FACTORS AFFECTING THE STORAGE AND REPRODUCTION OF PREDICTIVE SMOOTH PURSUIT EYE MOVEMENTS

Stephen G. Wells

Thesis submitted for the degree of Doctor of Philosophy
of the University of London

MRC Human Movements and Balance Unit,
Institute of Neurology,
23, Queen Square,
London, WC1N 3BG
United Kingdom

1999

Abstract

The eyes take 100ms to react to a moving visual target. Anticipatory production of internally generated eye velocity can reduce this delay. However, smooth velocities up to only about 5°/s can be voluntarily generated without a moving target. In contrast, fast predictive movements without visual feedback occur during anticipatory smooth pursuit (ASP) eye movements. Frequent repetition of brief target ramp movements appears to charge an internal store that is later released as ASP before each ramp.

This thesis shows that ASP velocity increases when 1) faster ramps are used (for 12-50°/s ramps, the eye typically reaches 60% of target velocity by 100ms after ramp onset), 2) alternate direction rather than unidirectional ramps are used and 3) when audio timing cues are given 600ms before the onset of each ramp. It decreases when a fixation target is present before ramp onset.

Several results suggest ASP velocity is not precisely controlled. Variability to consecutive identical stimuli is quite high and some subjects have large directional asymmetries. Furthermore, appropriately scaled ASP velocities cannot be produced when an increase in target velocity is expected.

The putative store's longevity was assessed by repetitively presenting brief ramps with different intervals of darkness between each ramp up to 7.2s. Ability to generate fast ASP declined with increasing interval, even with audio timing cues. Similar decreases were not seen in anticipatory tracking movements by the hand.

The magnitude of anticipatory eye acceleration before each ramp started and of anticipatory deceleration before each ramp ended was altered by changing the target briefly into an visual acuity target that had to be identified at a set time during each ramp. However, the changes were small suggesting that subjects cannot greatly modify the predictive compromise between optimal tracking of different parts of the target motion waveform.

ASP eye movements appear to be a rough estimate of target velocity released with appropriate timing and direction. This rough estimate can significantly improve pursuit whilst awaiting the visual feedback needed for precise pursuit.

Acknowledgements

I would like to thank my supervisor Dr. Graham Barnes for his guidance and inspiration. I am also extremely grateful for the support from the staff at the Human Movement and Balance Unit and the encouragement from my family.

Table of contents

CHAPTER 1: INTRODUCTION

The Function of Smooth Pursuit Eye Movements

For a moving visual target to be observed with maximum clarity, smooth pursuit eye movements are used to keep the target's image stationary on the central retina. The eye rotates at an angular velocity that roughly matches that of the target to reduce its blur whilst largely ignoring the smeared image of the background. Our eye movements perform so well that we often do not realise how severe the degradation caused by blur can be. Retinal motion of about 2-3°/s can be tolerated (Westheimer & Mckee 1975) but greater blur impairs vision (Barnes & Smith 1981; Murphy 1978). Thus even a sluggardly object taking over a minute to cross our entire visual field would not be seen clearly if we did not move our eyes.

Ocular smooth pursuit is the object of research of this thesis but it is just one of a family of types of eye movement used in different situations to improve vision. Whilst the different types of eye movements are intimately related to each other, broad distinctions can be drawn between them. The four other major types (saccades, vergence, optokinesis and vestibulo-ocular reflex) will be described here briefly.

Other types of eye movements

Saccades are rapid shifts of gaze to an object of interest. They are a consequence of the fact that our retinae, like those of many other animals are not uniformly sensitive. Only about the central one degree of the visual image that lands on the fovea of the retina can be seen with maximum clarity. Thus even a horse that can see almost all round its head still needs to make eye movements to shift its gaze since its highest sensitivity is restricted to a thin 'visual streak'. Saccades can be very fast (up to around 1000°/s) and typically last 50-200 ms.

Fig. 1.1 shows an example of smooth pursuit and saccades being used to track a visual target after it starts to move. The target is initially stationary, but then moves with a ramp motion at 50°/s. A high-velocity saccade is used to correct most of the positional error before the eye starts to move smoothly at about target velocity.

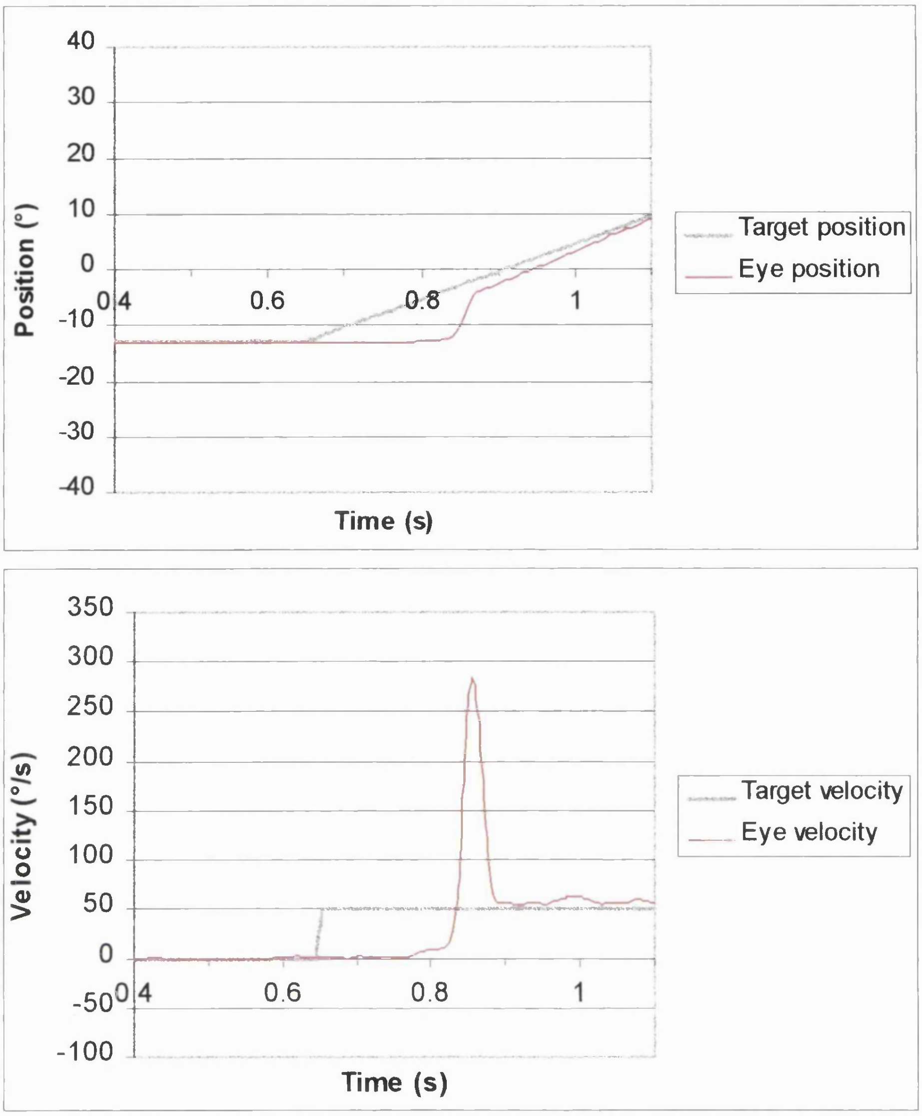


Fig. 1.1 Example of the eye tracking movements. The upper graph shows position and the lower graph velocity. After the target starts to move with a constant velocity ramp at 50°/s, the eye makes a high-velocity saccade then uses smooth pursuit to match target velocity.

Vision is improved if the fovea at the centre of both retinae can be directed at the same object of interest. Detection is better since the light from two eyes can be pooled and the two slightly different viewpoints allow a perception of depth. If the object is far away then the eyes are yoked to move together. However if the object is quite close then vergence movements are needed e.g. for an object one metre away the eyes must converge (i.e. move in opposite directions) by about 3.5° in order to maintain fusion of the images on the two retinae.

Optokinesis are reflexive eye movements that compensate for movements of the entire visual field. Usually these are small, brief corrections for transient image movements. However, when looking out of a train window for example, an optokinetic nystagmus is produced where each eye moves smoothly to compensate for the continual image motion before a saccade-like movement flicks the eye back in the opposite direction.

The pattern of movement depends on the subject's attention. If a subject stares passively at the moving image then a small amplitude nystagmus with frequent saccades is produced and the average eye deviation is in the opposite direction to the image motion. If a subject actively tracks the image then a large amplitude nystagmus with fewer saccades is produced and the average eye deviation is in the direction of the image motion. Both optokinesis and smooth pursuit usually take over a tenth of a second to process the visual input and respond appropriately.

If we relied on visual processing to correct all image motion then this relatively slow response would result in frequent blurring. Most of the movement of the visual world is due to movements of our head and fortunately the eyes can use the vestibulo-ocular reflex (VOR) to compensate for this motion much more promptly. When the head rotates, the walls of the inner ear canals move with it but the fluid within the canals tends to get left behind. Detectors of this relative motion can, by the most direct route, drive the eye muscles via a three-neuron arc within just a hundredth of a second. This can be easily demonstrated by the fact that we can see our hand more clearly when we shake our head (VOR) than when we shake our outstretched arm (smooth pursuit).

Retinal inputs that drive smooth pursuit

If a target suddenly moves, there is a latency of around 100 ms before pursuit is initiated in humans (Carl & Gellman 1987). Tychsen & Lisberger (1986) showed that enlarging the target from a 6' of arc spot to 10° disc decreased latency by about 10ms. Decreasing the intensity of the target increased the latency by 20 ms. Both reports showed that the eye's acceleration during at least the first 100 ms of pursuit was independent of how the target moved once pursuit had started, since delays in the processing of visual information prevent any new retinal error signals affecting this initial acceleration. Thus it takes about 100 ms to *initiate* pursuit and about 100 ms to *correct* pursuit in the light of visual feedback telling the system if the eye movements are appropriate for the current target motion. Tychsen & Lisberger (1986) found that eye acceleration in the first 20 ms of pursuit was much less than 80-100 ms after pursuit onset. This later interval was also more strongly dependent on the visual properties of the stimulus. Acceleration was higher when the position from which the target started moving was closer to the fovea, but was actually highest when starting 2-3° eccentric and moving towards the fovea.

What aspects of the target motion drive pursuit? In its simplest form, the smooth pursuit system can be characterised by a closed-loop negative velocity feedback controller which drives the eye to reduce retinal slip. This stems from the observation that steps in target position usually lead to saccades whereas if the target moves with a gradual ramp then smooth pursuit is evoked. To confirm if it was target position on the retina or the actual motion that was the stimulus for smooth pursuit, Rashbass (1961) used a 'step-ramp' stimulus where the target first stepped away from current eye position then moved with a ramp back towards centre. In this situation, the first reaction was a smooth eye movement in the direction of ramp *velocity* and away from current target *position*. Thus the smooth pursuit system only seemed to be concerned with target velocity, leaving any positional errors to be corrected by the saccadic system. Lisberger *et al.* (1981) concluded that visual inputs provide an eye acceleration signal which under optimal conditions can lead to maximum smooth pursuit velocities as high as 115-150°/s.

Several studies have shown that position clearly does have a role in pursuit. If a target moves away from the fovea with a simple ramp rather than a step-ramp then by the time the smooth pursuit system has matched target velocity there will be a positional error which usually has to be corrected by a catch-up saccade. Robinson (1965) demonstrated that if the initial catch up saccade fell slightly short then pursuit velocity would often exceed target velocity until the remaining positional error had been corrected. During this period, eye velocity is actually in the opposite direction to retinal slip, and in the direction of the retinal positional error. He also noticed that pursuit of a step-ramp stimulus appeared to start around 26 ms later than for a simple ramp showing that the positional step does not go unnoticed. Further evidence for the production of smooth pursuit in the direction of positional errors has come from studies where a target is stabilised on the peripheral retina so that its position relative to the fovea cannot be altered by any eye movements. An example of a stabilised image is the afterimage seen after having a flash photograph taken that stays in the same place on the retina regardless of what eye movements are made. Kommerell (1972) showed that the eye tended to drift smoothly towards afterimages placed eccentrically from the fovea. An image can also be stabilised by detecting a subject's eye movements and simultaneously moving a target to compensate for them so that it always falls on the same part of the retina. Wyatt & Pola (1981) demonstrated smooth pursuit towards an eccentric target when its position was electronically stabilised with respect to saccades but not for smooth pursuit. Barnes *et al.* (1995) electronically stabilised a row of targets on the retina and found that smooth velocities of over 80°/s could be built-up by alternately directing visual attention to targets on either side of the fovea. All three stabilised image studies elicited faster movements for larger target eccentricities (tested up to 10, 6 and 5° respectively). The reason for the apparent increase in latency of pursuit to Rashbass-like step-ramps was revealed by Carl & Gellman (1987) and Wyatt & Pola (1987). They used accurate recording techniques to prove that the first response is actually a small pursuit acceleration in the direction of the step after about 100 ms. The eye then reverses direction and accelerates in the direction of the ramp about 50 ms later.

It is apparent that the likelihood of generating smooth pursuit from position steps is dependent on context. Carl & Gellman (1987) showed that position steps of a stationary fixation target were more likely to induce some presaccadic pursuit if they were presented amongst several ramp pursuit trials. They also found that the responses to position steps were more vigorous if presented when the subject was already tracking. Morris & Lisberger (1987) examined pursuit in monkeys, revealing that positional errors stabilised on the retina could not initiate pursuit from fixation but were effective at altering the velocity of ongoing pursuit (for backward offsets up to 1° but saturated for onward offsets above 0.5°). In contrast, fixed velocity errors imposed on the retina were equally effective at generating accelerations from fixation or from pursuit. Barnes *et al.* (1987) showed that smooth pursuit could be initiated (with velocities up to 3-4°/s) if subjects tracked position steps that were repetitive, forming a staircase-like positional trajectory.

Visual inputs do not have to be on the fovea in order to generate smooth pursuit. Winterson & Steinman (1978) evoked smooth pursuit easily using an eccentric target moving sinusoidally. Pursuit can still be stimulated when subjects attempt to pursue an imaginary target placed midway between two eccentric moving cues up to ±20° apart. For these stimuli however, there appears to be a gradual decrease in effectiveness at inducing pursuit with eccentricity of the cues for both sinusoidal (Barnes & Hill 1984) and step-ramp (Wyatt & Pola 1994) target motion. Generation of pursuit by areas away from the fovea would be important for pursuit of large objects, where the moving edges may all be peripheral, and under dark, scotopic conditions, where the fovea is blind.

Volition is not essential for smooth eye movements to be evoked by a small moving target. Pursuit-like eye movements can still be evoked when subjects stare passively at a moving object (Barnes and Hill 1984; Wyatt & Pola 1987; Ohashi & Barnes 1996). These responses are similar to those produced when subjects actively attend to a moving target but are usually of lower velocity.

Smooth pursuit generated without any retinal motion

In an illuminated, structured environment without moving objects the optokinetic response would be expected to inhibit any self-generated smooth movement. For the visual system, such a movement would be most detrimental producing an unnecessary blur. However, even in darkness, where there is no visual scene to smear over the retina, smooth movements are not readily produced. These basic observations meant that smooth pursuit used to be referred to as a 'reflex' since it was thought that it could never be voluntarily produced in the absence of a moving target.

However, there have been numerous reports suggesting that retinal image velocity and position are not the only stimuli that can generate pursuit. For example, Deckert (1964) claimed that smooth pursuit could be generated when imagining pendulum motion with the eyes closed. Westheimer & Conover (1954b) demonstrated apparently smooth movements when subjects moved the eyes rapidly between two stationary targets placed 30° apart (but at the improbable velocity of 280°/s). In contrast, Kowler & Steinman, (1979a) found that subjects were unable to generate smooth movements when moving the eyes between two targets placed much closer together. Other studies have claimed that smooth pursuit can be evoked in darkness by tracking a moving acoustic target (Zambarbieri *et al.* 1981) and some have shown smooth tracking of the hand in darkness (e.g. von Noorden & Mackensen 1962). However Steinbach (1969) estimated that only one in three subjects could do this and only for slow hand movements. Smooth eye movements have been reported during sleep (0.17-0.33Hz oscillations; (Dement 1964) and fixational shifts may become smoother with drowsiness (Miles 1929).

Whilst there is undoubtedly some truth in these findings, they must be viewed with some caution since in many experiments, the presence of repeated small saccades cannot be ruled out. Firstly, some authors only examined eye position traces which do not show saccades as clearly as eye velocity traces where saccades appear as prominent spikes. Secondly, many of the eye movement recordings were by electro-oculography

(EOG)[†] which will not reveal small saccades below its relatively poor resolution limit (~1°). Collewijn *et al.* (1982) recorded eye movements simultaneously with search coils[†] and EOG and found that small saccades could be hidden on the pursuit EOG trace. All of these demonstrations of pursuit without retinal motion appear to have required repetition of quite large amplitude non-visual stimuli before any smooth movement was produced. More recent studies with higher resolution recording techniques have found that subjects can generate smooth movements in darkness purely by volition but only at velocities up to about 6°/s with frequent saccadic interruptions (Becker & Fuchs 1985; Kao & Morrow 1994). Thus while the positional gain of the eye (smooth and saccadic eye displacement / target displacement) may match the non-visual target, the smooth movements alone do not. In conclusion, it appears that smooth movements can be generated without visual target motion but these movements are of low gain. Therefore it is misleading to say that smooth pursuit can be generated in a particular situation without quoting the velocity achieved and whether this velocity could be sustained.

This section has emphasised the importance of visual inputs for initiating pursuit but the role of efferent information is also crucial. During tracking that is almost perfect there is very little retinal image motion so pursuit is not sustained by retinal error feedback. but by the subject's perception of the target motion. If there is no motion on the retina

---

[†] Methods of recording eye movements:-

There is no ideal system for recording eye movements. All methods have to compromise on price, accuracy, comfort, robustness or range of recordable movement. The simplest and cheapest method is EOG. This uses the fact that the front of the eye is around 1mV positive with respect to the back of the eye. Therefore when a subject looks to the left for example an electrode placed on the lateral external canthus will become positive with respect to one placed on the medial canthus. The equipment is comfortable, operates over a large range and can be used on patients at the bedside, but is only accurate to about 1°. Infra-red recorders (used for this thesis) are worn like spectacles and use arrays of emitters and detectors. The position of the eye can be deduced from that fact that the detectors facing the dark iris will receive less reflection than those facing the white sclera. They are accurate to about a tenth of a degree, but are generally more expensive than an EOG system and the signal is only linear over a range of about ±15°. Alternatively, high-speed infra-red video cameras and image processing software can be used to locate the position of the black disc of the pupil. They are particularly suited for studying eye movements in two dimensions. Another accurate system is the scleral search coil that uses a tiny coil of wire embedded in an annular contact lens. When the coil moves in a rotating magnetic field, the phase of the induced current in the coil varies depending on its angle. The drawback with this method is that the coils are expensive, fragile and can only be used comfortably for up to 30 minutes.

but the efference copy of the drive sent to the eyes indicates that the eyes have moved then the brain has to conclude that the target has moved as well. The efference copy is important for movement perception and for recalibrating the retinal spatial values relative to the coordinates of extrapersonal space during the eye movement. It is likely that the perceived visual motion and the input used to drive the eyes are constructed by adding the oculomotor efference copy to the retinal slip velocity signal (Yasui & Young 1984). The perceived movement does not have to be real in order to sustain pursuit. Heywood & Churcher (1971) elicited smooth movements by asking subjects to follow the apparent drift of a foveal afterimage. Heywood (1973) also showed that the apparent motion of a row of stroboscopically illuminated stationary dots could be tracked smoothly (sigma pursuit). In this situation if the eye moves at one dot per flash then the retinal image does not change and there is the perception of the whole row moving in the direction of pursuit. This can also be extended to the apparent rotation and pursuit of a circle of stroboscopically illuminated stationary dots where only the foveal image stays the same from one flash to the next (Collewijn *et al.* 1982; see Grüsser 1986 for a review of sigma phenomena). Lamontagne *et al.* (1993) took this idea to the limit by demonstrating pursuit along a solid line in continuous illumination after a period of training.

Predictive smooth pursuit

The difficulty in voluntarily initiating and sustaining smooth movements of substantial velocity contrasts with the ease with which they are produced during the tracking of a predictably moving target. It has been known since the work of Dodge *et al.* (1930) that when following a sine wave, the phase lag is smaller than would be expected from the known feedback delays. Additionally, the eye can sometimes reverse direction before the target has reversed. Often within just half a cycle of motion, a subject can track a sine wave with no phase lag (Dallos & Jones 1963; van den Berg 1988). Such behaviour is clearly not directly due to retinal image motion and must involve prediction. Prediction dramatically increases the gain for tracking a normal sine wave compared to a random walk of half sine cycles joined together at their zero velocity points (e.g. smooth pursuit gain of 0.79 for 1Hz, ±15° sine waves compared to 0.38 for a random walk; (Lisberger *et al.* 1981). Zero latency tracking is not just limited to the ubiquitous sinusoid. Bahill & McDonald (1983) showed that zero latency tracking of predictable parabolic trajectories could be achieved within a few cycles and of cubic waveforms (a visual stimulus that does not occur naturally) after several minutes practice.

The superior pursuit of regular over irregular target motion implies that the system is not simply a linear servo mechanism responding to retinal error and must receive a predictive input. Furthermore, predictive behaviour is not completely absent during tracking of supposedly "unpredictable" stimuli. Becker & Fuchs (1985) claimed that subjects consistently "interpret" certain epochs of Gaussian noise motion as segments of sinusoids. The pursuit system is non-linear in that it is not possible to predict the response to one type of motion by linearly combining the responses to other types of motion. Several studies have shown that gain and phase relations derived from responses to single sinusoids cannot predict the responses to a 'pseudorandom' stimulus made from summing several unharmonically related sinusoids. When subjects pursue such a stimulus, Collewijn & Tamminga (1984) demonstrated that although there are phase lags in the pursuit of the higher frequency components, there can be phase leads of 10-20° for the lower frequency components. For similar stimuli Yasui & Young (1984) recorded a phase lead as large as 84° for a 0.046Hz component. This would imply anticipation of the target motion by as much as 5.1 s which is implausible, so they suggested that the predictive system tried to optimise the response to minimise phase shift at some intermediate frequency component.

In agreement with these last two studies, Barnes *et al.* (1987) confirmed that eye position gain for higher frequency components between 1-3Hz of a pseudorandom stimulus could be greater than one i.e. higher than for sinusoids of the same frequency presented on their own. When there is a component above about 0.4Hz present in the motion, smooth velocity gains are always lower than for single sinusoids but the reduction is least for the highest frequency component. Thus it seems that more effort is put into pursuit of the highest frequency. Barnes & Ruddock (1989) showed that increasing the velocity of the highest frequency component a) further reduced the smooth velocity gain of the lower frequency components, b) slightly increased the phase lead of the lowest frequency component, c) further increased the phase lag of the second to highest frequency, but d) reduced the phase lag of the highest frequency component. Thus pursuit of the highest frequency component became more like that of a single sinusoid as it became a more dominant part of the stimulus. They explained these effects using a non-linear model that altered the dynamic characteristics of the visual feedback depending on the composition of the stimulus.

Exposing the predictor

Briefly blanking the target

An understanding of prediction is desirable since it clearly plays a crucial role in continuous pursuit. However, during on-going pursuit, it is difficult to separate the predictive component from that caused by the visual feedback loop of the pursuit system. The effect of visual feedback can be removed by making the moving target suddenly disappear. Any smooth pursuit produced in addition to a rapid deceleration around 100 ms after target extinction must be self-generated. von Noorden & Mackensen (1962) showed that sinusoidal pursuit could continue during brief blank periods as long as these lasted less than 1 s. Whittaker & Eaholtz (1982) showed that although pursuit velocity decayed, subjects could continue to produce appropriate reversals in direction for over 1 s after prolonged pursuit of a sinusoidally moving target that was suddenly blanked. Becker & Fuchs (1985) found that when the target disappeared, smooth pursuit velocity dropped rapidly but then maintained a lower 'residual velocity' instead of falling to zero. This residual velocity was typically around 60% of the previous pursuit velocity for targets between 5 and 20°/s. In these cases, subjects expected the target to reappear which seems crucial in maintaining the velocity. Indeed Becker & Fuchs (1985) sometimes noticed reaccelerations before the expected reappearance of the target.

Stabilising the target on the retina

Although pursuit can continue in darkness in the absence of retinal input, the predictive response is obscured by the transient response to the sudden removal of retinal stimulation. One method of opening the visual feedback loop whilst maintaining a target on the retina is to stabilise the image. However, there have been conflicting reports about the relationship between open and closed-loop pursuit. Wyatt & Pola (1983) found that, for sine tracking, open-loop responses could be used to predict closed loop responses by applying the rules of a simple, linear system. However Cushman *et al.* (1984) and Collewijn & Tamminga (1986) found large idiosyncratic differences in the ability of subjects to produce open-loop pursuit. van den Berg & Collewijn (1987) found that subjects could continue sinusoidal pursuit for several seconds after the image was suddenly stabilised with crude control over amplitude and velocity. However, once subjects realised that pursuit was open loop then instructions became of paramount importance. The goal of pursuit (to maintain the target on the fovea) becomes meaningless when subjects realise that a foveally-stabilised target will always be on their fovea or that an eccentrically-stabilised target can never be foveated. Inferences about closed loop pursuit from such conditions should be treated with caution.

Brief periods of undetected open-loop motion during on-going pursuit are much more likely to reveal normal predictive responses. For example, comparison of open and closed loop responses to step ramps reveals that corrective feedback about how well the eye is matching target velocity takes between about 126 ms (Tychsen & Lisberger (1986) and 200 ms (Carl & Gellman 1987). Morris & Lisberger (1987) showed that monkeys could continue pursuit at 15°/s for over 600 ms in the absence of any retinal errors. van den Berg (1988) masked the onset of 1.5 s periods of stabilisation by switching during a saccade, or when the retinal error was very small, and found that the acceleration when stabilised was context specific i.e. depended on whether the stabilisation occurred at peak or zero target velocity during sine tracking. Although he estimated that over 75% of closed-loop sine pursuit is predictive, the oscillations after stabilisation were rapidly damped implying that the predictive mechanism requires continuous updating. In a similar experiment, Barnes *et al.* (1995) showed that subjects could produce a wide range of frequencies and velocities after switching to the open-loop mode but that the responses were more variable than during closed-loop tracking.

Anticipatory pursuit

Another method of isolating the underlying predictive process is the study of anticipatory smooth pursuit (ASP) produced in expectation of retinal motion. The movements are anticipatory because they occur before visual feedback of the target motion can influence the eyes. ASP was first studied by Kowler & Steinman (1979a) who found that the eye tended to drift smoothly before making saccades in expectation of small (up to 7°) repetitive target steps. The movements started about 350 ms before the target step and the velocity increased with the frequency of stepping up to around 0.5°/s. Such ASP represents the initiation of a new pursuit movement rather than the extrapolation of an existing pursuit movement as happens when the target disappears or is stabilised. The movements are unusual since subjects must ignore the self-generated retinal slip of the stationary target during the period before it steps. In a later study, (Kowler & Steinman 1979b), it was shown that ASP also occurs before small single steps and slow ramps (<1°/s). However, they were unable to demonstrate ASP when a period of darkness was inserted between each target step. ASP still occurred, although at reduced velocities and in preferred directions, when guesses were made before unpredictable direction target displacements (Kowler & Steinman 1981). Kowler (1989) later confirmed that cognitive expectations could be used to guide the direction of ASP rather than simply being a repetition of a motor habit i.e. they could be directed when told verbally which direction the target would move in. Slightly faster ASP was elicited by Becker & Fuchs (1985) using 10°/s ramps. They noticed that the self-generated retinal slip could lead to a nystagmus-like pattern of occasional corrective saccades back to the fixation target. Interestingly, if the target occasionally disappeared at the exact moment when the ramp was expected to start then a fast pursuit acceleration was still seen at the appropriate instant reaching peak velocities of up to 8°/s. Boman & Hotson (1988) showed that extinguishing the fixation target for 800 ms before ramp onset enhanced the velocity of ASP, presumably due to the absence of any retinal errors. Velocities of around 3°/s were reached before 10°/s ramps. However, the velocity was not further increased by extinguishing the target for 2000 ms before the ramp. These relatively low velocities of ASP led to the view that they are not useful in the subsequent matching of target velocity during closed loop smooth pursuit (Boman & Hotson 1992). Furthermore, Boman & Hotson (1988) claimed that the fact that ASP moved the fovea away from the fixation target meant that it was not corrective and hence different from closed-loop smooth pursuit which always reduces errors. This is not necessarily true since although ASP may increase errors of a target that is stationary, it can reduce the initial tracking error once the target moves.

More recent studies have evoked higher ASP velocities compatible with the predictive velocities that must be produced to achieve the small phase lags observed during continuous pursuit of predictable target motion. Many of these have relied on repetition of a stimulus to build-up the magnitude of anticipatory responses. A sawtooth waveform of repetitive unidirectional ramps (up to 40°/s) allowed Kao & Morrow (1994) to elicit anticipatory velocities of several degrees per second and occasionally as high as 20°/s. Moschner *et al.* (1996) used repetitive target steps of large amplitude (20-70°) to elicit fast ASP (>3°/s in over 50% of responses by some subjects and occasionally up to 40°/s). They were also occasionally seen when the steps occurred at random times with random amplitudes. Whereas fast ASP may hasten the subsequent matching of target ramp velocity by closed loop smooth pursuit, fast ASP before large target steps, the majority of which is matched by a saccade, cannot serve such a function and may therefore merely reflect the release of fixation or the transfer of attention.

Barnes & Asselman (1991) studied the effect of repetition on the transition from reactive to predictive responses. ASP before each saccade to regular square wave target displacements of up to 8° at 0.52-1.3Hz built up over 2-4 cycles to a mean of 4-6°/s. They next studied triangular waves at 0.69Hz but only briefly exposed the target for 40-320 ms as it passed through the midline. Both the peak velocity achieved during each response and the ASP before each target exposure increased with repetition to reach an asymptote after about two cycles. This asymptote was higher for faster targets and for longer exposures. For these stimuli, fast ASP was regularly seen e.g. *mean* velocity of 26°/s for a 41°/s ramp exposed for 240ms. They explained the findings by the charging of a putative internal store of motor drive that can be released under the control of a periodicity estimator. In support of this idea, if the target motion suddenly changes, the store still appears to be discharged with an inappropriate direction and velocity until visual feedback corrects the mismatch (Barnes & Asselman 1991; Kao & Morrow 1994). Indeed the response can be so well consolidated that anticipatory pursuit can be produced even against a stationary structured background (Barnes *et al.* 1997). For these repetitive ramp stimuli, the ASP is stimulus specific in that the velocity is scaled with target velocity (Barnes & Asselman 1991; Kao & Morrow 1994; Barnes *et al.* 1995). If the target is stabilised on the retina during such responses then the response is very similar to the normal closed-loop situation showing that only a small amount of the drive is provided by visual feedback (Barnes *et al.* 1995).

Despite the fact that ASP is heavily influenced by expectations, subjects are largely unaware of these anticipatory movements. Kowler & Steinman (1979a) claimed that subjects could not abolish ASP voluntarily and when Barnes & Asselman (1991) asked subjects to stare passively at the stimulus, very similar ASP velocity characteristics were observed despite the fact that eye position made a nystagmus like pattern. Although the high velocities of ASP produced under these conditions are compatible with the velocities of predictive movements during sine pursuit, there may be reason to believe that the underlying processes are different. Barnes & Asselman (1991) and Deno *et al.* (1995) have suggested that there might be two predictive processes operating during continuous pursuit. Firstly a short-term process that extrapolates the current target motion in the same way as a Taylor series (weighted addition of derivatives such as velocity and acceleration to current target position will give future target motion providing there are no discontinuities). Secondly a long-term process where information from several cycles is used in order to predict events such as target reversals during a triangular wave. ASP may be more closely related to this second type of prediction where cognitive inputs can guide the anticipation of future events.

Neural substrate of smooth pursuit

The visual systems of monkeys have been extensively studied. The primary visual cortex (V1) contains "complex" cells that respond to retinal image motion. These project directly and indirectly via extrastriate cortex (V2) to the ipsilateral middle temporal visual area (MT) (Tusa & Zee 1989). This area lies in the superior temporal sulcus. Most neurons here encode stimulus speed and direction. Extrafoveal lesions of MT cause a scotoma for moving stimuli in the affected contralateral peripheral part of the visual field. Area MT projects to the medial superior temporal area (MST) in monkeys and also via the corpus callosum to the contralateral MT and MST areas. The neurons here have larger receptive fields and some also encode a non-visual signal that is probably an efference copy of the eye movement command (Newsome *et al.* 1988). Human studies of this area, also called V5, using stroke patients with selective motion perception deficits (Zihl *et al.* 1991), positron-emission tomography (Watson *et al.* 1993) and functional MRI (Barton *et al.* 1996b) suggest it is located just posterior to the junction of the ascending limb of inferior temporal sulcus and the lateral occipital sulcus. In monkeys, MST, unlike MT continues to be active during pursuit if the target is blanked due to a blink or if the target is stabilised on the retina. Lesions of MST cause a retinotopic deficit, as seen in MT, but also a unidirectional deficit in horizontal pursuit for a target moving towards the side of the lesion (Dursteller & Wurtz 1988). Deficits in smooth pursuit may or may not be accompanied by deficits in motion perception (Barton *et al.* 1996a).

In monkeys, both MT and MST project to the posterior parietal cortex where the neuronal responses seem to be more concerned with selective attention (reviewed in Eckmiller 1987). This aspect of control is important outside the sterile visual environment of the laboratory where there may be many different objects in motion. All three of these areas project to the frontal eye fields (FEFs) located in the arcuate sulcus in monkeys but the precentral sulcus in humans (Petit *et al.* 1997). There appear to be two descending pathways that project to the dorsolateral pontine nucleus (DLPN). One from the FEFs and one from areas MT/MST/posterior parietal cortex. From here the major projections are to the paraflocculus, flocculus and vermis of the cerebellum, an area that is essential for normal pursuit (Zee *et al.* 1981). These areas receive inputs encoding retinal error velocity, eye velocity and head velocity signals (Noda 1986). Electrical stimulation of the flocculus will generate pursuit within 10 ms (Belknap and Noda 1987). The cerebellar output is relayed via the vestibular nuclei and ocular motor nuclei to the extra-ocular muscles.

Although most studies have implicated each cortical hemisphere in controlling ipsilateral pursuit, there appears to be a smaller contribution to contralateral pursuit. This is supported by occasional observations of bidirectional deficits after discrete unilateral cerebral lesions in humans (Morrow & Sharpe 1990) and the fact that hemidecorticate patients can produce some ipsilateral pursuit when tested 8-12 years after surgery (Sharpe *et al.* 1979). The wide distribution of the smooth pursuit network may make it susceptible to damage. Lekwuwa & Barnes (1996a) found that only 20/72 patients with cerebral lesions had pursuit gains within the range of patients with no neurological disorders.

Possible neural substrate for predictive smooth pursuit

The frontal eye field is an important component of the saccadic system. Electrical stimulation here in monkeys can elicit contralateral saccades indistinguishable from natural ones (Robinson & Fuchs 1969). More recent reports show that the FEF also participates in the control of pursuit. FEF stimulation produces ipsilateral smooth pursuit which increases with applied current and ablations degrade ipsilateral smooth pursuit (MacAvoy *et al.* 1991). There is recovery of pursuit several months after a lesion but the more cognitive aspects of pursuit such as anticipatory pursuit and predictive continuation during target blanking are permanently degraded. In monkeys and in humans (Petit *et al.* 1997), the pursuit area appears to be adjacent to the saccade area. The elicited smooth eye movements have a latency of around 39 ms (Gottlieb *et al.* 1993). These smooth eye movements can be elicited from fixation whereas stimulation of the MST area only has a small effect during fixation compared to the much larger modulation of eye velocity during on going pursuit (Komatsu & Wurtz 1989). Keating (1993) found that FEF-lesioned monkeys had greater deficits in the predictive aspects of pursuit than in normal visually guided pursuit. However there was not a complete absence of prediction showing that the deficit was probably not due to an inability to predict but a problem with its expression. He concluded that the FEF deficit lies in the premotor part of the circuit, downstream of the guiding inputs but before the oculomotor plant that drives the eyes. Similarly, in none of the 53 patients with cerebral lesions studied by Lekwuwa & Barnes (1996b) was there a complete loss of prediction. Even in patients with large phase errors for sinusoidal tracking there was still some evidence of anticipatory pursuit and an advantage in the first 200 ms of tracking predictable ramps compared with unpredictable ramps.

None of the four patients with cerebellar ataxia syndrome examined by Moschner *et al.* (1996) produced the normal fast anticipatory smooth pursuit movements that occur before saccades made to large regular target steps in alternate directions. Similarly, Lekwuwa *et al.* (1995) found that the velocity of anticipatory pursuit before ramps was reduced, although not eliminated, in cerebellar patients. Braun *et al.* (1996) also studied the effect of brain damage on the predictive aspects of smooth pursuit. All four patients with unilateral cortical lesions studied had reduced velocities in visually guided smooth pursuit, anticipatory pursuit and predictive continuation of pursuit during target blanking. The patients had the capacity to achieve higher velocities than the chosen ramp speeds so the impairment was not due to a motor output limit. Neither was it due to a retinal signal since the anticipatory pursuit was produced in the dark. These results suggest that the anticipatory movements follow the normal smooth pursuit pathway.

The Dorso-Medial Frontal Cortex (DMFC) or Supplementary Eye Field is a plausible candidate for a source of long-term predictive signals. It has inputs from MST and the parietal lobe and is interconnected with the FEF. Activity in this area seems to rise in a way that is related to the timing of events in a predictable waveform rather than in response to stimulus position or velocity (Heinen 1994). For ramp tracking, the activity of some cells rises to a peak shortly before the predictable onset of a ramp while others peak just before the predictable offset (Heinen and Liu 1997). The size of this peak increased as the monkeys learnt a new pattern of target motion. Stimulation of this region in darkness does not produce pursuit, but a stimulation train that ends just before the monkey expects a ramp will increase anticipatory acceleration and initial visually guided acceleration (Heinen 1996). The facilitation seems to depend on the end of the stimulation since if the train ends just after ramp onset then pursuit is suppressed. Stimulation during pursuit just before ramp offset hastens deceleration.

This thesis

This thesis attempts to characterise anticipatory smooth pursuit eye movements and explores how they are controlled. There are three main sections. The first deals with how much cognitive control subjects have over the velocity of ASP. An abstract of this work was published in the proceedings of the Physiological Society (Wells & Barnes 1996). The second section explores the ability to reproduce previous movements after different intervals of time and compares this ability to tracking with the hand. This work was published in Experimental Brain Research (Wells & Barnes 1998). The final section assesses the extent to which anticipatory movements can be modified to suit the current task requirements. This work is currently in press with Vision Research.

CHAPTER 2: COGNITIVE CONTROL OF ANTICIPATORY SMOOTH PURSUIT VELOCITY

Introduction

If a visual target moves with a brief ramp that is repeated every few seconds then for the first ramp there is a reaction time delay of around 100 ms before ocular pursuit starts. However, for subsequent ramps, the delay becomes shorter, then negative as there is a build-up of anticipatory smooth pursuit (ASP) before the onset of each ramp as shown in Fig. 2.1 The convention of positive points on a graph representing rightwards position or velocity is used is this and all other figures.

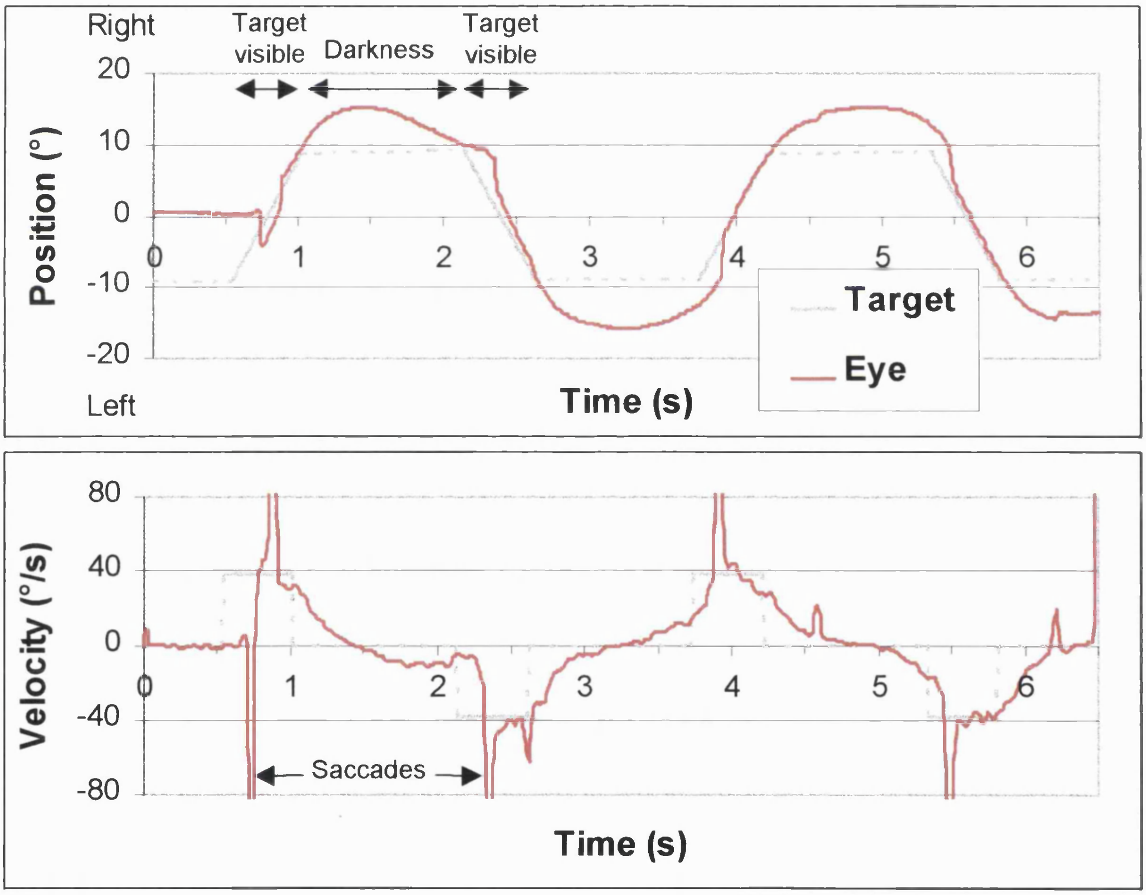


Fig. 2.1 Position and velocity responses to the first of four repetitive ramps. The target (grey) moved in alternate directions at 38.4°/s for 480 ms with 1120 ms intervals of darkness between ramps. Dotted lines show when the target was invisible and the subject was in darkness. The first response starts after a reaction time delay but subsequent responses become more anticipatory.

A steady state velocity profile is achieved by the third or fourth ramp. When Barnes & Asselman (1991) used much briefer ramps (≤320 ms) they found that the peak eye velocity built up over a few presentations as well as the ASP. Indeed, for the faster ramps, target velocity could only be matched once a reasonable anticipatory response had been established. In contrast, the longer presentations used for this figure (480 ms), usually allowed enough time for visual feedback to match target velocity on the very first presentation.

Several studies have shown that for repetitive ramp stimuli, ASP velocity increases with target velocity over quite a wide range of target velocities (Barnes & Asselman (1991) used ramp velocities between 9-45°/s; Kao & Morrow (1994) used 5-20°/s ramps; Barnes *et al.* (1995) used 10-50°/s ramps; Ohashi & Barnes (1996) used 12.5-50°/s ramps). The anticipatory responses are therefore stimulus specific rather than just a default response.

Scaling of ASP velocity is less obvious for repetitive target steps. Kowler & Steinman (1979a) found weak scaling of ASP velocity with step amplitude (ASP velocity increased from ~0.15°/s to just ~0.34°/s as step size increased from 0.17° to 7.1°). Moschner *et al.* (1996) found faster ASP before much larger target steps but found no change in ASP velocity when step amplitude was varied between 20 and 70°. This could be related to the argument that ASP before target steps merely reflects a default response to the release of fixation whereas ASP before target ramps has the additional benefit that it may help in the actual tracking of the target movement.

There are two possible causes for the scaling of ASP before repetitive target ramps. It may be due to subjects using their knowledge of the target motion to predict velocity of the upcoming ramp. Alternatively, since all the above studies used repetitive ramps of the same velocity, the only reason that responses are appropriate for a particular target velocity may be because subjects merely replay the previous response to that target velocity. This first section of the thesis aimed to differentiate these two possibilities. The first experiment of this section explored the general characteristics of ASP before ramps at many different target velocities. Using this information, suitable parameters were chosen for assessing the cognitive control of ASP velocity in the second and third experiments.

General Method

The following description applies to all experiments described in chapters 2 and 3 of this thesis. Each subject sat in a dark room at the centre of a 1.5m radius semi-circular screen onto which the horizontally moving target was projected via a servomotor-controlled mirror. The head was immobilised using clamps and a chin rest. Left eye movements during binocular viewing were recorded with 5-10min arc resolution by infra-red limbus tracking (Iris, Skalar Medical, Netherlands). A picture of the apparatus is shown in Fig. 2.2.

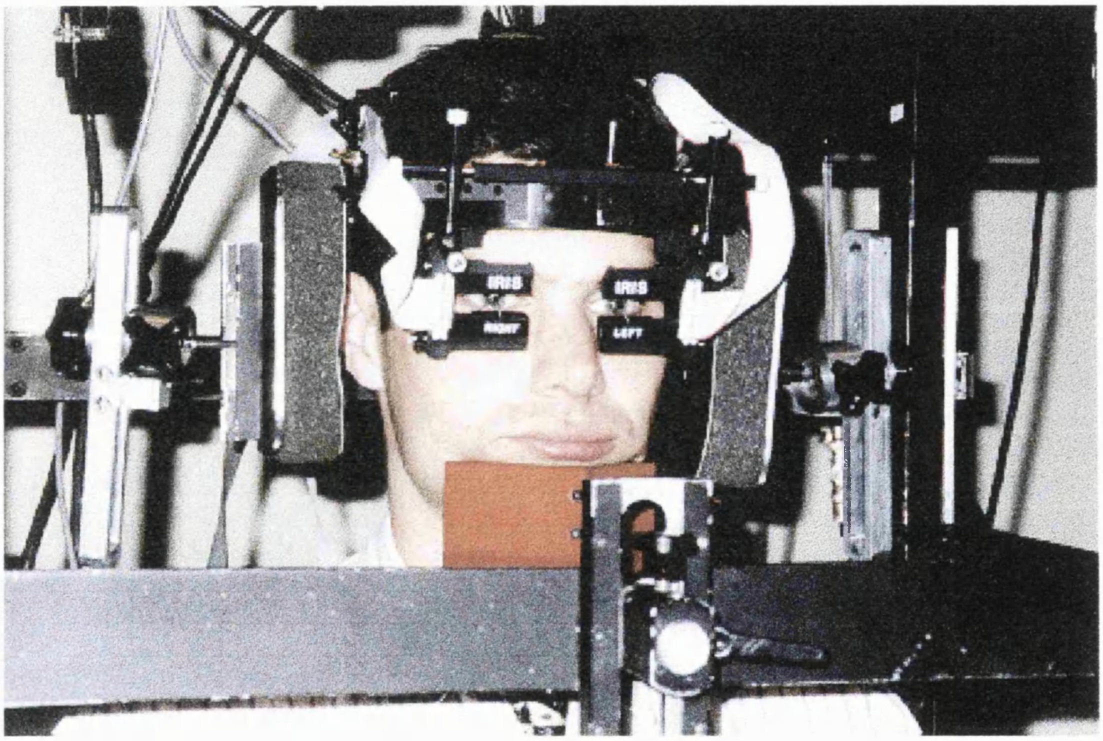


Fig. 2.2 Apparatus used for monitoring the subject. Eye movements were recorded by infra-red detectors while a chin rest and head clamps stabilised the head.

The white target was a 1.22° diameter circle with cross hairs, with two 0.30° wide x 1.22° high white rectangles above it and two below it centred at ±1.13° and ±1.76° from the middle of the circle. Target illumination was controlled by an electro-mechanical shutter that could produce flashes as short as 8ms. Immediately before each trial, the eye position signal was calibrated with the target signal by requiring the subject to pursue a ±16°, 0.4Hz sinusoidal target motion as shown in Fig. 2.3.

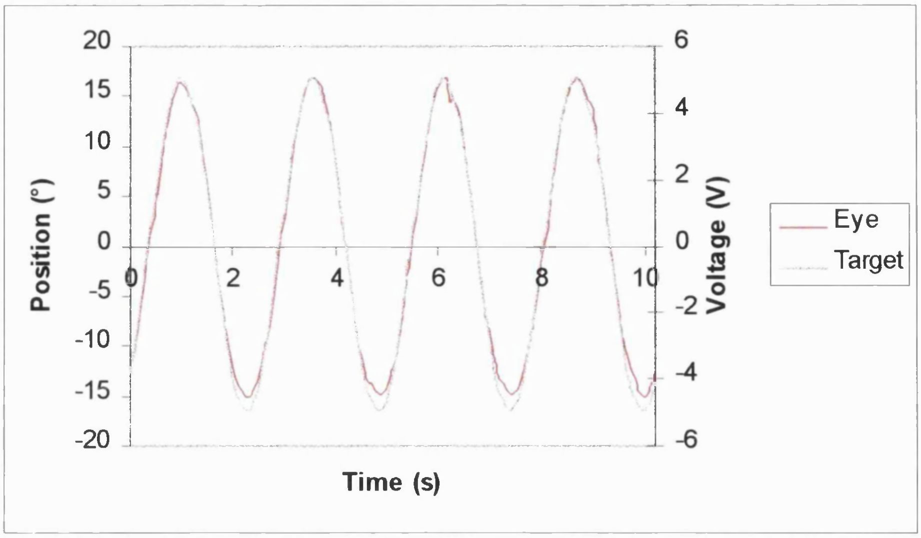


Fig. 2.3 Pursuit of 0.4Hz sinusoidal target motion used to calibrate the voltage from the eye movement recorder to actual angular position.

The subjects performed this easily and four cycles of the overall eye position signal (including the few saccadic corrective movements) were then correlated with target position as shown in Fig. 2.4 using a least-squares error-fitting procedure.

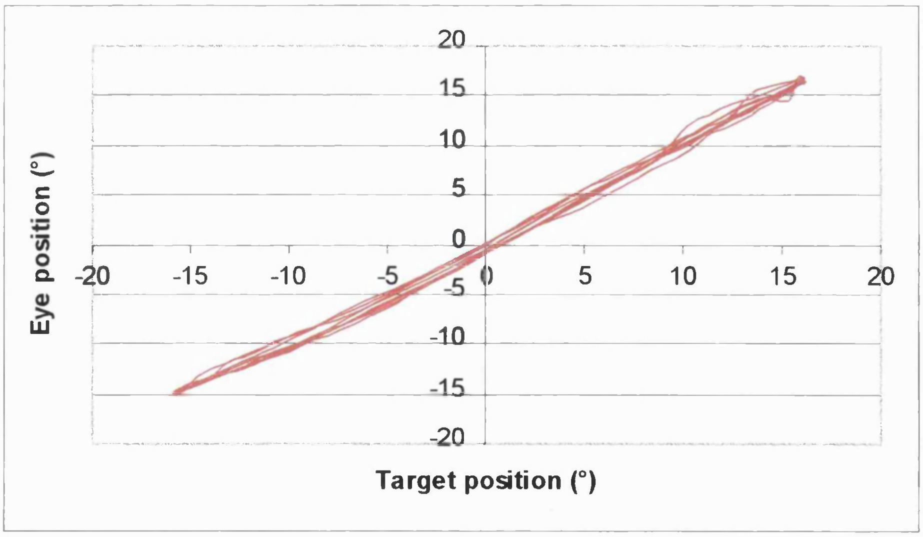


Fig. 2.4 Correlation of eye and target position during calibration of the eye position signal.

During an experiment, eye and target position signals were sampled with 12-bit resolution and eye velocity was obtained by digital differentiation using a two-point difference algorithm. Saccades were identified by an acceleration criterion (on a velocity trace, a saccade is a prominent spike but is even more easily detected on an acceleration trace as two distinctive spikes in opposite directions). An acceleration threshold (typically 300-400°/s/s) that separated the high acceleration of saccades from the lower acceleration of smooth pursuit / noise was set by eye. Where a double spike exceed both the threshold for both rightwards and leftwards acceleration then the intervening period plus one data point either side was removed from the velocity trace. The removed section was replaced by linear interpolation to obtain the smooth eye velocity traces used for averaging multiple responses. These were passed through a digital zero-phase low-pass filter at 40Hz.

Statistical analysis

For eye movement experiments, it is often desirable that each subject participates in all experimental conditions i.e. repeated measures are taken, rather than assigning different groups of subjects to each condition. Firstly, a smaller and more practical number of subjects can be tested. Secondly, the variability between the eye movement responses of different subjects may be much larger than the variability within a subject (i.e. the variability between responses to two conditions by the same subject).

All experiments in this thesis are based on repeated-measures factorial ANOVA. This was performed using the General Linear Model Repeated-Measures SPSS software function. Each factor has a certain number of factor levels and the total number of conditions is the product of the number of levels of each factor. To assess which factors were significant main effects and which interactions were significant, the multivariate F test approach was used. The more powerful univariate approach could have been used with a Greenhouse-Geisser correction, but this requires homogeneity of variance across the different within-subject factor levels. There was some doubt over the validity of this so it was decided to use the more robust mulitvariate approach. This assumes that the observations for each condition come from a normal distribution. Since the number of subjects participating in each experiment was only between 6 and 9, it was difficult to reliably detect departures from normality. Nevertheless, for each condition, a Shapiro-Wilks test was performed on the n responses by the group of n subjects. Around 5% of the conditions described in this thesis were assessed as not being drawn from a normal population. A note was also made of outliers (i.e. if the mean response of a subject lay beyond the 75th percentile by an amount greater than 1.5 times the magnitude of the inter-quartile range). Occasional mean responses were classified as being outliers. However no subject consistently produced outlying responses so it was not felt necessary to exclude any particular subject from the analysis. After considering these points for each experiment it was concluded that the data were acceptably normal and that the loss of clarity from using transformed variables or the loss of statistical power from using non-parametric data would not be justified.

The criterion of $p < 0.05$ was used to decide if a result was significant. Once a factor had been shown to have a significant effect, contrasts were performed to find which factor levels were the source of this effect. The more comparisons are made, the higher the probability of making a Type I error (i.e. rejecting the null hypothesis when it is true). The accepted probability of making a Type I error may be 0.05 for each separate comparison but the family-wise type I error rate must also be considered (the probability of making one or more Type I errors in the entire set of comparisons). The relationship is:

$$\text{family-wise error probability} = 1 - (1-0.05)^{c}$$

where c is the number of comparisons. Most researchers appear to be willing to perform as many comparisons as the number of degrees of freedom, without correcting for family-wise error (Keppel 1982). For example if there are 5 conditions then the maximum number of planned comparisons (i.e. not post-hoc comparisons) that will be conducted without correction is equal to df = 4. For a significance level of 0.05 the acceptable family-wise error rate will then be $1-(1-0.05)^4 = 0.185$. If 5 comparisons are required, this figure is divided by 5 to give 0.04 which is the adjusted significance level used to evaluate each of the five individual comparisons. This is referred to as the modified Bonferroni test.

Experiment 2a: Scaling of anticipatory eye velocity with target velocity

Specific method for this experiment

This experiment aimed to confirm the ASP velocity scaling results of Barnes & Asselman (1991), Kao & Morrow (1994), Barnes *et al.* (1995) and Ohashi & Barnes (1996) but over a larger range of target velocities. Each constant velocity target ramp was presented for 480 ms with the motion centred about the straight ahead position. Consecutive ramps were in alternate directions. There was a regular inter-stimulus interval of 1.6 s between the start of each target appearance (equivalent to a 0.3125Hz triangular wave; 1120 ms of darkness between ramps). Eye and target displacement signals were sampled at 100 Hz. Target velocities between 6.4 and 64°/s were used in increments of 6.4°/s. The five slowest target velocities were tested in one trial and the five fastest in another trial with each target velocity being presented for a block of 10 consecutive ramps. To control for training effects, the order of presentation of blocks at each ramp velocity was randomised across subjects. An example of responses to 10 consecutive 38.4°/s ramps by one subject is shown in Fig. 2.5

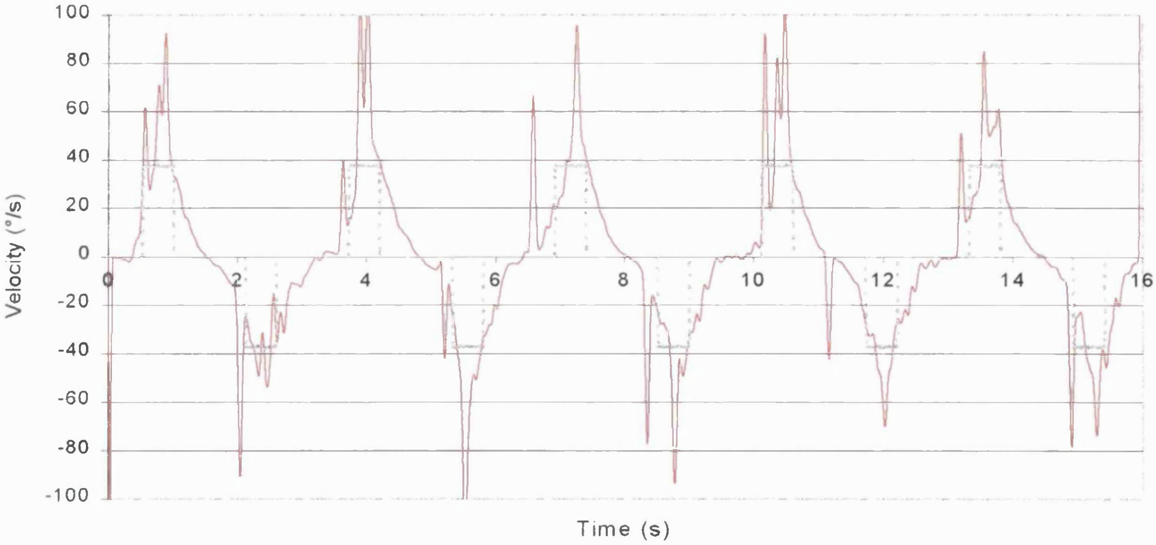


Fig. 2.5 Example of eye velocity responses (red) by one subject in response to ten consecutive 38.4°/s target ramps (grey) each lasting 480 ms.

Only the last 8 ramps at each velocity were analysed to give the "steady state" response after the anticipatory velocity had reached an asymptotic level. The six subjects (aged 23-49, 4 male) all had prior experience of oculomotor testing.

Results

The upper graph of Fig. 2.6 shows the last 8 responses from Fig. 2.5 overlaid and aligned with respect to ramp onset. The saccades were removed as described in the General Method. The lower graph shows eight responses to 12.8°/s ramps.

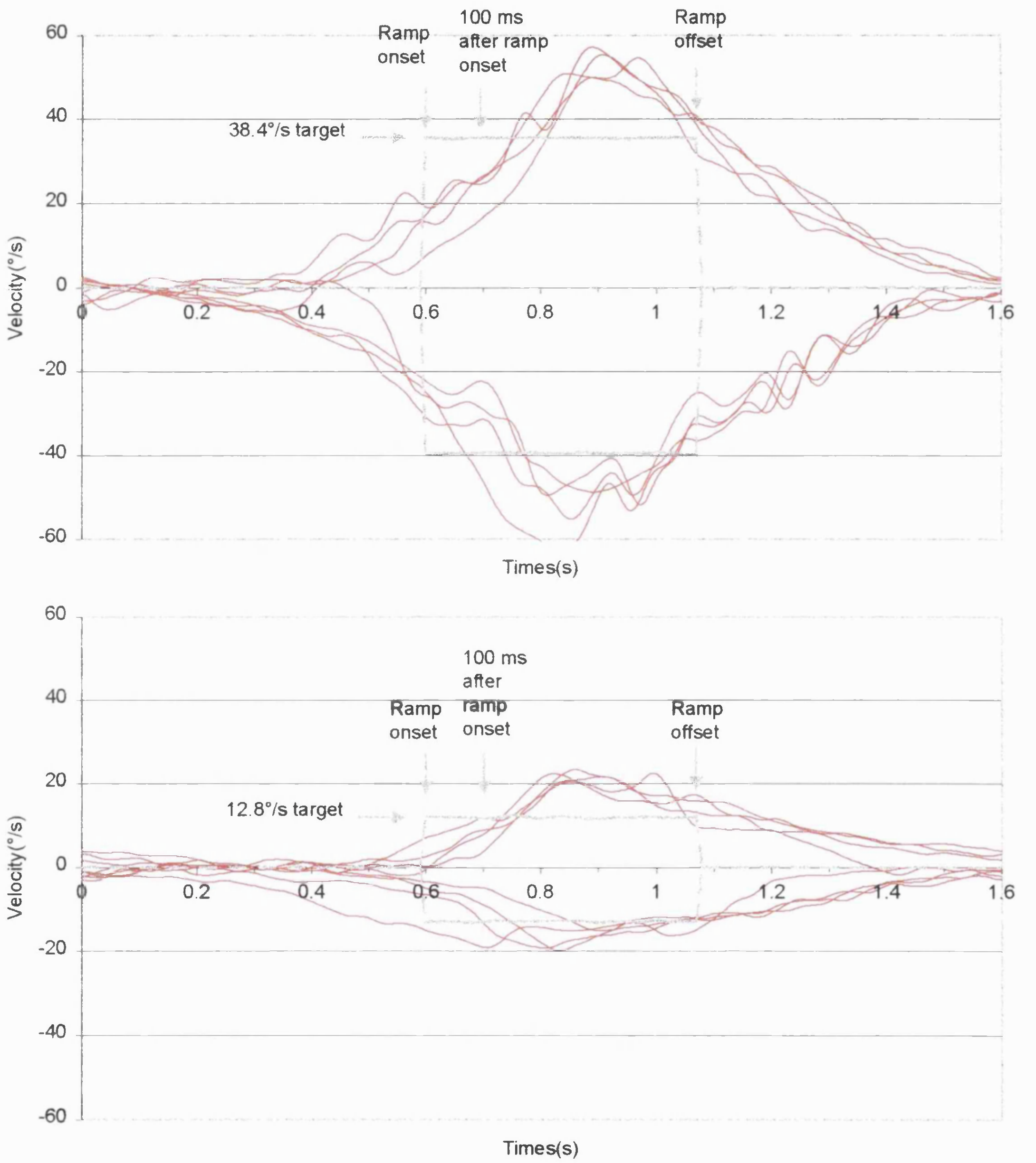


Fig. 2.6 The red lines in the top graph show the last eight responses to ten consecutive 38.4°/s target ramps (shown in grey) moving alternately to the left and right. The bottom graph shows responses to 12.8°/s ramps. These responses are considered to be steady state since the anticipatory velocity has reached an asymptotic level.

The anticipatory velocities often reached a sizeable proportion of target ramp velocity before the target had appeared. There was considerable variation in the magnitude of the anticipatory velocity to identical consecutive ramps. However, ASP velocity increased with target velocity so for example, anticipatory velocity before 38.4°/s ramps was nearly always higher than before 12.8°/s ramps. This was achieved through higher accelerations and the response starting earlier.

During tracking of the ramp, eye velocity often exceeded target velocity as has been noticed before (Robinson 1965; Wyatt & Pola 1987; Luebke & Robinson 1988; Krauzlis & Miles 1996b; Ohashi & Barnes 1996). The overshoot of target velocity may reflect an attempt to correct a positional error, or an overestimated predictive response exerting an influence beyond 100 ms after ramp onset

The magnitude of ASP was assessed as the eye velocity 100 ms after ramp onset (V100). Although the anticipatory movement starts several hundred milliseconds before ramp onset, it is desirable to measure the response as late as possible when the velocity is greatest in comparison to the noise in the signal. However, if the measurement is made too late then part of the response may be due to visual feedback and not be purely anticipatory. The latest time was therefore chosen as 100 ms after ramp onset since 100 ms is the minimum time that visual feedback takes to influence smooth pursuit (Carl & Gellman 1987). Thus the response is purely anticipatory up until this point. The plots in Fig. 2.7 show the results from 6 subjects to all the target velocities tested.

Generally, all subjects increased their V100 in proportion to target velocity. On average V100 was around 60% of target ramp velocity for targets between 12.8 and 51.2°/s, but the exact percentages varied widely between subjects. Some subjects would achieve nearly 100% of target velocity whilst others would only achieve around 25%. Experience seemed to have little effect on the V100 magnitude. The two most experienced subjects (GB & SG) produced the highest and lowest values of the group. Outside of this range where V100 was roughly proportional to target velocity, V100 fell to around 40% on average for the fastest targets but increased to around 100% for the slowest. Nearly all subjects showed this pattern.

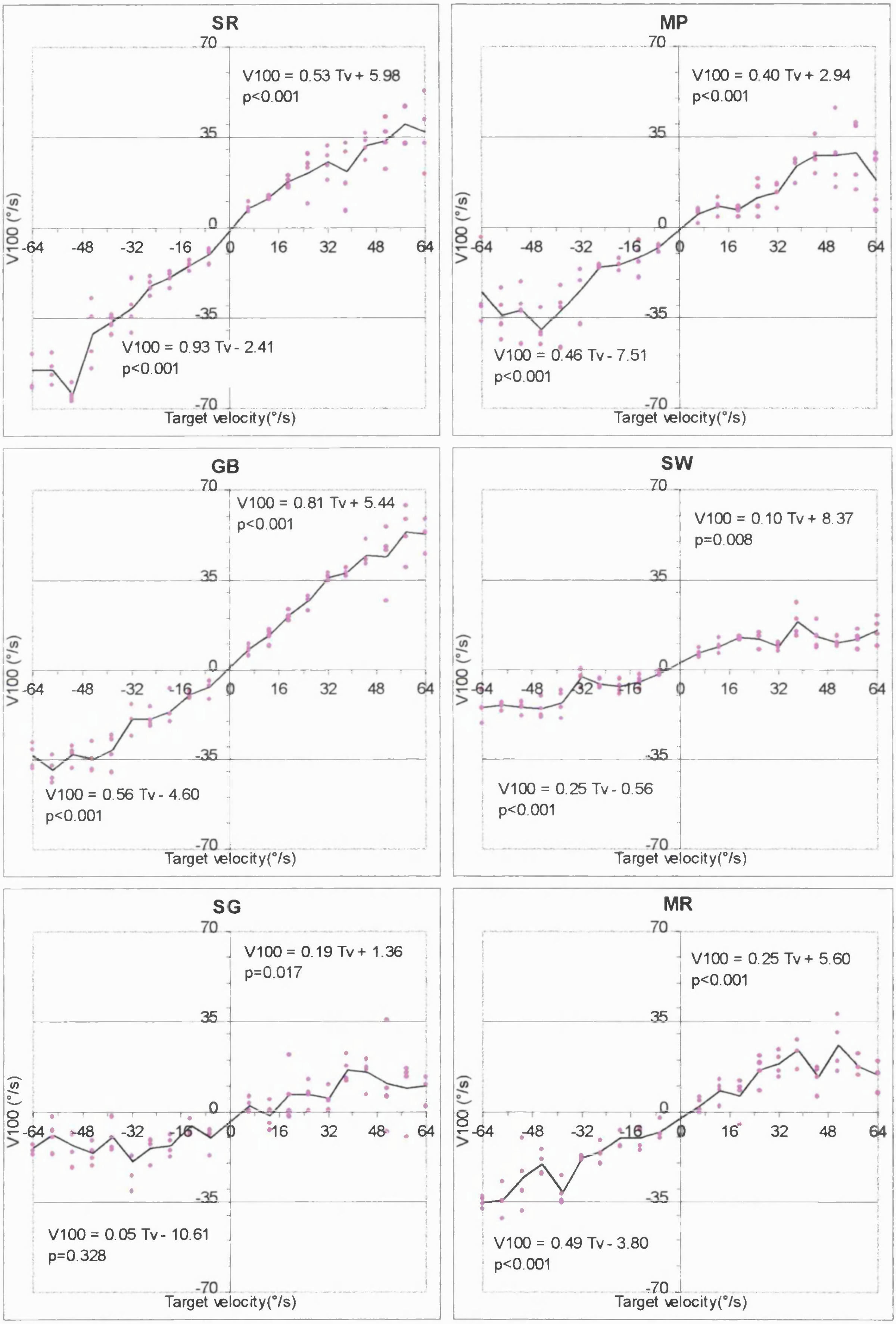


Fig. 2.7 Responses by six different subjects to repetitive ramps at particular velocities. Positive values represent rightwards motion. Each pink point shows anticipatory eye velocity at 100 ms after ramp onset (V100) for a single response. The black line shows the average. The formulae show the function of the best fit linear regression line for estimating V100 from target velocity (Tv), calculated separately for rightwards and leftwards motion.

Regressions were carried out to statistically analyse how well the scaling of V100 with target velocity could be described by a linear function. Separate regressions were performed on each subject's responses in each direction. The resulting coefficient and intercept for predicting V100 from the target velocity are shown on each graph for rightwards and leftwards motion separately. All regressions were significant ($p<0.02$) except for subject SG for leftwards motion where there was little variation in V100 with target velocity. Although V100 was generally around 60% of target velocity, the mean coefficient was 0.42 since the regression line was not forced to have an intercept of zero. The mean intercept was 4.9°/s. For some subjects there was a clear directional asymmetry in the anticipatory responses. For example, subject SR's V100 to the right was around 100% of target velocity for most ramps but only around 70% to the left (coefficients of 0.93 and 0.53 respectively). This asymmetry disappeared, as might have been expected, during closed loop pursuit later in the ramp.

Discussion

V100 was scaled appropriately over a wide range of target velocities in all subjects. Mean V100 was well described as a linear function of target velocity with each subject achieving quite a constant percentage of target velocity. However, there appeared to be a tendency for V100 to be a higher percentage of low target velocities and a lower percentage of high target velocities. This was also shown by the fact that the best-fit lines did not have zero intercepts. This was not a range effect whereby the responses were scaled to the mean ramp velocity in a trial since the five slowest target velocities and five fastest velocities were presented in separate trials. The decrease for the fastest ramps was probably not due to the ramp duration being too brief. Firstly, even the highest ramp velocity could be matched within this time and secondly Ohashi & Barnes (1996) showed that for similar repetitive ramps V100 did not increase further when ramp duration increased above 240 ms. It was probably due to a limitation in the maximum velocity of anticipatory pursuit that can be produced. It seems likely that this limit might approach the maximum velocity that can be achieved for visually guided smooth pursuit (115-150°/s; Lisberger *et al.* 1981). It should be remembered that the limitation during visually guided pursuit is not due to mechanical constraints since smooth VOR movements can achieve velocities of up to 400°/s (Atkin & Bender 1968).

The increase in V100 relative to the lowest target velocities was perhaps due to an overestimation of ramp velocity or perhaps because the ramp velocity was near to the velocity of pursuit that can be generated at will in the dark. Indeed the mean intercept of the regressions was close to this value (≤5°/s; Kao & Morrow 1994). It appears that a more complex function would better describe the extremities of the relationship between V100 and target velocity. However more target velocities below 10°/s and above 60°/s would be needed to fit such a function with confidence.

The consistent directional asymmetry in V100 seen in some subjects was not surprising. Large asymmetries in closed-loop pursuit can be seen in patients with cortical lesions (Morrow & Sharpe 1990; Lekwuwa & Barnes 1996a) but should not be seen in normals. However, small asymmetries in normals are more likely to become apparent during open-loop pursuit. Indeed they have been reported when trying to sustain smooth movement in the dark (Becker & Fuchs 1985; Braun *et al.* 1996) and in the first 100 ms of pursuit initiation (Carl & Gellman 1987). The asymmetry in V100 has important implications for when the putative store is charged. It cannot be a repetition of the last anticipatory movement since for subject SR for example, a fast anticipatory movement to the right is produced after a slow anticipatory movement to the left. It seems likely that the putative 'store' is charged during the closed loop part of the response (where the eye is always near target velocity) and then the subsequent release of the response is modulated by an open-loop motor asymmetry.

High variability between consecutive responses to identical stimuli has been noticed before. Robinson (1965) described it as "embarassing to the attempt to describe analytically the smooth pursuit system". Likewise, many authors have noticed a considerable variation in the magnitude of anticipatory responses between subjects for both repetitive ramps (Kao & Morrow 1994) and repetitive steps (Moschner *et al.* 1996). These findings emphasise the need to obtain many responses from several subjects before drawing any general conclusions about the pursuit system.

Experiment 2b: Scaling of anticipatory eye velocity during repetitive target velocity sequences: Alternate direction ramps

Introduction

Experiment 1a revealed that subjects could produce a wide range of anticipatory velocities that were scaled to target velocity. However it was uncertain whether this scaling was a cognitive strategy or merely the reproduction of a prior movement. To answer this question subjects were presented with simple sequences of fast and slow targets. Would subjects produce an anticipatory response appropriate to the expected ramp velocity or merely repeat the response to the previous ramp?

Specific method for this experiment

Eight normal subjects (aged 22 - 50, 5 male) with varying experience of oculomotor testing participated. The target moved with a ramp lasting 480 ms with its motion centred about the straight ahead position. The ramp was repeated in alternate directions every 1.6 s (1120 ms of darkness between ramps). Ramp velocity was either "fast" (38.4°/s) or "slow" (12.8°/s) and varied according to a simple sequence of n fast ramps followed by n slow ramps. Three different length velocity sequences were studied (n = 2,3 or 4) and are illustrated in Fig. 2.8. The actual target motion for one of the velocity sequences is shown in Fig. 2.9. In each trial, one of the sequences would be repeated 12 times without a break, with subjects having full prior knowledge of the motion. Only the responses during the last 11 repetitions were analysed to reveal the steady state response. A second trial for each sequence was later presented but with all the target directions reversed. Normalising the responses over direction and averaging across the two trials would allow any directional asymmetry in pursuit to be cancelled out. The eight trials were presented in a pseudorandom order over the eight subjects using a Latin square design. This controlled for training effects over time and carry over effects from one trial to the next. Two further trials where the velocity was either always fast or always slow were also presented for comparison. Eye and target displacement signals were sampled at 100Hz.

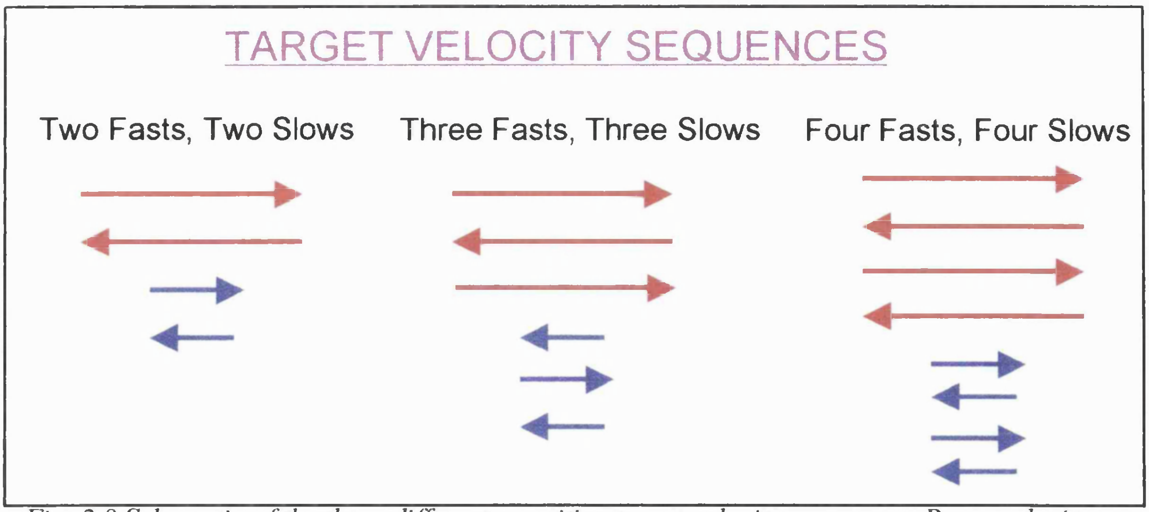


Fig. 2.8 Schematic of the three different repetitive target velocity sequences. Ramp velocity was either "fast" (38.4°/s, shown in red) or "slow" (12.8°/s, shown in blue) and varied according to a simple sequence of n fast ramps followed by n slow ramps (n = 2,3 or 4). Each arrow represents the amplitude and direction of the ramp with the next ramp in the sequence drawn below it.

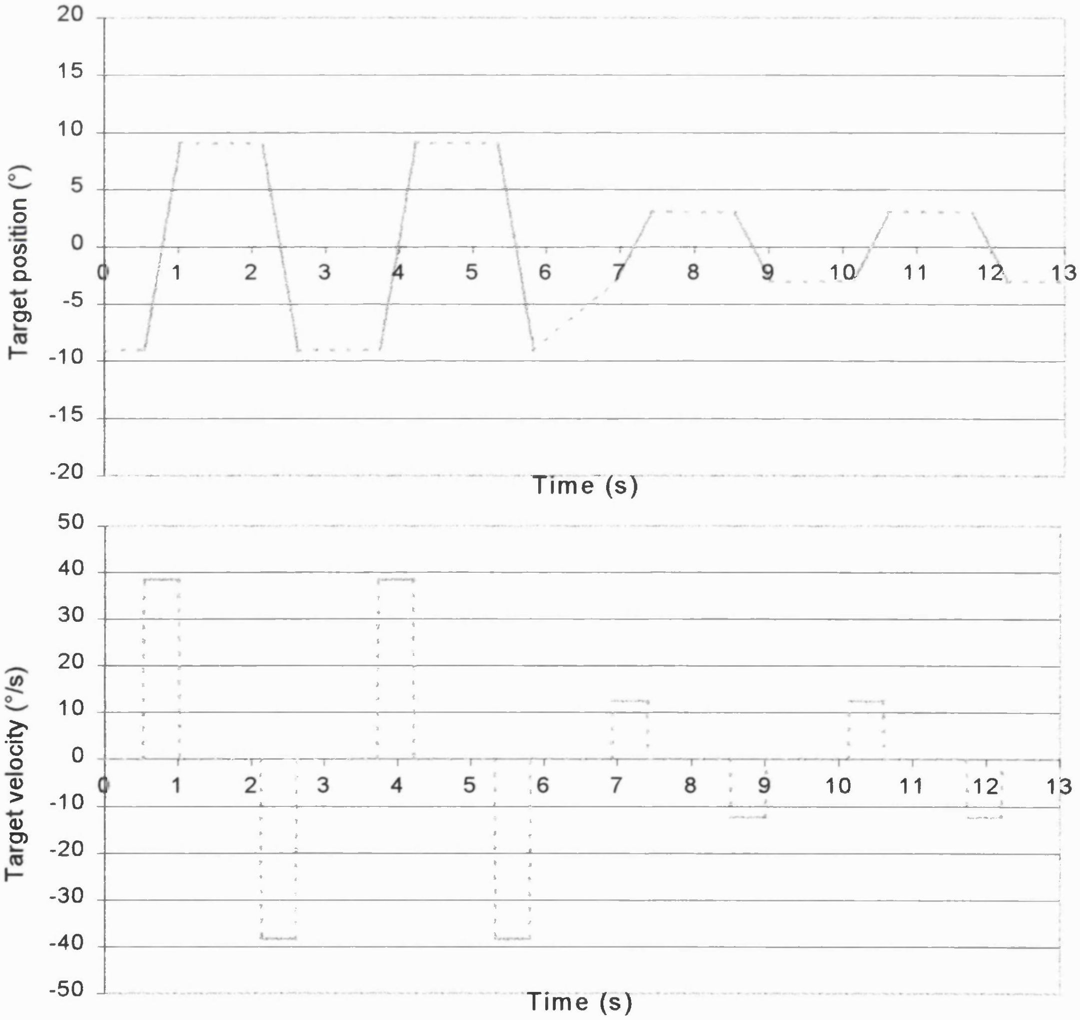


Fig. 2.9 Example of the target motion used in this velocity sequence experiment. Target position (upper plot) and target velocity (lower plot) used in the Four Fasts, Four Slows sequence. The eight ramps shown here were repeated 12 times in a trial. Dotted lines show when the target was invisible and the subject was in darkness.

Results

Subjects did not just produce the same anticipatory response to all parts of the sequence but cyclically varied their anticipatory velocity depending on which part of the sequence they were responding to.

Fig. 2.10 shows many steady state responses by one subject to the Four Fasts Four Slows sequence which typifies the results of this experiment. The responses were averaged along with all the steady state responses from a second trial where the target motion was reversed. Leftward responses in a trial were reversed in sign before averaging. As before, the magnitude of the anticipatory response was assessed as average eye velocity 100 ms after ramp onset (V100), just before visual feedback could have an effect. V100 for this velocity sequence for this subject are shown in Fig. 2.11. In this case, the anticipatory responses to the 2nd, 3rd and 4th Fast ramps were appropriately fast and the responses to the 2nd, 3rd and 4th Slow ramps were appropriately slow. This is unsurprising since in all these cases, the preceding ramp was at the same velocity. The crucial responses were those when the next ramp velocity was faster or slower than the previous ramp to reveal if an appropriately scaled anticipatory response could be produced or merely a repetition of the previous movement. For the 1st fast ramp of each sequence repetition, V100 was only slightly faster than the anticipatory response to the preceding ramp (the 4th slow ramp). Thus this subject was unable to increase V100 appropriately, despite the fact that the velocity sequence was very simple and was repeated many times. In contrast, for the 1st slow ramp of each sequence repetition, V100 was much less than the anticipatory response to the previous ramp (the 4th fast target) and hardly different from the responses to the other slow targets. Thus an appropriate anticipatory response could be produced when a decrease in target velocity was expected.

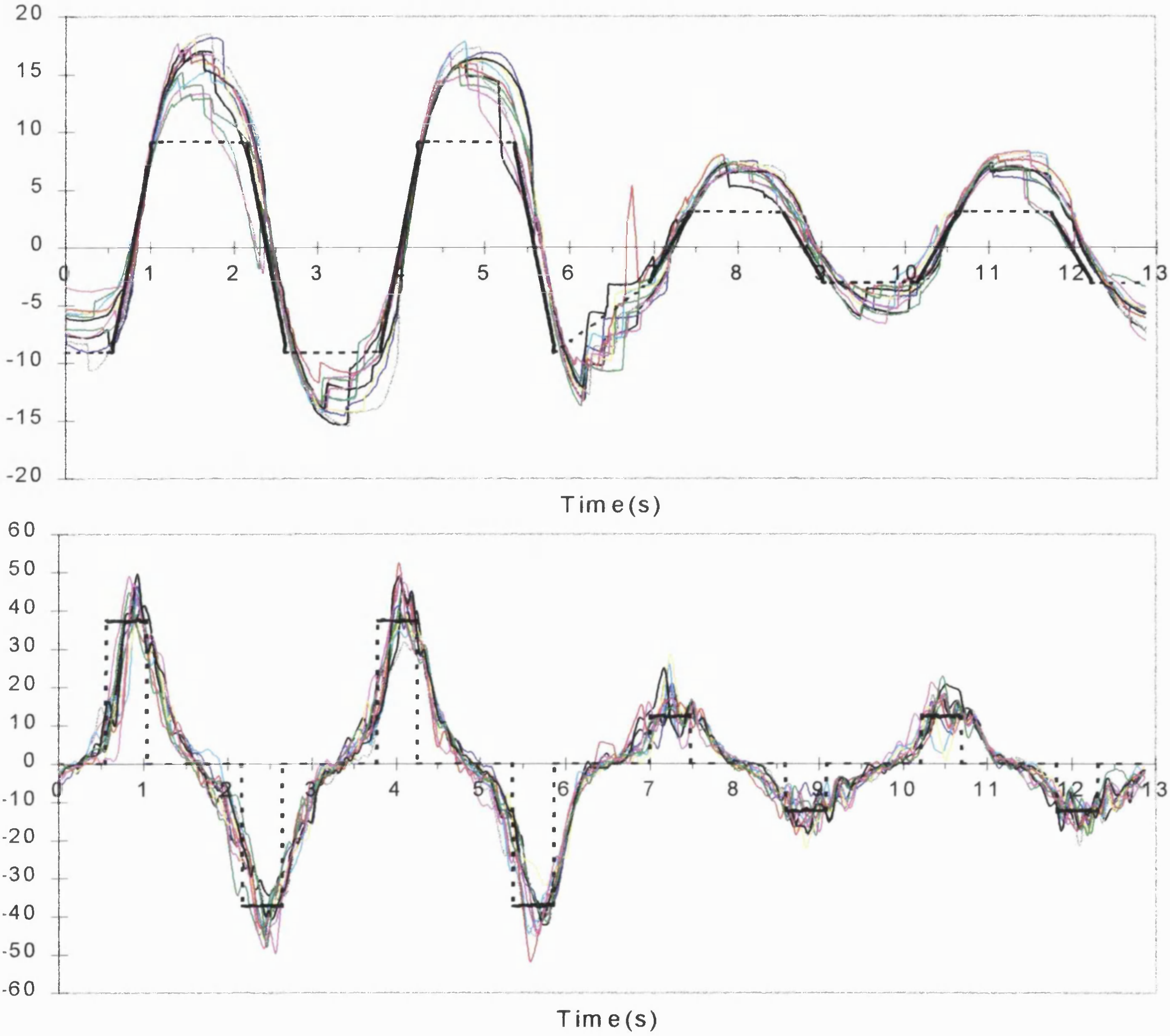


Fig. 2.10 All steady state responses by one subject to a trial of the Four Fasts Four Slows sequence. The upper graph shows position and the lower graph velocity. The last 11 sequence repetitions of the 12-repetition trial have been overlaid. The thick black line shows target motion (the dotted line shows when the target was invisible) and the coloured lines show the eye responses. Saccades have been removed from the eye velocity traces.

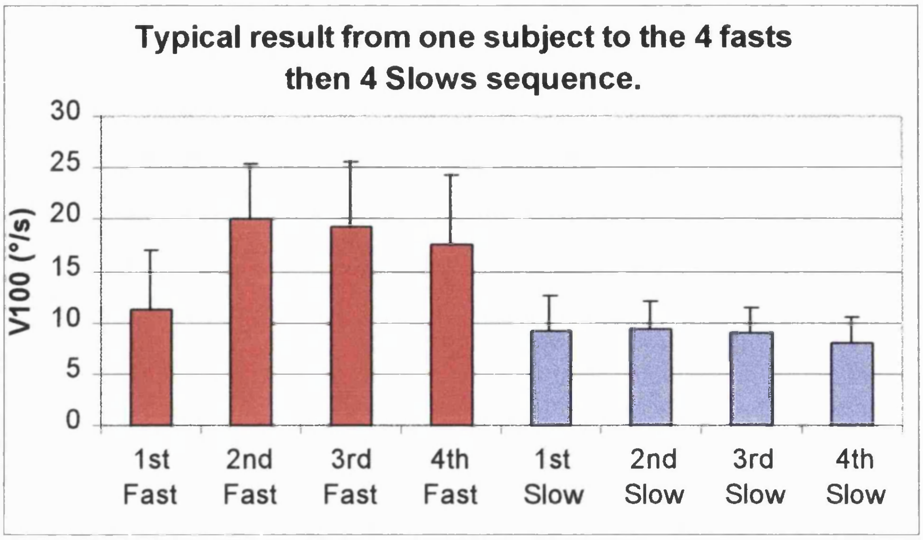


Fig. 2.11 Typical response by one subject to the repetitive velocity sequences. Each column shows mean V100 with standard deviation from 22 responses normalised over direction, for each component of the Four Fasts then Four Slows sequence.

A similar pattern was seen in all the other subjects and for all three types of velocity sequence. The three different length velocity sequences had four common sequence components: the 1st Fast, Last Fast, 1st Slow and Last Slow ramps. Mean V100s for each common component, from each of the velocity sequences from all eight subjects were entered in a repeated-measures factorial ANOVA. The factors were *Sequence component* (4 levels) and *Sequence length* (3 levels). The ANOVA results are shown in Table 2.1

	F	Degrees of freedom	Significance
Sequence component	34.25	3	0.001
Sequence length	0.66	2	0.550
*Sequence component * Sequence length*	13.63	6	0.070

Table 2.1 Results of factorial ANOVA on V100. Planned contrasts between the four factor levels of 'Sequence component' revealed which levels were significantly different (1st Fast vs Last Fast, $p<0.001$; Last Fast vs 1st Slow, $p<0.001$; 1st Slow vs Last Slow, $p=0.133$; Last Slow vs 1st Fast, $p=0.001$). Modified Bonferroni test (see Statistical analysis section) accepts p values less than 0.036 as being significant for these four comparisons.

Sequence length was not a significant factor (p=0.550), but *Sequence component* was (p=0.001). The mean smooth responses of the four common sequence components for the three velocity sequences are shown in Fig. 2.12.

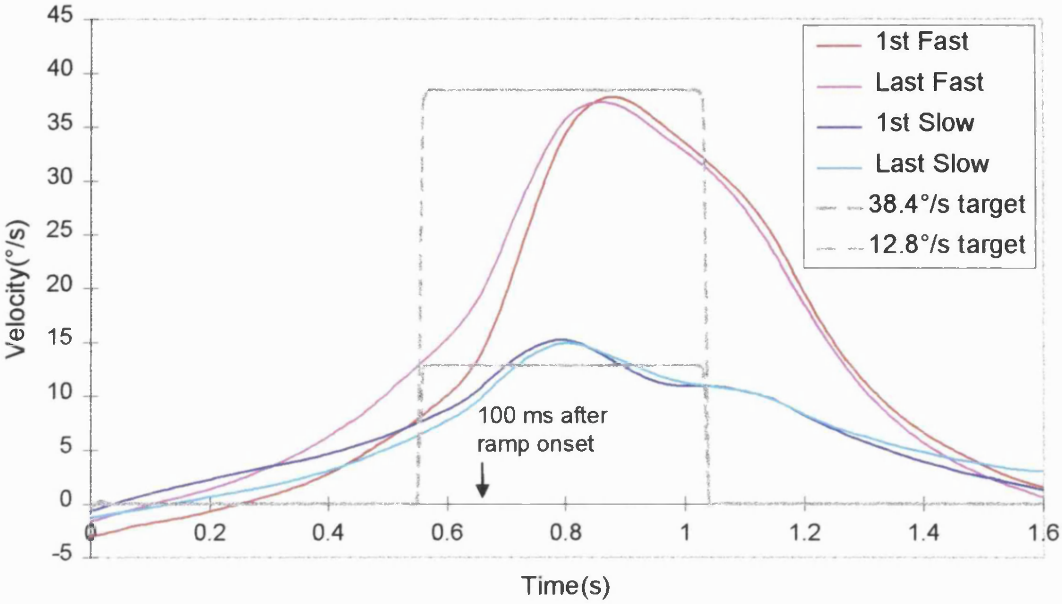


Fig. 2.12 Mean response by all subjects to each of the common components of the velocity sequences.

Mean V100 for the 1st Fast ramp of each sequence repetition was 14.3°/s. This was slightly but significantly faster (p=0.001) than V100 for the preceding Last Slow (10.0°/s) but still significantly slower (p<0.001) than V100 for the upcoming Last Fast (19.9°/s). Thus when subjects expected a ramp that was faster than the preceding one, they increased their anticipatory velocity slightly but were unable to make it sufficiently fast to be appropriate for that target velocity. In contrast when subjects expected a slower ramp, an appropriately slow response was produced (for the 1st Slow ramp, mean V100 (11.0°/s) was significantly slower (p<0.001) than for the preceding Last Fast ramp and not significantly different (p=0.133) from the upcoming Last Slow ramp.

The similarity of this effect on the three different length sequences is shown in Fig. 2.13 for the three velocity sequences tested.

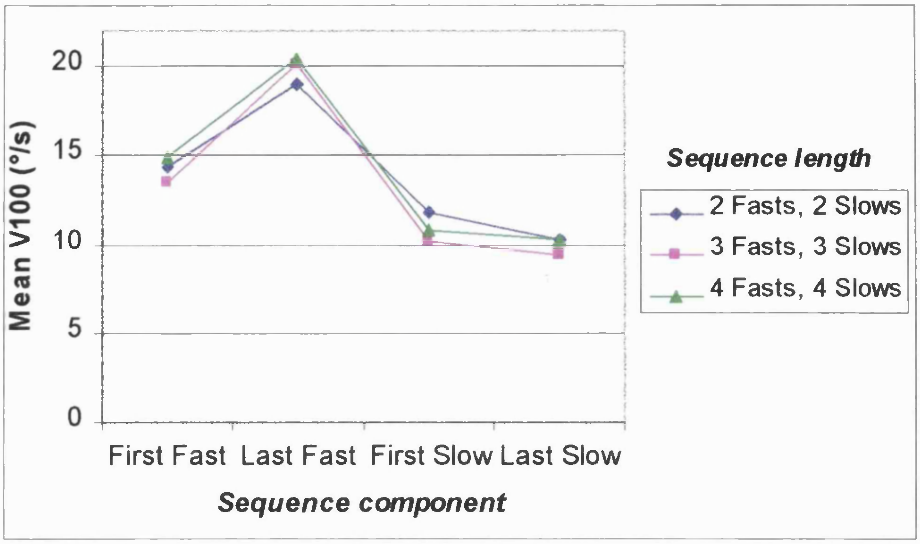


Fig. 2.13 Mean V100 over all subjects to each of the common components from each of the three different length target velocity sequences.

The fact that this effect was not significantly different for all three sequence lengths implies that increasing the number of intervening slow ramps between the Last Fast and 1st Fast ramp had a negligible effect. Indeed a pilot study suggested that just one slow ramp was enough to prevent an appropriately fast V100 being produced subsequently (the sequence was One Fast, One Slow).

Although subjects generated different magnitude anticipatory velocities as was seen in experiment 2a, all subjects showed the same pattern. Namely, that they were able to generate an appropriate anticipatory velocity when a decrease was required but were less do so for an increase. Thus the pattern of responses did not depend on whether subjects generally produced anticipatory velocities that were always a high percentage of target velocity or always a low percentage. Fig. 2.14 shows each subject's mean V100 to all the different sequence components of all three lengths of velocity sequence. Responses to the trials where ramp velocity never changed are also included for comparison.

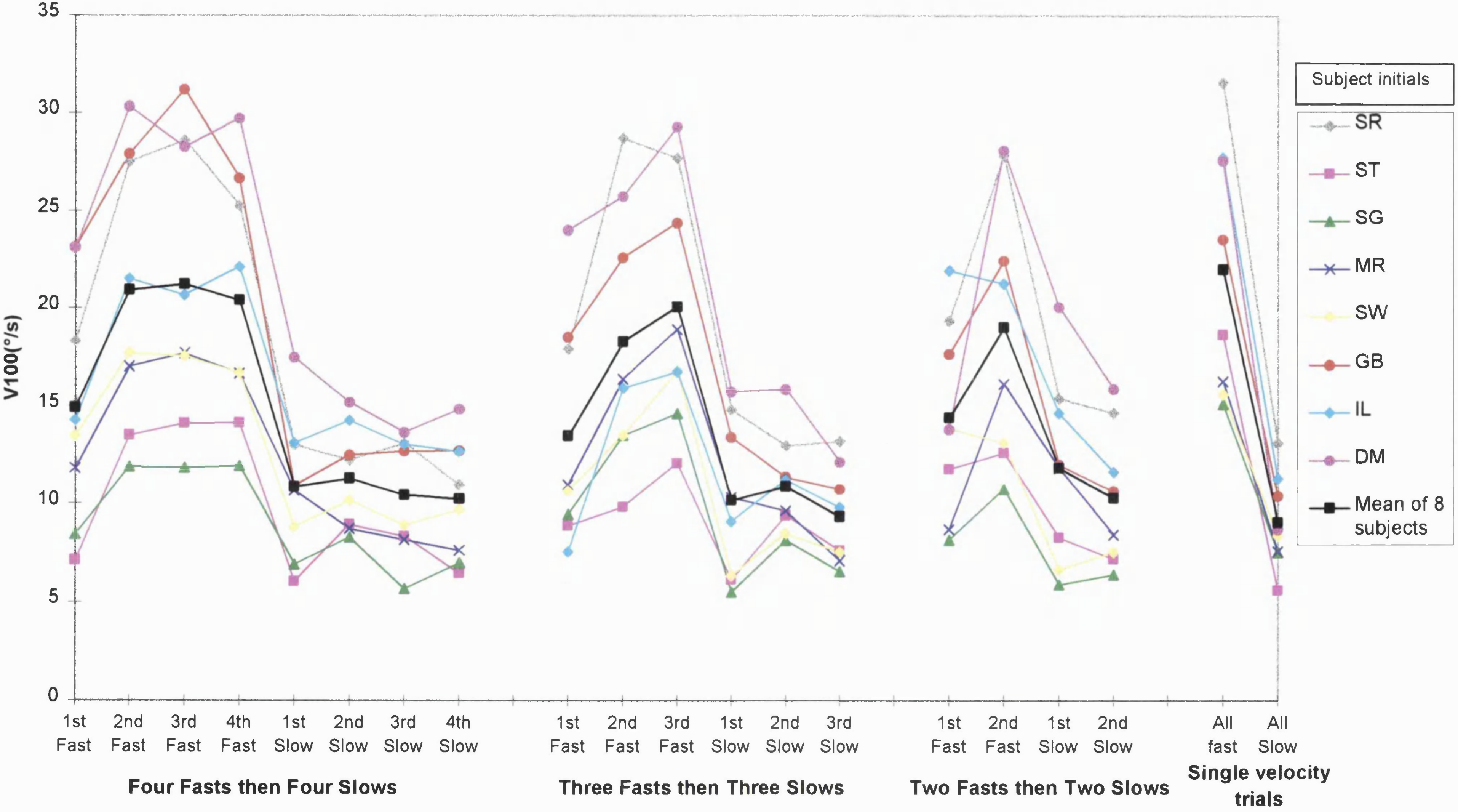


Fig. 2.14 Mean V100 by each subject to each sequence component of each target velocity sequence. Responses to trials where the target velocity never changed are also included on the right.

Change in anticipatory velocity with practice

It is possible that the reason why the anticipatory response to the first fast target was too slow was due to insufficient time to practice. This seems unlikely since the known sequences were simple and were repeated 12 times in each trial. Fig. 2.15 shows the mean V100 averaged over all subjects for the 1st Fast, Last Fast, 1st Slow and Last Slow ramp of each velocity sequence as a function of the number of sequence repetitions. To assess if there was a gradual increase in V100 with repetition of each sequence, a least-squares linear function was fitted to each subject's V100 for each sequence component against repetition number (excluding the first repetition). This yielded a value for the increase in V100 per repetition and these values were entered into a repeated-measures factorial ANOVA (Sequence Length (3 levels) x Sequence Component (4 levels)). Neither factor was significant. Thus there was no consistent difference in the way that V100 changed as the sequence was repeated. V100 for the 1st Fast ramp of each sequence repetition did not increase with practice (actually decreased on average by 0.16°/s per repetition). Similarly, V100 before the 1st Slow target (Dark blue traces) was always appropriately slow (slight increase of 0.01°/s per repetition). For the other common components there was a similarly small change with each repetition (V100 decreased by 0.08°/s for both the Last Fast ramp and the Last Slow ramp).

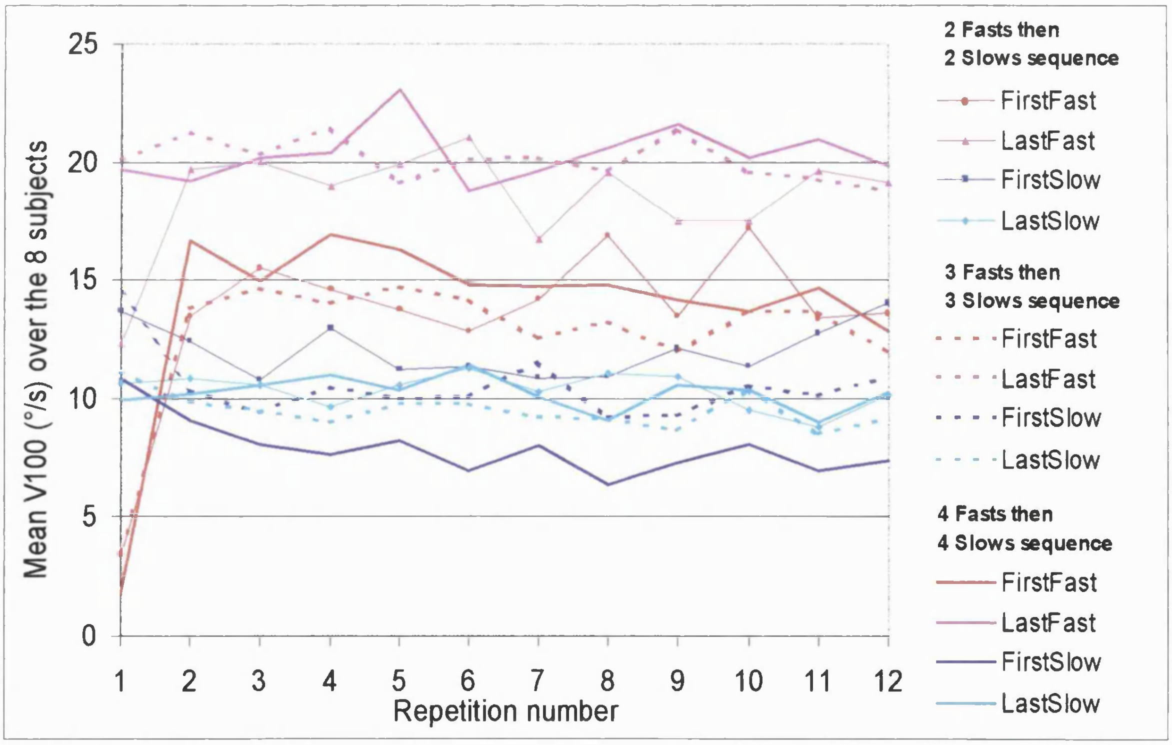


Fig. 2.15 Mean V100 for each of the 12 sequence repetitions averaged over all subjects for the 1st Fast, Last Fast, 1st Slow and Last Slow ramp of each velocity sequence.

Directional asymmetry

Although V100 to the 1st Fast ramp was generally too slow, V100 to the 2nd Fast ramp was always appropriately fast, despite the fact that it was in the opposite direction. This is an important point. If the response is viewed as the release of a store, charged during the preceding response, then this suggests that the store is reversible i.e. recently pursuing a fast target to the right is not necessary for producing a fast rightwards V100, provided that a fast leftwards target has just been pursued.

The issue of directional asymmetry will now be addressed. Most subjects made quite similar magnitude anticipatory responses before leftwards and rightwards ramps. However, two subjects showed large asymmetries. Subjects GB and SG made much faster anticipatory movements to the right and left respectively. For example, when GB was presented with ramps that were always 38.4°/s, his V100 to the left was 17°/s on average (red column labelled All Fast on the far right hand side of Fig. 2.16) but 30°/s to the right (green column labelled All Fast).

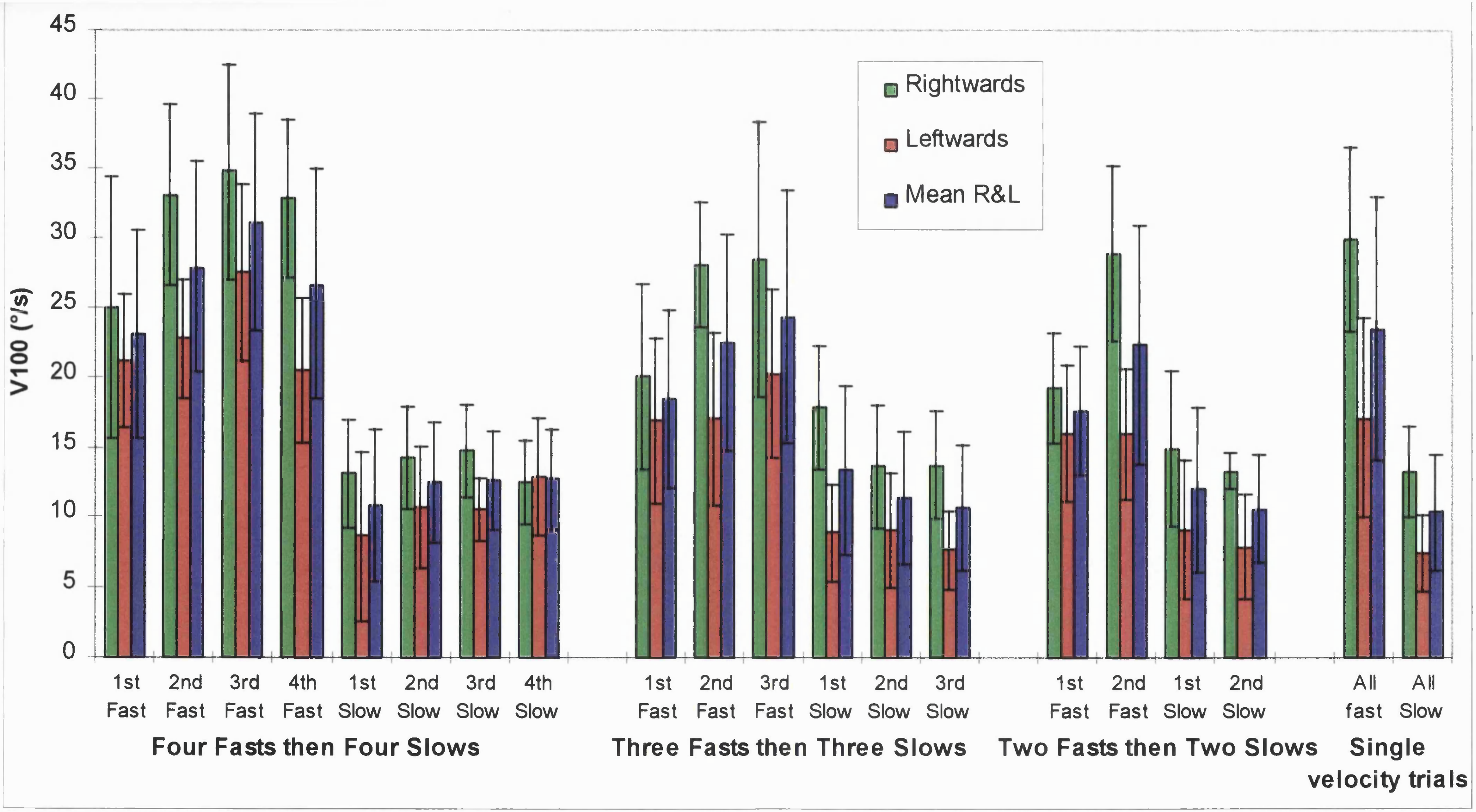


Fig. 2.16 Mean V100 by subject GB. Green columns show mean V100 when each sequence component was a rightwards ramp. Red columns show responses for leftwards ramps and blue columns show the mean response averaged over direction. The error bars show the standard deviation. Consecutive ramps were in alternate directions so alternate green and red columns are from one trial.

For the velocity sequence trials, the asymmetries of GB and SG were still present but the ratio of rightwards to leftwards anticipatory velocity was not always of the exact same magnitude as in the single velocity trials. This is shown in Fig. 2.16 for subject GB. The ramps were in alternate directions so for each sequence there was one trial where the sequence components were presented left-right-left etc (red-green-red in Fig. 2.16) and one trial with the directions reversed i.e. right-left-right etc (green-red-green in Fig. 2.16). The blue columns are the responses from both trials averaged over direction, which show the usual pattern of V100 being too slow for the 1st Fast ramp of each sequence repetition. However, for this subject with a large asymmetry, the underlying pattern was modulated by the directional asymmetry so that the pattern was not obeyed on individual trials. For example, consider the right-left-right etc (green-red-green in Fig. 2.16) trial for the Four Fasts then Four Slows sequence. Here the 1st Fast was actually faster than the 2nd Fast. However, when these responses were averaged over direction with the second trial, the blue average columns showed the usual pattern of V100 for the 1st Fast being slower than for the 2nd Fast.

Response variability

The standard deviation bars in Figs. 2.11 and 2.16 show that each subject had quite high variability in V100 for each velocity sequence component from one sequence repetition to the next. The standard deviation for each sequence component was typically around 32% of V100. However for some sequence components for some subjects it could be as low as 14% or as high as 89%.

Discussion

This experiment has shown that subjects can use their knowledge of a target velocity sequence to exert some control over the velocity of anticipatory pursuit. This control is limited in that subjects are unable to produce an appropriately fast anticipatory movement when an increase in target velocity is expected. However it should be remembered that this is a general trend rather than an absolute rule since the relatively high variability in V100 from one response to the next means that the trend may not hold for every repetition. The variability suggests that the control is rather imprecise. However, a crude estimate of target velocity released at the appropriate time may be adequate to make a significant reduction in the time at which precise closed-loop matching of target velocity can be achieved.

It seems unlikely that the inability to produce an appropriately high V100 before the 1st Fast target was due to the target velocity being too high since 38.4°/s is below the limit at which anticipatory velocities start to saturate (see first experiment in this section). A pilot experiment suggested that the general trends seen here would apply to other target velocities between about 6 and 50°/s.

Barnes & Asselman (1991) and Kao & Morrow (1994) showed that if a ramp does not appear as expected, an erroneous prediction will be made as if the store is being discharged with a velocity appropriate to the previous target before it's output is halted by visual feedback. The fact that subjects seem less able to generate an appropriate V100 when a faster ramp is expected than when a slower ramp is expected may reflect the level of the putative store of motor drive for making these movements. It seems plausible that a fast ramp charges the store to a higher level than a slow ramp. Thus when a faster ramp is expected the contents of the store are inadequate and can only be increased slightly. However, when a slower ramp is expected, the contents of the store can just be scaled down. It seems likely that this is connected to the claim by Steinman *et al.* (1969) that subjects can quite easily produce pursuit that is a required amount slower than target velocity but not faster.

A possible alternative explanation is the effect of target position. After the Last Slow ramp of each repetition, subjects had to move their eyes outwards to the starting position of the larger amplitude 1st Fast ramp movement i.e. a position error in the opposite direction to the direction of the next ramp had to be corrected. A positional error can generate smooth pursuit as described in the Introduction to this thesis. However it could only be the *expectation* of a positional error that could affect the anticipatory pursuit in this case. The eye did indeed start its movement further from the straight ahead position for the Last Fast ramp than for the 1st Fast ramp. However, by 100 ms after ramp onset, there was no significant (p=0.374) difference between the mean positions (see Fig. 2.17)

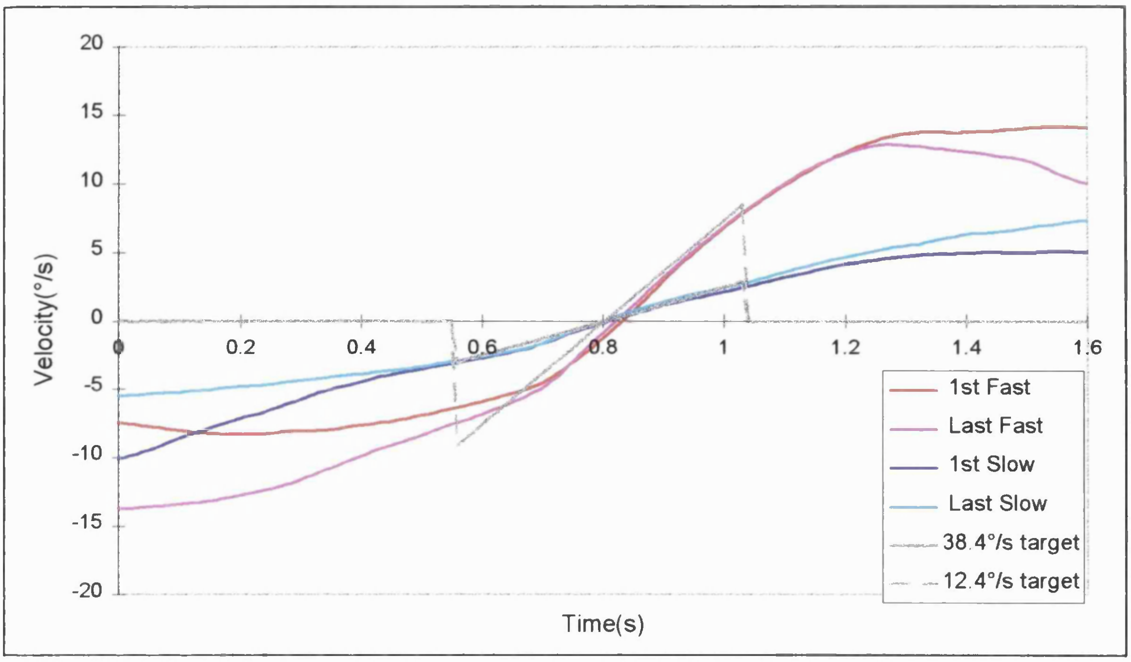


Fig. 2.17 Mean positional trajectory for the common components of the target velocity sequences.

The explanation also seems unlikely for two further reasons. Firstly, although expected positional errors will generate anticipatory movements (Moschner *et al.* 1996), subjects had over 1 s to move to the new starting position and presumably directed their eyes to where they thought the target would appear. Secondly, V100 was not faster for the 1st Slow ramp despite the fact that subjects had to move their eyes inwards to the starting position from the end point of the Last Fast ramp (i.e. a positional error in the same direction as the next ramp).

Experiment 2c: Scaling of anticipatory eye velocity during repetitive target velocity sequences: Unidirectional ramps

Introduction

This experiment was designed to assess whether the results of experiment 2b would apply to waveforms other than alternate direction ramps. The experiment was repeated but with all ramps moving in the same direction (rightwards) and all starting from the same position.

Methods

Five of the subjects from the previous experiment plus two others participated. Conditions were identical to the previous experiment (480 ms ramps every 1.6 s) except that all ramps moved rightwards and started at 9.2° to the left of straight ahead. The fast ramps (38.4°/s) were thus centred about the straight ahead position but the slow ramps (12.8°/s) were not. The same three velocity sequences were studied (n fast then n slow, where n = 2, 3 or 4) and are illustrated in Fig. 2.18. The actual target motion for one of the velocity sequences is shown in Fig. 2.19. All movements were in the same direction so directional asymmetries in the magnitude of anticipatory responses were irrelevant. Therefore there was no need for repeat trials with the target motion reversed. Each trial consisted of 12 repetitions of one sequence of which the last 11 were analysed as the steady state response. Two further trials where the target velocity was either always fast or always slow were also presented. To control for training effects, the order of presentation of the five trials was randomised over the subjects.

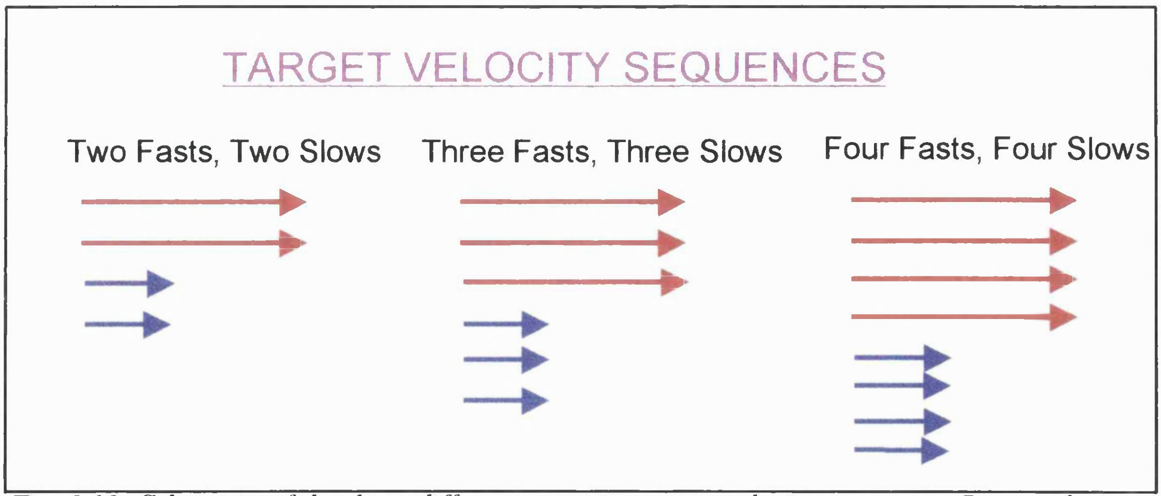


Fig. 2.18 Schematic of the three different repetitive target velocity sequences. Ramp velocity was either "fast" (38.4°/s, shown in red) or "slow" (12.8°/s, shown in blue) and varied according to a simple sequence of n fast ramps followed by n slow ramps (n = 2,3 or 4). Each

arrow represents the amplitude and direction of the ramp with the next ramp in the sequence drawn below it.

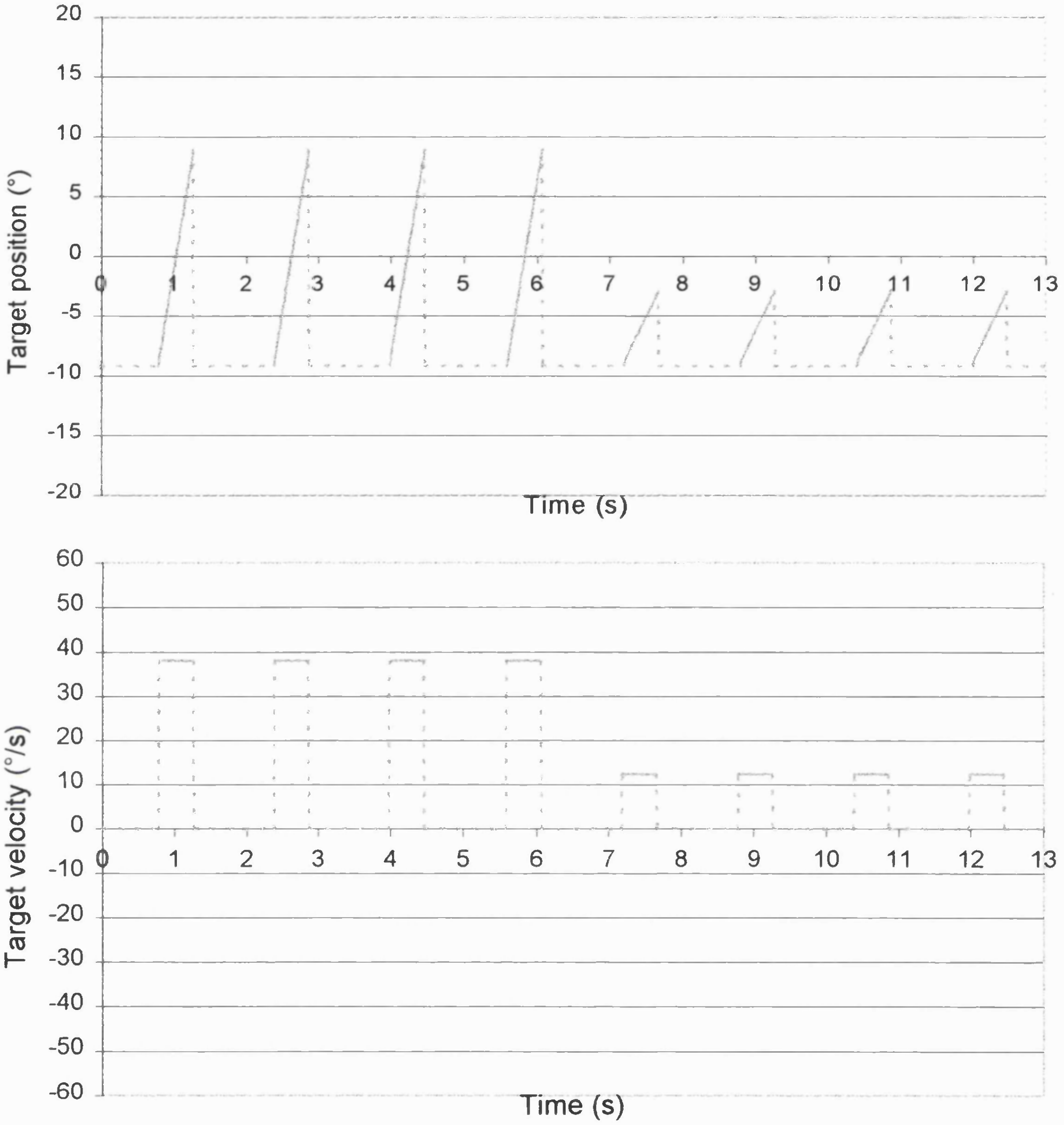


Fig. 2.19 Example of the target motion used in this velocity sequence experiment. Target position (upper plot) and target velocity (lower plot) used in the Four Fasts, Four Slows sequence. The eight ramps shown here were repeated 12 times in a trial. Dotted lines show when the target was invisible and the subject was in darkness.

Results

Fig. 2.20 shows an example of the responses to unidirectional target velocity sequences (steady state responses by one subject to the Four Fasts Four Slows sequence). The magnitude of the anticipatory response was assessed as average eye velocity 100 ms after ramp onset (V100), just before visual feedback could have an effect.

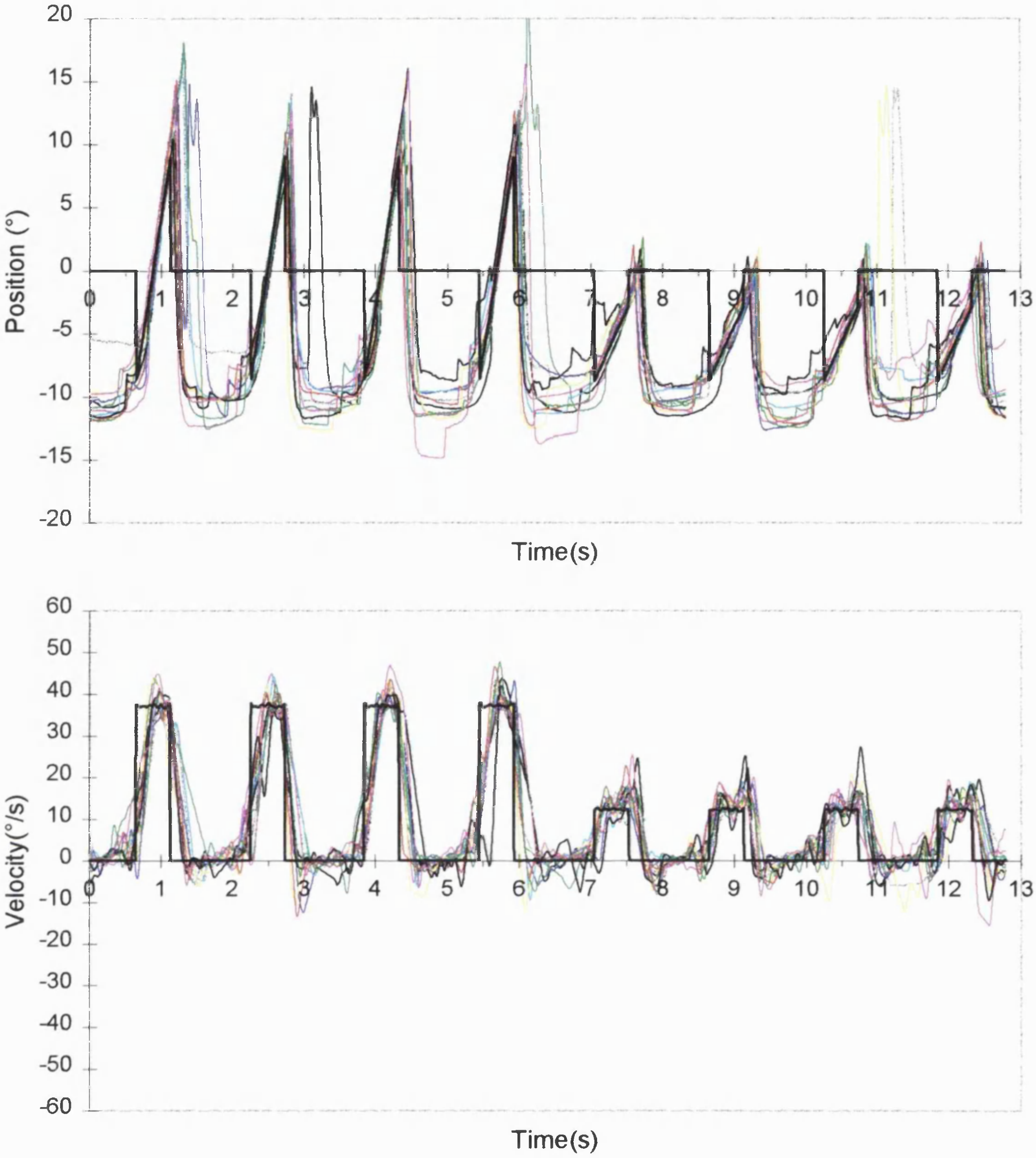


Fig. 2.20 All steady state responses by one subject to a trial of Four Fasts, Four Slows. The upper graph shows position and the lower graph velocity. The last 11 sequence repetitions of the 12-repetition trial have been overlaid. The thick black line shows target motion (the dotted line shows when the target was invisible) and the coloured lines show the eye responses. The eye velocity traces have been desaccaded.

V100 was generally around 10-30% less than the values obtained for the alternate direction velocity sequences (experiment 2b). However, a cyclical variation in anticipatory velocity was still seen in expectation of each component of the velocity sequence. Whereas all subjects in the previous experiment showed a similar pattern of responses, the responses to the unidirectional stimuli were more irregular. The three sequences had four common sequence components: the 1st Fast, Last Fast, 1st Slow and Last Slow ramps. The velocity profiles for these common components averaged over all 7 subjects are shown in Fig. 2.21.

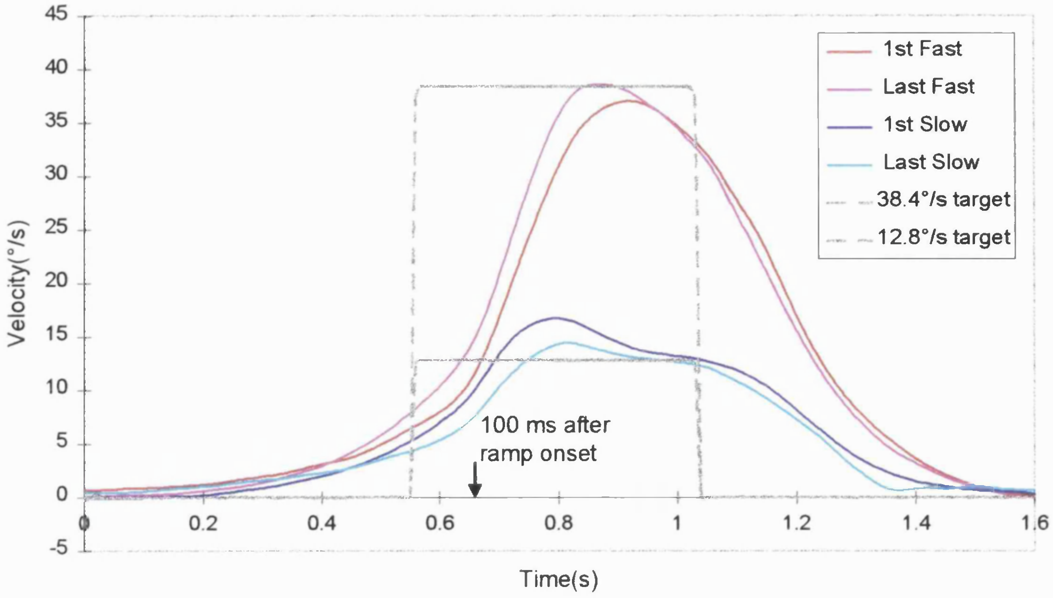


Fig. 2.21 Mean response by all subjects to each of the common components of the target velocity sequences.

The anticipatory response to the 1st Fast ramp of each sequence repetition was faster than the preceding response to the Last Slow ramp but slower than the response to the upcoming Last Fast ramp. Similarly, the anticipatory response to 1st Slow ramp of each sequence repetition was slower than the preceding response to the Last Fast ramp but faster than the response to the upcoming Last Slow ramp. Thus some cognitive scaling of anticipatory velocity was possible but the influence of the previous ramp was still powerful. The difference between these results and those of the last experiment was that the response to the 1st Slow ramp could not be scaled appropriately. Each subject's mean V100 for each sequence component was analysed by repeated-measures factorial ANOVA (*Sequence length* (3 levels)**Sequence Component* (4 levels)). The results are shown in Table 2.2.

	F	Degrees of freedom	Significance
Sequence component	8.77	3	0.031
Sequence length	0.13	2	0.878
*Sequence component * Sequence length*	27.28	6	0.146

Table 2.2 Results of factorial ANOVA on V100. Planned contrasts between the four factor levels of 'Sequence component' revealed which levels were significantly different (1st Fast vs Last Fast, $p<0.006$; Last Fast vs 1st Slow, $p<0.078$; 1st Slow vs Last Slow, $p=0.051$; Last Slow vs 1st Fast, $p=0.026$). Modified Bonferroni test (see Statistical analysis section) accepts p values less than 0.036 as being significant for these four comparisons.

The mean responses by the 7 subjects are shown in Fig. 2.22 separated into the three different velocity sequences.

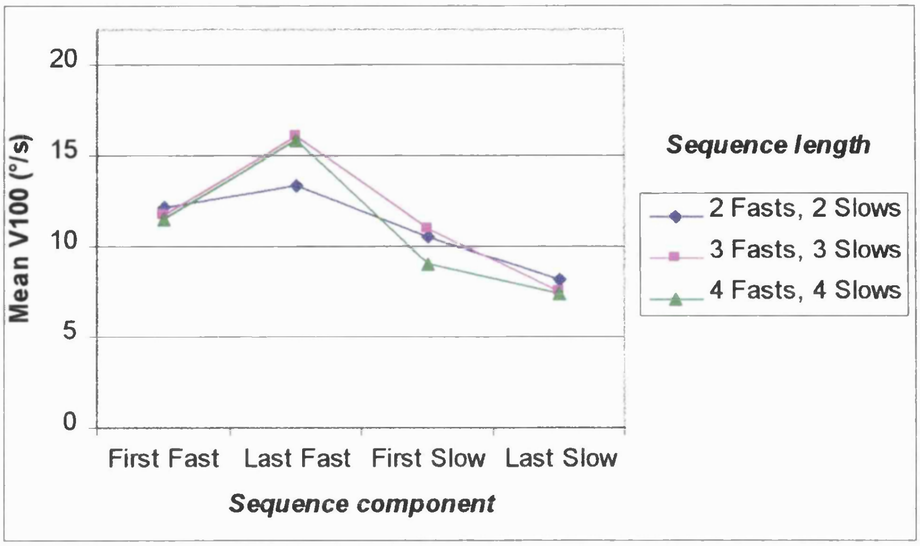


Fig. 2.22 Mean response by all subjects to each of the common components of the three different target velocity sequences.

Analysis revealed that there was no significant difference between the three different sequences (*Sequence length* factor, p=0.878). *Sequence component* was a significant factor though (p=0.031). Contrasts revealed that V100 for the 1st Fast ramp was significantly faster (p=0.026) than for the Last Slow ramp but significantly slower than V100 for the Last Fast ramp (p=0.006). Thus when an increase in target velocity was expected, the anticipatory response was faster but not sufficiently fast. V100 for the 1st Slow ramp was slower (but not significantly; p=0.078) than for the Last Fast ramp and was faster (but not significantly; 0.051) than for the Last Slow ramp. Thus when a decrease in target velocity was expected, the anticipatory response tended to be slower but was not sufficiently slow. This suggests that the response is intermediate between the response for the Last Fast ramp and that for the Last Slow but that inter-subject variability means that the trend does not apply to all subjects. This variability can be seen in Fig. 2.23 which shows each subject's mean V100 to each sequence component for each sequence.

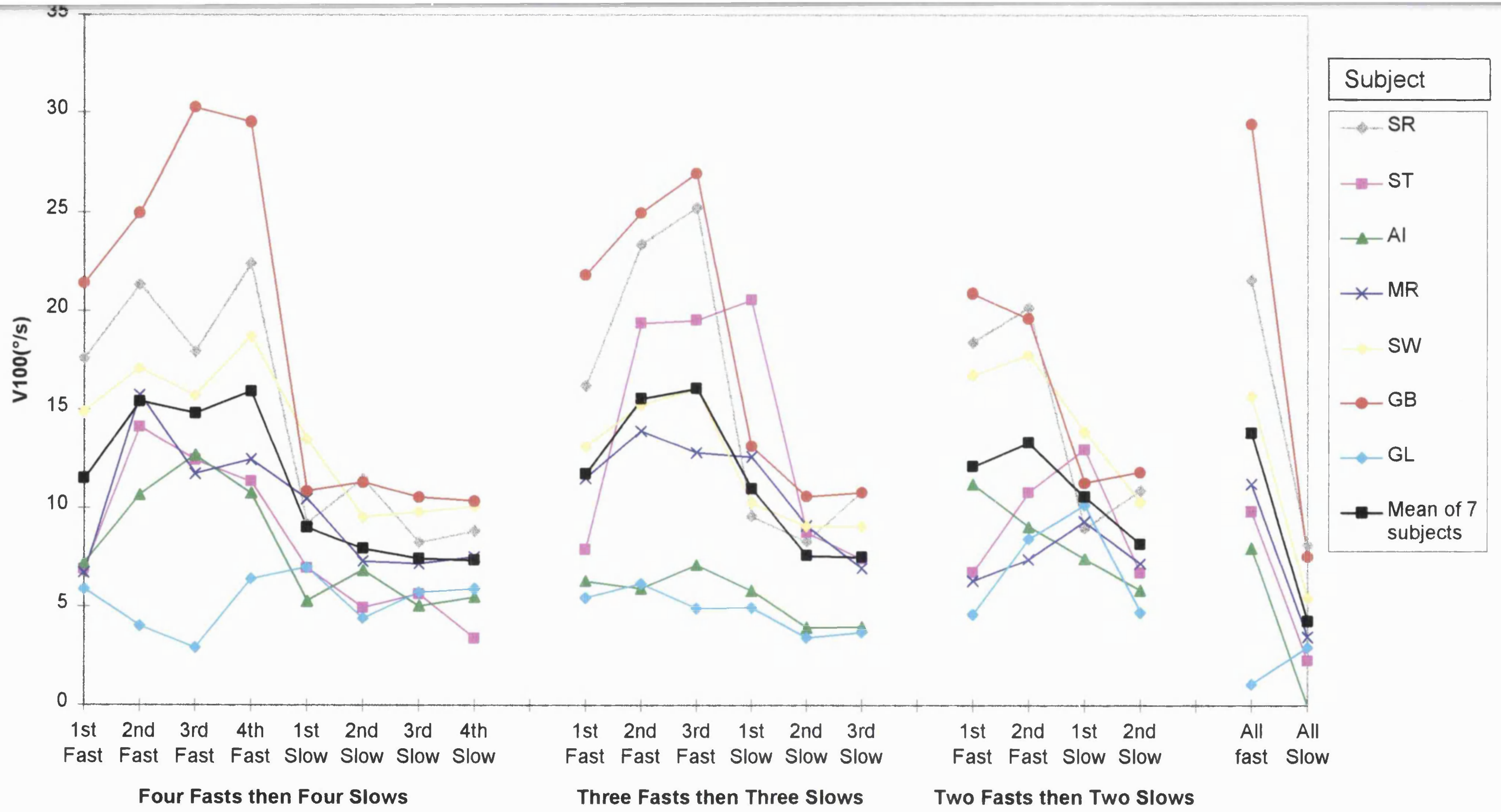


Fig. 2.23 Mean V100 by each subject to each sequence component of each target velocity sequence. Responses to trials where the target velocity never changed are also included on the right

Conclusions

Some cognitive control over the scaling of anticipatory velocity before ramps which always move in the same direction has been shown. However, for both increases and decreases in target velocity, subjects were not able to produce an appropriate anticipatory velocity that was significantly different from the response to the previous ramp velocity and not significantly different from subsequent responses to the current target velocity. Thus there appeared to be a larger carryover effect from the previous ramp than was seen in the previous experiment when ramps moved in alternate directions. The variability between subjects was greater than in the previous experiment making the velocity scaling results for unidirectional ramps less clear. It may have been better to increase the interval between ramps for this stimulus. Although the ramps occurred with the same frequency as in the previous experiment, the required movement was actually at twice the frequency since between ramps a large saccade was needed to return the eyes to the starting position. Thus less of the waveform could be matched by smooth pursuit alone. This perhaps disrupted the response and made the smooth movements more erratic. This may also be the reason for the 10-30% reduction in V100 compared to the alternate direction ramp stimulus.

Several results in this chapter suggest that anticipatory eye velocity is not a precise estimation of expected target velocity: 1/The mean response is usually only a fraction of the target velocity. 2/ There appears to be some cognitive control over this velocity but this is limited especially if an increase is required. 3/ There is considerable variability between subjects and within subjects in the magnitude of the response.

The coarseness of this control may have implications for the function of these movements. Accurate tracking generally only occurs once closed loop pursuit has been established, usually after a saccade has been made to correct any initial positional error. Therefore the anticipatory velocity may not need to be extremely precise. A crude estimate of target velocity may be sufficient to improve pursuit. The initial retinal slip is reduced giving a clearer image of the target and there is a smaller magnitude initial velocity error to correct. Fine control can then occur more quickly once visual feedback is available. The fact that anticipatory velocities only match a fraction of target velocity may be a conservative underestimation intended to prevent overshoots and oscillations if a large predictive estimation turns out to be inaccurate. This may be why a higher fraction of target velocity is produced for the slowest ramps. In this situation if the prediction turns out to be incorrect, even an anticipatory velocity of 100% of expected target velocity can only produce an error a few degrees per second larger than if the eyes had remained stationary.

Summary of Chapter 2

- Subjects produce characteristically scaled anticipatory smooth eye velocities when repetitively presented with ramps at one particular velocity.
- The eye achieves an anticipatory smooth velocity of about 60% of target velocity 100 ms after ramp onset for ramp velocities between around 12 and 50°/s.
- When subjects are presented with repetitive sequences of ramp velocities, there is a cyclical variation in anticipatory velocity across the sequence rather than the same response being made to all ramps.
- After just one ramp at a particular velocity, subjects will produce a characteristically scaled anticipatory velocity for all subsequent ramps at that velocity providing each ramp lasts more than a few hundred milliseconds.
- However for the first ramp at a new velocity, subjects have a limited ability to use their cognitive expectations to appropriately scale their anticipatory velocity:-

  For alternate direction ramps, cognitive expectations can be used to generate an appropriately slow V100 when the ramp is expected to be slower than the previous one. Subjects were somewhat less able to accomplish this for unidirectional stimuli.

  For both alternate direction and unidirectional ramps, cognitive expectations can be used to increase V100 slightly when the ramp is expected to be faster than the previous one but the response is generally not fast enough to be appropriate.
- There are considerable differences in response magnitude between subjects. For alternate direction ramps, different subjects produce V100s that are widely differing percentages of ramp velocity. However, they show similar patterns of responses to velocity sequences. For unidirectional ramps, subjects produce widely differing percentages of ramp velocity and also show different trends in response to velocity sequences.

CHAPTER 3: DEPENDENCE OF ANTICIPATORY PURSUIT ON A SHORT-TERM STORE

Experiment 3a: Smooth pursuit of repetitive ramps with different intervals between ramps

Introduction

In recent studies, procedures have evoked fast anticipatory velocities compatible with the predictive velocities that must be produced to achieve the small phase lags observed during continuous pursuit of predictable target motion (Barnes & Asselman 1991; Kao & Morrow 1994; Moschner *et al.* 1996; Ohashi & Barnes 1996). Comparable velocities cannot be generated voluntarily in the dark. All these studies have required repetition of a stimulus before sizeable anticipatory movements are produced. Barnes & Asselman (1991) studied this repetition using brief (320 ms or less) target ramps and showed a build-up of anticipatory velocity and peak eye velocity over the first three or four presentations. This was explained by the charging of a putative internal store of motor drive. These authors and Kao & Morrow (1994) showed that during such tracking, inappropriate anticipatory responses are produced if the target motion suddenly changes, as if a stored response is released, then corrected. Experiment 2a showed that the stored anticipatory response could be scaled over a wide range of target velocities as if faster targets charge the store to higher levels. Experiment 2b showed how during a sequence of two different ramp velocities, subjects were only partially able to scale their anticipatory responses to a different ramp velocity. This suggests that subjects have only a limited ability to alter the output of the response stored during the previous presentation.

If such a store exists, it is unlikely to be permanent. Firstly, fast anticipatory movements are rarely seen unless a moving stimulus has been recently presented i.e. the store has been charged. Secondly, a permanent store could be detrimental when responding to future stimulus changes. In the following experiment, to assess the store's longevity, repetitive ramps were presented to subjects with different Inter-Stimulus Intervals (ISIs) between 1.8 and 7.2 s. Two different target velocity ramps (25 or 50°/s) were used to assess whether the ability to appropriately scale the anticipatory velocity also changed with increasing intervals between ramps.

Knowing exactly when the first target will appear does not appear to be sufficient to evoke high velocities. In addition, fast anticipatory guesses can sometimes be made before repetitive presentations with short but random intervals where the timing is not certain (Moschner *et al.* 1996; Lekwuwa & Barnes 1996). For such stimuli, anticipatory velocities are generally much lower than for predictable stimuli but can be fast when a committed guess is made. The build-up of the response appears to be partly due to learning the pattern of the target motion and partly due to charging the store. Thus both timing and repetition are important. Evidence shows that it is harder to accurately estimate a long interval than a short one (Mates *et al.* 1994). Therefore to assess the importance of accurate timing knowledge, conditions were either presented without or with an audio cue before each ramp, the latter leaving the subject with no doubt as to when each target would appear. The experiment was carried out using two different Waveforms (Alternate direction ramps or Unidirectional) to assess how the results would generalise across different target motions.

The 500 ms ramps used in this current experiment normally allowed target velocity to be matched on the very first presentation, and one appeared sufficient to completely charge the store unlike the more brief ramps used by Barnes & Asselman (1991). However, an anticipatory response the same as the 'steady-state' was not seen until about the third presentation in general since although subjects knew the stimulus parameters, two presentations were often needed to fully appreciate the future pattern of target motion.

Methods

The eight normal subjects (aged 23 - 50, 4 male) had varying experience of oculomotor testing. The constant velocity target was presented for 500 ms with the motion centred about the straight ahead position. A 500 ms audio tone accompanied each ramp. For cued conditions, subjects also heard a triplet cue consisting of three 40 ms duration 150Hz square wave tones at 600, 400 and 200 ms before ramp onset. The cue reminded subjects of the interval between consecutive ramps and also the exact interval between the cue and ramp onset since this was explicitly reiterated by the fact that it was a triplet (audio pulses shown in Fig. 3.2). Each experimental session, lasting about 30 minutes, consisted of 8 trials of 32 presentations each, with a calibration before each trial. The order of trials was pseudorandomly balanced across subjects.

There were 32 different stimulus conditions characterised by the level of 4 factors:-

- ISI (either 1.8, 3.2, 5.4 or 7.2 s intervals between consecutive ramp onsets),
- Waveform (ramps in Alternate directions or Unidirectional ramps in the same direction),
- Cueing (audio Cue before target presentation or No Cue)
- Target Velocity (50°/s or 25°/s)

Four stimulus conditions per trial were studied by splitting each trial into four sectors of 8 identical presentations. The Waveform and Cueing variables stayed the same throughout each trial. The first two sectors of each trial were at one ISI and the last two sectors at another. The first and third sectors were at 50°/s and the second and fourth at 25°/s. Typical instructions were "Track the target as accurately as possible. The target will always move rightwards with a cue before each presentation. There will be 8 fast then 8 slow presentations at 1.8 s intervals then 8 fast and 8 slow presentations at 7.2 s intervals". From each sector of 8 identical presentations, only the last 6 were analysed to observe the steady state response without a carryover effect from the condition of the previous sector. To counter any possible pursuit directional asymmetry, all 32 conditions were repeated in a second session with the target motion reversed. For a Unidirectional trial, all ramps were in the opposite direction to those in the first session. For an Alternate direction trial, the sequence of alternate direction ramps started with a rightwards rather than leftwards target movement. Pooled with the first session, this gave 12 responses overall per condition from each subject. In each session, the trials were presented in a pseudorandom order over the eight subjects using a Latin square design to control for any training effects.

Results

Changes in anticipatory velocity

Typical raw eye position and velocity response profiles from one sector of a trial are shown in Fig. 3.1. Only the last 6 responses from each sector were averaged to give the steady-state mean response. To obtain each subject's mean response, the eye movements during leftwards ramps were reversed in sign and averaged with the rightwards movements.

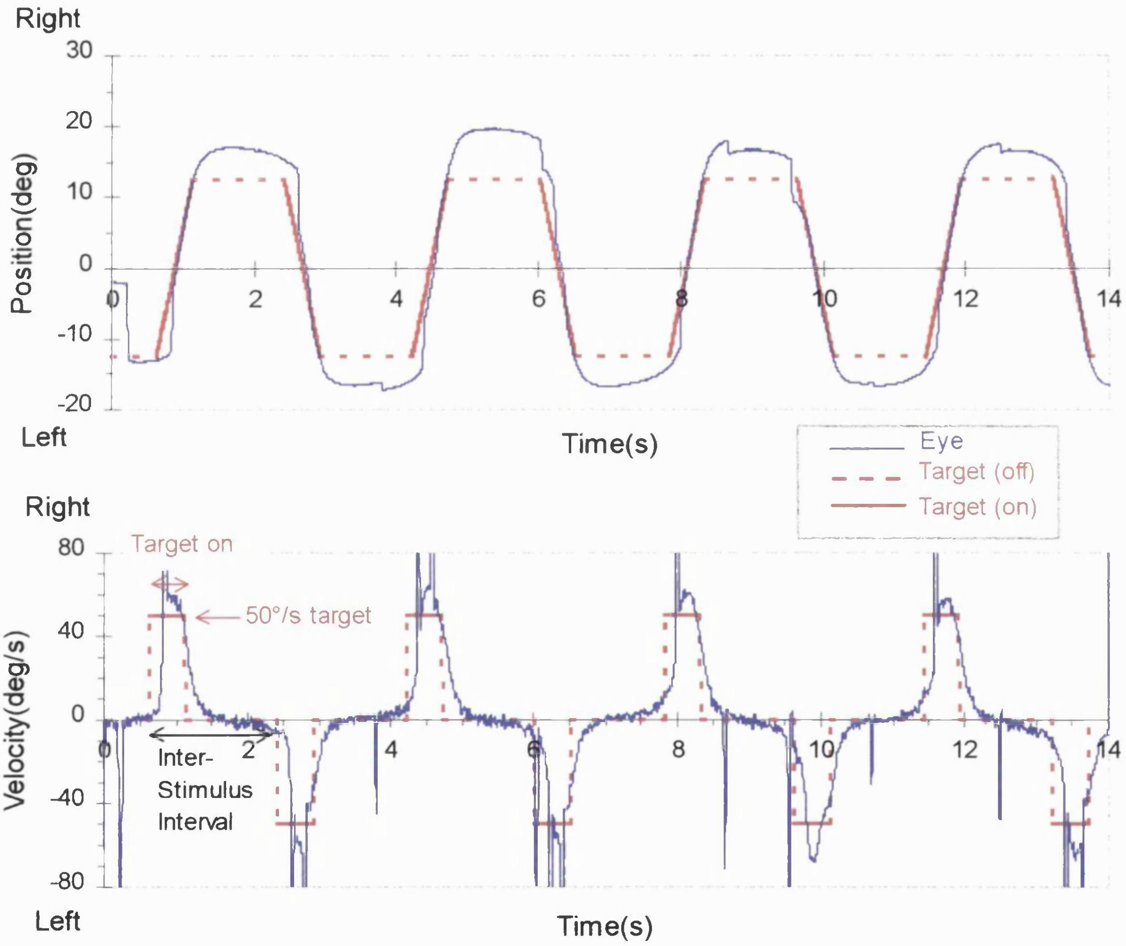
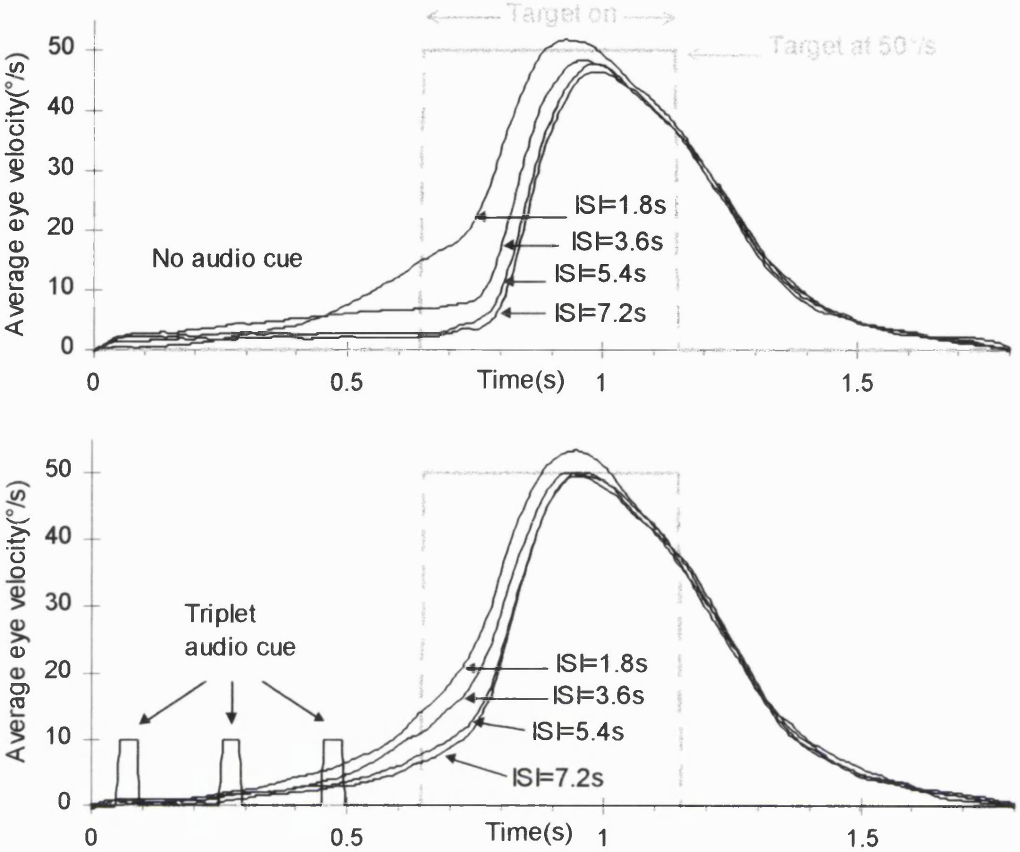


Fig. 3.1 Raw eye position (blue) trace in response to 50°/s target ramps (red) lasting 500 ms presented in alternate directions every 1.8 s. The accompanying velocity traces are shown in the lower graph. Spikes in the velocity trace are saccades.

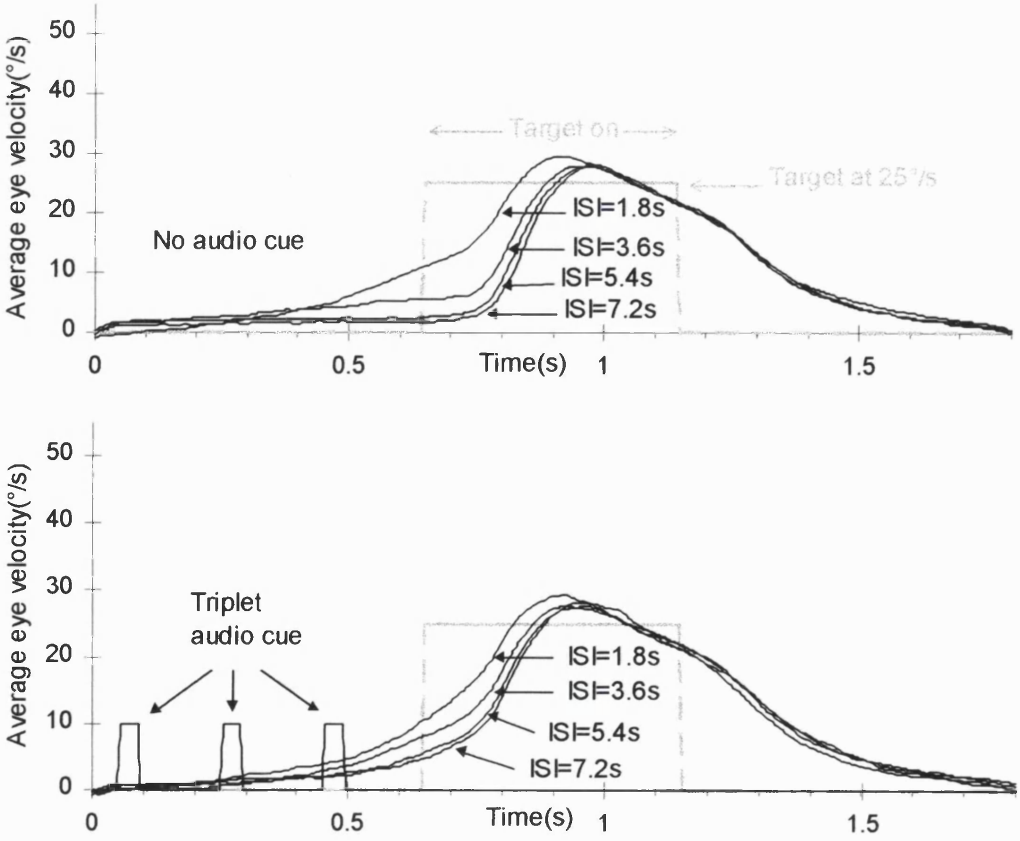
Fig. 3.2 displays the mean responses over the eight subjects for each of the 32 different stimulus conditions. Anticipatory velocity decreased sharply in sectors where the intervals between ramps were longer. This was only partially due to increased timing uncertainty, since there was still a considerable decrease, although less marked, when the audio triplet cues were provided. Similar decreases were seen for ramps at 50 and 25°/s and for both alternate direction and unidirectional ramps.

Fig. 3.2 Mean response by the eight subjects to each of the 32 different stimulus conditions

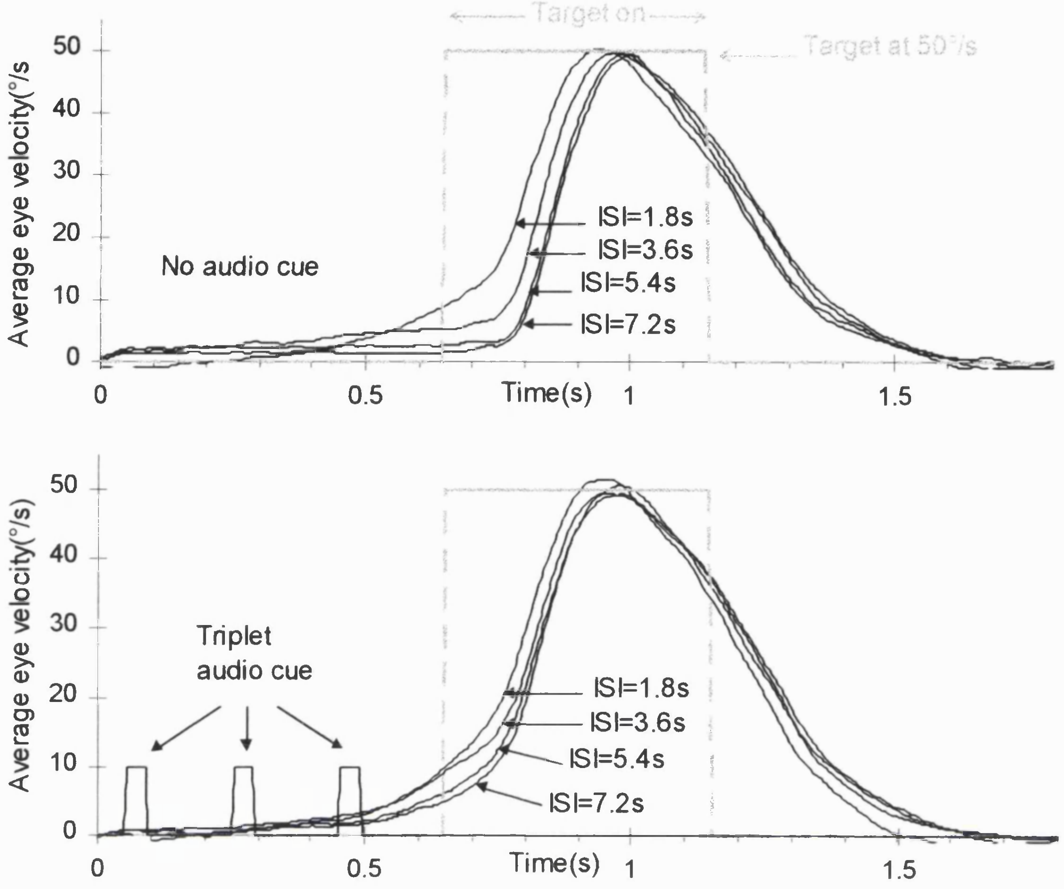
Alternate direction ramps at 50°/s. No Cue (upper plot), with Cue (lower plot)



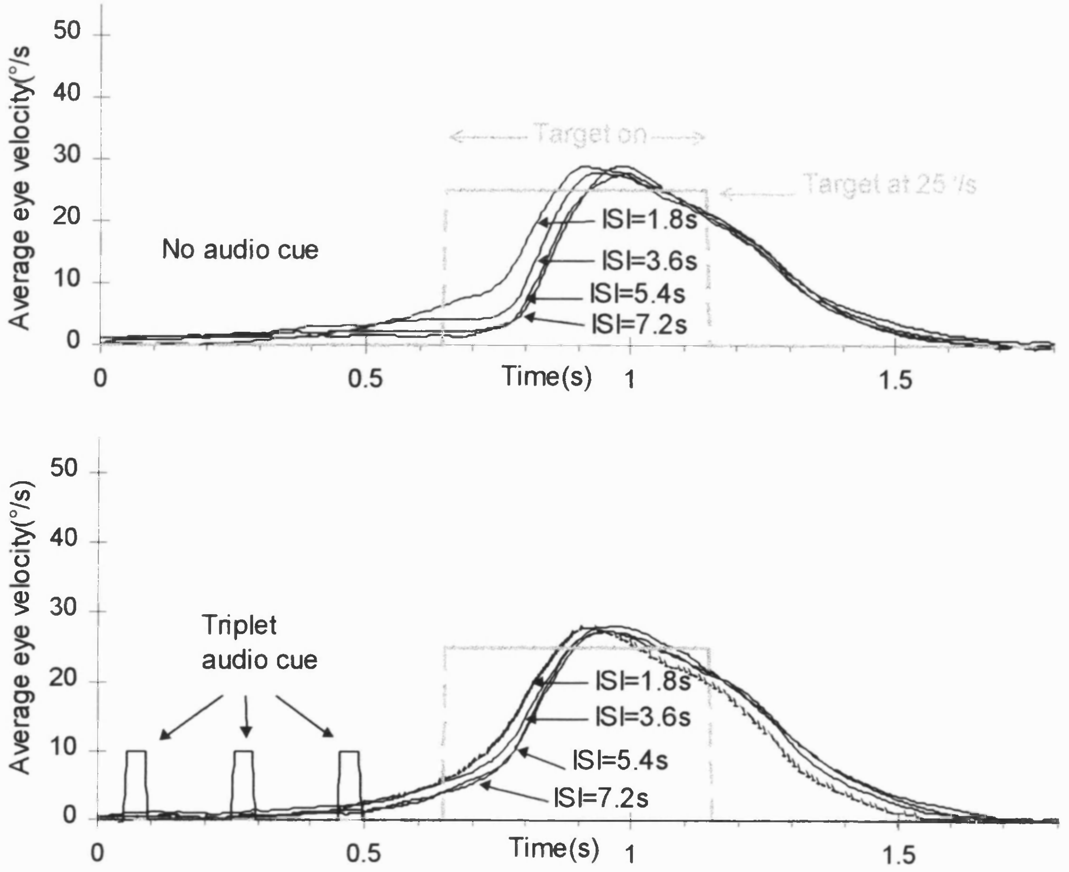
Alternate direction ramps at 25°/s. No Cue (upper plot), with Cue (lower plot)



Unidirectional ramps at 50°/s. No Cue (upper plot), with Cue (lower plot)



Unidirectional ramps at 25°/s. No Cue (upper plot), with Cue (lower plot)



The decrease, despite the presence of adequate timing cues, implies that there really is a decaying short-term store. For statistical analysis, anticipatory response magnitude was assessed as mean smooth eye velocity 100 ms after target onset (V100), just before the influence of visual feedback. The mean V100 values over the subjects with standard deviations for all of the 32 conditions are shown in Fig. 3.3.

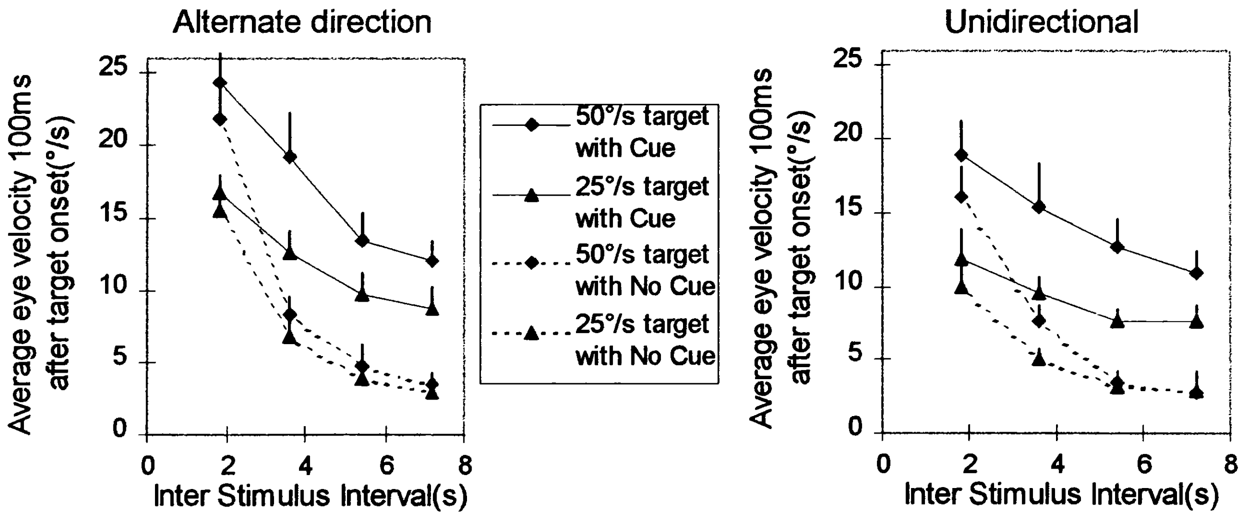


Fig. 3.3 Mean eye velocity at 100 ms after ramp onset (V100) by the eight subjects for all of the 32 different stimulus conditions. Error bars are the standard deviation of each mean.

Mean V100 from each of the 32 target motion conditions from each subject were entered into a repeated-measures factorial ANOVA. The results are shown in Table 3.1

	F	Degrees of freedom	Significance
ISI	9.99	3	0.015
Waveform	18.21	1	0.004
Cueing	26.54	1	0.001
Target velocity	46.65	1	<0.001
*ISI * Waveform*	9.41	3	0.017
*ISI * Cueing*	6.54	3	0.036
*ISI * Target velocity*	6.24	3	0.038

Table 3.1 Results of factorial ANOVA on V100. To reduce complexity, only interactions with a p value < 0.05 are shown..

Since there was a significant interaction between the ISI and Cueing factors, a further ANOVA was performed on the conditions with No Cue alone and a separate ANOVA performed on the conditions with a Cue. The results for the No Cue condition are shown in Table 3.2.

No Cue conditions only	F	Degrees of freedom	Significance
ISI	7.42	3	0.027
Waveform	8.28	1	0.024
Target velocity	23.51	1	0.002
*ISI * Target velocity*	9.83	3	0.015

Table 3.2 Results of factorial ANOVA on V100. To reduce complexity, only interactions with a p value < 0.05 are shown.. Planned contrasts between the four factor levels of ISI revealed that V100 for ISI=1.8 s was significantly higher than for ISI=3.6 s (p=0.002) which was significantly higher than for ISI=5.4 s (p=0.001) which was significantly higher than for ISI=7.2 s (p=0.001). Only three contrasts were planned so no Bonferroni correction was considered necessary (see Statistical analysis section).

V100 decreased sharply and significantly (p=0.027) with ISI when no cues were given (dotted lines in Fig. 3.3). For example, mean V100 ± S.D. over the 8 subjects was 21.8±10.4°/s for ISI=1.8 s but only 3.4±2.6°/s for ISI=7.2 s (for Alternate direction, 50°/s ramps with No Cues). Higher anticipatory velocities were evoked by Alternate direction stimuli compared to Unidirectional (p=0.024) and by 50°/s ramps compared to 25°/s ramps (p=0.002). However the difference between responses to 50°/s and 25°/s ramps decreased with interval as subjects tended towards making no anticipatory movement at all (significant ISI * Target velocity interaction, p=0.015).

Cued conditions (solid lines in Fig. 3.3) evoked higher anticipatory velocities than No Cue conditions (p=0.001). The results of the separate ANOVA on Cued conditions are shown in Table 3.3.

Cued conditions only	F	Degrees of freedom	Significance
ISI	12.92	3	0.009
Waveform	23.37	1	0.002
Target velocity	50.22	1	<0.001
*ISI * Waveform*	19.47	3	0.003

Table 3.3 Results of factorial ANOVA on V100. To reduce complexity, only interactions with a p value < 0.05 are shown.. Planned contrasts between the four factor levels of ISI revealed that V100 for ISI=1.8 s was significantly higher than for ISI=3.6 s (p=0.009) which was significantly higher than for ISI=5.4 s (p=0.007) which was significantly higher than for ISI=7.2 s (p=0.034). Only three contrasts were planned so no Bonferroni correction was considered necessary (see Statistical analysis section).

Despite the accurate timing information provided by the Cue, V100 after long intervals was still significantly less ($p = 0.009$) than that achieved for short intervals e.g. 24.3±6.4°/s for ISI=1.8 s but only 12.0 ±4.0°/s for ISI=7.2 s (for Alternate direction, 50°/s ramps with Cues). V100 for each ISI was significantly higher than for the next longest ISI for all four ISIs tested in this experiment. However the shape of the solid lines in Fig. 3.3 suggest that V100 would tend towards an asymptotic non-zero level at longer intervals, a level that could be generated from a fully decayed store. Alternate direction presentations produced anticipatory velocities around 25% higher than Unidirectional stimuli ($p=0.004$). A similar difference between Alternate and Unidirectional ramps was noticed when experiments 2b and 2c were compared. In the current experiment, although the magnitude of V100 was less for Unidirectional stimuli, the trends for both types of waveform were identical showing that the effects were neither limited to just one pattern of target motion nor reliant on the decay of a prior response.

V100 increased with Target Velocity ($p<0.001$) as found previously (first section of this thesis) but this difference decreased with longer ISIs. This may be taken to imply that without a recently refreshed store it is more of a default response than a stimulus specific response at this time. However, for cued conditions alone, this interaction was not significant ($p=0.121$). In fact, V100 for 50°/s targets was larger by quite a constant percentage (40-60%) compared to V100 for 25°/s targets for all cued intervals, suggesting that the system was still scaling appropriately but that there was less drive in the store to scale. Experiment 1a suggested that V100 was almost proportional to target velocity for ramps every 1.6 s between 12.8°/s and 51.2°/s. However, for all cued intervals in the current experiment, V100 for 50°/s ramps was only 40-60% larger than V100 for 25°/s ramps, not 100% as it should have been if V100 had increased in proportion with target velocity. This suggests that V100 probably started to saturate for these subjects at a ramp velocity slightly less than 50°/s.

Time to reach 80% of target velocity

To assess the extent to which high anticipatory velocities reduce the delay in subsequently matching target velocity, the average time after ramp onset for the eye to reach 80% of target velocity, $t_{80\%}$, was analysed. 80% of target velocity was chosen since this was always reached, even on presentations when subjects never quite matched 100% of target velocity. Furthermore, eye velocity at this time was generally rising quite sharply, making the measure more reliable than if 100% of target velocity had been chosen where the eye velocity may take a large amount of time to change by just a small percentage of target velocity.

Mean $t_{80\%}$ is shown in Fig. 3.4.

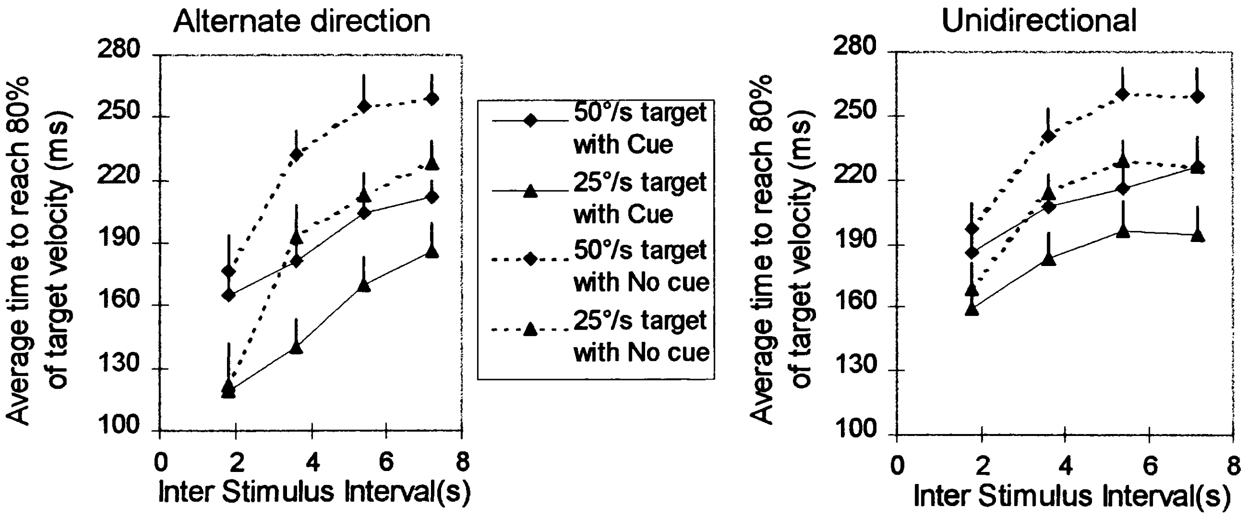


Fig. 3.4 Mean time to reach 80% of target velocity after ramp onset ($t_{80\%}$) by the eight subjects for all of the 32 different stimulus conditions. Error bars are the standard deviation of each mean.

As anticipatory velocity increased from the lowest values where the response was driven almost solely by visual feedback to the highest values, $t_{80\%}$ became shorter. For Alternate direction ramps, $t_{80\%}$ for 50°/s and 25°/s targets was shorter by around 94 ms and 109 ms respectively. For Unidirectional ramps, $t_{80\%}$ for 50°/s and 25°/s targets were both shorter by around 70 ms. Looking at all individual responses by each subject for 50 and 25°/s ramps separately, the relationship between eye velocity at target onset (V_0) and $t_{80\%}$ was well described by a linear function (regression was significant for all subjects; $p<.001$). Typical examples from two subjects are shown for 50 and 25°/s targets in Fig. 3.5. The values of the line that was fitted to each subject's data are shown in Table 3.4. For the 8 subjects, each 1°/s increase in anticipatory velocity at target onset reduced $t_{80\%}$ by 4.3-6.2 ms for 50°/s targets and by 7.5-10.2 ms for 25°/s targets, thus emphasising the utility of anticipatory pursuit in reducing the time required to match target velocity. This suggests that even the relatively slow anticipatory velocities elicited by cues after long intervals are genuinely beneficial in matching target velocity more promptly. Alternatively the cues may have simply raised the subjects attention at the correct time thus enhancing a visually guided reaction to the ramp. This seems unlikely though since all intervals were predictable, so even for ramps without cues, subjects could estimate when to raise their attention and expect an imminent ramp.

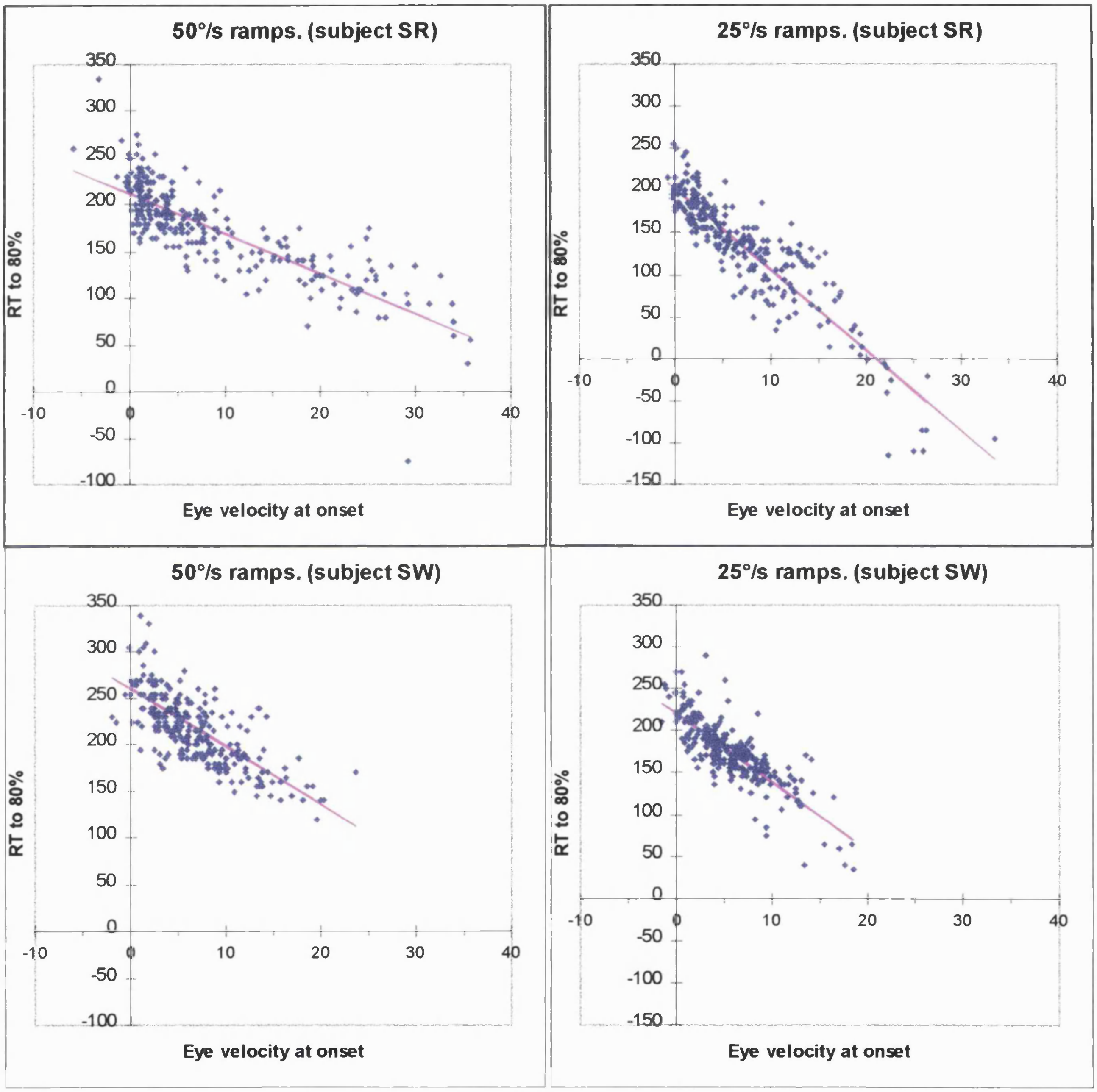


Fig. 3.5 The relationship between eye velocity at ramp onset and the time taken to reach 80% of target velocity after ramp onset. In the upper plot on the left, each blue point represents individual responses from all stimulus conditions where the ramp velocity was 50°/s by subject SR. The upper plot on the right shows all responses where the ramp was 25°/s. The lower plots show the corresponding responses by subject SW.

Subject	50°/s ramps	25°/s ramps
SG	$-6.0\ V_0 + 239.0$	$-9.2\ V_0 + 202.6$
JM	$-6.0\ V_0 + 268.4$	$-8.2\ V_0 + 235.7$
IL	$-4.7\ V_0 + 261.6$	$-10.2\ V_0 + 247.3$
GB	$-5.0\ V_0 + 259.4$	$-10.2\ V_0 + 231.5$
ST	$-4.5\ V_0 + 285.5$	$-7.5\ V_0 + 248.3$
SR	$-4.3\ V_0 + 212.1$	$-9.6\ V_0 + 202.0$
SW	$-6.2\ V_0 + 260.7$	$-8.2\ V_0 + 220.6$
RX	$-5.8\ V_0 + 275.9$	$-8.3\ V_0 + 240.7$

Table 3.4 Values of the line fitted to the relationship between eye velocity at ramp onset (V_0) and the time to match 80% of target velocity ($t_{80\%}$). The regression was carried out on all individual responses by each subject for 50°/s and 25°/s separately. All regressions were significant ($p<0.001$).

In the current experiment, different subjects had different magnitude responses but all showed the same effects to the experimental factors. For each of the significant effects found in the group analysis, at least seven out of eight subjects showed the same effects. The intra-subject variability was relatively high with typical standard deviations, for each subject's mean V100 for each of the conditions, being around 3-7°/s. Thus although the average velocity of anticipatory responses was much lower after long intervals, fast movements were still seen occasionally. The highest V100 achieved by any subject after a 7.2 s interval was 22.6°/s (Alternate direction, 50°/s target with Cue). This is indeed much higher than this subject's *mean* V100 after this interval (14.2°/s) which was used for the ANOVA, but is only half his *maximum* for the same stimulus after a 1.8 s interval (44.4°/s). This supports the idea of a decaying store rather than simply high velocities being achieved less often. This subject's two maximum anticipatory velocity responses for 1.8 and 7.2 s intervals are shown in Fig. 3.6.

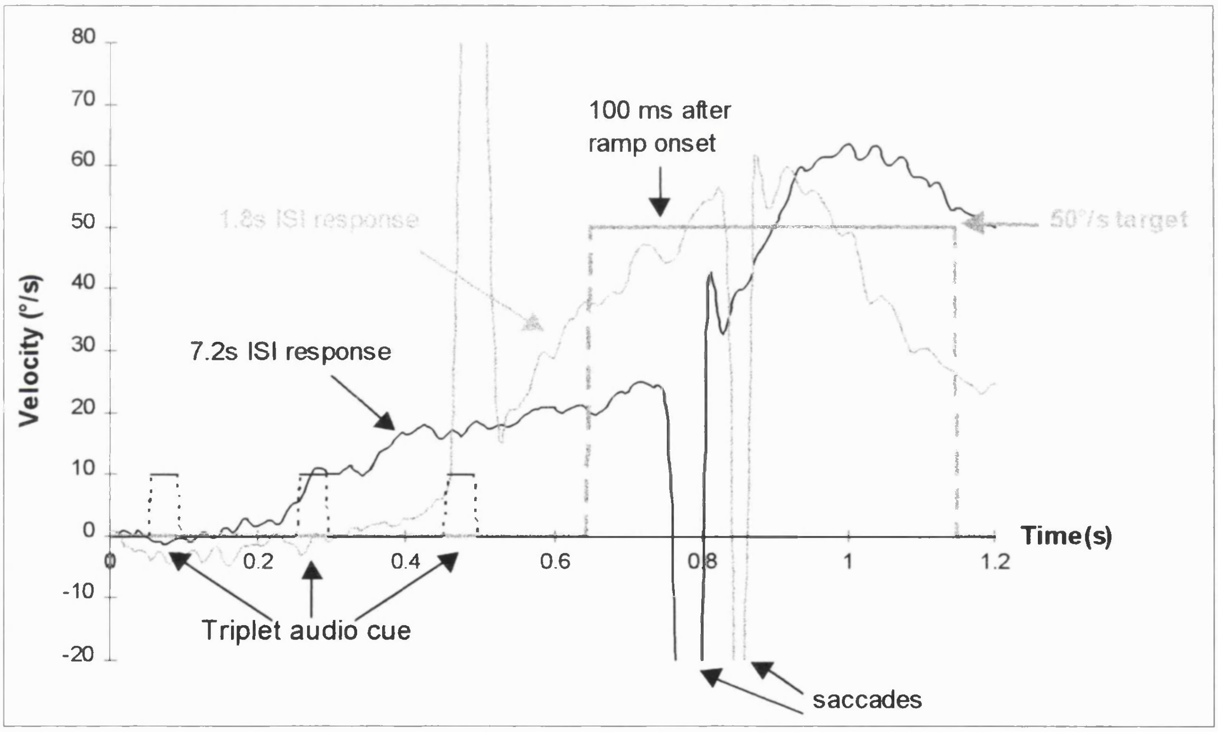
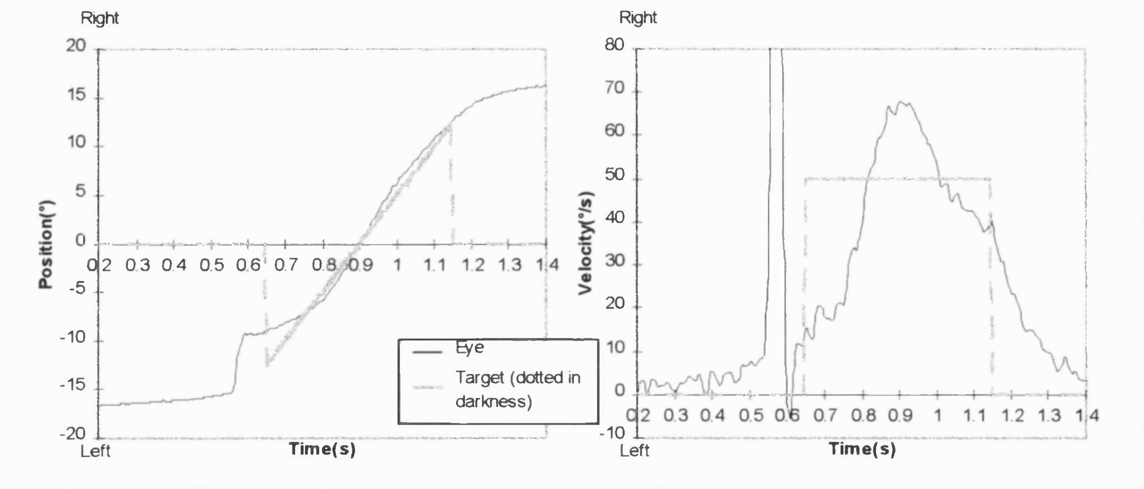


Fig. 3.6 The two responses by one subject with the highest anticipatory velocities achieved when the Inter-Stimulus Interval was 1.8 s and 7.2 s.

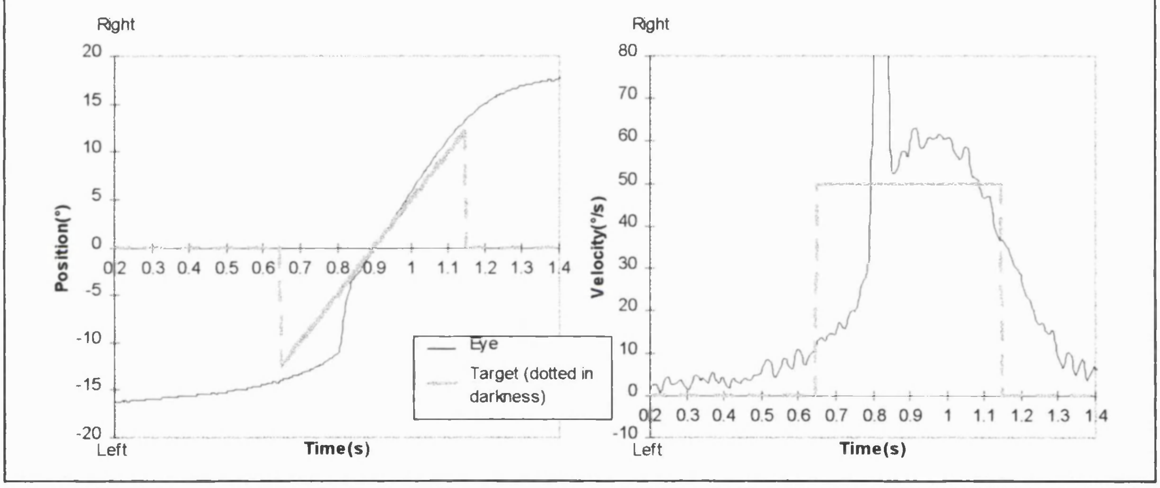
Eye position

An identical ANOVA was performed on eye position at target onset as was performed on eye velocity. None of the factors, ISI, Cueing or Waveform had a significance p value less than 0.05. The average position of the eyes at target onset was 0.4° in front of the target for ISI=1.8 s and 0.2° behind the target for ISI=7.2 s. The dim background light in the room gave subjects peripheral orienting cues but did not inhibit anticipatory pursuit as a foveal fixation target might. The intra-subject standard deviations for eye position at target onset were quite high, ranging from ±2.6 to ±4.1°. However, there was no significant effect of any experimental factor on the level of this variability. Thus there was no tendency for the eyes to drift back to centre after long intervals and subjects did not become more uncertain about where the moving target would appear. Although the eye was near the target when it appeared, its velocity was always lower than target velocity. Thus the eye lagged behind the target, often necessitating a catch-up saccade occurring after 120-200ms. In 49% and 34% of responses there were one or two saccades respectively whilst the target was visible. Sometimes (11% of responses) there were no saccades at all. This usually occurred when a slight positional lead (similar to a Rashbass step-ramp) combined with a fast anticipatory velocity kept the positional lag to a level that could be corrected by the smooth pursuit system alone. The average number of saccades while the target was visible did not change with ISI. On average there were 1.48 saccades during 50°/s ramps and 1.17 saccades during 25°/s ramps. Examples of individual position and velocity responses with 0, 1 or 2 saccades whilst the target was visible are shown in Fig. 3.7.

No saccades whilst target visible



One saccade whilst target visible



Two saccades whilst target visible

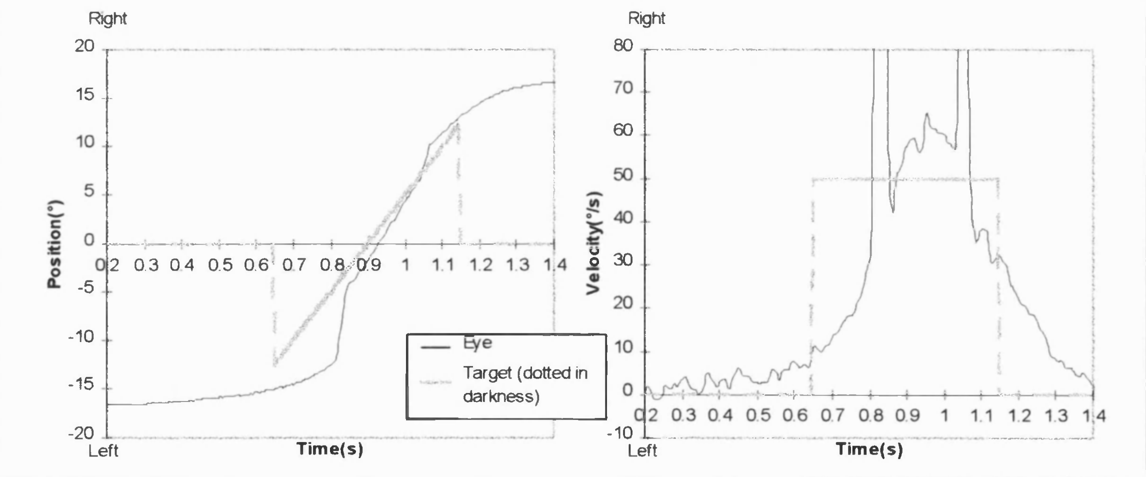


Fig. 3.7 Individual responses by one subject where different numbers of saccades were used to track identical ramps (taken from a trial for 50°/s Alternate direction ramps every 1.8 s with No Cue).

Discussion

These results present strong evidence for the existence of a short-term store lasting a few seconds for the production of fast anticipatory smooth pursuit. They accord with the idea that fast targets charge the store to a higher level than slow targets (see chapter 2), since the decaying store remains reasonably well scaled with the target velocity. This is an important indication of its functional relevance. An exponentially decaying store that can be charged to different starting levels seems a plausible explanation. The asymptotic level produced by a fully decayed store would be the level that can be produced by volition alone (Becker & Fuchs 1985; Kao & Morrow 1994).

The store appears to be directionally reversible in that a movement to the right can charge it for a subsequent movement to the left. For example, rightwards V100 before Alternate direction presentations with ISI=3.6 s was much higher (19.2°/s) than before Unidirectional presentations with ISI=7.2 s (10.9°/s), despite the fact that both of these have consecutive rightwards movements 7.2 s apart. The intervening leftwards movement of the Alternate direction condition seems to recharge the store, making the subsequent anticipatory rightwards movement faster than it would otherwise be. This agrees with the velocity sequence results of experiment 2b where recently pursuing a fast target to the right was not necessary for producing a fast rightwards V100, provided that a fast leftwards target had just been pursued. Similarly, unpublished experiments have shown that if the subject knows that there will be three rightwards movements then one to the left, the appropriate direction anticipatory responses can be generated.

The anticipatory response magnitude appears to be heavily influenced by previous stimuli (velocity sequence experiments of chapter 2), but the direction is largely under voluntary control. Kowler (1989) showed that during pursuit of a 2°/s vertically moving target, subjects could make anticipatory horizontal movements of around 0.3°/s when verbally cued about whether the target was going to veer right or left. The ability to use cognitive expectations to direct anticipatory movements is surely related to the anticipatory reversals in direction seen during the tracking of continuous target motion (Dodge *et al.* 1930). Admittedly, a reversal can be extrapolated from the target's instantaneous motion for a sine wave, but this is impossible with a predictable triangular wave (Boman & Hotson 1992) or during an unpredictable triangular wave where each half-cycle is of an unknown length (Barnes *et al.* 1987).

Taken alone, the linear relationship between anticipatory velocity at ramp onset and $t_{80\%}$ (Fig. 3.5) appears to indicate that there is a constant acceleration from ramp onset up to the 40 or 20°/s thresholds. However, in a simple linear velocity error feedback system, acceleration would be expected to increase with the size of velocity error. Fig. 3.2 shows that in conditions where there was very little anticipatory movement, and the velocity error was large, the abrupt acceleration that started at around 100 ms after ramp onset was indeed high. However, it was not high enough to match target velocity at the same time as in conditions with considerable anticipatory movement, where there was a relatively smooth acceleration that continued after visual feedback became available. Further research is needed to establish whether the system responds to visual inputs in the normal way during an anticipatory movement. What is clear though is that high velocity anticipatory pursuit allows target velocity to be matched at an earlier time and is the key to its role in reducing phase errors in sinusoidal pursuit at high frequencies (≥1.2Hz) (Lekwuwa & Barnes 1996a).

The decrease in anticipatory velocity with ISI is unlikely to be a fading cognitive memory of the stimulus parameters i.e. velocity, start time and start position. Firstly, Magnussen & Greenlee (1992) showed that target velocity information can be retained for at least 30 s in a velocity comparison task. Secondly, the triplet Cue allowed the time of target onset to be accurately predicted without the need to additionally recall the previous interval between cue and onset. Thirdly, the subjects' eye position at target onset did not become more variable with increasing interval.

The importance of short-term memory in motor control is well recognised. Miall *et al.* (1995) showed that open-loop wrist movements made without visual feedback by a deafferented patient decreased in positional accuracy as little as 6 s after the last visually guided movement. This brief visuo-motor memory thus appeared to aid the accuracy of *positional* control in the immediate future. In contrast our results show that a short-term store of similar longevity is also important for generating the appropriate *velocity* of smooth eye movement which could not otherwise be reconstructed from position and time information. The importance of this velocity memory in other motor systems is uncertain. However, similar anticipatory movements to intermittent stimuli are made by the hand (see next experiment in this chapter). They are also produced by the head during combined head and eye tracking and anticipatory VOR suppression is seen whilst fixating an intermittently illuminated head-fixed target during whole body oscillation (Barnes & Grealy 1992). The functional significance for pursuit of such a short-term velocity store is evident. Anticipatory pursuit is clearly useful for improving visual acuity by reducing velocity error but if the prediction is wrong then the retinal blur could be worse than if the eyes had remained stationary. A short term store is sufficient to overcome the relatively short time delays but minimises continued errors after unexpected target motion changes.

Experiment 3b: Hand and eye tracking of repetitive ramps with different intervals between ramps

Introduction

Experiment 3a showed that the ability to make fast anticipatory ocular pursuit before repeated brief presentations of a moving target appears to depend upon some sort of short-term store that decays over a few seconds. Hand movements in contrast can be produced voluntarily at anytime. For example, the finger can move in anticipation of a timing cue in order to synchronise tapping movements with a metronome rather than reacting late to each cue (Mates *et al.* 1994). Musicians and sports players make anticipatory movements all the time to compensate for processing delays. Prediction is also used on a continuous basis during manual tracking movements. Weir *et al.* (1989) showed that humans could track sine targets with smooth movements and a lag of just 25 ms. It is clear that the hand often adopts similar predictive strategies to the smooth pursuit system for optimising its performance. Experiment 3a was therefore repeated but with simultaneous hand tracking movements in order to make a comparison of the smooth pursuit system with a system that has the same goals but different dynamics and a different degree of voluntary control.

If the velocity of anticipatory hand movements decreased with longer ISIs, this would suggest that the decrease seen in smooth pursuit velocity in the last experiment was not due to a fading store, but merely a change in volitional strategy i.e. a shift from an anticipatory mode to a reactive, "wait and see" mode. If, on the other hand, there was no decrease in anticipatory hand velocity then this would be further evidence for some sort of store for anticipatory smooth pursuit.

It should not be assumed that anticipatory hand and eye movements are completely independent. If for example both anticipatory hand and eye velocity were still high after long ISIs, this could mean that a large anticipatory hand movement can be used by the eye to drive a faster than normal anticipatory smooth movement. Indeed there have been many reports of a hand-related command, either efference copy or afferent feedback, being used by the oculomotor system. von Noorden & Mackensen (1962) claimed that smooth pursuit could be generated by following the hand in the dark despite the fact that normally only saccades can be generated in darkness. However, Steinbach (1969) found that only about one in three subjects could do this and only for slow hand movements. Nevertheless, he suggested that the eye could use an efference copy of the hand movement command since smooth pursuit was better when subjects tracked their own visible hand when it was actively moved by themselves in an irregular way than when it was passively moved by the experimenter (Steinbach & Held 1968). The role of prediction was ignored though. Gauthier *et al.* (1988) also found an improvement when the hand was the target of pursuit. In addition, they found that ocular pursuit of an external target was better if the hand simultaneously tracked it; the movements were smoother with fewer saccades and maximum smooth eye velocity was increased from around 40°/s to over 100°/s (Leist *et al.* 1987 also found an increase from around 60°/s to 75°/s). This effect was even found when the hand was masked from view. Gauthier & Hofferer (1976), in accord with von Noorden & Mackensen, showed that smooth pursuit could be generated by tracking the imaginary image of the finger in the dark when it was moved actively or passively but not when afferent input was disrupted by an ischaemic block to the arm. Afferent input is therefore necessary and sufficient for this ability. Gauthier & Hofferer showed that efferent finger signals were important too. If the efferent finger signal was increased, either by loading the finger or asking subjects to move a less responsive ischaemic finger, then smooth pursuit often exceeded the velocity of the finger that was being tracked. They concluded that efference copy may be more important for the timing of coordinated tracking. In support of this, Vercher *et al.* (1996) showed that smooth pursuit started to track a target actively moved by the arm with a negative latency of -5 ms and that this was even possible in deafferented patients but not when the arm was passively moved by the experimenter (mean latency 130 ms for controls). They concluded that efferent signals are necessary and sufficient for initiating short latency smooth pursuit and attributed the role of afferent input from the hand to enhancing performance in terms of gain, phase and accuracy.

Method

Six of the eight right-handed subjects that took part in the last experiment were re-tested (aged 24-51; 3 male). The target motion conditions were identical except that only alternate direction targets were used. Unidirectional target motion had produced identical effects in the last experiment so these were not repeated to halve the number of runs. The target was presented for 500 ms at regular Inter-Stimulus Intervals (ISIs). A repeated-measures factorial design tested V100 for 16 stimulus conditions by combining all levels of the following factors:-

- ISI (either 1.8, 3.2, 5.4 or 7.2 s intervals between consecutive target onsets),
- Cueing (a triplet audio Cue before each target ramp or No Cue)
- Target Velocity (50°/s or 25°/s)

The order that the trials were presented in was randomised over the six subjects to control for any training effects.

The lower right arm was immobilised by strapping it to an arm rest, leaving the wrist free to move. The hand held a lightweight manipulandum which was constrained to move in the horizontal plane. The manipulandum consisted of a padded gutter, the centre of rotation of which was located beneath the wrist joint. It was coupled to a high-quality potentiometer, the voltage from which drove a mirror galvanometer to project the hand cursor at the current angle of the hand. Fig. 3.8 shows a picture of the manipulandum.

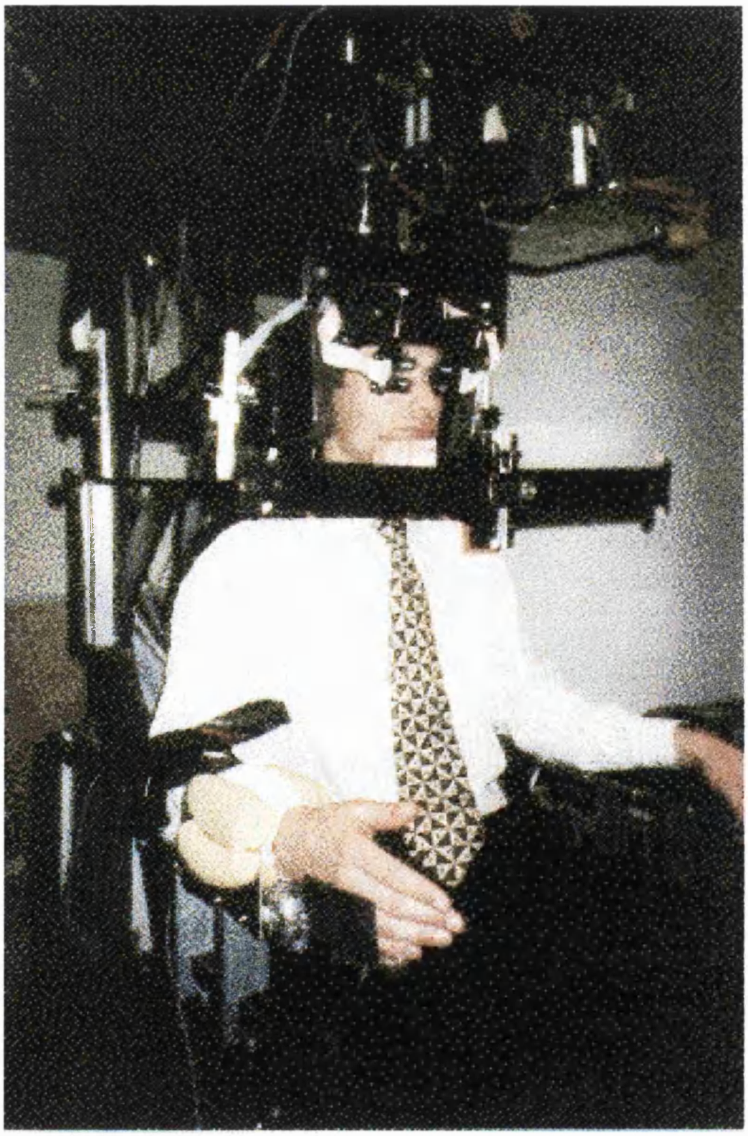


Fig. 3.8 Photograph of the manipulandum moved by the wrist in order to move the cursor on the screen

The cursor was illuminated in the same intermittent manner as the target leaving the subject in complete darkness between ramps. The hand cursor was green and was always easily distinguishable from the white target. It consisted of a circle of identical diameter to the target but there was only one rectangle above and below it and these were aligned so that they fell in between the white rectangles of the target.

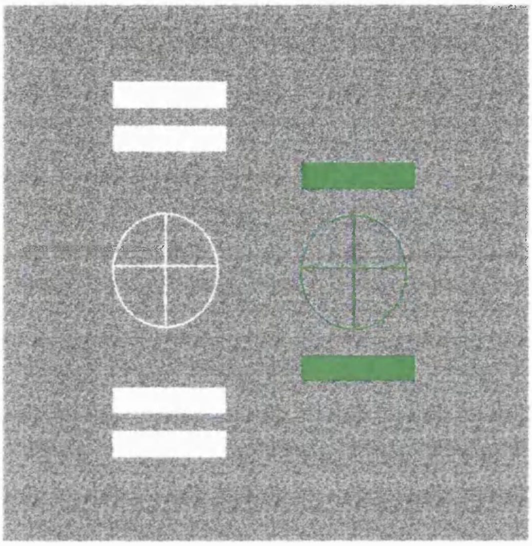


Fig. 3.9 Diagram showing the appearance of the white target and green hand-controlled cursor

Results

Typical hand and eye tracking position responses are shown in Fig. 3.10.

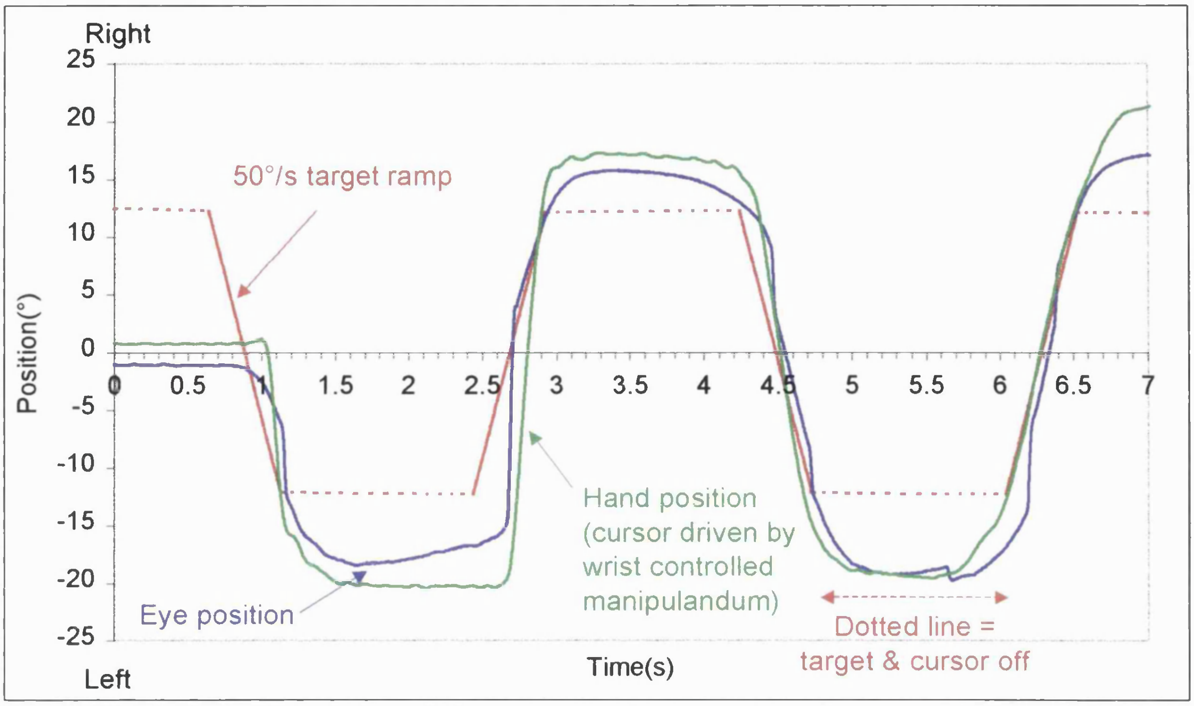


Fig. 3.10 Typical hand and eye responses. The plot shows responses to the first four 50°/s ramps of a trial with intervals of 1.8 s and No Cue.

The corresponding hand and eye velocity responses are shown in Fig. 3.11. There are several points to notice. For the first ramp of the trial there was a reaction time delay before the hand or eye started to move. For subsequent ramps, both the hand and the eye showed a build up of anticipatory velocity over the first two ramps with no major change after about the third response. Whereas peak smooth pursuit velocity did not greatly exceed target velocity, peak hand velocity could be very high. It reached velocities similar to those of catch-up saccades. Catch-up hand movements lasted much longer due to the higher inertia of the hand. The ability of the eye to quickly correct positional errors with saccades meant that even on the first or second ramp, the eye was able to achieve a period of smooth tracking when it moved with a velocity approximately equal to target velocity. In contrast, this was not achieved by the hand until the third response. The reactive, visually guided responses of the hand and eye look quite different due to their different dynamics. In contrast, the predictive steady state profiles of the hand and smooth eye velocity were more similar in shape, suggesting that the brain used a similar predictive tracking strategy for both effectors. However for the third and fourth presentation, the anticipatory hand velocity was somewhat faster than the anticipatory smooth pursuit.

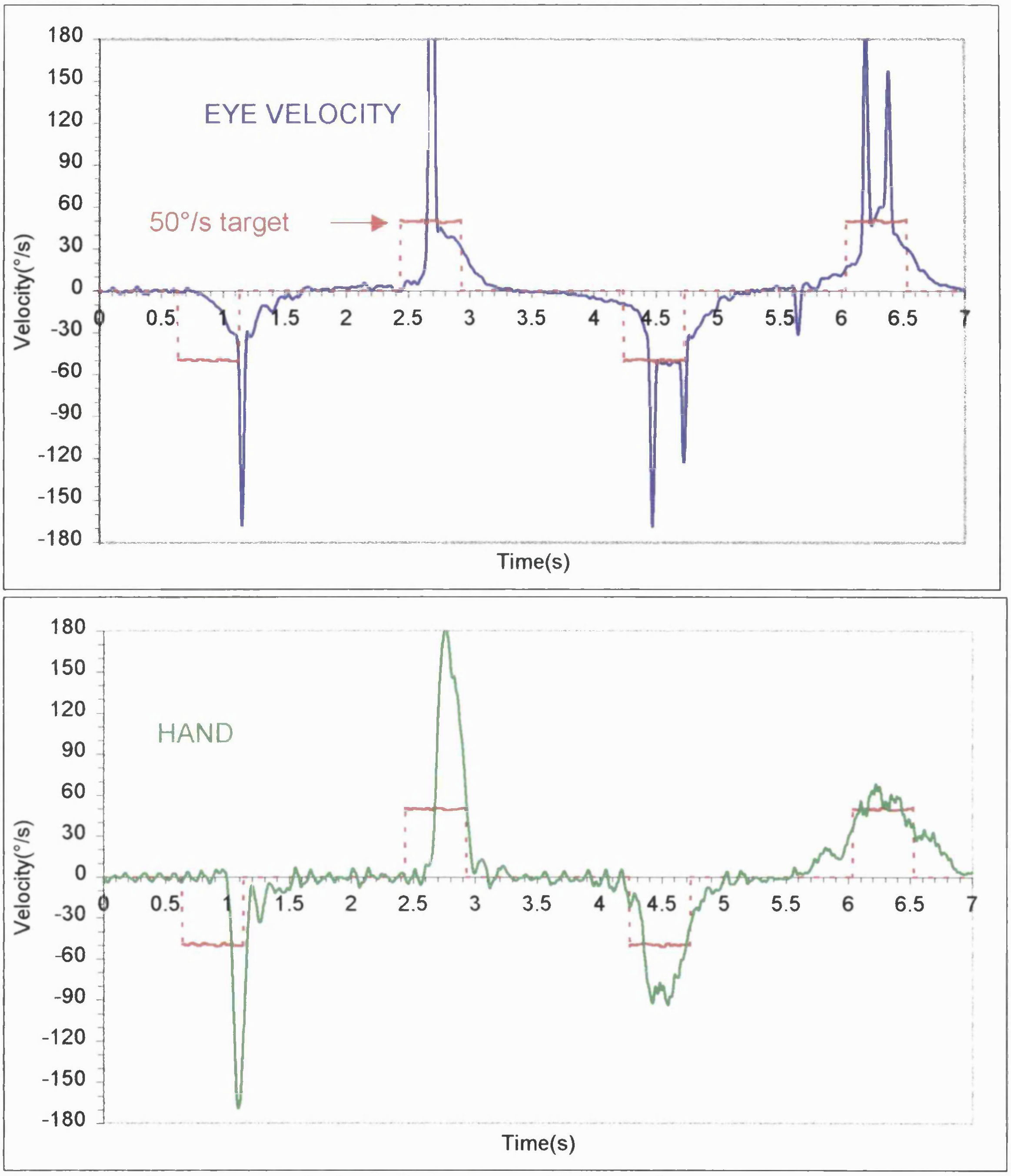


Fig. 3.11 The upper graph shows the corresponding eye velocity traces to the position traces from Fig. 3.10. The lower graph shows the corresponding hand velocity traces.

Fig. 3.12 shows the mean velocity profiles averaged over the six subjects for each of the eight stimulus conditions with 50°/s ramps and Fig. 3.13 shows the results for 25°/s ramps.

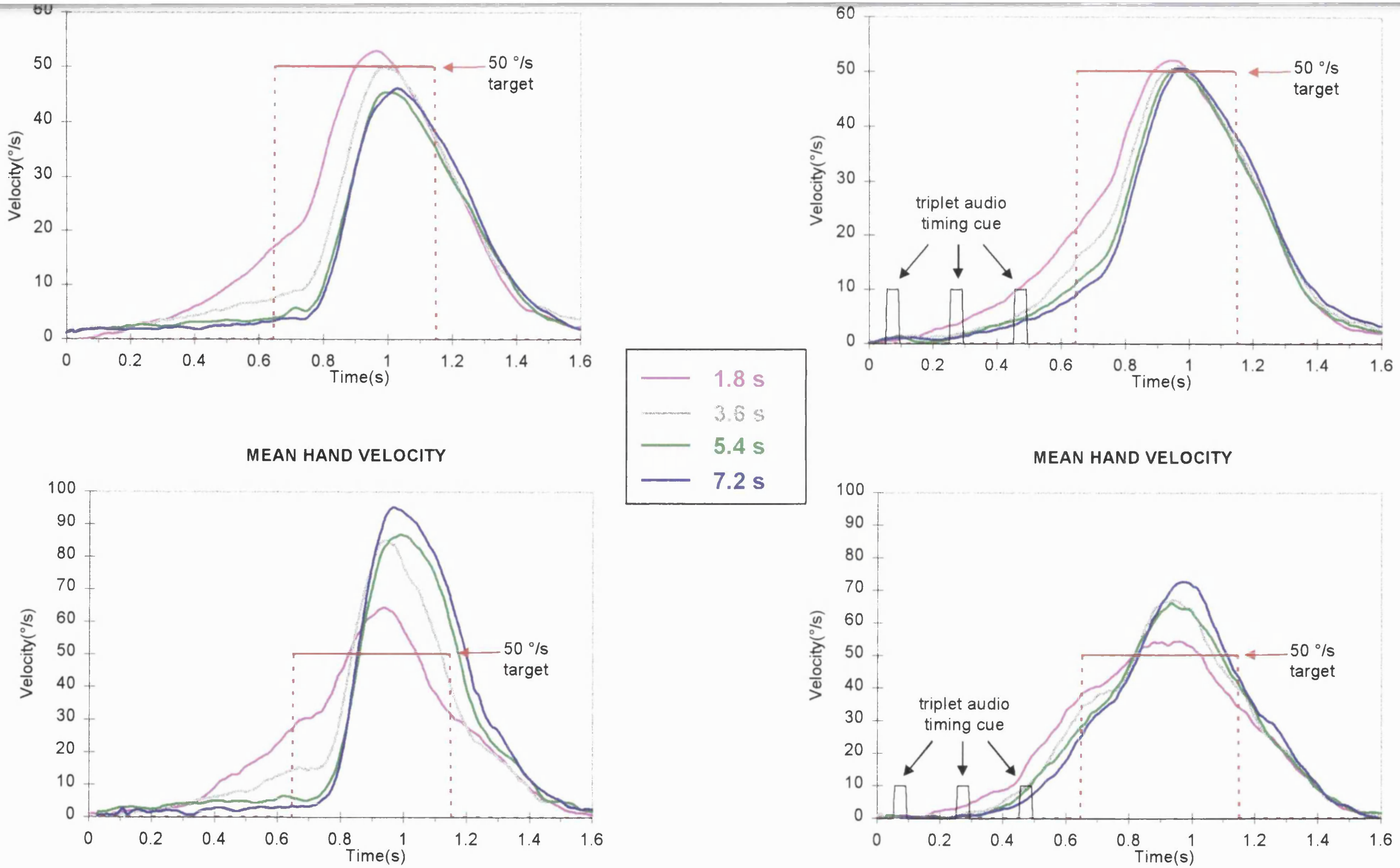


Fig. 3.12 Each graph displays the smooth eye responses for four of the eight stimulus conditions where the ramp velocity was 50°/s with the corresponding hand velocity responses in the graph below (Note that the hand and eye velocity scales are different). Each colour represents a different ISI.

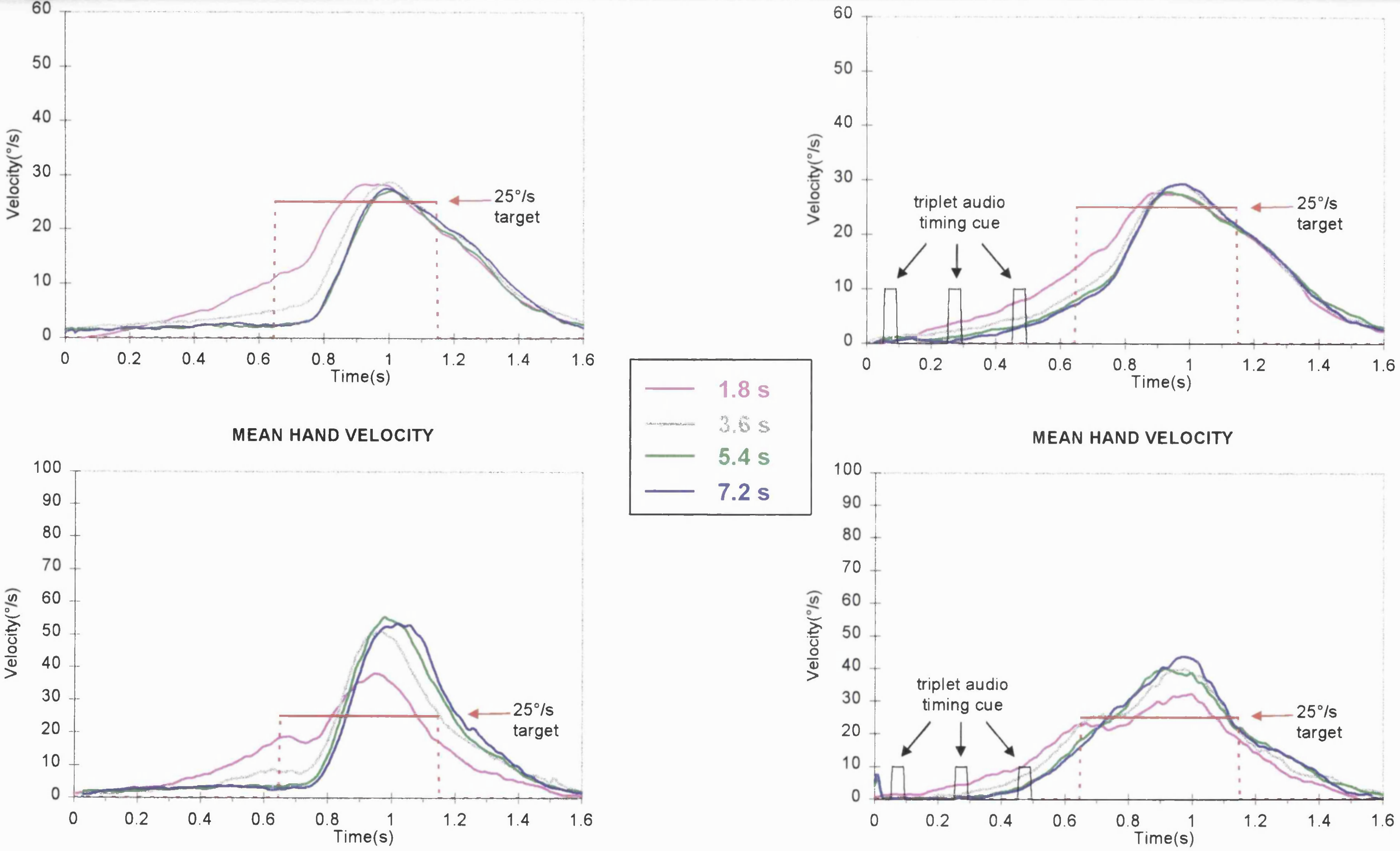


Fig. 3.13 Each graph displays the smooth eye responses for four of the eight stimulus conditions where the ramp velocity was 25°/s with the corresponding hand velocity responses in the graph below (Note that the hand and eye velocity scales are different). Each colour represents a different ISI.

To assess what experimental factors had a significant effect on the anticipatory velocities, each subject's mean steady state V100 for each experimental condition was entered into a repeated-measures ANOVA (EyeOrHand * ISI * Cueing * Target Velocity). The mean V100 for each of the 16 conditions is shown in Fig. 3.14.

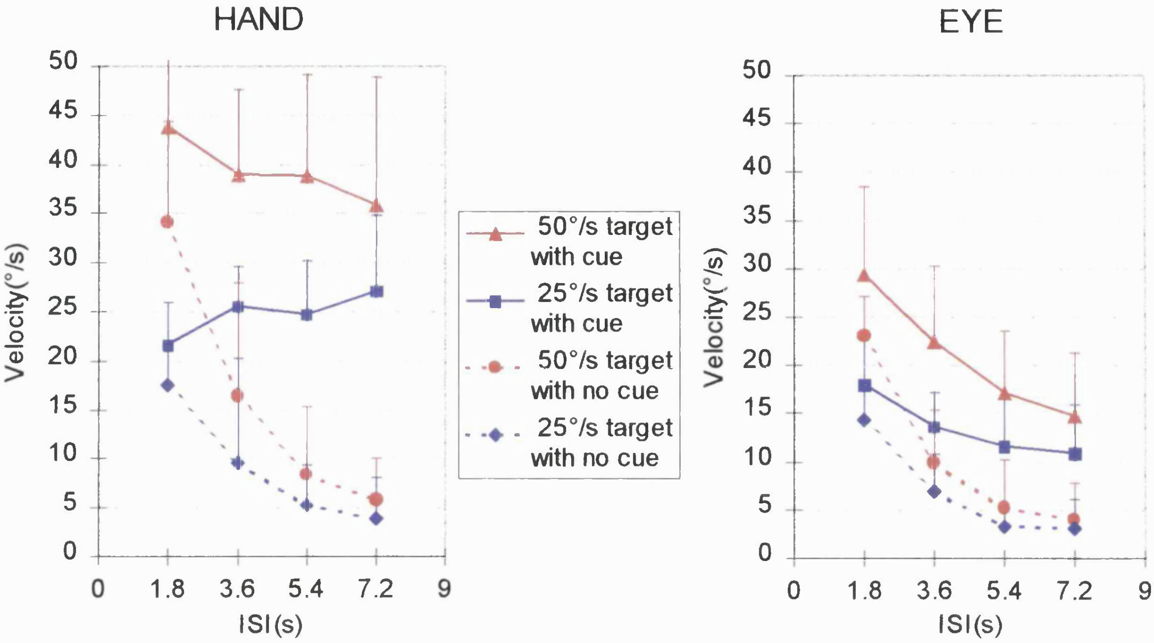


Fig. 3.14 The left plot shows mean hand V100 for each of the 16 stimulus conditions. The right plot shows smooth eye V100. The error bars are the standard deviation over the six subjects.

The results of the ANOVA are shown in Table 3.5

	F	Degrees of freedom	Significance
EyeOrHand	39.05	1	0.002
ISI	41.69	3	0.006
Cueing	126.72	1	<0.001
Target velocity	34.48	1	0.002
*EyeOrHand * Target velocity*	11.23	1	0.020
*EyeOrHand * Cueing*	25.13	1	0.004
*ISI * Cueing*	11.83	3	0.036
*ISI * Target velocity*	94.06	3	0.002
*Cueing * Target velocity*	84.51	1	<0.001

Table 3.5 Results of factorial ANOVA on V100. To reduce complexity, only interactions with a p value < 0.05 are shown..

All factors were significant main effects. V100 was lower for eye movements compared to hand movements (p = 0.002), for long intervals compared to short intervals (p = 0.006), for conditions with No Cue compared to those with a Cue (p < 0.001) and for 25°/s ramps compared to 50°/s (p = 0.002). There were several significant interactions though so these will be explained by separating the conditions into conditions with No Cue and those with a Cue.

Conditions with No Cue (dotted lines in Fig. 3.14):-

The results of a separate ANOVA performed on the conditions with No Cue alone are displayed in Table 3.6.

No Cue	F	Degrees of freedom	Significance
EyeOrHand	10.54	1	0.023
ISI	23.40	3	0.014
Target velocity	17.17	1	0.009
*EyeOrHand * Target velocity*	10.06	1	0.025
*ISI * Target velocity*	13.54	3	0.030

Table 3.6 Results of factorial ANOVA on V100. To reduce complexity, only interactions with a p value < 0.05 are shown..

Hand V100 was significantly faster than for the eye (p = 0.023). However, both the hand and eye exhibited a sharp and significant decrease (p=0.014) with ISI, as the intervals became longer and thus harder to predict. For the eye, mean V100 decreased from 23.1±4.1°/s to 4.0±3.8°/s for 50°/s ramps and from 14.4±4.0°/s to 3.1±3.1°/s for 25°/s ramps. For the hand, mean V100 decreased from 34.1±10.4°/s to 5.9±4.2°/s for 50°/s ramps and from 17.6±3.3°/s to 3.9±4.3°/s for 25°/s ramps. Thus, both systems responded to timing uncertainty in the same way by tending to produce only minimal accelerations until the target appeared. The hand did not adopt an alternative strategy such as generating an expectant nystagmus. The similar way in which anticipatory hand and eye velocity decreased with increasing ISI when there were No Cues shows that timing uncertainty was the dominant factor affecting the responses of the two systems.

Both the hand and the eye V100 were faster for 50°/s ramps compared to 25°/s ramps (p = 0.009) but this scaling decreased with ISI (significant Target Velocity*ISI interaction; p = 0.030) as subjects tended towards making no anticipatory movements at all.

Cued Conditions (solid lines in the Fig. 3.14)

The results of a separate ANOVA performed on the Cued conditions alone are displayed in Table 3.7.

Cued	F	Degrees of freedom	Significance
EyeOrHand	40.62	1	0.001
ISI	4.08	3	0.139
Target velocity	50.55	1	0.001
*EyeOrHand * ISI*	12.51	3	0.033
*EyeOrHand * Target velocity*	7.9	1	0.038
*ISI * Target velocity*	15.17	3	0.026

Table 3.7 Results of factorial ANOVA on V100. To reduce complexity, only interactions with a p value < 0.05 are shown..

Hand V100 was always faster on average than eye V100 (p=0.001) apart from in 2/6 subjects for 1.8 s ISIs. Although the steady state predictive hand and eye responses resembled each other, there were still some clear differences. The hand acceleration was much higher during the 200 ms before target onset for cued conditions and reached a higher percentage of target velocity. After this time, for ISI=1.8 or 3.6 s conditions, the hand appeared to cruise at about target velocity until visual feedback presumably started to have an effect. For longer cued intervals however, the hand continued accelerating and often exceeded target velocity, presumably in order to correct any positional errors. In contrast for all cued intervals the eye made quite a smooth continuous acceleration and positional errors could be corrected by brief saccades.

The significant EyeOrHand * ISI interaction (p=0.033) shows that there was a greater decrease in V100 for the eye than for the hand. To explore this difference, separate ANOVAs were performed on eye V100 for Cued conditions (Table 3.8) and on hand V100 for Cued conditions (Table 3.9).

Cued eye responses	F	Degrees of freedom	Significance
ISI	13.53	3	0.030
Target velocity	32.83	1	0.002
*ISI * Target velocity*	4.90	3	0.112

Table 3.8 Results of factorial ANOVA on eye V100 for Cued conditions. Planned contrasts between the four factor levels of ISI revealed that V100 for ISI=1.8 s was significantly higher than for ISI=3.6 s (p=0.022) which was significantly higher than for ISI=5.4 s (p=0.018) which was significantly higher than for ISI=7.2 s (p=0.041). Only three contrasts were planned so no Bonferroni correction was considered necessary (see Statistical analysis section).

Cued hand responses	F	Degrees of freedom	Significance
ISI	0.16	3	0.916
Target velocity	33.01	1	0.002
*ISI * Target velocity*	6.18	3	0.084

Table 3.9 Results of factorial ANOVA on hand V100 for Cued conditions. Planned contrasts between the four factor levels of ISI revealed that V100 for ISI=1.8 s was not significantly higher than for ISI=3.6 s (p=0.734) which was not significantly higher than for ISI=5.4 s (p=0.787) which was not significantly higher than for ISI=7.2 s (p=0.871). Only three contrasts were planned so no Bonferroni correction was considered necessary (see Statistical analysis section).

When the triplet audio cue was provided, eye V100 still exhibited a significant (p=0.030) decrease for longer ISIs, although it was less marked than when there was No Cue (mean V100 decreased from 29.4±9.0°/s to 14.7±6.6°/s for 50°/s ramps and from 18.1±5.2°/s to 11.0±4.9°/s for 25°/s ramps). All 6 subjects showed decreases with ISI for 50°/s ramps and 5 subjects for 25°/s ramps. In contrast, hand V100 decreased only slightly on average for longer Cued ISIs for 50°/s ramps (mean V100 decreased from 43.8±7.6°/s to 35.8±13.0°/s). Three subjects showed slight decreases but the other three produced quite constant velocities. For 25°/s targets there was actually a slight increase with ISI from 21.7±4.4°/s to 27.0±7.7°/s on average. Four subjects showed this slight increase. Thus, there was no overall tendency for anticipatory hand velocity to decrease after longer intervals suggesting that unlike smooth pursuit, the production of hand movements is not dependent on a short-term store. Although ISI had no significant effect on the velocity attained by Cued anticipatory hand responses (p=0.92), the acceleration profiles do not look identical and there appears to have been a slightly larger difference in anticipatory velocity at the time of ramp onset. However, a further ANOVA of hand velocity at ramp onset for Cued conditions did not show that ISI was a significant factor (p=0.113).

The slight decrease in anticipatory hand responses to 50°/s ramps and the slight increase for 25°/s ramps suggest that, although the hand can always make a movement, it may be produced with less velocity specificity. In this experiment, hand V100s for 50°/s ramps were 102% larger than responses to 25°/s ramps for 1.8 s ISIs but only 33% larger for 7.2 s ISIs, meaning that there was reduced velocity scaling. However the ISI*Target Velocity interaction did not reach significance for the hand (p=0.084).

Similarly for the eye, the difference between responses to 50 and 25°/s targets decreased with increasing ISI. In Experiment 3a, although the absolute difference between responses to the two target velocities decreased, there was quite a constant ratio between them (responses to 50°/s ramps were 40-60% faster than to 25°/s ramps). In this experiment, responses to 50°/s ramps were 63% faster than responses to 25°/s ramps for 1.8 s ISIs but only 34% faster for 7.2 s ISIs. However, as with the hand, there was not a significant ISI*Target Velocity interaction (p=0.112) for the eye. For the shortest Cued ISI, the fact that hand V100 increased in proportion with target velocity (V100 for 50°/s ramps was 102% faster than for 25°/s ramps) whereas eye V100 for 50°/s ramps was only 63% faster than for 25°/s ramps suggests that the hand was more able to scale its anticipatory movements appropriately for these target velocities.

Although there was no significant decline in mean V100 produced by the hand, the movements may have become more variable for conditions with longer intervals. To assess this possibility, each subject's standard deviation about his or her mean hand V100 for each Cued condition was entered into an ANOVA. The standard deviation about V100 increased from ±13.1°/s to ±19.0°/s for 50°/s ramps and from ±7.9°/s to ±13.5°/s for 25°/s ramps as ISI increased from 1.8 s to 7.2 s. However this increase was not significant (p =0.237) showing that the hand movements did not become markedly less precise.

Time to match 80% of target velocity ($t_{80\%}$)

To assess how quickly subjects matched target velocity, the time after ramp onset taken by subjects to reach 80% of target velocity was measured ($t_{80\%}$). This is shown in Fig. 3.15.

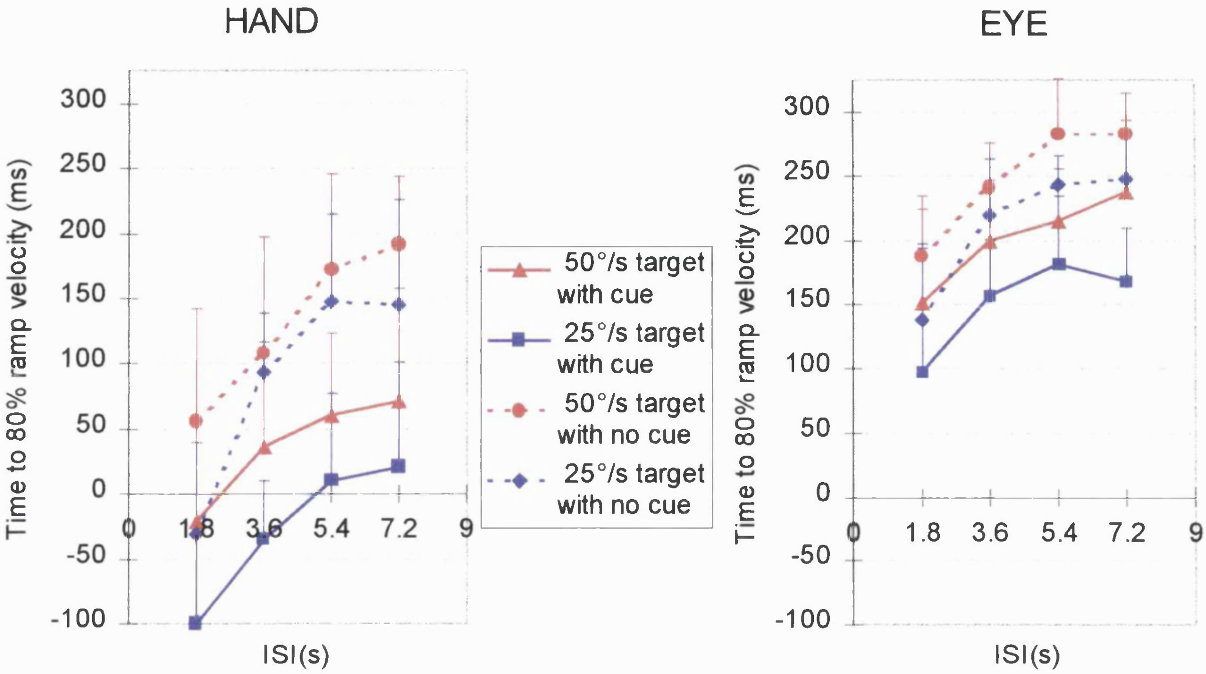


Fig. 3.15 The left graph shows mean time for the hand velocity to reach 80% of target velocity for all 16 stimulus conditions. The right graph shows the time taken by the smooth eye velocity. The error bars are the standard deviation between the six subjects.

On average, $t_{80\%}$ for the hand was always earlier than for the smooth eye velocity. For Cued 50°/s targets, $t_{80\%}$ for hand velocity was around 170 ms earlier for all ISIs than the smooth component of the eye velocity. Similarly, for 25°/s Cued targets, $t_{80\%}$ for hand velocity was on average 120 ms earlier than for smooth eye velocity. This is not due to the removal of fast catch-up saccades in this analysis since these occurred with latencies of at least 100 ms which is longer than hand $t_{80\%}$ for all Cued ISIs. Thus the hand was much more able to match ramp velocity around target onset. Indeed, hand $t_{80\%}$ often occurred before the target had even appeared hence the negative values in Fig. 3.15. At longer ISIs, $t_{80\%}$ increased in a similar way for all conditions for both the hand and the eye. The largest increases were for the No Cue conditions between ISIs of 1.8 and 3.6 s in accord with the largest decrease in V100. As was seen in the previous experiment, 80% of 25°/s ramps was reached earlier than for 50°/s ramps (by around 50-80 ms for both the hand and eye).

For the eye, $t_{80\%}$ always occurred after the time when visual feedback could have had an effect (apart from Cued 25°/s targets $t_{80\%}$ = 98ms). This does not necessarily imply that 80% of target velocity cannot be reached by the eye without visual feedback since the predictive response does not just finish at 100 ms but is the dominant factor for at least another 100ms. Thus it was no surprise, as was seen in the last experiment, that higher anticipatory velocities led to shorter $t_{80\%}$. For the hand too, there was an overall trend for faster anticipatory velocities at 0 ms to lead to shorter $t_{80\%}$. However, there was a much larger spread in $t_{80\%}$ for the hand. Whereas the eye nearly always reached 80% of target velocity a short interval after visual feedback could have an effect, the hand often reached 80% long before this time. Thus the same anticipatory hand velocities at ramp onset could be associated with a wide range of $t_{80\%}$.

Although $t_{80\%}$ for the hand occurred earlier than for the eye, its tracking in terms of velocity error was worse overall. Average hand velocity did not accurately match target velocity apart from for the 1.8 s ISIs (both with and without a Cue). Although the eye has a lower initial acceleration, it can make brief catch up saccades and then pursue at approximately target velocity. The hand however, has no such ability and must make a more prolonged movement in excess of target velocity to correct a positional error. For longer Cued intervals, mean hand velocity overshot target velocity by around 20°/s for both 50°/s ramps and 25°/s ramps.

For 5.4 & 7.2 s ISIs with No Cue, where there was virtually no anticipatory movement, the hand still reached 80% of target velocity around 95 ms before the smooth eye velocity. This seems surprising given the more sluggish dynamics of the hand. Looking at the velocity profiles, the eye and the hand responses appear to start around the same time but the hand acceleration is much higher. This faster hand acceleration will be compared to the composite eye velocity (includes saccades) in a later paragraph. Additionally, the hand appeared to start from a more eccentric position in the dark than the eye, thus necessitating a larger catch-up movement. So for the long ISIs with No Cue, although the hand was initially faster than the smooth eye velocity, its tracking was worse overall. The hand often took nearly the whole presentation to correct the positional error requiring average catch up velocities up to 45°/s in excess of target velocity.

Eye and hand Position

The 50°/s ramps started at 12.5° from the straight ahead position and moved to 12.5° on the opposite side. 25°/s ramps started and ended at ±6.25°. To assess the resting position where the anticipatory movements started from, an ANOVA was performed on position at 400 ms before ramp onset. Very little anticipatory movement started before this time (Figs. 3.12 and 3.13). The results are shown in Table 3.10.

	F	Degrees of freedom	Significance
EyeOrHand	220.56	1	<0.001
ISI	19.831	3	0.018
Cueing	28.97	1	0.003
Target velocity	106.00	1	<0.001
*EyeOrHand * Target velocity*	11.78	1	0.019

Table 3.10 Results of factorial ANOVA on eye position at 400 ms before ramp onset. To reduce complexity, only interactions with a p value < 0.05 are shown..

Between ramps, the eye was at around 13.4° from straight ahead for 50°/s ramps i.e. at a slightly more eccentric position than where the next ramp would start. The hand was more eccentric than the eye ($p<0.001$) by 4.2° on average for 50°/s ramps. This was probably due to the hand's greater inertia making it overshoot the end point of the preceding ramp (see fig. 3.10 for example). As expected, both the hand and the eye started from a more eccentric position for the larger amplitude 50°/s ramps ($p<0.001$) than the 25°/s ramps. Mean eye position at this time for 25°/s ramps was 7.6° from straight ahead with the hand being 3.0° more eccentric to this. For conditions with No Cue both the hand and the eye tended to be around 0.9° less eccentric on average than for Cued conditions ($p=0.003$). This is probably due to occasional centripetal guesses starting inappropriately early. ISI did not have a significant effect on either hand or eye position showing that there was no overall tendency for the eye or hand to drift in a particular direction with longer intervals. A similar ANOVA at 100 ms after ramp onset revealed that the hand was still wider than the eye at this time ($p=0.002$). By this time both the hand and eye were now closer to the midline when there was a Cue compared to No Cue ($p=0.002$) since the timing information prompted centripetal anticipatory movements. ISI was not a significant factor overall at this time despite that fact that it had a significant effect on V100. Perhaps the changes in velocity did not have enough time to produce significant differences in position.

Saccades

Clear differences have been shown between hand tracking and smooth pursuit. However, it is interesting to ask how much of this was due to excluding saccadic eye movements from the analysis. To assess this, the mean composite eye velocity (smooth pursuit and saccades combined) was studied. Whilst the averaging smears out the saccadic spikes, it gives an idea of when the saccades usually occurred. The composite velocity responses were filtered in the same way as the smooth responses since the shape of the saccadic velocity spikes was not important for this analysis. If saccades occurred randomly in the forwards and backwards directions then there would be no net difference between the average smooth velocity profile and the average composite velocity profile. Only if saccades normally occurred in the same direction at a particular time would there be a net difference. The comparison is shown in Fig. 3.16 for 50°/s ramps at ISI=1.8 s with Cues.

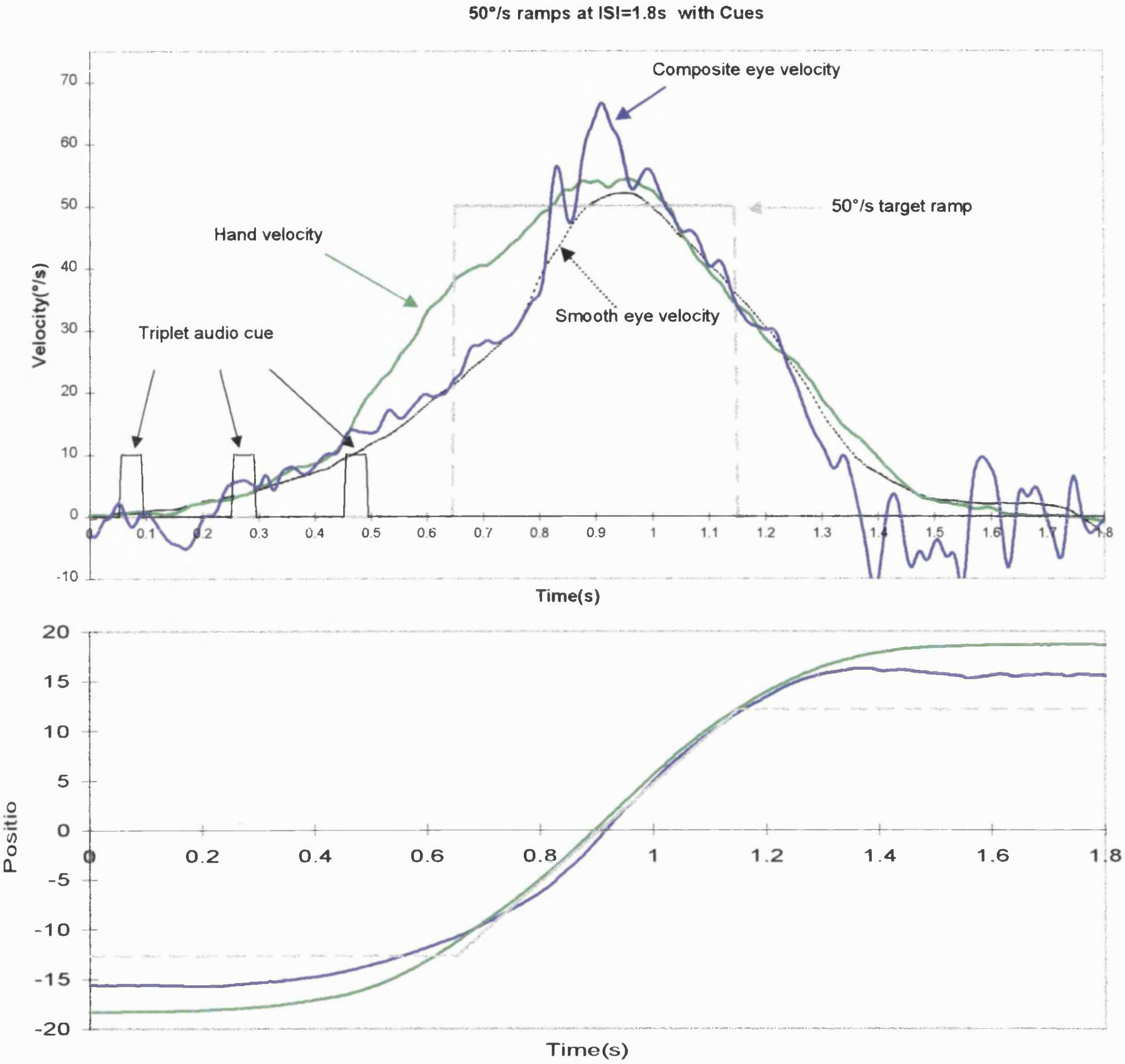


Fig. 3.16 Upper plot shows mean hand velocity, smooth eye velocity and composite (smooth + saccadic) eye velocity by the six subjects for 50°/s ramps at intervals of 1.8 s with timing Cues. Lower plot shows mean hand and eye position.

In this figure, the composite eye velocity trace is very similar to the smooth eye velocity trace. This shows how the movement was mainly smooth and that the few saccades were distributed randomly in the forwards and backwards direction. The only place where there is a small discrepancy is between 150 and 350 ms after ramp onset when catch up saccades in the forwards direction commonly occurred. The oscillations at about 200 ms after ramp offset are due to repositioning saccades and blinks. The earlier observation that the anticipatory hand velocity was much faster than the anticipatory smooth eye velocity cannot be explained by the exclusion of saccades since there is almost no difference between the smooth and the composite eye velocity profiles during the anticipatory phase. Thus the hand clearly made an anticipatory movement of greater velocity than the eye. An identical pattern was seen for all the other cued conditions. Fig. 3.17 shows the results for 7.2 s ISI. For this Cued ISI, the fact that the anticipatory smooth eye movement was hardly different from the composite eye movement means that extra saccades were not used to make up for the reduced anticipatory smooth pursuit for this condition. Thus whereas the hand made similar anticipatory movements for short and long Cued ISIs, the eye did not, even when saccades were taken into consideration.

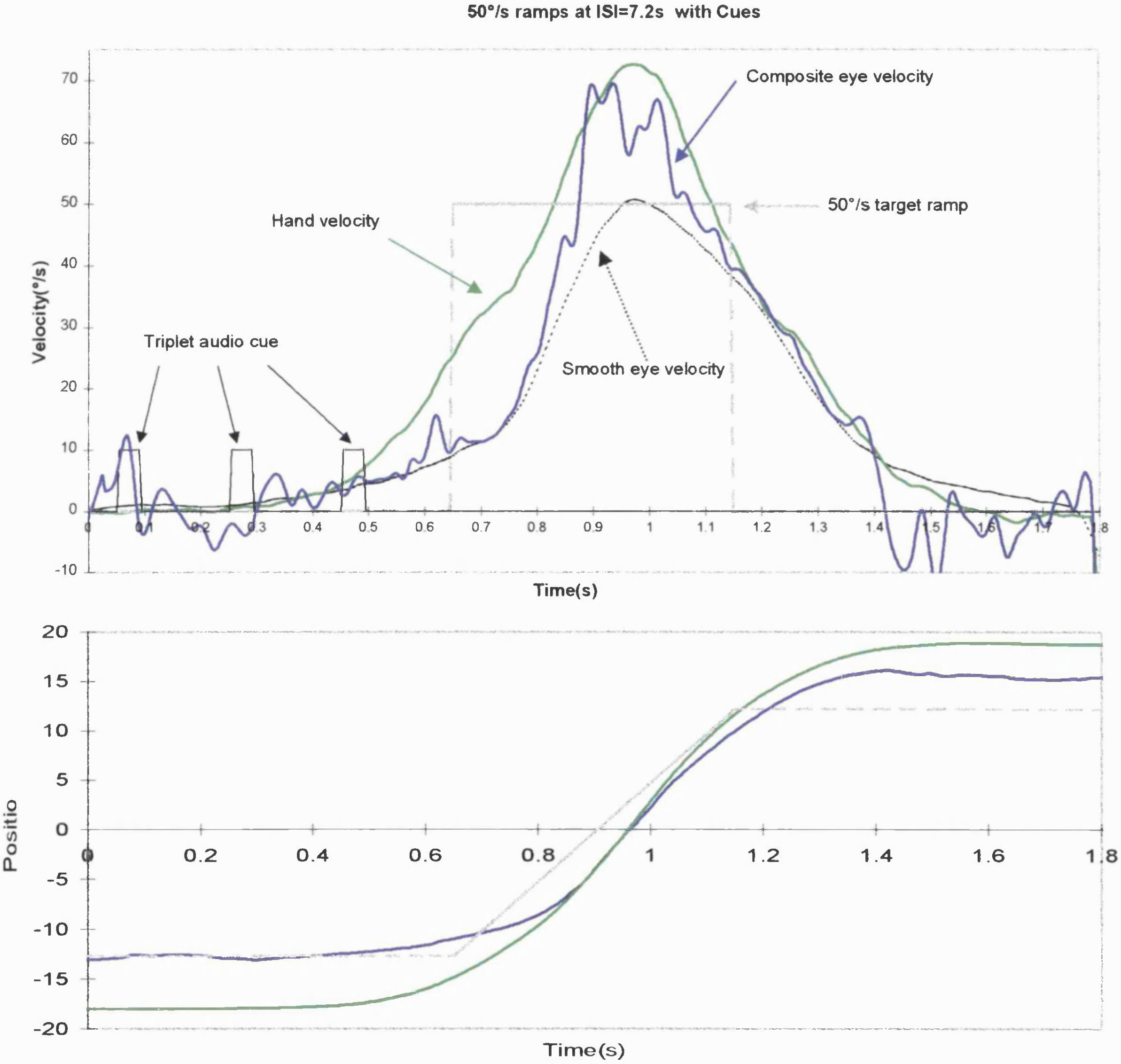


Fig. 3.17 Upper plot shows mean hand velocity, smooth eye velocity and composite (smooth + saccadic) eye velocity by the six subjects for 50°/s ramps at intervals of 7.2 s with timing Cues. Lower plot shows mean hand and eye position.

The V100 results showed that for ramps with No Cue, where the ISI was greater than 1.8 s, the responses were mainly reactive. The hand and composite eye velocity profiles are shown in Fig. 3.18 for 50°/s ramps with ISI=7.2 s with No Cue. The hand and eye accelerated with about the same latency after ramp onset. The composite eye velocity showed a higher acceleration at this point due to the large catch up saccade that nearly always occurred at this point. It then dropped promptly towards target velocity but was still faster than the smooth eye velocity trace due to further catch up saccades sometimes being needed. In contrast the hand velocity remained high much longer due to catch up movements by the hand being more prolonged.

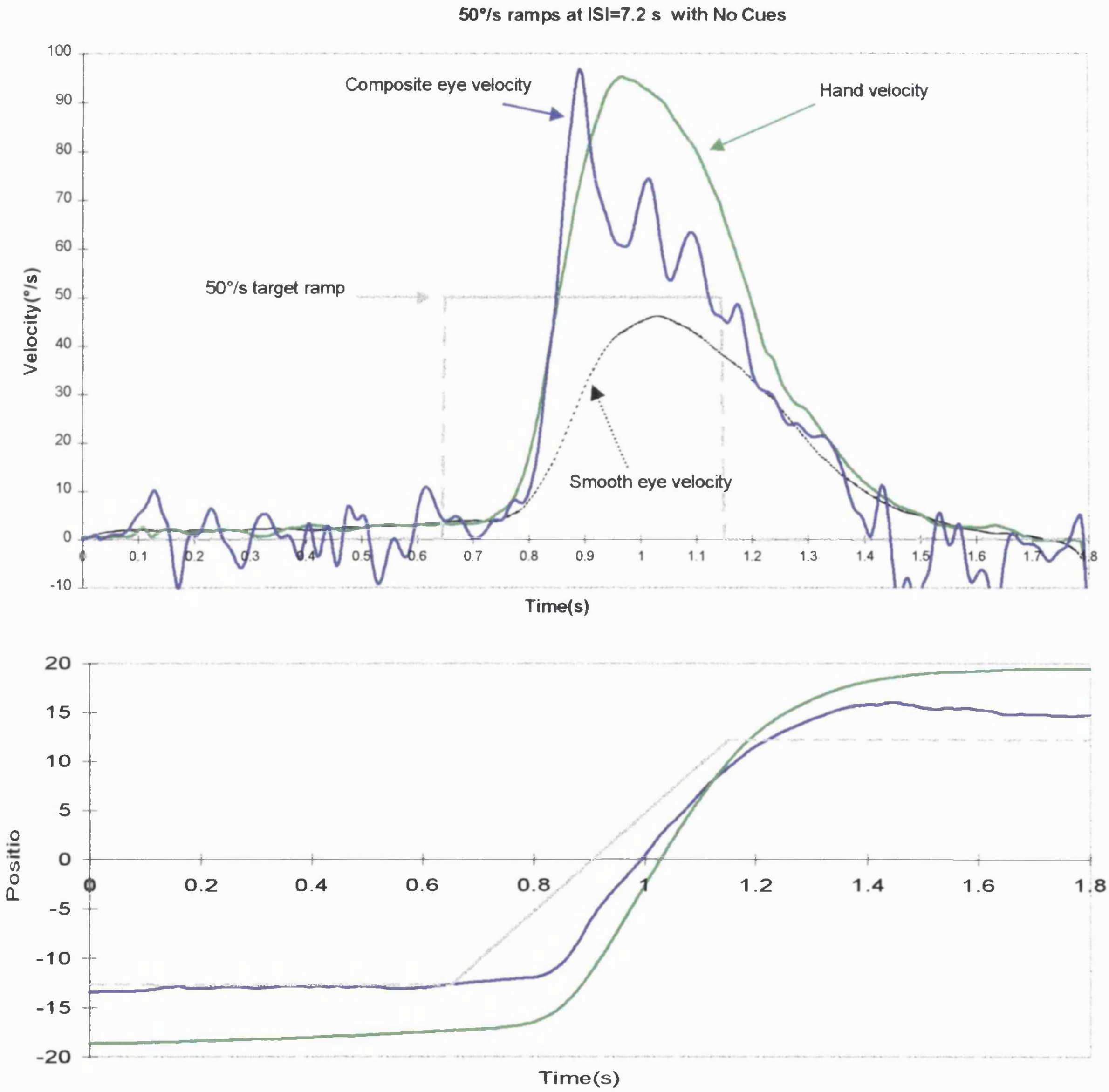


Fig. 3.18 Upper plot shows mean hand velocity, smooth eye velocity and composite (smooth + saccadic) eye velocity by the six subjects for 50°/s ramps at intervals of 7.2 s with No Cue. Lower plot shows mean hand and eye position.

Comparison of eye responses during 'eye alone' and 'eye and hand' tracking

The eye responses from this experiment were compared to those from Experiment 3a for the six subjects that participated in both. Anticipatory smooth eye velocity at 100 ms showed slight differences depending on whether the movement was accompanied by a hand movement or not. For No Cue there were only small inconsistent differences. For Cued conditions, the anticipatory velocities were slightly higher for 'eye and hand' tracking (on average between 0.5-3.4°/s faster) but idiosyncratic differences meant that this was not significant [smooth eye velocity data from all six subjects that took part in experiments 3a and 3b were entered into an ANOVA for all the common conditions. An extra factor which had the levels 'Eye and Hand' and 'Eye Alone' was not found to be significant (p=0.177)].

Deceleration

For all ramps described so far in this thesis, the ramp duration was constant for each experiment. Therefore subjects knew exactly when each ramp would end. It has often been noticed that in such situations, subjects tend to slow down in expectation of the ramp ending rather than responding reactively 100 ms after ramp offset when they have visual feedback of the offset. This aspect of predictive pursuit will be dealt with more thoroughly in the next chapter of the thesis. In this experiment however, the velocity profile of this deceleration was remarkably independent of target motion condition. The deceleration must be programmed to occur at a set time after ramp onset since it is unaffected by the amount of anticipatory pursuit near target onset. By 100 ms after ramp offset, instead of pursuit being maintained near target velocity, all 6 subjects showed anticipatory decelerations for all conditions. Smooth eye velocity decelerated to an average of 25°/s for 50°/s ramps and to 16.8°/s for 25°/s ramps. For cued conditions, the hand decelerated to an average of 26°/s for 50°/s ramps and to 14°/s for 25°/s ramps. However, for *No Cue* conditions at long intervals, the hand velocity at this time was often higher since the catch-up period where hand velocity exceeded ramp velocity had only just ended.

Discussion

Hand movements can always be generated voluntarily if appropriately cued, so the fact that the anticipatory hand velocity did not decrease in the same way as eye velocity suggests that the audio cues did give sufficient timing information. Thus for longer intervals with cues subjects did not, for example, shift to a reactive mode to avoid exacerbating tracking errors by making inaccurate predictions. Thus the inability to generate fast, smooth anticipatory eye movements after a long interval is unlikely to be due to a change in strategy and is probably due to a decaying short-term store.

For long ISIs with a Cue, there was no major enhancement of anticipatory eye velocity by the fast anticipatory hand movements that were made. Thus proprioceptive feedback or efference copy of the hand movement was not used by the eye to compensate for a decayed store. The slight but insignificant enhancement could perhaps have been due to a raised attentional level caused by the added demand of making a hand movement. After the anticipatory movement, the eye velocity profiles appeared to be very similar regardless of whether there was an accompanying hand movement or not.

For longer intervals with No Cue, the hand looks as though it is driven in a similar way to the eye but the velocity profiles differ due to the hand's higher inertia. For Cued ramps, both the hand and eye make bell-shaped velocity profiles but with some important differences. By 100 ms after ramp onset the hand reached between 72-108% of target velocity for the different conditions with Cues. In contrast the eye reached only 59-72% of target velocity for 1.8 s ISI and only 29-44% of target velocity for 7.2 s ISI. This shortfall in smooth eye velocity in comparison to the hand was not made up by saccadic movements (Fig. 3.16). Experiment 2a suggested that the eye is driven to match around 60% of target velocity by 100 ms after ramp onset. The reason why the oculomotor system does not aim to match 100% of target velocity cannot be to avoid oscillations and overshoots since visual feedback stability problems are likely to be similar for the hand. Before visual feedback occurs, hand tracking is better than the eye i.e. there is less velocity error. Perhaps fast anticipatory movements are not as important for the eye since it can make quick and accurate saccades to correct position errors and then immediately pursue at about the correct velocity. In contrast, the higher inertia hand can only track a brief ramp properly if a reasonable anticipatory movement is made. The fact that the eye always has a clear view of the target around 300 ms after ramp onset could mean that there is little incentive to increase anticipatory acceleration or eliminate anticipatory deceleration. This idea will be explored in the next chapter. The differences between anticipatory hand and eye movements at short intervals suggest that they probably do not access the same store. If each effector has its own store then the decline in anticipatory eye velocity suggests that the store for smooth pursuit has a shorter longevity or that retrieval becomes impaired.

Anticipatory hand movements increased in proportion to target velocity. In contrast, the increase in anticipatory eye velocity with target velocity was less than proportional so it is possible that the short-term store effects are due to a system working near its limits. However, it seems unlikely that a similar decrease in anticipatory hand velocity would be seen even if target velocities nearer the velocity limit of the hand were used. The hand can always attempt to make a movement, if appropriately cued, unlike the smooth pursuit system. The lack of proportionality between anticipatory smooth pursuit and high target velocities bears some similarity to the acceleration saturation seen in the initial pursuit when a retinal slip is suddenly imposed. In this situation, the initial eye acceleration increases with retinal slip velocity up to a certain velocity but then saturates above this (the values vary depending on the exact experimental conditions: around 10°/s (Carl & Gellman 1985); around 20°/s (Kao & Morrow 1994); over 30°/s (Robinson *et al.* 1986); over 90°/s (Tychsen and Lisberger 1986)). This can be related to the way that the ratio of neuronal firing rate of velocity-sensitive cells to retinal slip velocity diminishes with increasing velocity (reviewed by Barnes 1993). In contrast to these reactive movements, the anticipatory movement is made in the absence of visual feedback. Thus while the anticipatory reproduction of eye velocity cannot be directly related to acceleration saturation, it may be indirectly related by the storage of these movements being affected by this non-linearity.

Summary of Chapter 3

- There is a sharp decrease in anticipatory smooth pursuit by the eye and anticipatory tracking by the hand when the interval between ramps is long and there is No Cue. Thus both the hand and eye respond to timing uncertainty in the same way.
- There is a still a significant decrease in anticipatory ocular smooth pursuit, although less marked, when an audio timing cue is given before the onset of each ramp. This decrease is unaffected by whether there are simultaneous hand tracking movements or not and suggests that these movements depend on a short-term store.
- This decrease occurs for both 25 and 50°/s targets and for unidirectional and alternate direction ramps.
- In contrast, there is no significant decrease in anticipatory hand velocity when the time of onset of each ramp is preceded by an audio cue. These results suggest that

appropriate anticipatory hand tracking movements can always be made when a timing cue is provided.

- High anticipatory eye velocities lead to target velocity being matched at an earlier time.
- Anticipatory eye velocity is around 25% higher for alternate direction ramps than unidirectional ramps.
- Anticipatory hand velocities are higher than anticipatory eye velocities even at short intervals.

CHAPTER 4: DYNAMIC VISUAL ACUITY AND PREDICTIVE SMOOTH PURSUIT

Introduction

Static Visual Acuity

Visual acuity is a measure of the ability to discriminate small objects or resolve fine details subtending small angles at the eye. This is usually tested with the observer and target stationary and is referred to as Static Visual Acuity (SVA). The exact level of acuity that can be achieved depends on the actual task. Subjects can detect the presence of a dot just ½ min of arc in diameter (i.e. a 0.15mm spot at one metre) (Boff & Lincoln 1986). However, for identifying a letter, rather than just detecting a presence, critical details must subtend around 1 min of arc (i.e. a letter written with a pen tip of thickness 1 min, so that the letter B would subtend 5min in height for example). These Snellen letters are not ideal since they are not all equally legible. Therefore it is often better to ask subjects to identify the orientation of a letter **E** or a 'Landolt' **C**.

Sometimes visual acuity is expressed as a ratio, rather than a minimum angle, which for “normal” vision is 6/6. The ratio is the viewing distance (6 metres) divided by the distance at which the critical detail would subtend 1 min. So visual acuity of 6/9 means that a letter whose details would subtend 1 min at 9 metres away can only be read when placed at 6 metres. This can be easily tested using a chart with rows of letters with decreasing size of critical detail. The correlation between different varieties of acuity target test is not always very good, and results can vary depending on viewing conditions and instructions.

These tests only measure the ability to resolve high spatial frequencies. However, low spatial frequency discrimination is vital for shape discrimination, viewing at large distances, viewing moving targets and vision under low illumination. Therefore testing with gratings of different spatial frequencies is often better. The level of contrast needed to resolve the grating bars or perceive their orientation is tested. Peak sensitivity is around 3 cycles/degree (Burr & Ross 1982). Retinal cones are around 1.5μm wide so to detect a dark gap, there would need to be one darkly lit, unstimulated cone between two brightly lit, stimulated cones as shown in the top half of Fig. 4.1. This would give a resolving power of around 20 seconds of arc, which agrees with the measures above.

Hyperacuity or vernier acuity is the ability to resolve the displacement of one bar relative to another as shown in the bottom half of Fig. 4.1. Surprisingly, subjects can detect displacements of just 2-4 seconds of arc i.e. less than the width of a retinal cone. This is thought to be due to integrating information from many cones over the entire length of each bar.

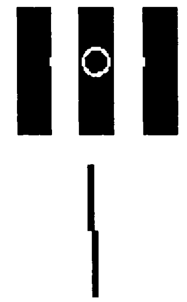


Fig. 4.1
Upper: schematic of the minimum grating spacing that can be detected by retinal cones.
Lower: Vernier acuity test.

Dynamic Visual Acuity

Dynamic Visual Acuity (DVA) is the ability to resolve targets when there is relative motion between the observer and the target. It therefore depends on the ability of the visual system to decipher blurred images and on corrective eye movements to reduce this blur. Visual motion over the retina does not necessarily make objects less visible due to the spatial and temporal properties of the retinal response. Burr & Ross (1982) have shown that very low spatial frequencies are actually seen better when they are in motion on the retina. DVA is often a more functional test of vision than SVA. For example, someone with good SVA but poor DVA would be a dangerous driver.

Visual targets are almost never stationary on the retina, even in apparently static conditions, due to tiny fixational eye movements that constantly sweep the image across the photoreceptors. There are three classes of these movements (reviewed by Carpenter 1988: tremor (movements with velocities of the order 10'/s with amplitude decreasing above 10Hz, probably of peripheral origin); drift (amplitude ~2-5’, velocity of the order of 4’/s); and microsaccades (1 or 2 per second with median amplitude for a subject ranging from 1-23’ and the same dynamic characteristics as normal saccades). Microsaccades provide the only significant retinal motion. They may prevent images fading since perfect stabilisation actually impairs vision (reviewed in Ditchburn 1973). However, many animals manage without microsaccades and they may result from artificial laboratory conditions where subjects fixate a target for longer than its intrinsic interest (Steinman & Haddad 1973). Furthermore, they are not seen during fixational pauses while reading or in very high acuity tasks such as threading a needle (Winterson

& Collewijn 1976). In a sense, these miniature movements are irrelevant in natural situations due to imperfections in the vestibulo-ocular reflex or optokinesis. Steinman *et al.* (1982) report that during natural movements or even when subjects stay as still as possible, there is retinal slip and vergence velocities of a few degrees per second. A large part of the perceptual stability of vision is therefore due to visual processing of blurred images. A small but non-zero level of visual motion is probably desirable. However, movements above a few degrees per second often impair vision. In everyday life, there are often very high relative speeds between objects and the eye. For example, a car travelling at just 16kmph passes an observer 3m away at an angular velocity of 85°/s.

Most DVA studies have been performed by ophthalmologists on large numbers of subjects and usually used high target velocities (e.g. 60-150°/s). Eye movements were often not recorded. In contrast, oculomotor experiments usually use just a few subjects, in spite of high between-subject variability, and relatively low target velocities. Comparisons and inferences between the two bodies of research can therefore be difficult sometimes. These comparisons are important though since improved vision is the reason for moving the eyes. Thus it is important to consider DVA before making conclusions about the functional significance of different aspects of pursuit performance. For example if a patient with poor pursuit performs a certain DVA task as accurately as a subject with "normal" pursuit, then the presence of poor pursuit cannot be said to represent a functional impairment for this task.

Early observers such as Blackburn (1937) merely noted the velocity at which small moving objects became blurred. Ludvigh & Miller (1958) examined DVA more systematically using Landolt Cs moving at between 10 - 170°/s. They were presented for just 400 ms but could be seen moving behind frosted glass before this time. Acuity was around 2.2' at the lowest velocities but got markedly worse with increasing velocity. They fitted a curve of $\mathrm{DVA} = a + b*\mathrm{Velocity}^3$ to the results and found that subjects with similar SVAs could have very different DVAs. Similarly, Reading (1972) tested velocities of 22,43,83 and 167°/s exposed for between 6-120 ms and also fitted a cubic relationship between acuity and velocity.

The first simultaneous measurements of DVA and accompanying eye movements appears to have been by Barmack (1970). He looked at the velocity at which it became impossible to determine the orientation of stripes on a moving disc. Targets were visible for 400 ms or until they had covered 50°, whichever came first. He studied both humans and monkeys. Humans were found to have better SVA, but monkeys had better DVA due to a superior oculomotor performance (less variability, fewer saccades, shorter latencies and higher maximum pursuit speeds). Humans could discriminate 0.7' wide stripes that moved at up to around 60°/s and 1.6' stripes that moved at up to 125°/s.

In contrast to Ludvigh's cubic relationship, Brown (1972) found that DVA deteriorated linearly with target velocity from around 1.5’ at 20°/s to around 3.5’ at 90°/s. He used Landolt Cs exposed for 450 ms. Eye movements were simultaneously measured showing that velocity and position errors increased linearly with target velocity (Position error: ~2° for 20°/s targets, rising to ~10° at 90°/s. Velocity error: ~5°/s for 20°/s targets, rising to ~35°/s at 90°/s.)

Whilst it is clear that there is some degradation in DVA with increased target velocity, it is probable that acuity would be much better if exposure times for faster targets were longer. With many of these experiments, the exposure times, limited by screen amplitude, were probably insufficient for the eye to match the highest target velocities. Smooth eye velocity itself does not appear to impair vision, and reductions in DVA can be explained in terms of velocity and positional errors. This was shown by Demer & Amjadi (1993) for both vertical target motion and head motion.

Long & Rourke (1989) investigated whether training could improve DVA for target velocities between 60 - 150°/s and presentation durations between 200 - 600 ms. Subjects were initially tested for 60 mins, then trained over four 30 min sessions then tested again for 60 mins. They found that Landolt C acuity deteriorated with higher target velocities and shorter durations. The largest improvements with training were for the hardest conditions and in subjects that were initially the worst. The experiment was later repeated with the head free to move naturally (Long & Riggs 1991). DVA was actually better than when the head was fixed. The DVA of athletes was also tested and found to be slightly but not significantly better than other students.

An important issue is whether the eyes move in the same way when trying to identify a moving target as they do when simply following its motion. Target identification (TI) of a novel target is perhaps more natural than the continual tracking of a familiar target used in most smooth pursuit experiments which may not produce the optimum performance. As mentioned in the introduction of this thesis, the basic pursuit response evoked when passively staring at a moving object can be enhanced by actively attending to the target. However, there have been suggestions of further improvement when subjects are asked to identify a moving target rather than simply follow its motion. Shagass *et al.* (1976) reported greatly improved pursuit (assessed by visual inspection of EOG traces) of moving letters compared to a simple spot in both controls and psychiatric patients. Sweeney *et al.* (1994) assessed that pursuit of a target that alternated between an O and an X was less saccadic than normal. In a more detailed study, Van Gelder & Lebedev (1995) found a similar improvement with fewer saccades, higher gain and reduced r.m.s. error when reading changing letters that moved with a 30°/s triangular wave. Somewhat counter-intuitively, these last authors also found that mild distraction (a listening task) improved pursuit, suggesting that the improvement during TI was due to *diverting* attentional effort away from misguided attempts to enhance smooth pursuit. This seems plausible since subjects often have a poor sense of their smooth eye velocity e.g. subjects can be unaware of anticipatory smooth pursuit (Kowler & Steinman 1981) or may think they are moving their eyes smoothly in the absence of a moving target whilst only making saccades (von Noorden & Mackensen 1962).

The two experiments described in this chapter are the first to study the effect of a TI task on the predictive components of smooth pursuit velocity. The problem with presenting an acuity target for the entire ramp, as done in most DVA experiments, is that eye movements will drastically alter the velocity and position errors of the target during the ramp for ramps longer than 100 ms. In the experiments described here, the annulus pursuit target changed into a Landolt C acuity target for only a brief period at a set time during each ramp as shown in Fig. 4.2.

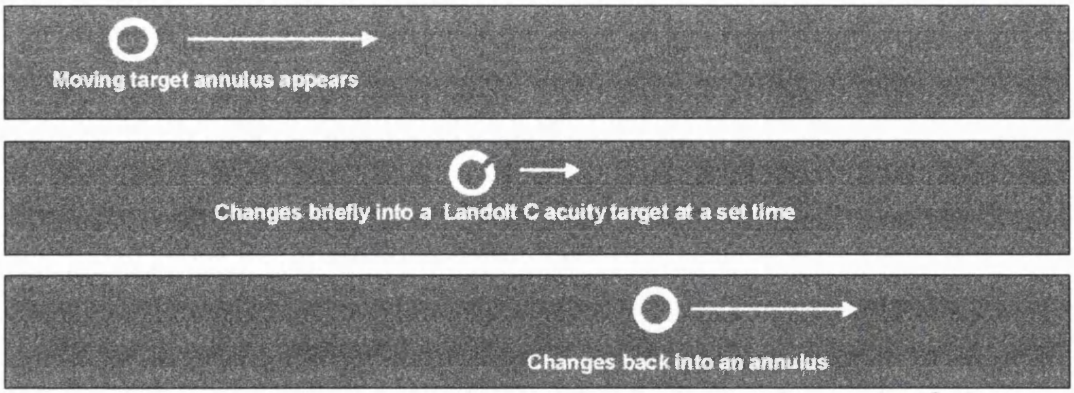


Fig. 4.2 Schematic of the target identifcation (TI) task. Subjects had to identify the orientation of the C.

This tested whether subjects could alter their anticipatory responses to optimise pursuit at one particular time during the ramp. Only one size of annulus (and C) was used to avoid pursuit being altered by the target size. The aim was to assess the effect of TI on predictive pursuit rather than to measure acuity very accurately.

Experiment 4a: Improvement of predictive smooth pursuit while attempting to identify moving acuity targets

Introduction

Experiment 2a showed that anticipatory acceleration only reaches about 60% of target velocity by 100 ms after ramp onset. It is possible that the system does not try to attain higher anticipatory velocities since there is always a period of accurate pursuit and clear vision during the middle of each ramp. To explore this possibility, an acuity target was always presented just after ramp onset to see if this would induce an increase in anticipatory acceleration to reduce retinal slip at this time.

Deceleration in anticipation of ramp offset before visual feedback of the actual offset can have had an influence is noticeable for all the constant duration ramps shown in this thesis. It is not obvious why visual feedback of the target that is still moving does not correct this self-induced error. Unlike anticipatory acceleration, it does not improve tracking of the ramp. Furthermore it cannot be produced in order to reduce an expected retinal slip in the future since for the ramps described so far, there was only darkness after the end of each ramp. Several authors have commented on this phenomenon (Kowler & Steinman 1979b; Boman & Hotson 1988; Ohashi & Barnes 1996) but the cause has not been previously studied. Robinson *et al.* (1986) claimed that it could not be eliminated voluntarily and in our experience, such attempts may only lead to saccades. This experiment examined if it could be reduced by requiring identification of a moving acuity target that always appeared near the end of each ramp.

Several authors have commented on the high variability between consecutive reactive responses to identical stimuli (Robinson 1965) and between consecutive anticipatory responses (Kao & Morrow 1994; Moschner *et al.* 1996). The possibility was tested that the requirements of an acuity task would reduce this variability and make the responses more reproducible.

Method

The complete method for this experiment is described here since it differs considerably from the General Method that applied to chapters 2 and 3. A computer-generated stimulus was needed to briefly display acuity targets since alternating photographic slides would have been impractical. A Hewlett Packard high-resolution monitor (1280 pixels wide x 1024 high) was used. Unfortunately, monitors are limited in resolution and amplitude. Larger amplitudes can be achieved by projecting the image or placing the subject closer to the screen but the accompanying loss of resolution means that small acuity targets cannot be displayed. Additionally, the finite refresh rate means that at high velocities, the target appears as discrete flashes across the screen rather than as a smoothly moving target. This is not really a problem for normal pursuit experiments since sequentially flashed stationary targets are an adequate pursuit stimulus (Barnes & Asselman 1992). However for DVA tasks it is undesirable. The refresh rate was 60Hz (once every 16 ms) so to traverse 1280 pixels at maximum smoothness (one pixel per refresh) would take 20.5 s, which is very slow. Therefore a small amount of 'jumping' had to be accepted. The screen was placed at 90cm from the subject's head at eye level. This is closer than in the previous experiments (1.5m) but only resulted in a convergence angle of ~3.8° for an inter-ocular spacing of 6cm. The screen had a certain amount of persistence which was accentuated by viewing in the dark. Two sheets of neutral density filter were therefore placed over the screen so that any 'tail' to the moving target was unnoticeable. The target had a luminance of 1.1 cd/m^2 and the background was <0.01cd/m^2. The graphics buffer was updated every 5 ms even though the screen only refreshed every 16 ms.

Each pixel subtended ~0.9min of arc. The target was an annulus (26 min of arc outer diameter, 20.8 min of arc inner diameter), chosen so that critical detail subtended 5.2 min of arc. During each ramp, the annulus changed into a Landolt C acuity target for just 100 ms at a set time during each ramp. The gap in the C was 5.2' wide. Subjects had to identify the C orientation and respond as quickly as possible, by pressing one of four buttons on the right armrest corresponding to the four possible C orientations. The gap in the C was in one of four pseudorandomly chosen positions at 45° from the vertical so that all orientations would be equally blurred during horizontal motion. Between responses, subjects kept their index finger on a central point around which the four, equidistant buttons were placed (Fig. 4.3). The middle of each 17mm^2 button was 38mm from the central point. This arrangement was thought to be the most intuitively obvious. A picture of a C in each orientation was drawn next to the appropriate button. The output of the response buttons was simultaneously recorded in the data files.

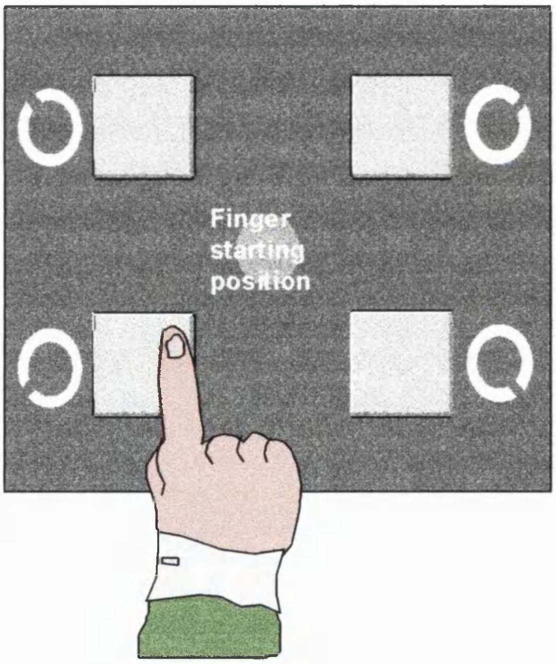


Fig. 4.3 Diagram showing the response box used by subjects to indicate the orientation of the Landolt C when it appeared.

When measuring reaction time it is desirable to have an estimation of certainty of the response. The interval between ramps was too short to obtain an additional estimation of certainty from the subject so to exclude guesses, subjects were asked to respond as quickly as possible but only when they were reasonably sure of being correct. This instruction was chosen so that button press response time could be used as the main measure of task difficulty. It was assumed that response time would be a more sensitive measure of performance than the percentage of correct responses, since for this experiment there were only 29 possible percentage scores but no such constraints on response time

The eight subjects (aged 22 - 50, 3 male) had normal or corrected-to-normal static visual acuity (at least 6/5 as measured using an E-letter chart). Their oculomotor testing experience ranged from naïve to experienced. Each subject sat in a very dimly lit room with the head fixed using a clamp and chin rest. The room was dark except for a small amount of background light from instrument panels, which seemed beneficial in maintaining arousal and reducing blinks.

Left eye movements during binocular viewing were recorded by infra-red limbus tracking (Microguide Inc, Illinois, USA), with resolution better than 6 min arc. Eye and target position signals were sampled at 200Hz with 12-bit resolution. Saccades were identified by an acceleration criterion using a semi-automatic procedure and replaced by linear interpolation to obtain the smooth eye velocity traces used for averaging.

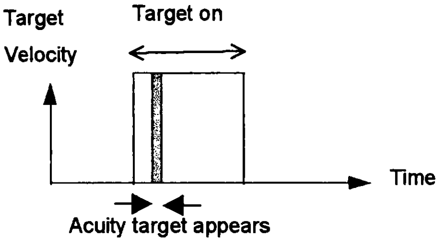
One combination of the experimental factors described below was tested in each trial of 32 ramps. Only the last 28 presentations were analysed to give the 'steady state' response. Before each trial, a calibration was performed (eye and target signals matched during pursuit of a 0.4Hz sine wave of amplitude ±8.8°). The fact that the screen was flat rather than concave meant that the angular velocity of a target near the edges was actually lower. The calibration extended to ±8.8° so this would represent a maximum error of 2.34% which was considered acceptable.

The target moved in a horizontal 15°/s ramp lasting 700ms, centred about the midline. Consecutive ramps were in alternate directions occurring at certain inter-stimulus intervals. There were 9 trials altogether each lasting slightly over a minute. Prior to each trial, subjects were informed of the target motion parameters produced by combining the following two experimental factors:-

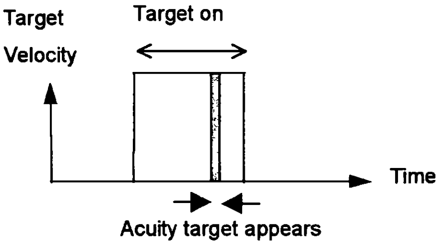
1) Interval Timing: Either *Regular* 2.4 s inter-stimulus intervals between the onset of consecutive ramps or *Random* intervals of 1.8, 2.2, 2.6 or 3.0 s, giving an average interval of 2.4 s. The intervals had to be long enough to allow a target identification response but short enough to encourage anticipatory pursuit.

2) C condition:

C after onset - the annulus target changed into a Landolt C for 100 ms starting 100 ms after target ramp onset



C before offset - the C appeared for 100 ms starting 200 ms before ramp offset



Random C - the C pseudorandomly appeared at either the *C after onset* or *C before offset* position

No C - the annulus never changed and subjects were just asked to accurately pursue the target

To control for training effects the eight trials were presented in a random order over the eight subjects using a Latin square design. At the start of each session, subjects were given a few minutes practice to check that they were happy with the instructions and were familiar with the procedure for pressing the buttons. A control trial was also performed for the *Random C* with *Random* Intervals but with the target stationary at the centre of the screen.

Results

Eye velocity

The upper graph of Fig. 4.4 shows the mean response by the eight subjects to each of the four different C conditions when there was a *Regular* interval of darkness between each ramp. The lower graph shows the responses when there was a *Random* interval.

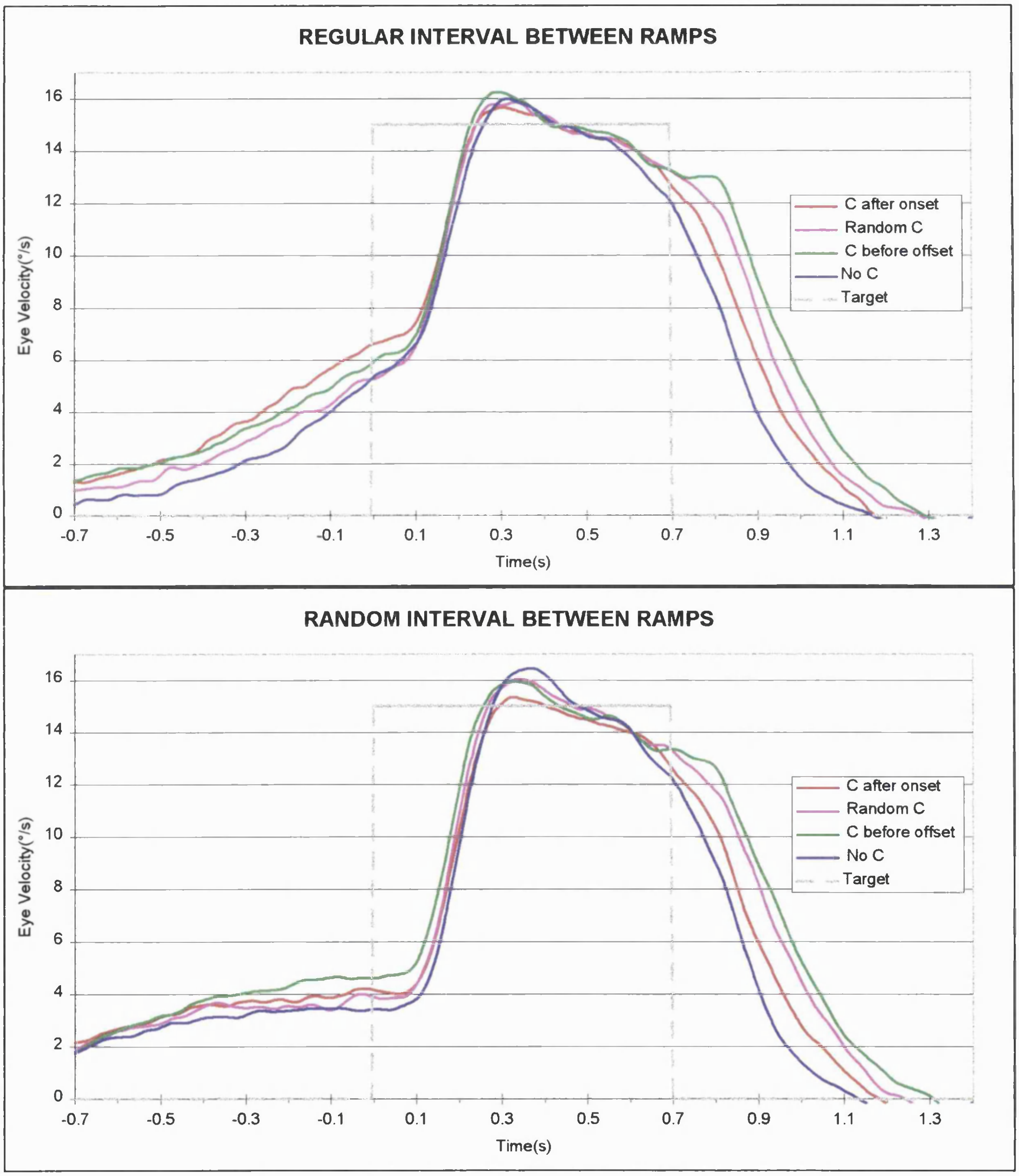


Fig. 4.4 The upper graph shows the mean response by the eight subjects to the four different C conditions when the intervals of darkness between ramps were regular. The lower graph shows the responses for random intervals.

Clearly there was not a dramatic difference between the smooth pursuit responses to the different C conditions despite the fact that the tasks were subjectively very different. For *Regular* intervals, the anticipatory acceleration to *C after onset* and *C before offset* was slightly higher than for *No C.* However there was no dramatic increase in anticipatory acceleration to reduce the initial retinal slip of the target when it appeared. The differences were no larger for *Random* intervals. The anticipatory deceleration seemed to be greatest for *No C* and reduced for the other conditions, especially *C before offset.* This suggests that concentrating on accurate pursuit of the end of the ramp can reduce, but not eliminate, anticipatory deceleration. During the middle part of the ramp, there was very little difference between any of the responses.

To statistically analyse the differences in anticipatory acceleration, each subject's mean smooth eye velocity 100 ms after ramp onset ($V100_{ON}$) was entered into a Repeated-measures factorial ANOVA (Interval Timing (2 levels) * C Condition (4 levels)). The values are shown in Fig. 4.5 and the ANOVA results in Table 4.1.

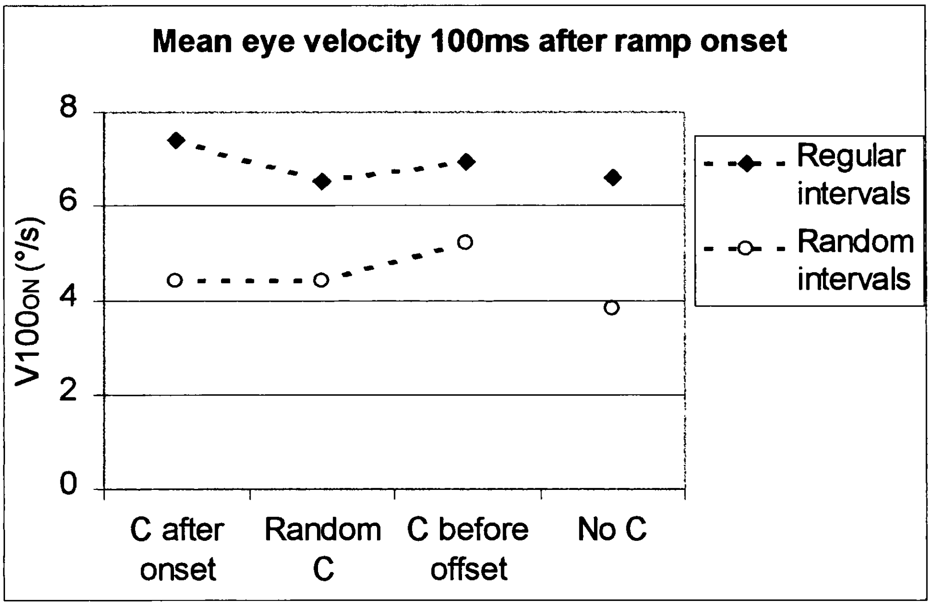


Fig. 4.5 Mean smooth eye velocity at 100 ms after ramp onset ($V100_{ON}$) by the eight subjects for the 8 different stimulus conditions.

$V100_{ON}$	F	Degrees of freedom	Significance
Interval timing	29.25	1	0.001
C Condition	4.02	3	0.084
*Interval timing * C Condition*	8.56	3	0.021

Table 4.1 Results of factorial ANOVA on smooth eye velocity 100 ms after ramp onset ($V100_{ON}$). Planned contrasts tested for significant differences between V100 for the No C condition with the other three C conditions: C after onset, p=0.064, Random C, p=0.634; C before offset, p=0.025. Only three contrasts were planned so no Bonferroni correction was considered necessary (see Statistical analysis section).

Interval Timing was a significant factor (p=0.001). V100 was high for *Regular* intervals since the release of anticipatory responses could be synchronised with ramp onset. In contrast, for *Random* intervals, there was a lower, more constant velocity. This was due to a slow expectant drift and also the averaging of occasional faster responses released at the wrong time. The C Condition factor did not reach significance (p=0.084). There was a tendency for conditions with Cs to evoke slightly higher anticipatory velocities as would be expected if subjects were trying to reduce the initial retinal slip but only V100 for *Late C* was significantly higher than for *No C* (p=0.025). However this difference was very small (on average 0.9°/s) and much less than the typical variability in eye velocity from repeated responses. For each subject, the standard deviation at 100 ms after ramp onset was around ±2-3°/s for all conditions. There was no indication that the acuity task made the responses more reproducible. Thus for these stimulus conditions it was clear that anticipatory acceleration was little affected by the acuity task.

To analyse the differences in anticipatory deceleration, a similar ANOVA was performed on smooth eye velocity 100 ms after ramp offset ($V100_{OFF}$). If there had been no anticipatory deceleration, eye velocity should still have been around ramp velocity at 15°/s. However, anticipatory deceleration was prominent for all conditions. At 100 ms after ramp offset, before subjects could utilise any feedback of the end of the ramp, eye velocity was 2-6°/s less than ramp velocity (Fig. 4.6). The results of the ANOVA are shown in Table 4.2.

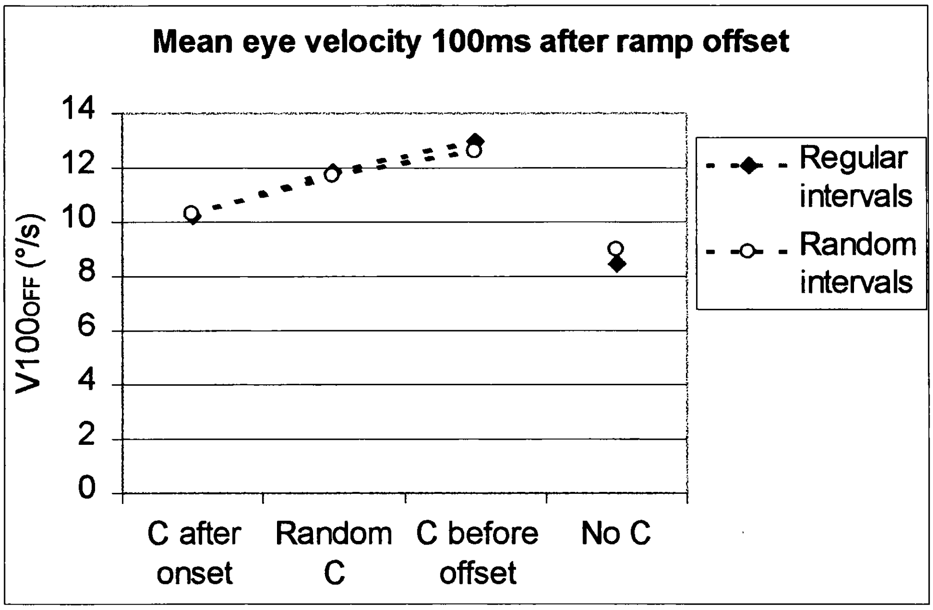


Fig. 4.6 Mean eye velocity at 100 ms after ramp offset by the eight subjects for the 8 different stimulus conditions

$V100_{OFF}$	F	Degrees of freedom	Significance
Interval timing	0.016	1	0.902
C Condition	20.21	3	0.003
*Interval timing * C Condition*	2.50	3	0.174

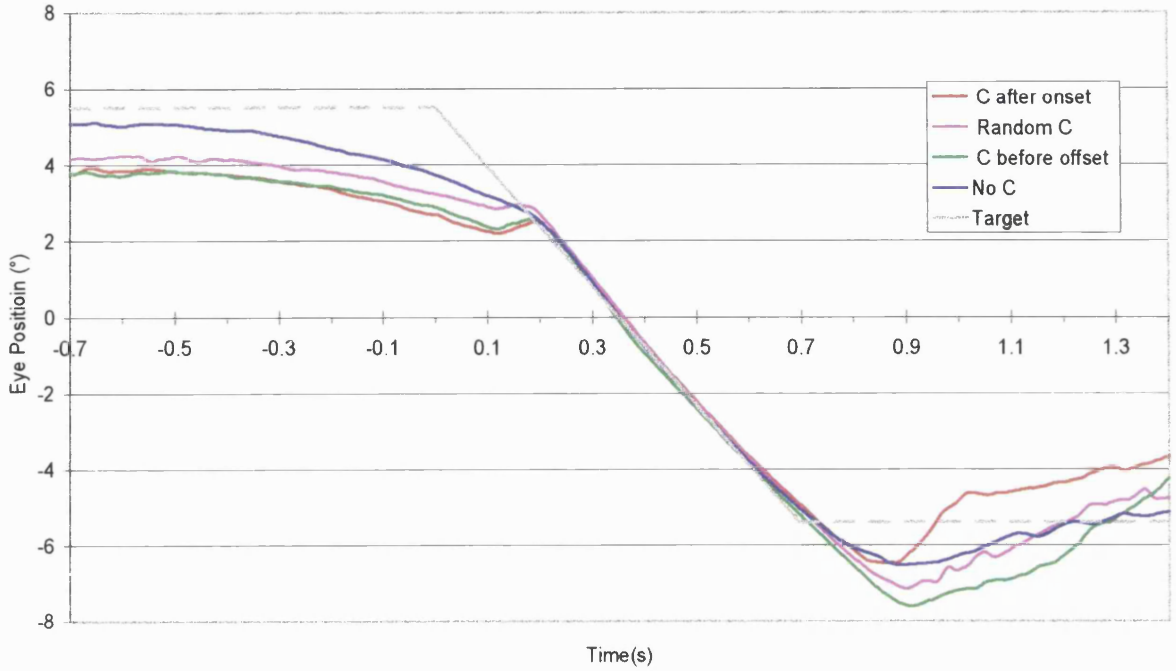
Table 4.2 Results of factorial ANOVA on smooth eye velocity at 100 ms after ramp offset ($V100_{OFF}$). Planned contrasts tested for significant differences between V100 for the No C condition with the other three C conditions: C after onset, p=0.132, Random C, p=0.001; C before offset, p<0.001. Only three contrasts were planned so no Bonferroni correction was considered necessary (see Statistical analysis section).

Interval Timing was not a significant factor since by this time, visual feedback had eliminated the initial advantage in knowing when the constant duration ramp would start. C Condition was a significant factor though (p=0.003). The system maintained significantly higher velocities at this time for both *Random C* (p=0.001) and *C before offset* (p<0.001). Thus the appearance of a C towards the end of the ramp reduced and/or delayed anticipatory deceleration but did not eliminate it. The effect of C condition had a larger effect on eye velocity at this time compared to near ramp onset.

Eye position

Fig. 4.7 shows the mean positional trajectories by the eight subjects to all eight stimulus conditions.

REGULAR INTERVAL BETWEEN RAMPS



RANDOM INTERVAL BETWEEN RAMPS

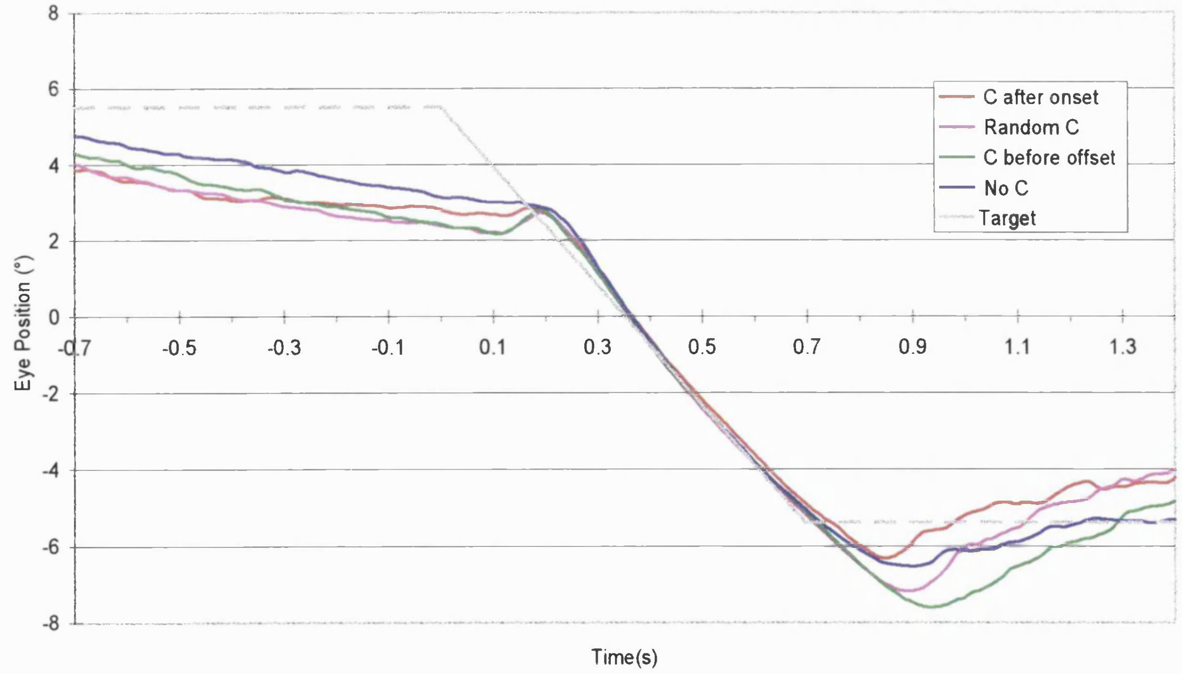


Fig. 4.7 Upper graph shows the mean positional trajectories by the eight subjects to the four C Conditions when the intervals of darkness between ramps was Regular. Lower graph shows the responses when the intervals were randomised.

The smooth accelerating anticipatory movement synchronised with ramp onset for *Regular* intervals contrasted with the relatively constant average velocity movement for *Random* intervals. For all conditions, the eye was often in a less eccentric position than the position where the ramp would start from. This often necessitated a back-up saccade. This was followed by a period of accurate tracking before the eye started to slow down in expectation of the end of the ramp. The eye seemed to start slightly more eccentrically for *No C* conditions. This is probably because there were often centripetal saccades after the end of each ramp for the acuity task conditions so that subjects would be ready for the next ramp as soon as possible. By 100 ms after ramp onset though, neither Interval timing nor C condition were significant factors in an ANOVA of mean eye position at this time.

A plot of mean position obscures saccades by smoothing them out. Therefore, Fig. 4.8 shows some raw data from one subject while tracking ramps with *Regular* intervals for three different C conditions. While the smooth pursuit is quite similar, there appear to be considerably more saccades between each ramp for the conditions with Cs. This is presumably an expression of the extra concentration that subjects reported was needed for the conditions with Cs. However, it seems that the repositioning saccades between ramps left the underlying smooth pursuit relatively unaffected.

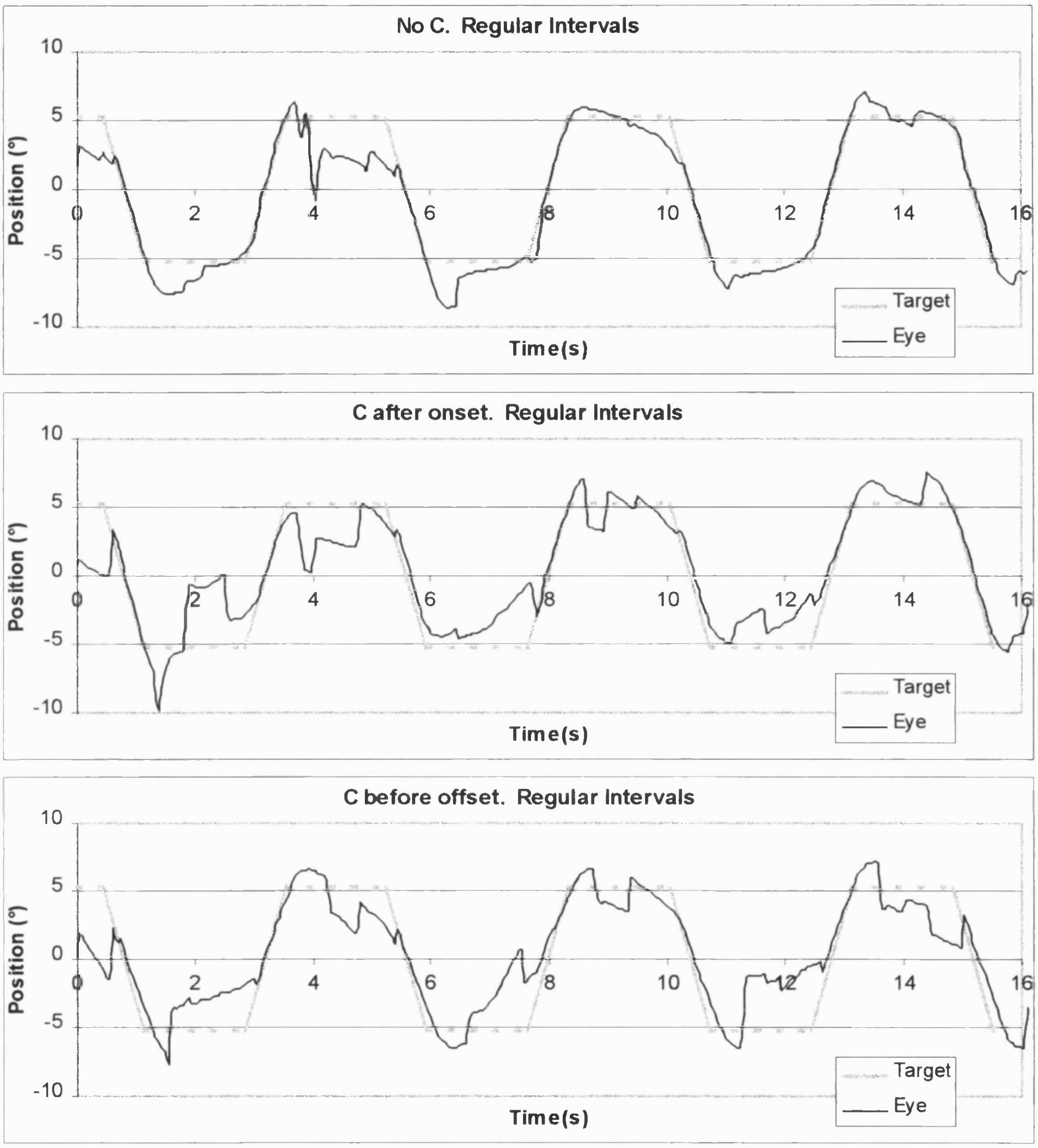


Fig. 4.8 Raw data before removal of saccades from one subject to illustrate the more frequent occurrence of saccades between ramps when there was an acuity task.

Accuracy of responses

Subjects were asked to only respond when they were reasonably sure of being correct. This instruction appears to have been adhered to since over 80% of the responses made were correct. Thus for the more difficult conditions, subjects made fewer responses rather than more guesses. Fig. 4.9 shows the percentage of correct responses as a proportion of the number of ramps.

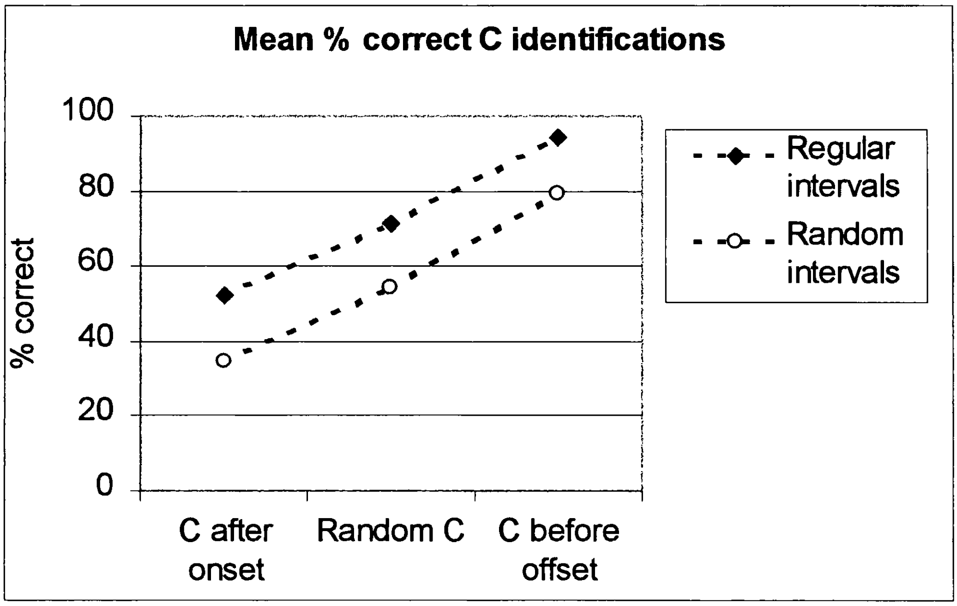


Fig. 4.9 Mean percentage of correct identifications by the eight subjects as a proportion of the number of ramps presented.

All subjects performed well in the control trial when the target was static, identifying over 90% of Cs correctly. For the conditions where a moving C appeared, *C after onset* was the hardest and *C before offset* the easiest, with an intermediate value for the *Random C*. For *Random C*, during exactly half of the number of ramps, the C appeared at the *C after onset* time and for the other half at the *C before offset* time. The fact that the percent correct is very close to the mean percent correct of the *C after onset* and *C before offset* conditions suggests that there is very little benefit in knowing that the C will always appear at a set time during the ramp. If there was an obvious benefit then accuracy for *C after onset* and *C before offset* would be high and accuracy for *Random C* would be low. This was not the case, which is in accord with the finding that subjects were unable to greatly modify their pursuit velocity profiles to optimise acuity at a particular time.

The randomisation of the interval between presentations systematically reduced the percentage of correct responses. For *C after onset*, this is presumably due to subjects having a lower V100 and hence higher initial retinal slip when the intervals were *Random*. Surprisingly this was even true for the *C before offset* / *Random* intervals condition despite the eye having 500 ms in which to establish accurate pursuit and the similarity of the eye velocity traces at this time.

The button press response times were generally quite long, probably because a choice decision has to be made between the four orientations as well as a decision about certainty before making a movement to the chosen button. The response time was measured from the time the C appeared to when the button contact was made (see Fig. 4.10 for values). The results of an ANOVA on response time are shown in Table 4.3.

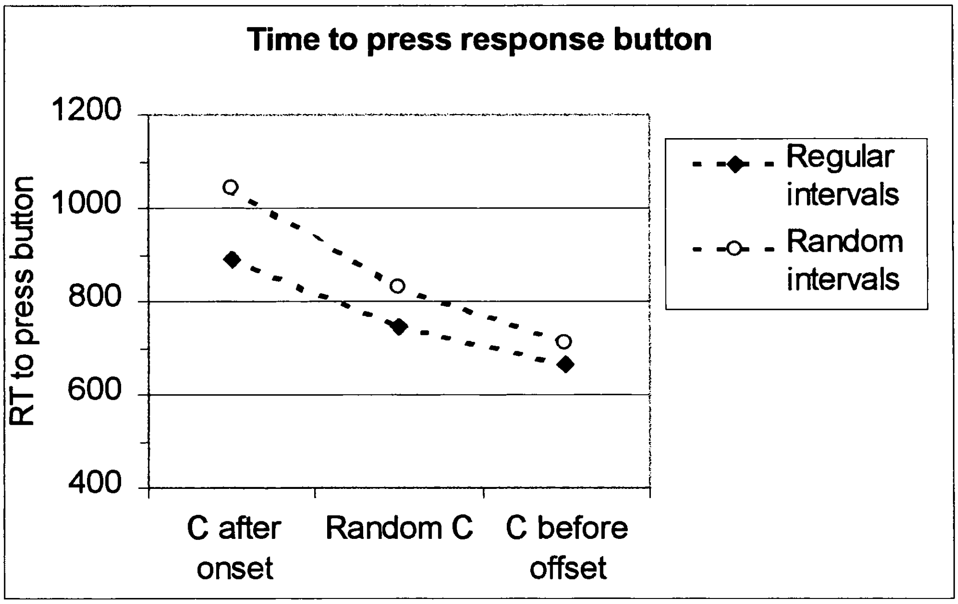


Fig. 4.10 Mean response time after appearance of the C by the eight subjects

Response time	F	Degrees of freedom	Significance
Interval timing	10.06	1	0.016
C Condition	7.74	2	0.022
*Interval timing * C Condition*	1.17	2	0.373

Table 4.3 Results of factorial ANOVA on the time after ramp onset for each subject to press a response button. Planned contrasts tested for significant differences between V100 for the C after onset condition with the other two conditions with Cs: Random C, p=0.032; C before offset, p=0.006. Only two contrasts were planned so no Bonferroni correction was considered necessary (see Statistical analysis section).

As would be expected, the harder conditions with lower percentages of correct responses led to longer reaction times. *Random* intervals led to significantly longer response times (p=0.016) than for *Regular* intervals. Response times were significantly shorter for *Random C* (p=0.032) and *C before offset* conditions (p=0.006) compared to *C after onset*, in accord with these conditions having a higher percentage of correct responses. Surprisingly there was not a significant Interval Timing*C Condition interaction (p=0.373) despite the fact that the *Regular* and *Random* interval lines seem to converge (Fig. 4.10). Convergence means that randomisation of the intervals had less of a deleterious effect when the C was presented late in the ramp. There was a general trend for this convergence but the pattern of interaction was quite variable between subjects. Thus, as was found for the percentage of correct responses, even 500 ms after ramp onset, there still appears to be a slight disadvantage in the onset having occurred at a random time.

The average response time for the control trial with a stationary target with *Random C* and *Random* intervals was 699 ms which is very similar to the values for *C before offset* with *Regular* or *Random* intervals. This shows that pursuit of the target at the end of the ramp provides comparable vision to fixation of a static target.

There were no significant differences in response times between the four possible C orientations (ANOVA on the mean response time to press each of the four different buttons by each subject, p=0.269). Thus subjects did not take longer to recognise one orientation and move their finger to the appropriate button. There was no large or consistent leftwards/rightwards asymmetry in the button pressing response times or percent correct in any subject.

There was a significant age effect with the older subjects (GB, GL, JSH) taking longer to respond as shown in Fig. 4.11 (regression of mean response time against age; p=0.003).

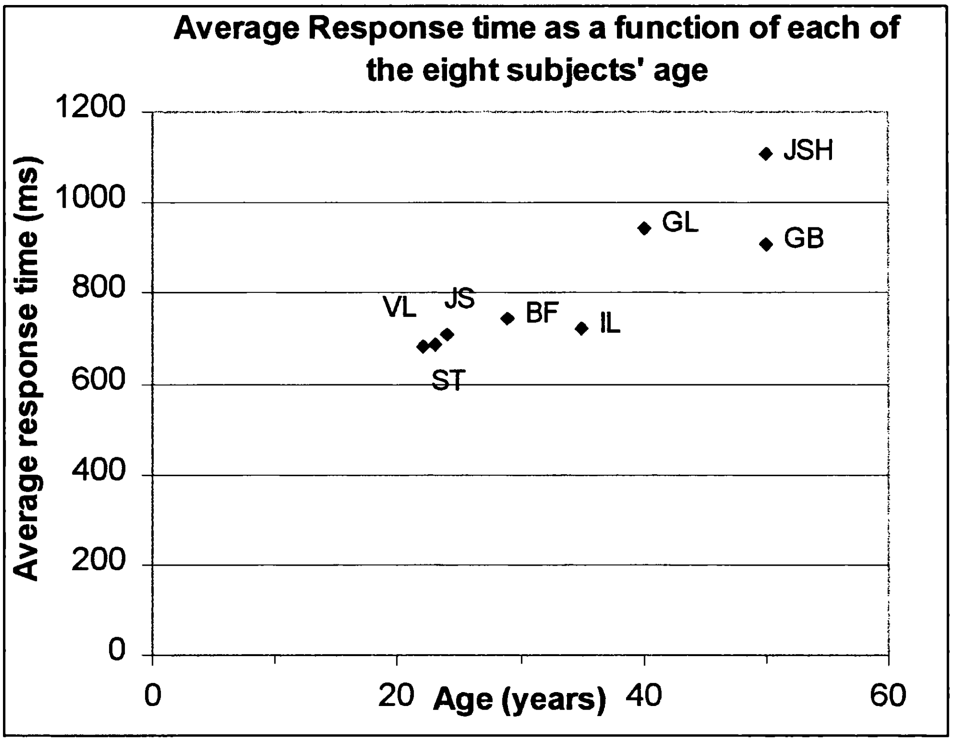


Fig. 4.11 Increase in response time with age

Conclusions

The surprising finding of this experiment is that the regular appearance of moving acuity targets during repetitive ramps makes little difference to the pattern of predictive pursuit. There was a tendency for anticipatory acceleration to be higher but this did not reach significance. Anticipatory deceleration was reduced when the C always appeared near the end of the ramp but the difference was quite small. It is unlikely that the task was too easy since performance was not perfect for any condition and was quite poor for *C after onset.* However it is possible that the retinal slip at the start and end of the ramp was not large enough to induce changes. To test this possibility the next experiment employed a similar paradigm using ramps that were twice as fast.

Experiment 4b: Ability to modulate predictive pursuit while attempting to identify fast moving acuity targets

Introduction

The last experiment showed that the pattern of predictive pursuit of 15°/s ramps separated by intervals of darkness is relatively unaffected by a simultaneous acuity task. Perhaps the reason that anticipatory acceleration was not greatly increased and anticipatory deceleration not eliminated was because the retinal slip was not large enough at the time when the C was presented. When the C was presented for *C before offset*, retinal slip was around 1 or 2°/s which will have little affect on acuity (Westheimer 1954a). In contrast, the retinal slip was substantial (8-12°/s) when the C was presented for *C after onset* in accord with the poor performance in the acuity task for this condition. To explore this further, a faster ramp velocity was used in this experiment since the velocity profiles from chapters 2 and 3 show that faster ramps lead to higher retinal slip near ramp onset and offset. In addition, the presentation time was made 50 ms closer to the start of the ramp for *C after onset* was and 50 ms closer to the end of the ramp for *C before offset*.

If a target is stationary and visible before it moves, it is clear that there must be a transition from fixation to pursuit. Similarly if it stops and remains visible at the end of a ramp there must be a transition from pursuit to fixation. When pursuit is initiated or terminated in the dark, as occurred in all trials described so far in this thesis, then the processes that occur in this transition are not so obvious. Since these processes are intimately related to anticipatory acceleration and deceleration, extra conditions were introduced in this experiment where the target was stationary and visible between ramps. This would allow a comparison of the transition between fixation and pursuit and between darkness and pursuit. To introduce this, some of the previous research on the transition from fixation to pursuit will be discussed.

Most laboratories studying smooth pursuit require subjects to fixate a stationary target before pursuing it once it moves. If the motion is relatively predictable then anticipatory acceleration is still produced (Kowler & Steinman 1979b; Becker & Fuchs 1985) and can even occur against a structured background (Barnes *et al.* 1997). However the magnitude is reduced, presumably due to the tendency for optokinesis to keep the eye still in the presence of a stationary target. Boman & Hotson (1988) showed that higher anticipatory velocities were reached when a period of darkness ("gap") was left between the disappearance of the fixation target and the appearance of the moving target. When there is no gap then in order to generate anticipatory acceleration, subjects must disengage fixation and ignore the self-induced retinal slip. To comply with the usual instruction to "track the target accurately" would, in principle, require an instantaneous switch from accurate fixation of the stationary target to accurate pursuit of the moving target. This is impossible due to the dynamics of the oculomotor system. The predictive response is therefore a compromise that must start at a time before the expected ramp onset in order to reduce velocity error at onset. To assess if an acuity task could alter this compromise, additional conditions were used where the target briefly turned into a C while it was stationary between ramps. The presence or absence of a fixation target does not just affect anticipatory pursuit but can also affect the reactive visually guided pursuit that occurs when the time of onset and direction of the ramp is unknown. The latency of this reactive pursuit can be reduced by the presence of a gap. Presumably the extinction of the fixation target allows fixation to be disengaged thereby reducing the time needed to release a pursuit reaction. Krauzlis & Miles (1996a) used a 200 ms gap to reduce pursuit latency from 146 to 119 ms. In contrast Morrow & Lamb (1996) found that the latency of reactive smooth pursuit was 109 ms for predictable motion and 149 ms for unpredictable motion regardless of the presence or absence of a gap. Knox (1996) found that a gap could reduce pursuit latency from around 245 ms to around 195 ms. However these latencies are so long that there must be some doubt about the method or analysis used in this experiment. Merrison & Carpenter (1995) claimed that short latency pursuit could be evoked by an audio cue just before ramp onset in an unpredictable direction but it is unclear how anticipatory guessing movements were eliminated from their data. While there is some disagreement over the existence of a gap effect for pursuit it has been well established for saccades. In addition to reducing the latency of saccades, there can sometimes (Fischer and Ramsperger 1984) but not always (Krauzlis & Miles 1996a) also be a separate population of "express" saccades with latencies around 100 ms separate from the population of regular saccades with latencies around 150 ms. Bekkering *et al.* (1996) showed that there was also a small gap effect for manual pointing and choice manual keypresses in response to the sudden movement of a visual target.

Against this background, the following experiment was designed to assess:

1) If a moving acuity target presented during each ramp could increase anticipatory acceleration and reduce anticipatory deceleration when the target velocity was high (30°/s).
2) If a stationary acuity target presented just before or after each ramp would decrease anticipatory acceleration and increase anticipatory deceleration.
3) If an acuity task could reduce the high variability between consecutive smooth pursuit responses to identical stimuli that several authors have commented on (Robinson 1965; Kao & Morrow 1994; Wells & Barnes 1998)

Methods

The nine volunteers (aged 24 - 51, 5 male) had normal or corrected-to-normal visual acuity. Their oculomotor testing experience ranged from naïve to experienced. Each subject sat in a very dimly lit room with the head fixed. A new display was constructed using a ring of 12 LEDs to produce a red target annulus, where each disc of light (1.1cd/m^2) abutted the two adjacent discs. This was projected via lenses and a servomotor-controlled mirror onto a tangent screen 1.5m away (<0.02cd/m^2). Extinguishing one LED produced a C shape with the same proportions as a Landolt C (outer diameter 1.0°, inner diameter 0.6°, gap in the C 0.2°). Only one size of annulus (and C) was used to avoid pursuit being altered by the target size. Although this ring of discs was not an annulus of uniform width, it was acceptable since the aim was to see the effect of TI on smooth pursuit rather than to measure acuity precisely. However, the percentage of correct responses for this one size gave some idea of acuity at different times during the response. There were several advantages of this target over one generated on a computer screen as used in Experiment 4a. There was less limitation in the amplitude of movement, the illumination was not interrupted by screen refreshes and the switching occurred in much less than a millisecond. Left eye movements during binocular viewing were recorded by infra-red limbus tracking (Skalar Iris), with 5-10min arc resolution. Eye and target position signals were sampled at 200Hz with 12-bit resolution.

Each subject performed 16 trials in a pseudorandom order over two 30-minute sessions. The target moved in horizontal 31°/s ramps lasting 700ms, centred about the straight ahead position, in alternate left and rightwards directions separated by a certain interval. Each trial consisted of 18 identical ramps characterised by one combination of the three experimental factors. Only the last 16 ramps (normalised over direction) were analysed to give the 'steady state' response. At the start of each trial, a calibration was performed and subjects were informed of the target motion parameters. The three experimental factors that were varied were:

1) Interval Timing: Either *Regular* 1.7 s intervals between ramp onsets or *Random* intervals of 1.1, 1.5, 1.9 or 2.3 s.

2) Visibility Between Ramps: The target was either visible and stationary (*Visible between ramps*) or invisible (*Invisible between ramps*).

Fig. 4.12 shows a schematic of the four basic waveforms.

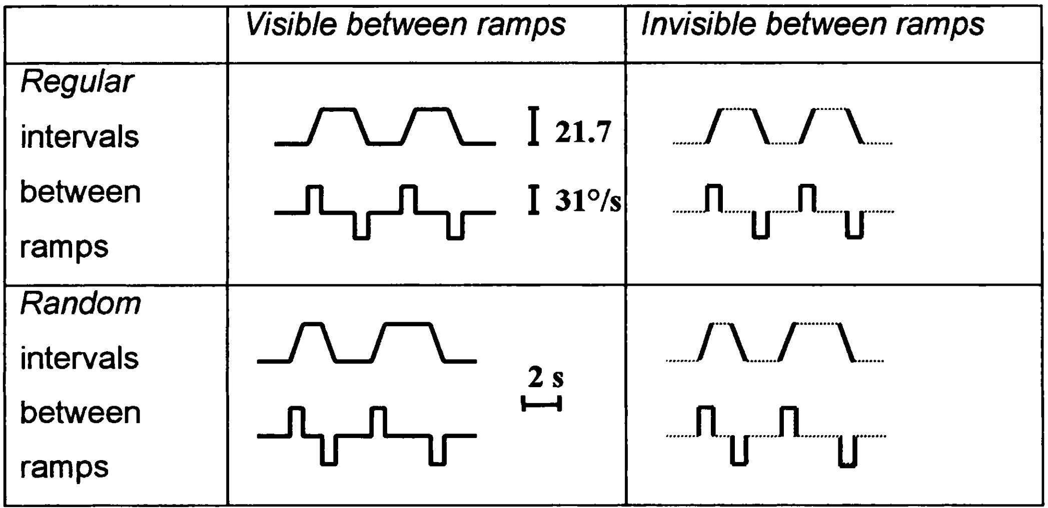


Fig. 4.12 Schematic of the position and velocity profiles of several consecutive ramps for the four basic combinations of the factors Interval Timing and Visibility Between Ramps. Dotted lines indicate when the target was invisible and the subject was in darkness.

To assess how the task of TI might alter the responses to these waveforms, they were combined with a third factor.

3) C condition: For TI conditions, the annulus target briefly changed into a Landolt C for 100 ms once per ramp. The C could be in 1 of 4 pseudorandomly chosen orientations with the gap at 45° from vertical. Subjects had to identify the C orientation and respond as quickly as possible, or guess if unsure, by pressing one of four buttons on the right armrest corresponding to the four possible orientations. Between responses, subjects kept their index finger on a central point around which the four, equidistant buttons were placed. For a TI trial, the C always appeared at the same set time relative to each ramp. There were five C conditions:

C before onset - a stationary C appeared for 100 ms at 150 before ramp onset (only possible for *Visible between ramps*)

C after onset - a moving C appeared for 100 ms at 50 after ramp onset

C before offset - a moving C appeared for 100 ms at 50 before ramp offset

C after offset - a stationary C appeared for 100 ms at 50 ms after ramp offset (only possible for *Visible between ramps*)

No C - the annulus never changed and subjects were just asked to track the target accurately at all times.

The 16 conditions produced by combining all the factors are shown in Table 4.4

	C Condition				
	C before onset	*C after onset*	*C before offset*	*C after offset*	*No C*
Visible between ramps	*1/ Regular* *2/ Random*	*3/ Regular* *4/ Random*	*5/ Regular* *6/ Random*	*7/ Regular* *8/ Random*	*9/ Regular* *10/ Random*
Invisible between ramps		*11/ Regular* *12/ Random*	*13/ Regular* *14/ Random*		*15/ Regular* *16/ Random*

Table 4.4

Statistical analysis was by repeated-measures factorial ANOVA where for each condition there were nine values which were the mean responses from the nine subjects for that condition. Quoted values are the mean ± SD over the nine subjects. Since some combinations of factor levels were not possible, a full factorial ANOVA could not be done. Therefore, for each variable e.g. eye velocity at 100 ms after ramp onset, one ANOVA analysed conditions 1-10 (Interval Timing (2 levels) * C Condition (5 levels)) and another ANOVA analysed conditions 3-6 plus 9-14 plus 15-16 (Interval Timing (2 levels) * Visibility between ramps (2 levels) * C Condition (3 levels)).

Saccades were identified by an acceleration criterion using a semi-automatic procedure and replaced by linear interpolation to obtain the smooth eye velocity traces used for averaging. These were passed through a digital zero-phase low-pass filter at 40Hz. The times at which the C appeared were chosen so that the probability of saccades was low. Saccades usually occurred between 150 and 300 ms after ramp onset (catch-up saccade) and between 250 and 350 ms after ramp offset (corrective saccade for overshooting the end of the ramp).

Results

Effects of Interval Timing and Visibility Between Ramps on Eye Velocity for the No C conditions

The responses to the four combinations of the factors Interval Timing and Visibility Between Ramps without TI will be considered first since these are the simplest. Fig. 4.13 shows the mean smooth eye velocity response by the nine subjects to each of these stimuli.

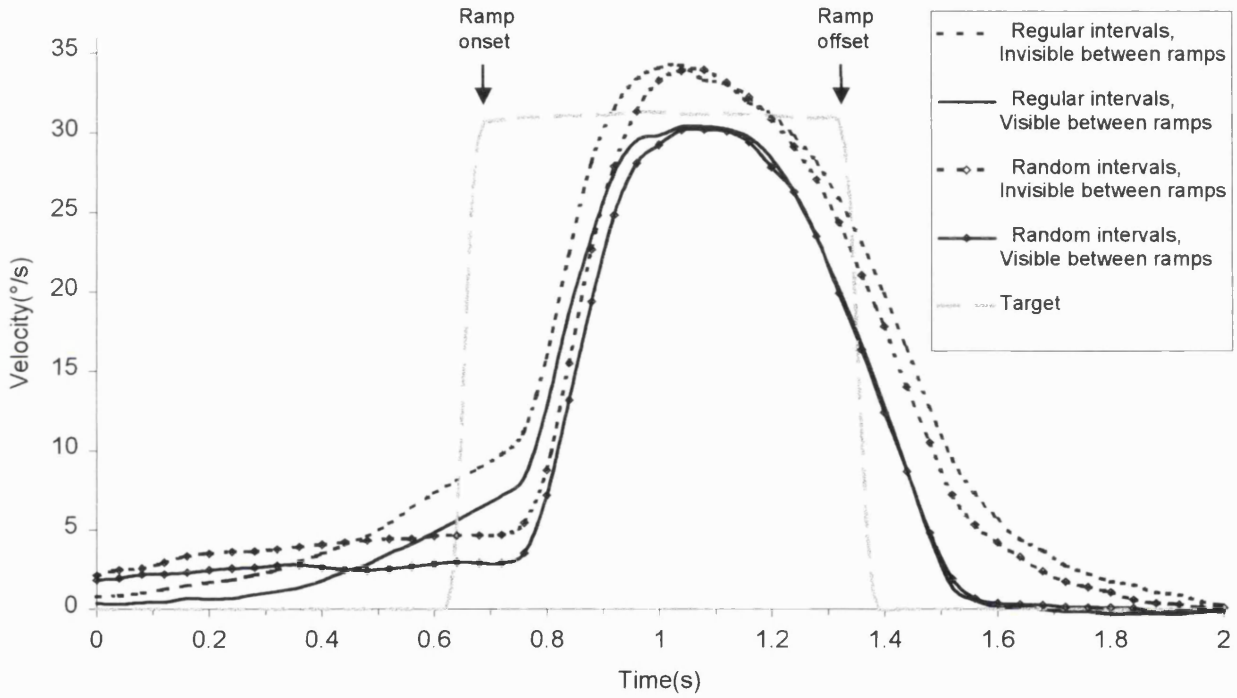


Fig. 4.13 Mean smooth eye velocity by the nine subjects to the four No C conditions where no target identification was required.

Anticipatory acceleration

The inflection around 100 ms after ramp onset shows where visual feedback first had an effect (somewhat smoothed here due to averaging many responses). To statistically analyse differences in the magnitude of anticipatory acceleration, mean smooth eye velocity was measured at 100 ms after ramp onset ($V100_{ON}$). ANOVA (results displayed in a later section) revealed significant effects of both Interval Timing and Visibility Between Ramps on $V100_{ON}$. For *Regular* intervals (lines without diamonds in Fig. 4.13), the acceleration could be synchronised with the time of ramp onset, so $V100_{ON}$ was high (7.9±3.5°/s for *Visible between ramps*). In contrast, for *Random* intervals (lines with diamonds), where ramp onset varied unpredictably by over a second, $V100_{ON}$ was significantly ($p<0.001$) lower (3.2±1.2°/s). It was not zero even though the onset time was unpredictable, due to a slow expectant drift (Kowler & Steinman 1979b) and occasional higher velocity 'guesses' as observed before (Moschner *et al.* 1996; Lekwuwa & Barnes 1996b).

When the target was *Invisible between ramps* (dashed lines in Fig. 4.13), $V100_{ON}$ was significantly higher ($p<0.001$) at 5.1±1.8°/s and 10.6±4.0°/s, for *Random* and *Regular* intervals respectively, than when the target was *Visible between ramps* (solid lines). Thus the removal of a fixation target and its associated inhibitory optokinetic effect increased anticipatory velocity.

Anticipatory deceleration

For ramps of unknown duration, deceleration would not be expected to start until at least 100 ms after ramp offset (Robinson *et al.* 1986). In the current experiment though, subjects knew when and where each ramp would end so there was always anticipatory deceleration. The mean smooth eye velocity at 100 ms after ramp offset ($V100_{OFF}$) was measured to analyse statistical differences in the amount of anticipatory deceleration (note that a greater anticipatory deceleration leads to a lower $V100_{OFF}$).

ANOVA of $V100_{OFF}$ revealed no significant difference in anticipatory deceleration between *Regular* and *Random* intervals since any initial lag due to an unpredictable ramp onset was corrected by visual feedback by around half way through each constant duration ramp. Visibility Between Ramps was a significant factor though. When the target was *Visible between ramps*, the expectation that the moving target would suddenly stop and remain visible resulted in the eye decelerating to a significantly lower $V100_{OFF}$ (7.7±2.8°/s) than for *Invisible between ramps* (15.5±2.9°/s for *Regular* intervals, $p<0.001$). Admittedly this deceleration started from a lower mean peak velocity during the ramp when the target was *Visible between ramps* (31°/s compared to 34°/s for *Invisible between ramps* ($p=0.002$, ANOVA of mean peak smooth eye velocity)) but this difference was smaller than the difference in $V100_{OFF}$.

Effect of target identification (TI) on eye velocity

Anticipatory acceleration for the Visible between ramps condition

Fig. 4.14 shows how the mean velocity profile for *Visible between ramps* with *Regular* intervals in Fig. 4.13 was altered when a Landolt C acuity target was briefly presented once per ramp.

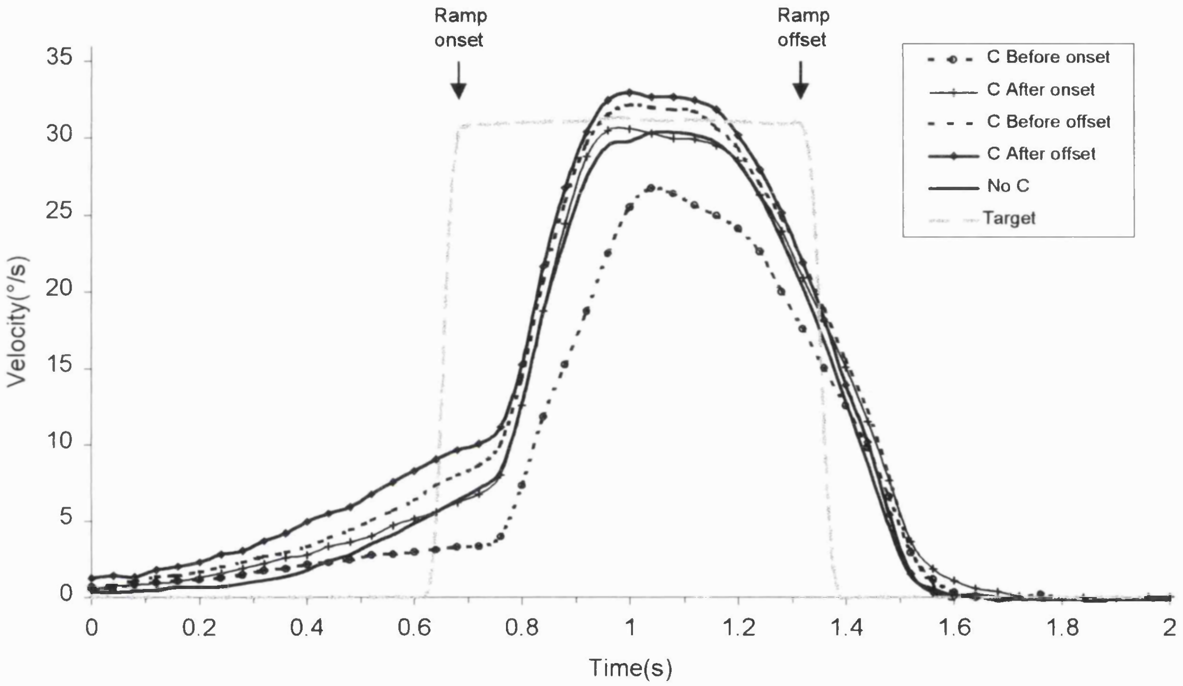


Fig. 4.13 Mean smooth eye velocity by the 9 subjects for all conditions with Regular intervals when the target was Visible between ramps.

$V100_{ON}$ for these responses is shown by the solid lines with squares in Fig. 4.15. Only these responses and those for *Visible between ramps* with *Random* intervals (solid lines with triangles) will be considered in the next two paragraphs.

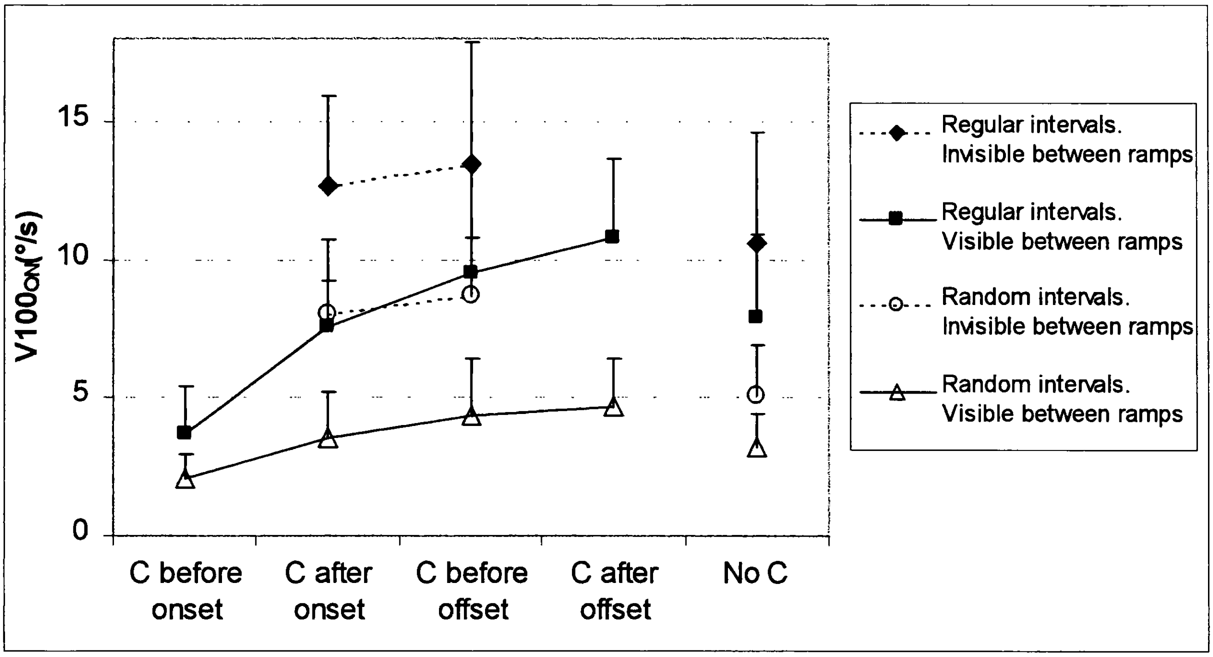


Fig. 4.15 Velocity reached by the anticipatory acceleration at 100 ms after ramp onset ($V100_{ON}$), just before the effect of visual feedback. Response to the four types of repetitive ramp stimuli are shown against the time relative to the ramp when the C could appear once per ramp. Values are the mean over the 9 subjects with the standard deviation.

$V100_{ON}$ was always higher for *Regular* rather than *Random* intervals when TI was required as was found for the *No C* conditions described above. Compared to *No C*, $V100_{ON}$ for *C before onset* was significantly reduced (p=0.003) to 2.1±0.9°/s and 3.7±1.8°/s, for *Random* and *Regular* intervals respectively. Thus subjects were able to reduce the retinal slip of the stationary C that appeared just before ramp onset, despite knowing that the target would move imminently. Fig. 4.14 also shows that the fast pursuit acceleration was delayed and target velocity was never matched. An indication of this delay is that the time for smooth eye velocity to reach 80% of target velocity for *C before onset*, was significantly later by 38 ms and 79 ms for *Random* and *Regular* intervals respectively compared to *No C* (p=0.002, ANOVA of time taken after ramp onset to match 80% of target velocity).

When the target changed into a moving C just after ramp onset (*C after onset*), subjects were unable to increase their anticipatory acceleration compared to *No C*. The predictive response was a compromise between steady fixation of the stationary target and prompt pursuit once it moved. Subjects seemed unable to tip the balance in favour of pursuit. Surprisingly, $V100_{ON}$ was slightly higher (but did not reach significance; p=0.051) when the C was presented much later in the ramp for *C after offset* (Fig 4.14).

Anticipatory acceleration for the Invisible between ramps condition

Fig. 4.16 shows how the mean velocity profile for *Invisible between ramps* with *Regular* intervals in Fig. 4.13 was altered by TI.

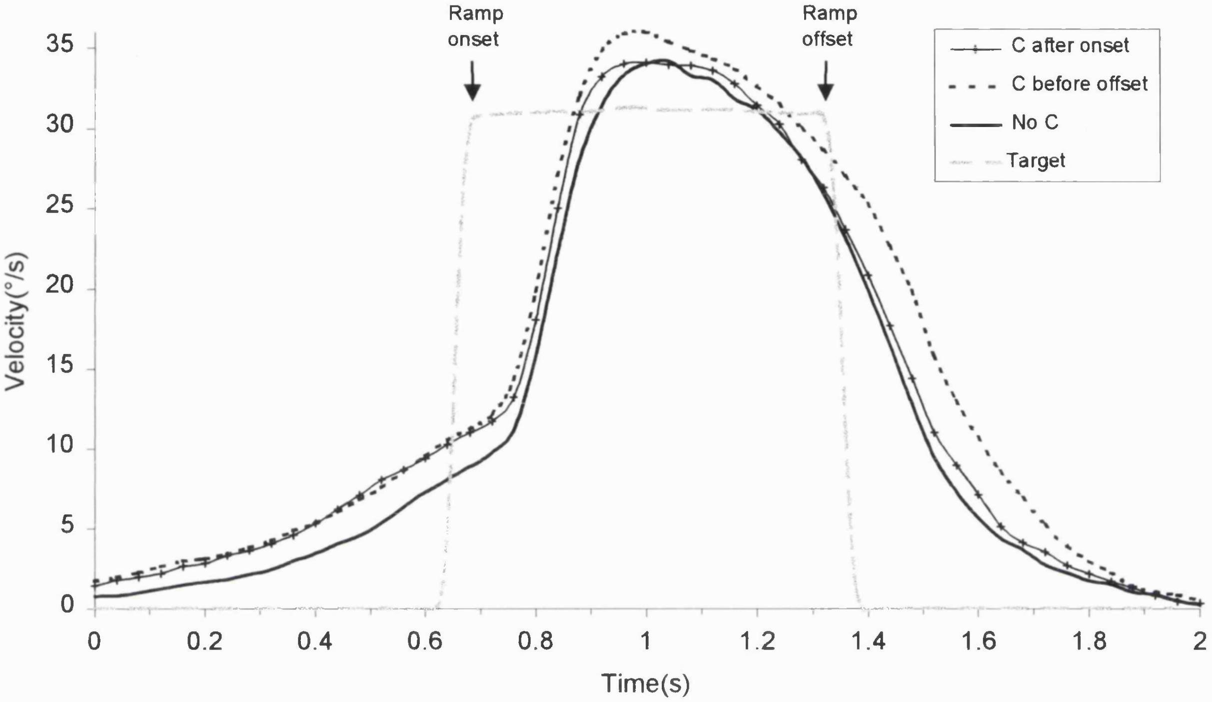


Fig. 4.16 Mean smooth eye velocity by the 9 subjects for all conditions with Regular intervals when the target was Invisible between ramps.

$V100_{ON}$ was higher when the target was *Invisible between ramps* rather than *Visible between ramps* for all TI conditions (dotted compared to solid lines in Fig. 4.15) as was found with *No C* conditions. Analysis of the *Invisible between ramps* conditions alone revealed that $V100_{ON}$ was significantly higher for *C after onset* ($p=0.001$) and *C before offset* ($p=0.017$) compared to *No C*. Thus when the subject was in darkness between ramps, the initial retinal slip of the ramp could be reduced by a few degrees per second when a moving acuity target was expected to appear during the ramp.

Anticipatory deceleration

As was found for the *No C* conditions, there was no difference in eye velocity at 100 ms after ramp offset between *Regular* and *Random* intervals for all the TI conditions. Similarly, $V100_{OFF}$ was higher when the target was expected to disappear at ramp offset (*Invisible between ramps*) than stop and remain visible (*Visible between ramps*). Fig. 4.17 shows how $V100_{OFF}$ changed with the different C Conditions.

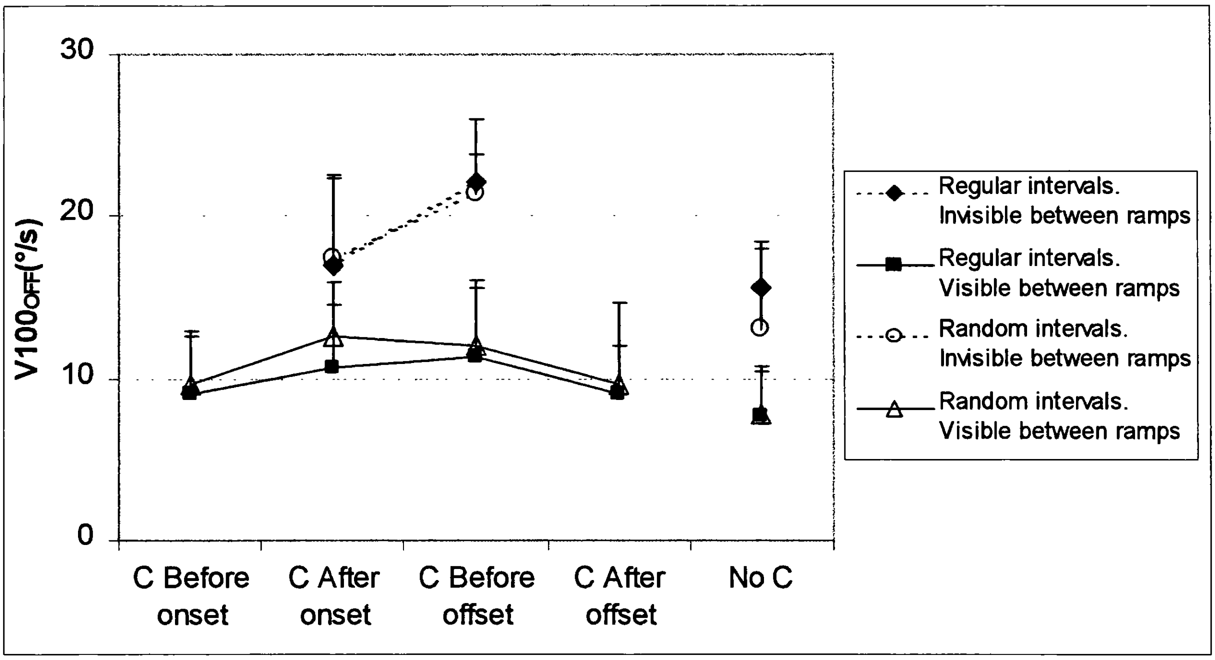


Fig. 4.17 Velocity reached by the anticipatory deceleration at 100 ms after ramp offset ($V100_{OFF}$), just before the effect of visual feedback. Response to the four types of repetitive ramp stimuli are shown against the time relative to the ramp when the C could appear once per ramp. Values are the mean over the 9 subjects with the standard deviation.

For the *Visible between ramps* condition (solid lines in Fig. 4.17), the deceleration was little affected by whether TI was required or not. $V100_{OFF}$ for *C before offset* was significantly faster than for *No C* (p=0.011) but only by 4°/s. Thus pursuit of the end of the ramp was still dominated by the anticipatory deceleration produced in expectation of the target suddenly stopping. When a stationary C appeared just 50 ms after ramp offset (*C after offset*) then, surprisingly, $V100_{OFF}$ was no lower compared to *No C* (Fig. 4.17). Subjects seemed unable to sacrifice accurate pursuit of the last part of the ramp in favour of more prompt fixation of the target once it stopped.

For *Invisible between ramps* (dotted lines in Fig. 4.17), the presentation of a moving C near the end of the ramp (*C before offset*) significantly reduced anticipatory deceleration ($p<0.001$) but did not eliminate it. $V100_{OFF}$ for *C before offset* was 6-8°/s higher than for than for *No C*. The whole velocity profile is shown in Fig. 4.16.

Statistical analysis of smooth eye velocity

The results of the two ANOVAs on eye velocity at 100 ms after ramp onset ($V100_{ON}$), used to assess anticipatory acceleration, are shown in Tables 4.6 and 4.7.

$V100_{ON}$	F	Degrees of freedom	Significance
Interval timing	44.254	1	<0.001
C Condition	10.48	4	0.012
*Interval timing * C Condition*	7.81	4	0.022

Table 4.6 Results of factorial ANOVA on smooth eye velocity at 100 ms after ramp onset ($V100_{ON}$) for conditions 1-10 as described in the Methods . Planned contrasts assessed which of the conditions with Cs produced significantly different$V100_{ON}$ compared to the No C condition (C before onset, p=0.003; C after onset, p=0.999; C before offset, p=0.136; C after offset, p=0.051).

$V100_{ON}$	F	Degrees of freedom	Significance
Interval timing	24.74	1	<0.001
Visibility between ramps	52.21	1	<0.001
C Condition	3.75	2	0.078
*Visibility between ramps * C Condition*	9.94	2	0.009

Table 4.7 Results of factorial ANOVA on smooth eye velocity at 100 ms after ramp onset ($V100_{ON}$) for conditions 3-6 plus 9-14 plus 15-16 as described in the Methods . Only the significant interactions are shown. Planned contrasts assessed which of the conditions with Cs produced significantly different $V100_{ON}$ compared to the No C condition (C after onset, p=0.049; C before offset, p=0.022).

The results of the two ANOVAs on eye velocity at 100 ms after ramp offset ($V100_{OFF}$), used to assess anticipatory deceleration, are shown in Tables 4.8 and 4.9.

$V100_{OFF}$	F	Degrees of freedom	Significance
Interval timing	2.24	1	0.173
C Condition	10.36	4	0.012
*Interval timing * C Condition*	0.42	4	0.787

Table 4.8 Results of factorial ANOVA on smooth eye velocity at 100 ms after ramp offset ($V100_{OFF}$) for conditions 1-10 as described in the Methods. Planned contrasts assessed which of the conditions with Cs produced significantly different$V100_{OFF}$ compared to the No C condition (C before onset, p=0.105; C after onset, p=0.001; C before offset, p=0.011; C after offset, p=0.102).

$V100_{OFF}$	F	Degrees of freedom	Significance
Interval timing	0.003	1	0.958
Visibility between ramps	69.32	1	<0.001
C Condition	16.03	2	0.002
*Visibility between ramps * C Condition*	7.94	2	0.016

Table 4.9 Results of factorial ANOVA on smooth eye velocity at 100 ms after ramp offset ($V100_{OFF}$) for conditions 3-6 plus 9-14 plus 15-16 as described in the Methods . Only the significant interactions are shown. Planned contrasts assessed which of the conditions with Cs produced significantly different $V100_{ON}$ compared to the No C condition (C after onset, p=0.003; C before offset, p<0.001).

Response variability

The standard deviation (SD) of each subject's sixteen eye velocity responses for each condition was used to assess whether the task of TI, where accurate pursuit was desirable, reduced the variability from one response to the next. The same analysis of variance and contrasts were performed on this measure at 100 ms after ramp onset and at 100 ms after ramp offset as were performed on smooth eye velocity. At 100 ms after ramp onset, velocity variability was ±3-4°/s for the four *No C* conditions. This was reduced to ±2°/s for *C before onset* (p=0.006) but actually increased to ±4-6°/s for the other C conditions (p=0.026) apart from *C after onset* (no increase). At 100 ms after ramp offset, velocity variability was ±3-4°/s for *No C* but increased to ±4-5°/s for TI conditions (p=0.03). Thus the acuity task generally made the responses less reproducible.

Eye position and saccades

An analysis of eye position can be informative since it reveals the net effect of smooth and saccadic components. The same analysis of variance and contrasts were performed on eye position at 100 ms after ramp onset and at 100 ms after ramp offset as were performed on smooth eye velocity. For *No C* conditions, differences in the eye position trajectories were less dramatic than in the velocity profiles. At 100 ms after ramp onset, the conditions that evoked the highest anticipatory velocities led to the eye being at a less eccentric angle. Thus the eye was less eccentric when the intervals were *Regular* rather than *Random* (p=0.008) and when the target was *Invisible between ramps* rather than stationary and *Visible between ramps* but this did not reach significance (p=0.08).

For the first half of the ramp, eye position generally lagged the target prior to correction by a high pursuit acceleration and/or catch up saccade (Fig. 4.18). The eye then remained close to the target for the remainder of the ramp. Although anticipatory deceleration reduced eye velocity near ramp offset for all conditions, the velocity was never zero so by 100 ms after ramp offset, the eye position overshot where the ramp ended. For *No C*, this overshoot was greater ($p=0.002$) when the target was *Invisible between ramps* compared to *Visible between ramps* (1.65±0.91° compared to 0.57±0.55°). This accords with the higher $V100_{OFF}$ values seen for *Invisible between ramps*.

The addition of an acuity task did not vary these trajectories greatly. However there were two noticeable effects. Firstly, for *C before onset*, where there was the least anticipatory acceleration, the eye lagged the first half of the ramp by a larger amount ($p=0.003$). Secondly, *C before offset* for *Invisible between ramps* evoked the greatest overshoot of the end of the ramp at 2.88±0.75° ($p=0.006$) in agreement with there being the least anticipatory deceleration (highest $V100_{OFF}$) for this condition.

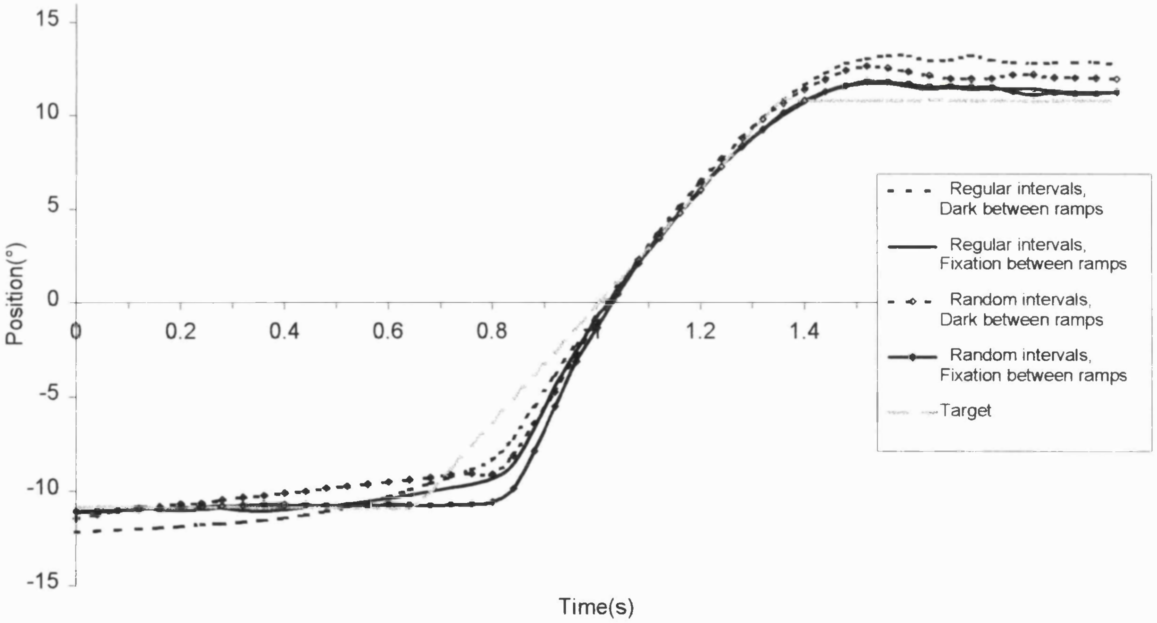


Fig. 4.18 Mean eye position by the nine subjects to the four No C conditions where no target identification was required.

To give an impression of the saccadic activity during tracking, Fig. 4.19 shows the velocity profiles of five responses by one subject where the saccades have not been removed. The responses are from trials with different C conditions for *Regular* intervals with the target *Visible between ramps*. It can be seen that catch-up saccades usually occurred between 150 and 300 ms after ramp onset and back-up saccades between 250 and 350 ms after ramp offset to correct any overshoot of the end of the ramp. As mentioned in the method, saccades rarely occurred during the anticipatory acceleration or anticipatory deceleration. Interestingly there is one response (black line) where the whole ramp is tracked without saccades highlighting the benefit of a high anticipatory velocity. The green line shows the delayed pursuit initiation and saccade typically seen for *C before onset* conditions.

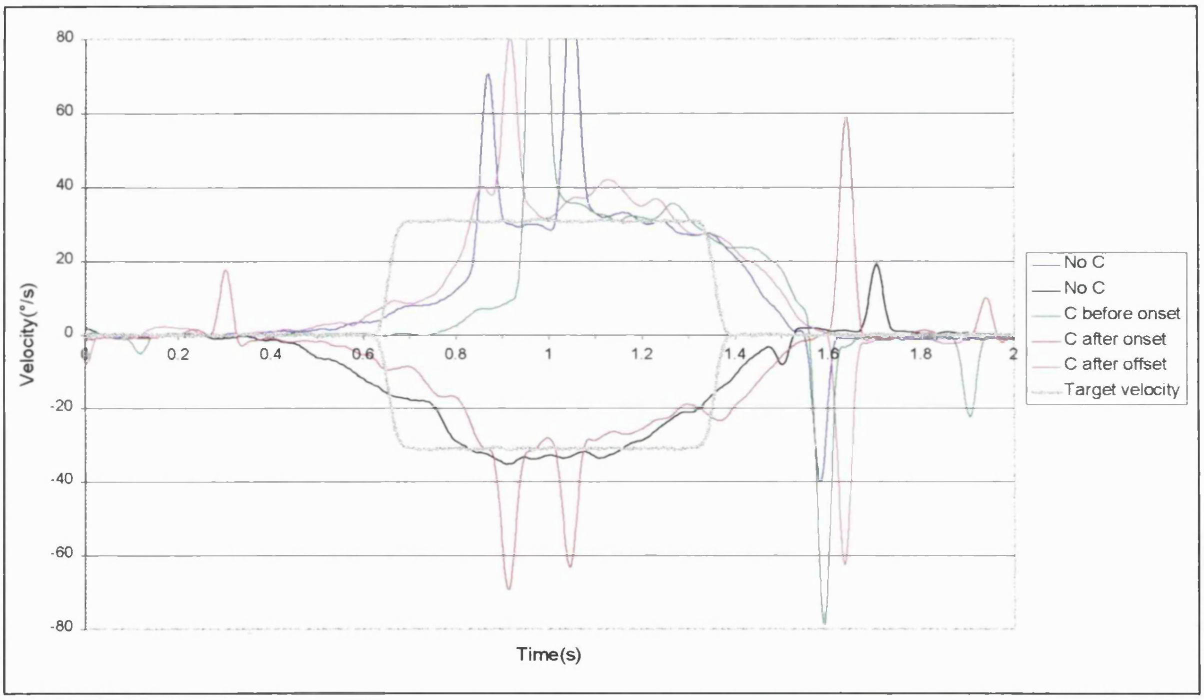


Fig. 4.19 Five example responses by one subject from trials with different C Conditions where the saccades have not been removed.

Promptness and accuracy of TI

Identification of C orientation was not impossibly difficult in any condition nor so easy that concentration was not required. Thus the task was suitable for studying the effect of TI on pursuit. For *C before onset* and *C before offset*, subjects were nearly 100% correct (Table 4.5). For *C after onset*, subjects were only slightly better than chance. For *C after offset* accuracy was around 80% on average. More difficult conditions led to later button presses and more guesses. Thus there was clear vision of the target before it moved, poor vision of the start of a ramp, clear vision of the end of the ramp and slightly worse vision just after it stopped.

Although accurate measures of acuity are not possible from these results, delayed or inaccurate TI was associated with high tracking errors during the 100 ms period when the C appeared. The errors for any one particular C condition varied slightly with Interval Timing and Visibility Between Ramps as indicated in the descriptions of anticipatory acceleration and deceleration. However, mean retinal slip and positional error during the 100 ms presentation of the C were 2°/s and 0.9° for *C before onset*, 22°/s and 3° for *C after onset*, 4°/s and 0.7° for *C before offset* and 9°/s and 1.4° for *C after offset*.

	C before onset	C after onset	C before offset	C after offset
Regular intervals. Invisible between ramps		854.7ms (41.0%)	555.4ms (97.9%)	
Regular intervals. Visible between ramps	677.1ms (95.8%)	1052.3ms (36.8%)	633.3ms (91.0%)	730.7ms (81.9%)
Random intervals. Invisible between ramps		946.1ms (40.3%)	537.3ms (100.0%)	
Random intervals. Visible between ramps	613.5ms (99.3%)	1045.0ms (29.2%)	650.1ms (91.0%)	712.0ms (79.2%)

Table 4.5 Promptness and accuracy of target identification of the Landolt C acuity target that briefly appeared during each ramp. Mean time to press a response button by 9 subjects with mean % correct in parenthesis.

Discussion

In agreement with previous findings, when TI was not required, anticipatory acceleration was increased by *Regular* rather than *Random* intervals (Moschner *et al.* 1996; Ohashi & Barnes 1996) and by the absence of a stationary target before ramp onset (Boman & Hotson 1988). Anticipatory deceleration was greater when the target stopped and remained visible between ramps than when it disappeared. Thus the expected conflict of the eye still moving after the target had stopped was more powerful than the expected conflict of the eye still moving in the absence of a target. In contrast, Boman & Hotson (1988) found no difference. Perhaps for their lower target velocities (≤10°/s), the conflict of the eye still moving at a low velocity after the target had stopped was of similar magnitude to the eye still moving in darkness. They did find that anticipatory deceleration started earlier for higher ramp velocities, and in a later experiment (Boman & Hotson 1992) that higher deceleration occurred when the target was expected to reverse direction and move at a higher velocity. All these findings suggest that earlier/greater deceleration is used to keep future retinal slip below an acceptable level.

We had considered a 700 ms ramp to be long enough to allow a period of accurate closed loop tracking in the middle of the ramp unaffected by the anticipatory acceleration near ramp onset or the anticipatory deceleration near ramp offset. However this appears not to be entirely true since the peak eye velocity for *Visible between ramps* was slightly lower than for *Invisible between ramps* (Fig. 4.13). This suggests that the greater anticipatory deceleration for *Visible between ramps* started as early as around 400 ms before ramp offset. As a percentage though, this difference in peak velocity was considerably less than the differences at ramp onset and offset.

When TI was required, there were significant changes in the responses but their magnitude was quite small, despite the fact that the conditions were subjectively very different. When TI was required just before the ramp started (*C before onset*), anticipatory acceleration was significantly reduced for *Visible between ramps*. Thus subjects were able to improve their fixation to view the stationary target clearly with the penalty of deficient pursuit of the ramp once the target moved. Anticipatory acceleration was not altogether eliminated though, showing that active fixation cannot totally override the expectation of imminent target motion. When TI was required just after ramp onset (*C after onset*), subjects could increase their anticipatory acceleration but only when the target was *Invisible between ramps*. This increase was significant in this experiment whereas for the same condition in experiment 4a it was not. Thus the higher target velocity induced a larger effect. However the increase was still surprisingly small (<3°/s) given that there was no retinal slip of a stationary target before ramp onset to inhibit a large anticipatory movement. Thus retinal slip during the first 200 ms of the ramp was still high and TI was poor. Anticipatory acceleration did not significantly increase for *C after onset* when the target was *Visible between ramps*, suggesting that subjects were unable to ignore a stationary target close to where the moving C would imminently appear. There was however, an increase when the C always appeared later in the ramp (*C after offset*) which nearly reached significance ($p=0.051$). Perhaps this resulted from a spatial shifting of attention that encouraged fixation to be released, since subjects knew that the C would appear around 20° away.

This could be related to the finding that faster smooth movements tend to be evoked when a target is stabilised at a more eccentric position on the retina (Wyatt & Pola 1981; Barnes *et al.* 1995). The changes in anticipatory acceleration were larger than in the first experiment of this chapter. This suggests that the higher target velocity and accompanying higher initial retinal slip induced larger changes in anticipatory acceleration. However the changes were still less than 4°/s.

As in experiment 4a, anticipatory deceleration can be reduced but not eliminated by requiring TI just before the end of the ramp. Robinson *et al.* (1986) found that voluntary efforts to eliminate anticipatory deceleration failed. Our experiment shows that in a TI task where poor maintenance of smooth velocity should have been more obvious, subjects could reduce but not eliminate anticipatory deceleration. Attempts to increase anticipatory deceleration for *C after offset* were unsuccessful. For this condition, subjects probably attended closely to the end of the ramp (since they knew the target would imminently stop and change into a C), so were compelled to pursue its motion. This suggests that when the target is *Visible between ramps,* the anticipatory deceleration response cannot be greatly altered. Similarly, Pola & Wyatt (1997) found that the deceleration response when the target unpredictably stopped was independent of attentional mode. Krauzlis & Miles (1996b) found that monkeys were less sensitive to visual inputs (small target position steps just after ramp offset) when they knew the target would always stop compared to when it only sometimes stopped. In our current experiment, where anticipatory deceleration was always seen, subjects also appear to have been insensitive to the self-induced errors even when these led to significantly less prompt and accurate TI (TI was worse for *C before offset* for *Visible between ramps,* where anticipatory deceleration was higher, than for *Invisible between ramps*). These changes were proportionally larger than those seen in the first experiment of this chapter.

The requirement of TI appeared to increase the variability of responses slightly. This is perhaps because subjects tried to continually modify their movements rather than making stereotyped, semi-automatic responses. In most TI conditions, subjects were able to make small reductions in retinal slip on average compared to *No C* conditions in order to see the C more clearly when it appeared. However, the tracking was slightly worse in some cases so subjects were not always effective at improving their pursuit.

Volition is important in choosing the stimulus for pursuit. For example we can suppress eye movements when fixating a spot against a moving background (Murphy *et al.* 1975) or choose which of two identical moving stimuli to pursue (Kowler *et al.* 1984). Expectations are also important. Kowler (1989) convincingly showed that cognitive expectations could be used to alter the direction of smooth pursuit at low velocities (<0.5°/s). Experiments at higher velocities have confirmed that substantial anticipatory velocities can be directed and initiated by cognitive expectations provided that subjects have been recently exposed to a moving stimulus (chapter 3).

This current experiment suggests that predictive tracking is mainly determined by the system's expectations of future target motion rather than by the time at which the subject requires the best vision. TI can produce significant changes in the compromise between accurate pursuit of different parts of the target motion waveform but their magnitude is quite small. This is probably because a large part of the response for both acceleration and deceleration is, in effect, pre-programmed (Boman & Hotson 1992; Barnes *et al.* 1995) and therefore difficult to modify. Thus the usual instruction of asking the subject to produce what they think is accurate tracking does actually give similar results to a dynamic visual acuity task where functionally accurate tracking is required. The absence of larger changes may be because there is little room for improvement when healthy subjects actively track a target over a dark featureless background. Larger effects might be seen in the more natural situation of pursuit against a distracting structured background or when studying patients where TI may normalise pursuit deficits (Rosenberg *et al.* 1997).

Summary of Chapter 4

- Without Target Identification (TI), anticipatory acceleration increased when intervals between ramps were regular, rather than random. It increased further when, between ramps, the target was invisible rather than stationary and visible. Anticipatory deceleration increased when the target was expected to stop rather than disappear at ramp offset.
- Compared to no TI, anticipatory acceleration decreased when a stationary C always appeared just before ramp onset. It increased when a moving C appeared just after ramp onset, but only when the target was invisible between ramps. Anticipatory

deceleration was reduced when a moving C appeared just before ramp offset, but did not increase when a stationary C appeared just after ramp offset.

- The changes were significant, but of small magnitude, suggesting that predictive pursuit, especially with a visible target between ramps, cannot be greatly influenced by attempts to selectively improve acuity at a particular phase of the stimulus.

CHAPTER 5: GENERAL DISCUSSION AND FUTURE PROPOSALS

This thesis has shown that anticipatory smooth pursuit eye movements are produced in many situations. They can be evoked during darkness or fixation, they can be evoked by audio cues, they can produce accelerations or decelerations in the pursuit velocity and a wide range of velocities can be generated

The magnitude of anticipatory velocity can be increased by :-
1/ faster target ramps (expt. 2a)
2/ alternate direction ramps instead of unidirectional ramps (expts 2b, 2c and 3a)
3/ timing cues before each ramp (expt 3a)
4/ shorter intervals between ramps (expt 3a)
5/ the absence of a fixation target before the ramp (expt 4b)

Several results show that the velocity of anticipatory pursuit is not precisely controlled:-
1/ the variability within subjects and between subjects is high
2/ subjects only achieve around 60% of target velocity by 100 ms after ramp onset rather than 100%
3/ appropriately scaled responses cannot be produced when an increase in target velocity is expected
4/ subjects can have large directional asymmetries in the magnitude of their anticipatory velocity.

All these results suggest that the control of anticipatory velocity is rather imprecise and limited. The variability is not entirely surprising since they are open-loop movements and cannot be calibrated on line by visual feedback. The two aspects of the movement that do appear to be well controlled are the direction and timing. Anticipatory pursuit occurs before alternate direction or unidirectional ramps and experiments 2b and 3a suggest that the store can be easily reversed in direction. Recent pilot studies have shown that subjects can use a wide range of cues (audio, visual and tactile) to time the release of anticipatory movements. Thus it appears that anticipatory movements are a rough estimate of target velocity released at the appropriate time in the appropriate direction. This rough estimate can make significant improvements to pursuit whilst awaiting the visual feedback that is required for precise pursuit. This ability to direct anticipatory movements at the appropriate time would be of great functional benefit in everyday situations. There are often cues about an object's future motion. For example, cars and animals generally move forwards, gravity pulls objects downwards and balls bounce upwards.

Chapter 3 showed that low velocities of anticipatory pursuit can be evoked by an audio cue after a long interval of darkness. Ideally, experiment 3a would have been extended so that the decrease in ASP for trials with longer ISIs would have reached an asymptotic level. For the longest interval used in this experiment (7.2 s) the mean ASP velocity produced for alternate direction ramps was 12°/s. An asymptote of around 10°/s seems likely by visual inspection. This is higher than the velocities that Kao & Morrow (1994) and Becker & Fuchs (1985) reported for subjects trying to generate pursuit voluntarily in the dark where the mean velocity did not exceed 5°/s. This discrepancy can be explained by two fundamental differences. Firstly, for these two experiments, subjects tried to produce a sustained smooth movement in the dark and secondly there was no expectation of a real target appearing. In contrast, for experiment 3a, subjects produced a transient smooth movement in anticipation of the appearance of a real target. Barnes *et al.* (1997) confirmed the enhancement due to expectation of the appearance of a real target. Subjects pursued cued 50°/s ramps every 2 s but were informed that after nine ramps, the target would not appear for the next three cued intervals. Subjects were told to continue to make smooth movements during the time that the target was blanked. Steady-state V100 was 22.9°/s, but V100 for the first blank presentation was only 16.9°/s. Thus although the visual conditions were identical during the anticipatory phase (darkness), the expectation that a real target would not appear meant that subjects' efforts to produce a smooth movement were inhibited. For the next two responses in the dark, V100 fell to 5.3°/s as if the 'store' had been discharged. However, for the next presentation when the target was expected to reappear, V100 increased to 15.1°/s. This was less than the steady-state response but showed that the expectation of the appearance of a real moving target is more powerful than efforts to voluntarily generate smooth movements in the dark.

While there is good evidence that relatively low anticipatory velocities can be generated by volition alone, experiments 3a and 3b provided strong evidence for a short-term store for producing fast anticipatory velocities. If smooth pursuit could be produced at any time like hand movements then this would probably result in large retinal slips being inadvertently produced when the predictions were inaccurate. A short-term store however would restrict fast anticipatory pursuit to situations with frequent target movement where predictive pursuit is likely to lead to a net reduction in retinal slip.

It is uncertain whether visual feedback is used in the same way when predictive movements are being made. Visual inputs are partially ignored during anticipatory acceleration when a target is stationary and visible between ramps and during anticipatory deceleration. Although the response to an intermittent ramp is largely pre-programmed, visual feedback of the ramp itself is not ignored. If the ramp does not appear as expected then the anticipatory movement is quickly terminated (Barnes & Asselman 1991). Furthermore the anticipatory acceleration receives a boost around 100 ms after ramp onset during normal tracking compared to tracking a target that is occasionally stabilised on the retina for one ramp during a trial of many closed-loop ramps (Barnes *et al.* 1995). The results of the acuity task in experiment 4b were not sensitive enough to reveal if acuity was impaired during an anticipatory movement. It seems probable that visual inputs are not ignored but only used when they suggest a major conflict between target motion and the prediction.

Several reports have suggested that visual inputs are selectively used by the pursuit system. Krauzlis & Miles (1996b) showed that monkeys responded to step perturbations in target position at the end of a ramp when the target stopped unexpectedly but not when monkeys knew that the target would stop. Morris & Lisberger (1987) observed that retinal position errors had a much larger effect on smooth pursuit velocity when imposed during pursuit than during fixation. Goldreich *et al.* (1992) showed that monkeys could pursue high frequency sinusoidal vibrations in target position with higher gain if imposed during the pursuit of a ramp than if imposed during fixation. Thus a further benefit of anticipatory acceleration may be that it enhances the pursuit system's response to certain visual errors compared to the response generated from fixation.

Eye movements have many simplifying features compared to limb movements. For example there is only one joint, the load is constant and the moment never changes since the muscles act on the globe radius. In some respects they can therefore be thought of as a 'cartoon' of motor control i.e. a simplification that extracts the essence of the situation without complicating details (Robinson 1986). Obviously the study of eye movements will reveal nothing about load perturbation compensation but there is no reason why higher level movement control and planning such as prediction would be qualitatively different. Experiment 3b showed that the hand and eye make qualitatively similar anticipatory movements but with some quantitative differences. The study of these movements could therefore be of benefit in the treatment and diagnosis of movement control disorders which may be related to a deficit in prediction. It would be interesting to know if there are common cerebral areas controlling predictive smooth pursuit and predictive limb movements. One possibility is that there is an area for predicting future target motion that can use cognitive information and can be accessed by multiple movement systems. The finding that the store for anticipatory pursuit appears to be directionally reversible suggests that it operates above the lower level of motor control where most cells tend to be directionally selective.

The important task for future experiments is to link the findings on anticipatory pursuit to pursuit of a continuously moving target. Pilot experiments suggest that the pursuit of multiple consecutive ramps can be explained by multiple consecutive predictive pulses of motor drive. This would be an efficient method of tracking whereby occasional pre-programmed movements could be released at appropriate times leaving a lower level visual feedback control system to correct any discrepancies. The tracking of a continuous waveform may well be performed in a similar way. Indeed, the predictive pursuit of intermittent ramps and predictable continuous waveforms can be simulated by a single model (Barnes & Wells 1998).

The applicability of the moving acuity target experiments to pursuit in natural situations with the head free is uncertain. This stimulus certainly seems more natural than the continual tracking of an unchanging target. However, the usual precision of pursuit required in everyday situations is not known.

Human functional imaging studies would be useful to reveal the source of the anticipatory movements. If for example during tracking of intermittent ramps, the supplementary eye field could be shown to be active a few hundred milliseconds before the visual cortex became active due to the target's appearance then this would be good evidence that these movements originated here. This could then be compared to activity during tracking of continuously moving targets. The location of the putative short-term store will be harder to find since it is revealed as a difference in the magnitude of the anticipatory velocity which has been shown to be quite variable.

A simple extension of these experiments would be to test vertical anticipatory eye movements. Can the output of the store be directed orthogonally to the motion that charged it? Experiments with two-dimensional target trajectories suggest that this may be possible. Collewijn & Tamminga (1984) found that subjects cut the corner of rhomboidal target trajectories and Kettner *et al.* (1996) showed predictive pursuit by monkeys of Lissajou's figures. Boman & Hotson (1992) showed that similar anticipatory movements are made before the expected 180° reversal of target motion and before an expected 90° change in the direction. It has yet to be shown whether these movements are slow anticipatory velocities that can be produced by volition alone or if they are as fast as movements that can be generated after recently pursuing a moving target.

Glossary

ASP -anticipatory smooth pursuit i.e. smooth pursuit generated in expectation of target motion rather than visual feedback.

Ramp - the motion of a target moving at constant velocity. On a plot of position against time, the motion will appear as an inclined line or ramp.

Ramp onset -the time when a target starts moving at constant velocity

Ramp offset -the time when a constant velocity target stops moving

V100 or **$V100_{ON}$** - eye velocity at 100 ms after ramp onset

$V100_{OFF}$ - eye velocity at 100 ms after ramp offset

$t_{80\%}$ - the time after ramp onset for eye velocity to reach 80 % of target velocity

References

Atkin A, and Bender MB (1968) Ocular Stabilization during Oscillatory Head Movements. Arch Neurol 19: 559-566

Bahill AT, and McDonald JD (1983) Smooth pursuit eye movements in response to predictable target motions. Vision Res. 23: 1573-1583

Barmack NH (1970) Dynamic visual acuity as an index of eye movement control. Vision Res. 10: 1377-1391

Barnes GR, and Asselman PT (1992) Pusuit of Intermittently Illuminated Moving Targets in the Human. J.Physiol.(Lond) 445: 617-637

Barnes GR, and Smith R (1981) The effects on visual discrimination of image movement across the stationary retina. Aviation, Space and Environmental Medicine 466-472

Barnes GR, and Hill T (1984) The influence of display characteristics on active pursuit and passively induced eye movements. Exp Brain Res 56: 438-447

Barnes GR, Donnelly SF, and Eason RD (1987) Predictive velocity estimation in the pursuit reflex response to pseudo-random and step displacement stimuli in man. J.Physiol.(Lond) 389: 111-136

Barnes GR, and Ruddock CJS (1989) Factors affecting the predictability of pseudo-random motion stimuli in the pursuit reflex of man. J.Physiol.(Lond) 408: 137-165

Barnes GR, and Asselman PT (1991) The mechanism of prediction in human smooth pursuit eye movements. J.Physiol.(Lond) 439: 439-461

Barnes GR, and Grealy MA (1992) Predictive mechanisms of head-eye coordination and vestibulo- ocular reflex suppression in humans. Journal of Vestibular Research 2: 193-212

Barnes GR (1993) Visual-vestibular interaction in the control of head and eye movement: the role of visual feedback and predictive mechanisms. Progress in Neurobiology 41: 435-472

Barnes GR, Goodbody SJ, and Collins S (1995) Volitional control of anticipatory ocular pursuit responses under stabilised image conditions in humans. Exp Brain Res 106: 301-317

Barnes GR, Grealy MA, and Collins S (1997) Volitional control of anticipatory ocular smooth pursuit after viewing, but not pursuing, a moving target: Evidence for a Re-Afferent velocity store. Exp.Brain.Res. 116: 445-455

Barnes GR, Rathbone K, and Sira M (1997) Effects of a structured background on anticipatory ocular pursuit. J.Physiol.(Lond) 504P:

Barnes GR, Wells SG (1998) Modelling prediction in ocular pursuit: the importance of short-term storage. In: Becker W, Deubel H, Mergner T (eds) Current oculomotor research: physiological and psychological aspects. Plenum Press, New York (in press)

Barton JJS, Sharpe JA, and Raymond JE (1996a) Directional defects in pursuit and motion perception in humans with unilateral cerebral lesions. Brain 119: 1535-1550

Barton JJS, Simpson T, and Kiriakopoulos E (1996b) Functional MRI of lateral occipitotemporal cortex during pursuit and motion perception. Ann.Neurol. 40: 387-398

Becker W, & Fuchs AF (1985) Prediction in the oculomotor system: smooth pursuit during transient disappearance of a visual target. Exp.Brain.Res. 57: 562-575

Bekkering H, Pratt J, and Abrams RA (1996) The gap effect for eye and hand movements. Perception & Psychophysics 58: 628-635

Belknap DB, and Noda H (1987) Eye movements evoked by microstimulation in the flocculus of the alert macaque. Exp.Brain.Res. 67: 352-362

Blackburn RH (1937) Perception of movement. Am.J.Optom. 14: 365

Boff KR, Lincoln JE (1986) Spatial sensitivity. In: Boff KR, Lincoln JE (eds) Engineering Data Compendium: Human Perception and Performance. Wiley and Sons, New York, pp 199-199

Boman DK, and Hotson JR (1988) Stimulus conditions that enhance anticipatory slow eye movements. Vision Res. 28: 1157-1165

Boman DK, and Hotson JR (1992) Predictive smooth pursuit eye movements near abrupt changes in motion direction. Vision Res. 32: 675-689

Braun D, Boman DK, and Hotson JR (1996) Anticipatory smooth eye movements and predictive pursuit after unilateral lesions in human brain. Exp.Brain.Res. 110: 111-116

Brown B (1972) Dynamic visual acuity, eye movements and peripheral acuity for moving targets. Vision Res. 12: 305-321

Burr DC, and Ross J (1982) Contrast sensitivity at high velocity. Vision Res. 22: 479-484

Carl JR, Gellman RS (1985) Adaptive responses in human smooth pursuit. In: Keller E, Zee DS (eds) Adaptive processes in visual and oculomotor systems. Pergamon, Oxford, pp 335-339

Carl JR, and Gellman RS (1987) Human Smooth Pursuit: Stimulus-Dependent Responses. J.Neurophysiol. 57: 1446-1463

Carpenter RHS (1988) Miniature movements. In: Movements of the eyes. Pion, London, pp 124-138

Collewijn H, Curio G, and Grüsser O-J (1982) Spatially selective visual attention and generation of eye pursuit movements: experiments with sigma-movement. Human Neurobiol 1: 129-139

Collewijn H, and Tamminga EP (1984) Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. J.Physiol.(Lond) 351: 217-250

Collewijn H, and Tamminga EP (1986) Human fixation and pursuit in normal and open-loop conditions: effects of central and peripheral retinal targets. J.Physiol. 379: 109-129

Cushman WB, Tangney JF, Steinman RM, and Ferguson JL (1984) Characteristics of smooth eye movements with stabilized targets. Vision Res. 24: 1003-1009

Dallos PJ, and Jones RW (1963) Learning behaviour of the eye fixation control system. IEEE Transactions on Automatic Control AC-8: 218-227

Deckert GH (1964) Pursuit eye movements in the absence of a moving visual stimulus. Science 143: 1192-1193

Dement W (1964) Eye movements during sleep. In: Bender MB (ed) The oculomotor system. Harper & Row, New York, pp 366-416

Demer JL, and Amjadi F (1993) Dynamic visual acuity of normal subjects during vertical optotype and head motion. Invest.Ophthalmol.Vis.Sci. 34: 1894-1906

Deno DC, Crandall WF, Sherman K, Keller EL (1995) Characterization of prediction in the primate visual smooth pursuit system. Biosystems 34: 107-128(Abstract)

Ditchburn RW (1973) Eye movement and visual perception. Clarendon Press, Oxford,

Dodge R, Travis RC, and Fox JC (1930) Optic nystagmus III. Characteristics of the slow phase. Arch Neurol & Pscyhiatry,Chicago 24: 21-34

Dursteller MR, and Wurtz RH (1988) Pursuit and optokinetic deficits following chemical lesions of cortical areas MT and MST. J.Neurophysiol. 60 (3): 940-965

Eckmiller R (1987) Neural control of pursuit eye movements. Physiological Reviews 67: 797-857

Fischer B, and Ramsperger E (1984) Human express saccades: extremely short reaction times of goal directed eye movements. Exp.Brain.Res. 57: 191-195

Gauthier GM, and Hofferer JM (1976) Eye tracking of self-moved targets in the absence of vision. Exp.Brain.Res. 26: 121-139

Gauthier GM, Vercher J-L, Ivaldi FM, and Marchetti E (1988) Ocular-manual tracking of visual targets:control learning, coordination control and coordination model. Exp.Brain.Res. 73: 127-137

Goldreich D, Krauzlis RJ, and Lisberger SG (1992) Effect of changing feedback delay on spontaneous oscillations in smooth pursuit eye movements of monkeys. J.Neurophysiol. 67: 625-638

Gottlieb JP, Bruce CJ, and MacAvoy MG (1993) Smooth Eye Movements Elicited by Microstimulation in the Primate Frontal Eye Field. J.Neurophysiol. 69: 786-799

Grüsser O-J (1986) The effect of gaze motor signals and spatially directed attention on eye movements and visual perception. In: Freund H-J, Buttner U, Cohen B, Noth J (eds) The oculomotor and skeletal-motor systems: differences and similarities. Elsevier, Amsterdam., pp 391-404

Heinen SJ (1994) Evidence of a timing mechanism for predictive smooth pursuit in frontal cortex. In: Fuchs A, Brandt MD, Buttner U, Zee DS (eds) Contemporary ocular motor and vestibular research: a tribute to David A. Robinson. Thieme Medical Publishers, New York, pp 408-410

Heinen SJ (1996) Microstimulation in dorsomedial frontal cortex affects smooth pursuit eye movements. Soc Neurosci Abstr 22: 382.2(Abstract)

Heinen SJ, and Liu M (1997) Single-neuron activity in the dorsomedial frontal cortex during smooth-pursuit eye movements to predictable target motion. Vis.Neurosci. 14: 853-865

Heywood S (1973) Pursuing stationary dots: Smooth eye movements and apparent movement. Perception 2: 181-195

Heywood S, and Churcher J (1971) Eye movements and the afterimage-1. Tracking the afterimage. Vision Res. 11: 1163-1168

Kao GW, and Morrow MJ (1994) The relationship of anticipatory smooth eye movements to smooth pursuit initiation. Vision Res. 34, No. 22: 3027-3036

Keating EG (1993) Lesions of the frontal eye field impair pursuit eye movements, but preserve the predictions driving them. Behanioural Brain Research 53: 91-104

Keppel G (1982) Correction for multiple comparisons. In: AnonymousDesign and analysis. Prentice-Hall, Englewood Cliffs, pp 144-166

Kettner RE, Leung H, and Peterson BW (1996) Predictive smooth pursuit of complex two-dimensional trajectories in monkey: component interactions. Exp.Brain.Res. 108: 221-235

Knox PC (1996) The effect of the gap paradigm on the latency of human smooth pursuit of eye movement. Neuroreport 7: 3027-3030

Komatsu H, and Wurtz RH (1989) Modulation of pursuit eye movements by stimulation of cortical areas MT and MST. J.Neurophysiol. 62: 31-47

Kowler E (1989) Cognitive expectations, not habits, control anticipatory smooth oculomotor pursuit. Vision Res. 29: 1049-1057

Kowler E, and Steinman RM (1979a) The effect of expectations on slow oculomotor control-I. Periodic target steps. Vision Res. 19: 619-632

Kowler E, and Steinman RM (1979b) The effect of expectations on slow oculomotor control-II. Single target displacements. Vision Res. 19: 633-646

Kowler E, and Steinman RM (1981) The effect of expectations on slow oculomotor control: III. Guessing unpredictable target displacements. Vision Res. 21: 191-203

Kowler E, Van der Steen J, Tamminga EP, and Collewijn H (1984) Voluntary selection of the target for smooth eye movement in the presence of superimposed, full-field stationary and moving stim. Vision Res. 24: 1789-1798

Krauzlis RJ, and Miles FA (1996a) Release of fixation for pursuit and saccades in humans: evidence for shared inputs acting on different neural substrates. J.Neurophysiol. 76: 2822-2833

Krauzlis RJ, and Miles FA (1996b) Transitions between pursuit eye movements and fixation in the monkey: dependence on context. J.Neurophysiol. 76: 1622-1638

Lamontagne C, Desjardins FJ, and Pivik RT (1993) Smooth pursuit along a solid line: A new variation on the theme of efference-copy-bound eye tracking. Perception 22: 477-482

Leist A, Freund H-J, and Cohen B (1987) Comparative characteristics of predictive eye-hand tracking. Human Neurobiol 6: 19-26

Lekwuwa GU, and Barnes GR (1996a) Cerebral control of eye movements I. The relationship between cerebral lesion sites and smooth pursuit deficits. Brain 119: 473-490

Lekwuwa GU, and Barnes GR (1996b) Cerebral control of eye movements II. Timing of anticipatory eye movements, predictive pursuit and phase errors in focal cerebral lesions. Brain 119: 491-505

Lekwuwa GU, Barnes GR, Grealy MA (1995) Effects of prediction on smooth pursuit velocity gain in cerebellar patients and controls. In: Findlay JM (ed) Eye movement research. Elsevier Science B.V., pp 119-129

Lisberger SG, Evinger C, Johanson GW, & Fuchs A (1981) Relationship between eye acceleration and retinal image velocity during foveal smooth pursuit in man and monkey. J.Neurophysiol. 46: 229-249

Long GM, and Riggs CA (1991) Training effects on dynamic visual acuity with free-head viewing. Perception 20: 363-371

Long GM, and Rourke DA (1989) Training effects on the resolution of moving targets - dynamic visual acuity. Human Factors 31: 443-451

Ludvigh E, and Miller JW (1958) Study of visual acuity during the ocular pursuit of moving test objects. I. Introduction. J.Opt.Soc.Am. 48: 799-802

Luebke AE, and Robinson DA (1988) Transition dynamics between pursuit and fixation suggest different systems. Vision Res. 28: 941-946

MacAvoy MG, Gottlieb JP, and Bruce CJ (1991) Smooth-Pursuit Eye Movement Representation in the Primate Frontal Eye Field. Cerebral cortex 1: 95-102

Magnussen S, and Greenlee MW (1992) Retention and disruption of motion information in visual short-term memory. J.Exp.Psych.[Learn Mem] 18: 151-156

Mates J, Radil T, Poppel E, and Muller U (1994) Temporal integration in sensorimotor sychronisation. Journal of Cognitive Neuroscience 6: 332-340

Merrison AF, Carpenter RH (1995) "Express" smooth pursuit. Vision Res. 35: 1459-1462(Abstract)

Miall RC, Haggard PN, and Cole JD (1995) Evidence of a limited visuo-motor memory used in programming wrist movements. Exp Brain Res 107: 267-280

Miles W (1929) Horizontal eye movements at the onset of sleep. Psychol. 36: 122-141

Morris EJ, and Lisberger SG (1987) Different responses to small visual errors during initiation and maintenance of smooth-pursuit eye movements in monkeys. J.Neurophysiol. 58: 1351-1369

Morrow MJ, and Lamb NL (1996) Effects of fixation target timing on smooth-pursuit initiation. Exp.Brain.Res. 111: 262-270

Morrow MJ, and Sharpe JA (1990) Cerebral hemispheric localization of smooth pursuit asymmetry. Neurology 40: 284-292

Moschner C, Zangemeister WH, and Demer JL (1996) Anticipatory smooth eye movements of high velocity triggered by large target steps: normal performance and effect of cerebellar degeneration. Vision Res. 36: 1341-1348

Murphy BJ (1978) Pattern thresholds for moving and stationary gratings during smooth eye movement. Vision Res. 18: 521-530

Murphy BJ, Kowler E, and Steinman RM (1975) Slow oculomotor control in the presence of moving backgrounds. Vision Res. 15: 1263-1268

Newsome WT, Wurtz RH, and Komatsu H (1988) Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. J.Neurophysiol. 60: 604-620

Noda H (1986) Mossy fibres sending retinal-slip, eye and head velocity signals to the flocculus of the monkey. J.Physiol.(Lond) 379: 39-60

Ohashi N, and Barnes GR (1996) A comparison of predictive and nonpredictive ocular pursuit under active and passive stimulation conditions in humans. Journal of Vestibular Research 6: 1-16

Petit L, Clark VP, Ingeholm J, and Haxby JV (1997) Dissociation of saccade-related and pursuit-related activation in human frontal eye fields as revealed by fMRI. J.Neurophysiol. 77: 3386-3390

Pola J, and Wyatt HJ (1997) Offset dynamics of human smooth pursuit eye movements: effects of target presence and subject attention. Vision Res. 37: 2579-2595

Rashbass C (1961) The relationship between saccadic and smooth tracking eye movements. J.Physiol.(Lond) 159: 326-338

Reading VM (1972) Visual Resolution as measured by dynamic and static tests. Pflugers Arch. 333: 17-26

Robinson DA (1965) The mechanics of human smooth pursuit eye movements. J.Physiol.(Lond) 180: 569-591

Robinson DA (1986) Is the oculomotor system a cartoon of motor control? In: Freund HJ, Buttner U, Cohen B, Noth J (eds) Progress in Brain Research. Elsevier Science Publishers B.V., Amsterdam, pp 411-417

Robinson DA, & Fuchs A (1969) Eye movements evoked by stimulation of frontal eye fields. J.Neurophysiol. 32: 637-648

Robinson DA, Gordon JL, and Gordon SE (1986) A model of the smooth pursuit eye movement system. Biol.Cybern. 55: 43-57

Rosenberg DR, Sweeney JA, and Squires-Wheeler E (1997) Eye-tracking dysfunction in offspring from the New York High-Risk Project: diagnostic specificity and the role of attention. Psychiatry Res 66: 121-130

Shagass C, Roemer RA, and Amadeo M (1976) Eye-tracking performance and engagement of attention. Arch.Gen.Psychiatry 33: 121-125

Sharpe JA, Lo AW, and Rabinovitch HE (1979) Control of the saccadic and smooth pursuit systems after cerebral hemidecortication. Brain 102: 387-403

Steinbach MJ (1969) Eye tracking of self-moved targets: the role of efference. Journal of Experimental Psychology 82: 366-376

Steinbach MJ, and Held R (1968) Eye tracking of observer-generated target movements. Science 161: 187-188

Steinman RM, Skavenski AA, and Sansbury RV (1969) Voluntary control of smooth pursuit velocity. Vision Res. 9: 1167-1171

Steinman RM, Cushman WB, and Martins AJ (1982) The precision of gaze. Human Neurobiol 1: 97-109

Steinman RM, and Haddad GM (1973) Miniature eye movement. Science 181: 810-819

Sweeney JA, Haas GL, Li S, and Weiden P (1994) Selective effects of antipsychotic medications on eye-tracking performance in schizophrenia. Psychiatry Res 54: 185-198

Tusa RJ, Zee DS (1989) Cerebral control of smooth pursuit and optokinetic nystagmus. In: Lessel S, van Dalen JTW (eds) Current Neuro-Ophthalmology. Year Book Medical Publishers, Inc., pp 115-146

Tychsen L, and Lisberger SG (1986) Visual motion processing for the initiation of smooth-pursuit eye movements in humans. Neurophysiology 953-968

van den Berg AV (1988) Human smooth pursuit during transient perturbations of predictable and unpredictable target movement. Exp.Brain.Res. 72: 95-108

van den Berg AV, and Collewijn H (1987) Voluntary smooth eye movements with foveally stabilized targets. Exp.Brain.Res. 68: 195-204

Van Gelder P, and Lebedev S (1995) Anticipatory saccades in smooth pursuit: Task effects and pursuit vactor after saccades. Vision Res. 35: 667-678

Vercher J-L, Gauthier GM, Guedon O, Blouin J, Cole J, and Lamarre Y (1996) Self-moved target eye tracking in control and deafferented subjects: Roles of arm motor command and proprioception in arm-eye coordination. J.Neurophysiol. 76: 1133-1144

von Noorden GK, and Mackensen G (1962) Pursuit movements of normal and amblyopic eyes. Amer.J.Ophthalmol. 53: 325-336

Watson JDG, Myers R, Frackowiak RSJ, Hajnal JV, Woods RP, Mazzioatta JC, Shipp S, and Zeki S (1993) Area V5 of the human brain: Evidence from a combined study using positron emission tomography amd magnetic resonance imaging. Cerebral cortex 3: 79-94

Weir DJ, Stein JF, and Miall RC (1989) Cues and control strategies in visually guided tracking. Journal of Motor Behaviour 21: 185-204

Wells SG, and Barnes GR (1996) Anticipatory ocular smooth pursuit of repetitive target velocity sequences in humans. J.Physiol.(Lond) 494: 69P

Wells SG, and Barnes GR (1998) Fast anticipatory smooth pursuit eye movements appear to depend on a short-term store. Exp Brain Res 120: 129-133

Westheimer G (1954a) Eye movement response to a horizontally moving visual stimulus. Arch.Ophthalmol. 52: 932-941

Westheimer G, and Conover DW (1954b) Smooth eye movements in the absence of a moving visual stimulus. J.Exp.Psych. 47: 283-284

Westheimer G, and Mckee SP (1975) Visual acuity in the presence of retinal-image motion. J.Opt.Soc.Am. 65: 847-850

Whittaker SG, and Eaholtz G (1982) Learning patterns of eye motion for foveal pursuit. Invest.Ophthalmol.Vis.Sci. 23: 393-397

Winterson BJ, and Collewijn H (1976) Microsaccades during finely-guided oculomotor tasks. Vision Res. 16: 1387-1390

Winterson BJ, and Steinman RM (1978) The effect of luminance on human smooth pursuit of perifoveal and foveal targets. Vision Res. 18: 1165-1172

Wyatt HJ, and Pola J (1981) Slow eye movements to eccentric targets. Invest.Ophthalmol.Vis.Sci. 21: 477-483

Wyatt HJ, and Pola J (1983) Smooth pursuit eye movements under open-loop and closed-loop conditions. Vision Res. 23: 1121-1131

Wyatt HJ, and Pola J (1987) Smooth eye movements with step-ramp stimuli: The influence of attention and stimulus extent. Vision Res. 27: 1565-1580

Wyatt HJ, Pola J (1994) Smooth pursuit eye movements with imaginary targets defined by extrafoveal cues. Vision Res. 34: 803-820(Abstract)

Yasui S, and Young LR (1984) On the predictive control of foveal eye tracking and slow phases of optokinetic and vestibular nystagmus. J.Physiol.(Lond) 347: 17-33

Zambarbieri D, Schmid R, Prablanc C, Magenes G (1981) Characteristics of eye movements evoked by the presentation of acoustic targets. In: Fuchs A, Becker W (eds) Progress in oculomotor research. Elsevier, Amsterdam,

Zee DS, Yamazaki A, Butler PH, and Gucer G (1981) Effects of ablation of flocculus and paraflocculus on eye movements in primate. J.Neurophysiol. 46: 878-899

Zihl J, Von Cramon D, Mai N, and Schmid C (1991) Disturbance of movement vision after bilateral posterior brain damage: Further evidence and follow up observations. Brain 114: 2235-2252