701	0.761	0.688
	Static	-0.081	-0.309	0.146	0.072	-1.129	-0.505	1.000
	Conventional	-0.171	-0.398	0.057	0.072	-2.368	-1.059	0.213
Contracting	Static	-0.204	-0.432	0.023	0.072	-2.830	-1.266	0.091
	Conventional	-0.294	-0.521	-0.066	0.072	-4.069	-1.820	0.009
Static	Conventional	-0.089	-0.317	0.138	0.072	-1.239	-0.554	1.000
<i>Note.</i> Cohen's d does not correct for multiple comparisons.								

Note. P-value and confidence intervals adjusted for comparing a family of 6 estimates (confidence intervals corrected using the Bonferroni method).

Table 10 Results of the post-hoc analysis of stimulus type on the accuracy of eye positions.

In study it was observed that there was a significant difference between the Contracting and Conventional stimulus on the accuracy of eye positions.

In this study, there was no significant main effect of stimulus type on the precision of fixation [F(3,12) = 0.434, p = 0.733, $\eta^2 = 0.98$]. Precision of fixation did not seem to be affected and there were no other significant differences among the different

stimuli for fixation stability (Figure 41). As a reminder, the greater the value for precision, the greater the spread of the eye movements.



Figure 41 Comparison of eye position precision between the different stimulus types. Error bars indicate ±95% confidence intervals. As a reminder, larger values for precision indicate that eye positions had a greater spread. The graph shows that there was a similar precision (i.e. spread of eye movements) for each of the four stimulus types.

6.8. Discussion

The purpose of this research was to investigate whether a dynamic (i.e. nonstationary) target could be used to improve fixational stability by utilising a reflexive eye movement called OKN. The results show that the contracting stimulus resulted in more accurate fixation than the conventional stimulus. Nonetheless, main effect was only observed for the accuracy of fixational eye positions (how close eye position is to the target). The precision (the area of eye positions) did not seem to be affected by this stimulus type. This would suggest that the inward contracting target does provide better fixational accuracy than the conventional target. As for the outward and stationary sine wave target, they did not influence fixational stability in a significant way. Our results build upon the knowledge from Thaler et al (2013), however, there are a few key differences to be mentioned. The first would be the duration of the trials. In the current experiments, we opted for 90 seconds of continuous fixation trials, as for the conventional stimulus (Thaler et al. 2013) it was 17 seconds. It has been demonstrated before that fixational stability decreases as the trial progresses (Di Russo et al. 2003). Nonetheless, our stimulus resulted in more accurate fixation and no less precision than Thaler's stimulus, despite the trial duration being 5 times longer. We have not performed any analyses on varying excerpts of the 90 seconds continuous fixation data (e.g. 17 seconds to compare to the conventional stimulus). However, this would be of interest for future work, especially when considering quality of resulting fixation for shorter tasks.

Our experiment has focused on measuring the precision and accuracy of the eye positions. In contrast, one of the measures used for fixational stability was microsaccadic rate (Thaler et al. 2013). It should be noted that microsaccadic rate is not a conventional measure of fixation stability and would be dependent upon the ability of the eye tracker to resolve such small eye movements. In addition, Thaler et al (2013) measured precision using the bivariate probability density function, that, as discussed in Chapter 2, is not the optimal technique. Nonetheless, it is possible to compare the two results. In their experiment, they have found the precision of eye position gaze for the conventional stimulus across the 17 seconds of fixational data to be around $0.035^{\circ 2}$. Compared to the 90 seconds of fixation of the current contracting target, which yielded a result of $0.738^{\circ 2}$. This difference in the areas of precision could be attributed to the difference of duration between the trials, as generally gaze stability deteriorates with time.

This novel stimulus may be of benefit in applications when prolonged fixation is required, (e.g. laboratory-based studies). Possible application may be in clinical equipment used in eye care. An example of this could be where maintaining gaze over long durations is critical (visual field testing with or without impaired central vision loss, while viewing with an eccentric retinal locus) or potentially in training those with central vision loss to use residual peripheral retina. The typical duration of visual field testing can be in the order of minutes, and it is generally accepted that patients will have poor fixation, even if they are healthy. For this reason, the clinician performing the test needs to carefully monitor fixation performance to ensure accurate test results. In these two scenarios, a stimulus that allows for selfstabilisation could be of practical importance.

a) Limitations of the study

We only used a long epoch of 90 seconds per trial. We had assumed that fixation performance would decrease over an extended duration, however, it is unclear whether such a target would be appropriate for shorter durations. One would expect that the majority of the population would not have had previous experience with fixational research. Therefore, deterioration of fixational stability over time is to be expected. Hence, we consider the duration of this trial to be appropriate for keeping the gaze focused.

Another limitation would be the parameters of the target. The initial parameters were determined by trial and error, however, unless all combinations are systematically tested, it remains possible that other parameters could yield better results. Therefore, as this experiment included only a single iteration of the target, it would be interesting to further explore the capabilities of such a dynamic stimulus.

6.9. Conclusion

This study had demonstrated that:

 The inward drifting radial sine wave stimulus significantly improved the fixational accuracy but not precision when compared to the 'conventional' stimuli. Despite being larger in size, the inward drifting stimulus (3° diameter), resulted in similar eye position precision to the much smaller 'bull's eye and crosshair' stimulus (0.6° diameter)

Chapter 7. Conclusions and future work

This chapter considers the results of the experimental chapters (Chapter 3 - Chapter 6) in a wider context, as well as future directions for research.

7.1. Accuracy and precision of eye position during pursuit

In Chapter 3, it was found that eye positions during pursuit become less accurate and less precise as a function of target velocity, but not target direction. Of interest is how those who have lost foveal function due to pathology (e.g., a central scotoma due to age related macular degeneration) may perform under similar circumstances. Without an area dedicated to high resolution vison, it is not immediately clear how such a participant would follow a target, or whether, a similar trend with target velocity would be apparent in this population. Those individuals who have a central scotoma will develop a preferred retinal location, or PRL (Whittaker et al. 1988). This PRL serves as a replacement for their fovea. Use of a PRL would inevitably result in a scotoma being displaced to one side of the PRL. Therefore, depending upon the location of the PRL, there may be an effect of target direction during pursuit (see Figure 42).



Figure 42 A preferred retinal location (PRL) may be either behind or in front of a central scotoma, depending upon the target direction. In the diagram above, a scotoma located to the right of a PRL (left-hand side of the diagram) may result in the target disappearing during rightward pursuit (i.e. it would fall within the scotoma), since eye position tends to lag behind target position. In contrast, pursuit performance is likely to be better during leftward pursuit (right-hand side of diagram), since the PRL is in front of the scotoma and the pursuit target should always be visible.

For example, if an individual had a central scotoma to the right of their PRL, then during rightward pursuit, the PRL would be behind their scotoma. In chapter 3 it was found that eye positions lagged behind target position. This would suggest that the target would likely be imaged in the scotoma resulting in it disappearing from view and resulting in abnormal pursuit. In contrast, leftward pursuit is likely to be relatively unaffected since the target would be constantly visible.

How such individuals with central scotomas attempt to follow a moving target, and the strategies they employ would be worthy of further investigation. This could be initially studied using gaze contingent scotomas (McIlreavy et al. 2012) in typical individuals. This would involve displaying a mask to one side of a participant's gaze, and the position of the mask continuously updated using current eye position coordinates from the eye tracker.

Some studies have attempted to examine how pursuit changes in those with central scotomas due to age related macular degeneration (Shanidze et al. 2016a), however, this study suffers similar flaws to Shanidze et al. (2016b), in that the eye tracker was an SLO, with a low sampling rate, using a brief epoch of smooth pursuit, at a very slow, fixed target velocity. I would therefore argue that there are more investigations to be carried out in those with central visual loss. Nonetheless, this would be a fruitful area for exploration due to the potential translational benefits. It may be possible to devise techniques to help such individuals in their daily living. Example could include trying to read a bus number/destination while it is moving or trying to judge the flow of traffic/speed of vehicles before crossing a road.

A simple dot target has been used throughout the present work. However, future work could consider what impact any positional error between the eye and target would have for visual resolution, since the patient would not be placing their fovea (hence highest visual resolution) on the target. Perhaps this could be tested with a more detailed stimulus, similar to a radial sine wave of high spatial frequency or

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a Gabor that required some discrimination judgement regarding the target during each sweep.

A further area of research could examine to what extent the participants follow the edge of the target. Given the positional offset, it is logical to assume that the visual system would follow edges of targets rather than centres-of-mass. For example, if we consider a large (e.g. 5°) filled circular target, it would be difficult for the visual system to determine if there was any positional error or velocity error, using only the fovea, if an individual followed the centre of mass of the large target. This is because visual information about the target would be the same across the fovea. Therefore, in order for the visual system to determine if there was any error (whether positional or velocity), such information would have to come from the edge of the target. In this case the visual system would need to utilise retina that is more peripheral to the fovea (e.g. $\pm 2.5^{\circ}$ eccentricity for a 5° target). If the visual system uses the edge of a target to determine any pursuit error, this could be investigated using a line or bar-shaped pursuit target. If the bar was oriented horizontally during horizontal pursuit, then the position error should increase with the length of the bar if participants were following the edge rather than the centre of mass (i.e. due to a greater distance between the edge of bar and the centre of bar). In contrast, if the bar was oriented vertically during horizontal pursuit, then the position error should be independent of the length of the bar.

7.2. Saccades during pursuit

In Chapter 4 and Chapter 5, it was found that the positional error required to evoke a saccade increased as a function of target velocity, but not direction. Similarly, the targeting accuracy and precision of the saccade decreased as a function of target velocity, but not direction. In carrying out this work, it was apparent that a great deal of work has been undertaken on 'regular' saccades (i.e. saccades that are made to and from stationary targets), but not on saccades that are made during pursuit.

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The parameters (latency, main sequences, etc.) of 'regular' saccades are well established. However, such metrics have not been fully explored for catch-up saccades. Several key differences (highlighted in Table 7) suggest that their parameters may differ. For example, suppose a participant was viewing a grating that was drifting to the right. The optokinetic response of an individual would be to produce repeated cycles of a slow phase eye movement to the right followed by a fast phase to the left. While fast phases may be considered to be saccade like, the relationship between peak velocity and amplitude of the fast phases is different to saccades (Garbutt et al. 2001).



Figure 43 Figure from Garbutt et al. (2001). This figure shows a scatter plot of the peak velocity (°/s) for saccades and fast phases plotted against their amplitude. Quick phases (grey unfilled circles) have a lower peak velocity than saccades (black crosses) of the same amplitude.

In their study Garbutt et al. (2001) found that for a given amplitude, fast phases tended to have a lower peak velocity compared to saccades (Figure 43). This may be because the fast phases were deemed to be 'anti-compensatory', meaning that they were made in a direction that was opposite to the stimulus direction. It could be hypothesised that the lower peak velocity of the fast phases is because such

eye movements are needed to first overcome the slow phase velocity. For example, if slow phase eye velocity was 30°/s rightward, then a fast phase would need to counter this slow phase eye velocity as well as move the eye leftward.

Both catch up and back up saccades may show different peak velocity profiles in comparison to 'regular' saccades. Catch-up saccades will be made in the *same* direction of the pursuit eye movement whereas back-up saccades will be made in the *opposite* direction of the pursuit eye movement. Based on the data available for fast phases (Garbutt et al. 2001), this would suggest that back up saccades, may have a lower peak velocity that catch up saccades.

The latency of 'regular' saccades know to be approximately 200 ms (Purves 2001). However, it is not possible to establish the latency of either catch-up or back-up saccades. To address this issue, I have devised (and commenced data collection) on an experiment where a step change is introduced during pursuit (Figure 44).



Figure 44 A schematic position time plot of a typical trial. The target (solid black line) travels with constant velocity until at some time it either steps forwards or backwards in position before continuing with constant velocity (dashed black line). The simulated step is used to evoke both catch up (step forward) and back up (step back) saccades. This paradigm will allow for exploring the properties of saccades made during smooth pursuit.

In Figure 44, a schematic position-time plot for a trial is illustrated. In this trial a pursuit target moves with continuous velocity until at some time the target either

makes a fixed step either forwards (to evoke catch up saccades) or backwards (to evoke back up saccades), after which it continues travelling with constant velocity. The onset of the step is configured such that it will occur at a randomised time to avoid participants anticipating the onset. In addition, I have chosen a range of step sizes ranging from 0.25° up to 8°. Using this paradigm, the latencies (time from the step onset until the catch up/back up saccade was initiated), the peak velocities, velocity profiles and amplitudes of catch up and back up saccades could be explored. In addition, by using 'simulated' catch up and back up saccades in this paradigm, it should be possible to verify the data relating to 'real' catch up and back up saccades from chapter 4 and 5, for example the target accuracy and precision of such eye movements.

Similar to the findings on the accuracy and precision of eye position during pursuit, it would be fruitful to investigate clinical populations with impaired central vision (e.g. age related macular degeneration). If we refer to the scenario presented in Figure 42, the use of a PRL as a replacement for the fovea may result in unusual patterns of saccades. Saccades are gaze shifting eye movements where the fovea is redirected to various objects. However, when attempting to use a PRL, the oculomotor system will have to adapt the saccadic amplitude depending on the direction of the saccade to ensure that the image lands on, or near to the PRL. If, as in Figure 42, an individual were to saccade to the right, they would need a longer-than-normal saccade (since the PRL is located to the left of their former fovea). However, if they were to saccade to the left, they would need a *shorter*than-normal saccade (since the PRL is to the left of the former fovea). The extent to which such individuals adapts could be measured using the position error (both accuracy and precision) and may serve as a useful metric to assess how well an individual is likely to function in the real world and to better understand the timeline for any adaption process.

Finally, in some neurodegenerative conditions [i.e. Huntington's disease (Lasker et al. 1987), Schizophrenia (Abel et al. 1992)], saccades are known to be defective.
However, what remains unclear is to what extent these saccadic abnormalities will translate to abnormalities of catch-up and back-up saccades made during smooth pursuit.

7.3. Fixation

In Chapter 6 it was found that a novel dynamic radial sine wave target may offer a better fixation stimulus than conventional static fixation targets. The parameters for the novel fixation stimulus were serendipitously chosen. However, it remains possible that these parameters are not optimal. More accurate and more precise eye movements might be possible with different combinations of drift speed or spatial frequency. Determining the optimal parameters could be undertaken as part of a future study.

This stimulus may have broad application in vision science, since participants are often provided with fixation targets during long experiments so that stimuli can be presented at the correct location in their vision. It is also anticipated that this stimulus would be useful in a number of clinical settings, for example, it could be used instead of the dim amber LED that is currently used to aid fixation on some visual field machines. It may be useful for other clinical instruments that are used to examine those who have lost foveal function due to pathology (e.g. age related macular degeneration) as it is known that fixation performance is poorer in those individuals.

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Chapter 8. Appendix A

8.1. Copy of School Research Ethics Forms

a) Study number 1556





School of Optometry and Vision Sciences Ysgol Optometreg a Gwyddorau'r Golwg

Head of School Pennaeth Yr Ysgol Professor Yr Athro Marcela Votruba

College of Biomedical and Life Sciences Cardiff University Maindy Road Cardiff CF24 4HQ Wales UK

Tel *Ffôn* +44(0)29 2087 4374 Fax *Ffacs* +44(0)29 2087 4859 http://www.cardiff.ac.uk/optom/

Prifysgol Caerdydd Heol Maindy Caerdydd CF24 4HQ Cymru, Y Deyrnas Gyfunol

Document	Version	Date
Application Form for School Ethics Review 2020- 07-05 (blank).docx	Not specified	Not specified
Participant Information Sheet (blank).docx	Not specified	Not specified
Consent Form (blank).docx	Not specified	Not specified
Research protocol.docx	Not specified	Not specified
Participant data collection.docx	Not specified	Not specified
Invitation email.docx	Not specified	Not specified

Complaints/Appeals

If you are dissatisfied with the decision made by the Committee, please contact Professor Guggenheim (GuggenheimJ1@cardiff.ac.uk) in the first instance to discuss your complaint. If this discussion does not resolve the issue, you are entitled to refer the matter to the Head of School for further consideration. The Head of School may refer the matter to the University's Open Research Integrity and Ethics Committee (ORIEC), where this is appropriate. Please be advised that ORIEC will not normally interfere with a decision of the Committee and is concerned only with the general principles of natural justice, reasonableness and fairness of the decision.

Please use the Committee reference number on all future correspondence.

The Committee reminds you that it is your responsibility to conduct your research project to the highest ethical standards and to keep all ethical issues arising from your research project under regular review.

You are expected to comply with Cardiff University's policies, procedures and guidance at all times, including, but not limited to, its Policy on the Ethical Conduct of Research involving Human Participants, Human Material or Human Data and our Research Integrity and Governance Code of Practice.

OPTOM SREC Approval Form

b) Study number 1558





School of Optometry and Vision Sciences Ysgol Optometreg a Gwyddorau'r Golwg Head of School Pennaeth Yr Ysgol Professor Yr Athro Marcela Votruba		College of Biomedical and Cardiff University Maindy Road Cardiff CF24 4HQ
		Wales UK Tel <i>Ffôn</i> +44(0)29 2087 4 Fax <i>Ffacs</i> +44(0)29 2087 http://www.cardiff.ac.uk/op
		Prifysgol Caerdydd Heol Maindy Caerdydd CF24 4HQ Cymru, Y Deyrnas Gyfuno
The Committee must be informed of any unexpec adverse events that arise during the research project.	ted ethical issue	es or unexpected
Please provide an End of project report ONLY;		
notification should be made to <u>optomethics@cardi</u> research project completion. Documents reviewed by Committee The documents reviewed by the Committee were:	iff.ac.uk within	three months of
Document	Version	Date
Application Form for School Ethics Review 2020- 07-05 (blank).docx	Not specified	Not specified
Participant Information Sheet (blank).docx	Not specified	Not specified
Consent Form (blank).docx	Not specified	Not specified
Research protocol.docx	Not specified	Not specified
Participant data collection.docx	Not specified	Not specified
Complaints/Appeals		
If you are dissatisfied with the decision made by Professor Guggenheim (<u>GuggenheimJ1@cardiff.ac.t</u> your complaint. If this discussion does not resolve t	the Committee (1) in the first in the issue, you are	e, please contact stance to discuss e entitled to refer
the matter to the Head of School for further conside	ration. The Hea	d of School may
refer the matter to the University's Open Research	Integrity and E	thics Committee
interfere with a decision of the Committee and is	concerned only	with the general
principles of natural justice, reasonableness and fairn	less of the decision	on.
Please use the Committee reference number on all fu	ture corresponde	nce.
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School of Optometry and Vision Sciences Ysgol Optometreg a Gwyddorau'r Golwg	College of Biomedical and Life Sciences Cardiff University Maindy Road Cardiff			
Head of School Pennaeth Yr Ysgol Professor Yr Athro Marcela Votruba	CF24 4HQ Wales UK			
	Tel <i>Ffôn</i> +44(0)29 2087 4374 Fax <i>Ffacs</i> +44(0)29 2087 4859 http://www.cardiff.ac.uk/optom/			
	Prifysgol Caerdydd Heol Maindy Caerdydd CF24 4HQ Cymur X Devroas Gyfunol			
The Committee reminds you that it is your responsibility to conduct your research project to the highest ethical standards and to keep all ethical issues arising from your research project under regular review.				
You are expected to comply with Cardiff University's policies, procedures and guidance at all times, including, but not limited to, its Policy on the Ethical Conduct of Research involving Human Participants, Human Material or Human Data and our Research Integrity and Governance Code of Practice.				
OPTOM SREC Approval Form				

Chapter 9. Appendix B

9.1. Abstract and poster presented at the Association for Research in Vision and Ophthalmology (ARVO), May 2022

Title: Novel fixation target promotes more accurate fixation: initial proof-of-concept

Author Block: Viktor Nedelchev¹, Fergal Ennis¹, Peter Bex², Lee Mcilreavy¹

¹Cardiff University; ²Northeastern University

Purpose: When fixating a target, small eye movements (drift, microsaccades and tremors) cause the eyes to move. We have devised a novel fixation target (a radial sine wave grating) that, when drifting, recruits optokinetic-like responses. We predict that these drift-induced eye movements will either stabilize (contracting) or destabilize (expanding) fixation.

Methods: Five typical observers with normal vision were asked to fixate four different fixation targets for 90s each in random order. The target was either a radial sine wave luminance grating (3° diameter; 1 cpd; 100% contrast) that contracted (2Hz), expanded (2Hz) or was stationary (0Hz). As a control condition, observers fixated a 'bull's eye and crosshair' target (0.6° outer diameter; 0.2° inner diameter) previously reported to improve fixation performance (Thaler et al. 2013). All stimuli were presented against a 53 cd/m² mean luminance grey background. Observers viewed the targets binocularly and eye movements were recorded at 1000Hz from the eye with better acuity. Saccades and blinks were excluded from eye movement traces and a bivariate probability density function of target-relative eye position was calculated. The accuracy and precision of gaze were derived from the 68% isocontour that encompassed the eye position data.

Results: There was a significant main effect of stimulus type on the accuracy of eye position $[F(3,12) = 5.979, p = 0.010, \eta^2 = 0.599]$. The contracting stimulus resulted in more accurate fixation than the typical 'bull's eye and crosshair' stimulus ($p_{bonf} = 0.009$). There were no other significant differences among the different stimuli for fixation stability. Despite our novel fixation target being larger in diameter, there was no significant change in precision compared to the conventional target.

Conclusions: Our results suggest that our novel contracting concentric fixation targets improve the accuracy of fixation over an extended epoch. The constant level of precision with this target further suggests that functional benefits of fixational eye movements (Tulunay-Keesey, 1960) are preserved. We envision that our novel fixation target may be useful in applications where maintaining gaze over long durations is critical, for example during visual field testing, experiments in vision science, or for individuals with impaired central vision (e.g., age-related macular degeneration) when viewing with an eccentric retinal locus.



9.2. Abstract and poster presented at the Association for Research in Vision and Ophthalmology (ARVO), May 2022

Title: Two-dimensional eye velocity distributions of foveal fixation at different gaze angles **Author Block:** Lee Mcilreavy¹, Viktor Nedelchev¹, Fergal Ennis¹

¹Cardiff University;

Purpose: Small eye movements (drifts, microsaccades and tremors) keep the eye in continuous motion, even as observers attempt to fixate a target. In this study we examine eye velocity distributions from typical observers as they fixate targets presented at different gaze angle. We hypothesise that the mechanics of the oculomotor plant will bias eye velocity towards primary position.

Methods: Twelve typical observers with normal vision were asked to fixate a target (0.4° green dot) presented for 12s at either 0° (primary position) or at eccentricity of ±16° horizontal or ±16° vertical. The targets were presented in a random order against a black background in an otherwise dark room. Observers viewed the targets binocularly and eye movements were recorded at 1000Hz from the eye with better visual acuity. Saccades and blinks were excluded from eye movement data and a bivariate probability density function of target-relative eye velocity was calculated after filtering eye position data. The centroid of the isocontour that encompassed the highest 68% of data were examined to determine any directional bias.

Results: Preliminary results show the mean x coordinate of the centroid has a leftward bias (- $0.030 \pm 0.092^{\circ}$ /s) during right-gaze (+16°), and a rightward bias (+ $0.039 \pm 0.120^{\circ}$ /s) during left-gaze (-16°). This difference (0.072° /s) was statistically significant [t(11) = 2.697, p = 0.010, d = 0.779]. In contrast, the mean y coordinate of the centroid had a downward bias during up-gaze (- $0.217 \pm 0.310^{\circ}$ /s) and down-gaze (- $0.230 \pm 0.281^{\circ}$ /s). This difference (0.012° /s) was not statistically significant [t(11) = 0.101, p = 0.461, d = 0.029]. There were no significant differences between any of the eccentric gaze positions and primary position (i.e. 0°).

Conclusions: We have demonstrated that eye velocity during foveal fixation is dependent on gaze angle. Eye velocity is biased towards primary position during horizontal gaze, and downward during vertical gaze. These findings may relate to differences underlying horizontal and vertical oculomotor control. We speculate that the magnitude of the horizontal differences observed will increase with larger gaze angles (i.e. beyond 16°). Our results may have implications for aspects of foveal vision that are critically dependent on eye velocity, e.g., visual acuity, with thresholds potentially varying as a function of horizontal gaze angle.

