# Velocity Memory

*A thesis submitted to The University of Manchester for the degree of Doctor of Philosophy in the Faculty of Medical and Human Sciences*

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**Word Count =**

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## List of abbreviations

| | |
|---|---|
| ACC | Anterior Cingulate Cortex |
| ANOVA | Analysis of Variance |
| ASPEM | Anticipatory Smooth Pursuit Eye Movement |
| DLPFC | Dorsolateral Prefrontal Cortex |
| EEG | Electroencephalography |
| ERP | Event Related Potential |
| ERD | Event Related Desynchronization |
| ERS | Event Related Synchronization |
| FEFs | Frontal Eye Fields |
| fMRI | Functional Magnetic Resonance Imaging |
| HEOG | Horizontal Electro Oculogram |
| HSP | Hemifield Switch Positivity |
| ICA | Independent Components Analysis |
| IPS | Intraparietal Sulcus |
| M | Mean |
| MT | Medial Temporal |
| MST | Medial Superior Temporal |
| ORD | Occlusion Related Deflection |
| SEM | Standard Error of the Mean |
| SD | Standard Deviation |
| SEFs | Supplementary Eye Fields |
| SPEM | Smooth Pursuit Eye Movement |
| TMS | Transcranial Magnetic Stimulation |
| TTC | Time to Contact |
| VEOG | Vertical Electro Oculogram |

## Abstract

This Thesis, entitled ‘Velocity Memory’ is submitted to the University of Manchester by Alexis David James Makin (30/09/2010) for the degree of Doctor of Philosophy.

It is known that primates are sensitive to the velocity of moving objects. We can also remember velocity information after moving objects disappear. This cognitive faculty has been investigated before, however, the literature on velocity memory to date has been fragmented. For example, velocity memory has been disparately described as a system that controls eye movements and delayed discrimination. Furthermore, velocity memory may have a role in *motion extrapolation*, i.e. the ability to judge the position of a moving target after it becomes occluded. This thesis provides a unifying account of velocity memory, and uses electroencephalography (EEG) to explore its neural basis.

In Chapter 2, the relationship between oculomotor control and motion extrapolation was investigated. Two forms of motion extrapolation task were presented. In the first, participants observed a moving target disappear then reappear further along its path. Reappearance could be at the correct time, too early or too late. Participants discriminated reappearance error with a two-alternative forced choice button press. In the second task, participants saw identical targets travel behind a visible occluder, and they attempted to press a button at the exact time that it reached the other side. Tasks were completed under fixation and free viewing conditions. The accuracy of participant’s judgments was reduced by fixation in both tasks. In addition, eye movements were systematically related to behavioural responses, and small eye movements during fixation were affected by occluded motion. These three results imply that common velocity memory and pre-motor systems mediate eye movements and motion extrapolation.

In Chapter 3, different types of velocity representation were explored. Another motion extrapolation task was presented, and targets of a particular colour were associated with fast or slow motion. On identical-velocity probe trials, colour still influenced response times. This indicates that long-term colour-velocity associations influence motion extrapolation. In Chapter 4, interference between subsequently encoded velocities was explored. There was robust interference between motion extrapolation and delayed discrimination tasks, suggesting that common processes are involved in both.

In Chapter 5, EEG was used to investigate *when* memory-guided tracking begins during motion extrapolation. This study compared conditions where participants covertly tracked visible and occluded targets. It was found that a specific event related potential (ERP) appeared around 200 ms post occlusion, irrespective of target location or velocity. This component could delineate the onset of memory guided tracking during occlusion. Finally, Chapter 6 presents evidence that a change in alpha band activity is associated with information processing during motion extrapolation tasks.

In light of these results, it is concluded that a common velocity memory system is involved a variety of tasks. In the general discussion (Chapter 7), a new account of velocity memory is proposed. It is suggested that a velocity memory reflects persistent synchronization across several velocity sensitive neural populations after stimulus offset. This distributed network is involved in sensory-motor integration, and can remain active without visual input. Theoretical work on eye movements, delayed discrimination and motion extrapolation could benefit from this account of velocity memory.

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## The author

Alexis Makin completed his Undergraduate degree in Psychology and Neuroscience at the University of Manchester in 2006, and worked as a research assistant with Dr Ellen Poliakoff during this time. He was then awarded an Economic and Social Sciences Research Council (ESRC) 1+3 scholarship, and completed the M Res component in 2007.

## Publications

Parts of this thesis appear in other publications by Alexis Makin and colleagues:

Experiment 2 (Chapter 2) is due to appear in the Quarterly Journal of Experimental Psychology (Makin and Poliakoff, 2011).

Experiment 3 was published in Experimental Brain Research (Makin, Stewart and Poliakoff, 2009).

The results of Makin, Poliakoff Chen and Stewart (Vision Research, 2008) are discussed throughout.

The results of Makin, Poliakoff and El-Deredy (Neuropsychologia, 2009) are discussed throughout, and this work provides the rationale for Experiment 8.

A small ‘Journal Club Article’ by Ackerley, Wild and Makin (Journal of Neuroscience, 2009) is referenced discussion of Experiment 3.

## Acknowledgements

A great number of people have supported me during the production of this thesis. Most notable are my Supervisor Ellen Poliakoff and co-supervisor Wael El-Deredy. Ellen Poliakoff employed me as a research assistant while I was an undergraduate and has dedicated an incredible amount of time and energy to my development. Nearly everything in this thesis has evolved from our early work together, and literally everything in this thesis has benefited from her extreme clarity of mind. Likewise, Wael El-Deredy has been tremendously helpful: his expertise in EEG recording and analysis were invaluable, and his general energy was inspirational. I also thank the Economic and Social Sciences Research Council (ESRC) and University of Manchester for providing generous financial support.

I am extremely grateful to the people who volunteered to participate in these studies. Some experiments lasted several hours, and others involved uncomfortable brain recording procedures. Without their patience and good nature this thesis would not have been possible.

During my time at the University of Manchester I have enjoyed working with my collaborators immensely. In particular, I would like to mention my 'Journal Club' (Rochelle Ackerley, Emma Gowen, Paul Warren and Kelly Wild), with whom I have spent many afternoons critically evaluating some of the papers cited herein. I would also like to mention my office colleagues (Clare Allely, Anna Blackburn, Sarah Davies and Laura Mirams) for making my workdays so pleasant! Finally, I would like to mention my girlfriend Alisa. We have both been working on our PhD theses simultaneously for the last three years, and I will remember this period as one of the happiest of my life.

# Chapter 1

# Introduction to velocity memory

## 1.1 The common velocity memory system

Humans are sensitive to the velocity of moving objects (McKee, Silverman and Nakayama, 1986). We can also remember velocity information after moving objects disappear (Pasternak and Greenlee, 2005). This thesis characterizes velocity memory, and this introductory chapter reviews previous work that has described, or alluded to, velocity memory. It will be seen that many cognitive operations could potentially involve a common velocity memory system, although this has not always been recognized. These operations are outlined in the following sections. Finally, the neural basis of velocity memory is described, and the current experimental work is introduced.

## 1.2 Smooth pursuit eye movements

The most developed theories of velocity memory come from work on smooth pursuit eye movement (SPEM, for review see G. R. Barnes, 2008). Primates can use SPEMs to track a single moving target with a gain close to unity (i.e. the fovea remains on the target as it moves, Krauzlis & Stone, 1999). A general model of SPEM control, based on current understanding, is shown in Figure 1.1, and typical SPEM data is shown in Figure 1.2A (page 27). In this model SPEMs are controlled by a negative feedback loop, in which retinal velocity signals are cancelled by an SPEM of the same velocity. However, it takes 100 to 200 ms for the eyes muscles to respond to retinal stimulation (Schlag & Schlag-Rey, 2002). Therefore if SPEMs relied on visual feedback exclusively, eye position would always lag behind target position. This implies that ongoing SPEM must be enhanced by an internally generated, or extraretinal, velocity signal. For this reason, all SPEM can be described as 'predictive pursuit' (Dallos & Jones, 1963). In fact, predictive pursuit is controlled by at least two putative extraretinal velocity signals. The first is the *efference copy loop*, in which motor eye velocity commands are fed back to sensory modules (Churchland, Chou, & Lisberger, 2003; Robinson, Gordon, & Gordon, 1986). The second is the *reafferent loop,* in which pre-motor commands are recycled (G. R. Barnes, Grealy, & Collins, 1997).

Two experimental findings implicate extraretinal velocity information in SPEM control. First, SPEMs can continue after moving targets are retinally stabilized (i.e. feedback from an eye tracker is used to keep a visual target on the fovea) despite the fact that this procedure reduces retinal motion to zero. During retinal stabilization, SPEM must be produced by internally generated velocity signals alone (G. R. Barnes, Goodbody, & Collins, 1995). Second, SPEMs can continue uninterrupted across 100 - 200 ms intervals of target disappearance (Newsome, Wurtz, & Komatsu, 1988). These authors argue that all tracking requires extraretinal signals to overcome visuomotor delay, so pursuit across target disappearance periods with durations *shorter* than visuomotor delay requires no additional systems. However, when a moving target disappears for longer than 200 ms, eye velocity decays rapidly (Bennett & Barnes, 2003), or continues with reduced gain if volitional effort is applied (Becker & Fuchs, 1985; Pola & Wyatt, 1997). This suggests that the extraretinal velocity information used to maintain predictive pursuit is *not* stored for long periods, or that it is rapidly replaced by a subsequent input.

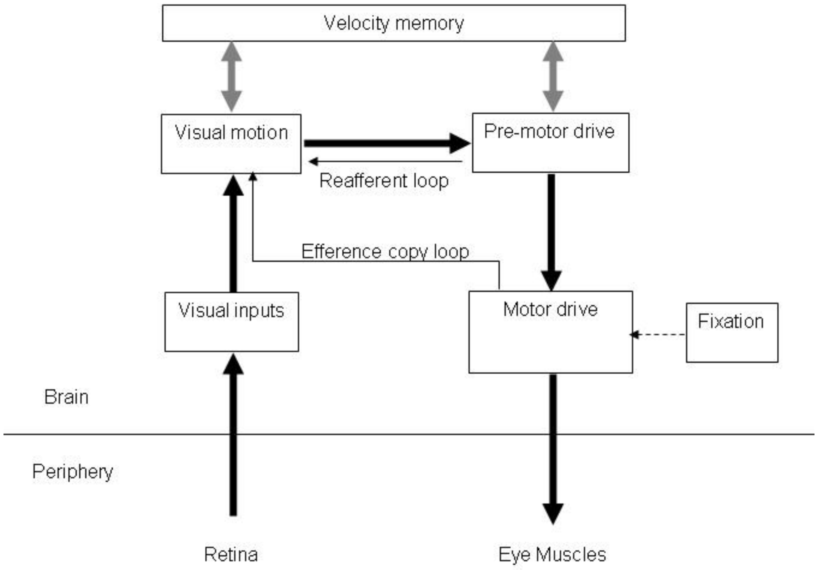


**Figure 1.1: Model of smooth pursuit eye movement control systems**. This diagram is based on models proposed by Barnes and his colleagues (e.g. Barnes and Asselman, 1991). The basis of the model is a negative feedback loop which converts visual velocity signals into SPEM of the same velocity (thick black arrows). Smooth pursuit may be maintained by efference copy and reafferent loops (thin black arrows). Sensory and pre-motor velocity signals may be retained in a short term store. Stored velocity information can guide anticipatory SPEM prior to target onset, or during occlusion (thick grey arrows). Fixation commands (dotted arrows) block motor drive, but do not inhibit pre-motor drive.

In addition to the very transient extraretinal velocity information that maintains predictive pursuit, more robust extraretinal velocity signals, from a velocity memory store can also drive SPEM. The velocity memory system in oculomotor control was first proposed to explain the observation that high velocity *anticipatory* SPEMs (ASPEMs) can occur before motion onset. In an early investigation, Barnes and Asselman (1991) presented moving targets with velocities ranging from 9 to 45°/s in blocked sequences. It was found that ASPEMs were *scaled* in accordance with the expected target velocity; expectation of faster targets elicited higher velocity ASPEMs and vice versa. In consideration of these results, Barnes and Asselman (1991) suggested that the copy of the pre-motor drive signal which maintains predictive pursuit may also be sampled and stored for longer durations. This stored velocity information could then be used to scale future ASPEMs (Figure 1.2A).

In another important study, Barnes et al. (1997) found that participants could still produce scaled ASPEMs despite fixating during all previous presentations. This showed that velocity information can be stored without activation of the efference copy loop (Figure 1.1). Further work suggests that more than one velocity can be encoded during fixation. Poliakoff, Collins and Barnes (2005) presented two targets travelling at different velocities while participants fixated. One of these was then cued, and repeated on the next presentation when tracking was allowed. It was found that the ASPEMs before the tracking presentation were scaled according to the cued, but not the un-cued velocity. This suggests that both were encoded simultaneously on the fixation presentation. In fact, these authors found that ASPEMs were also proportional to the velocity of the previous trial, despite that fact that it was no longer relevant to the task. As will be discussed later, such *past history effects* are a theme of the current work.

Further studies suggest that velocity memory controls eye movements after targets disappear or become occluded. Although occlusions shorter than 200 ms may be covered by predictive pursuit systems, tracking across longer occlusion intervals could be guided by stored velocity information. Evidence for this comes from Bennett and Barnes (2006a) who found that people could keep their eyes approximately aligned with the position of occluded targets for at least 900 ms. This was achieved via a combination of reduced velocity SPEM, saccadic eye movements and ASPEMs which were scaled to the expected velocity of the target after reappearance. In a similar experiment, by Bennett and Barnes, (2004), the target travelled at different velocities before and after occlusion. It was found that participants could learn different pre and post occlusion velocities, and modulate SPEMs which occurred in anticipation of reappearance to fit the expected velocity of the reappearing target. Finally, Bennett and Barnes (2006b) showed that oculomotor control is sensitive to target acceleration during occlusion; that is, ASPEMs were scaled according to the velocity an accelerating target would reach upon reappearance (see also Bennett, de Xivry, Barnes, & Lefevre, 2007; Bennett, de Xivry, Lefevre, & Barnes, 2010).

The model shown in Figure 1.1 raises a question; how long must target motion be visible before velocity information is stored? Barnes and Collins (2008) addressed this issue by presenting targets for very brief periods (50, 100, 150 or 200 ms) before an occlusion period (400 or 600 ms) and a second visible period. It was found that SPEMs were always initiated at around 100 ms after the onset of target motion. SPEM velocity then increased to reach an initial peak value early in the occlusion period. Barnes and Collins (2008) argued that a stored representation of the briefly presented retinal velocity signal could provide a goal for SPEM drive and that ocular pursuit of *visible* targets could be guided by retinal velocity signals, efference copy signals *and* stored velocity signals. However, after the initial period of occlusion, only stored velocity signals are available.

Further empirical work is required to determine the relative weighting of different extraretinal velocity signals in SPEM control. However, the important point with regard to the current work is that a velocity memory system is involved in guiding eye movements, at least before motion onset and during occlusions longer than visuomotor delay. In the following sections, it will be argued that the same velocity memory system mediates other cognitive operations as well.

## 1.3 Hand movements

The models developed by Barnes and colleagues are most directly applicable to SPEM control. However, it is likely that the velocity store component of this model may also guide other judgements and behaviours. In line with this, Barnes and Marsden (2002) demonstrated that the velocity memory system may also guide anticipatory *hand* movements. In this study, participants tracked moving target with a manually controlled cursor. As with SPEMs, anticipatory hand movements occurred prior to visual feedback, and this response was scaled according to the expected velocity of the upcoming target. In the second experiment, the interval between presentations was varied. The latencies for the onset of both hand and eye movements were affected in the same way. Finally, in a third experiment, blocks with predictable and random inter-presentation intervals were compared. Anticipatory responses were suppressed in the random condition for both hand and eye movements. These similarities can be explained by a common velocity memory module which guides both manual and oculomotor output channels.

In a more recent study, Vidoni et al. (2009) compared ocular and manual pursuit of moving targets. Predictable and random motion epochs were presented. It was found that both ocular and manual tracking became more accurate with practice, and this practice effect was exaggerated for the predictable epoch. This indicates that the predictable motion period was successfully encoded. There was a moderate trial-by-trial correlation in measures of ocular and manual tracking accuracy (although there were also differences in the pattern of learning for each effector type). Moreover, both forms of tracking were still more accurate for the predictable motion after a three day break. This suggests that long term retention of velocity information is possible, and that stored velocity information can guide both eye and hand movements.

Finally, Kerzel (2001) found that representation of the velocity of one's own hand movements may interfere with stored visual velocity representations. Participants viewed two subsequently presented visual targets separated by a short interval and judged whether the targets moved at the same velocity or not. During the inter-presentation interval, participants produced a hand movement which was either faster or slower than the first visual presentation. It was found that the velocity of the hand movement systematically interfered with the visual velocity judgement task. A fast hand movement resulted in the visual targets being remembered as faster than they actually were and vice versa. This cross-modal interference suggests that visual and manual velocity representations are stored in overlapping brain systems. This result again indicates that velocity memory has a function beyond oculomotor control.

## 1.4 The perceptual memory model

Velocity memory is often modelled as part of the oculomotor control system. However, velocity memory has also been discussed within the context of the *perceptual memory model*. The fundamental idea of this model is that the low-level sensory systems sensitive to a particular dimension of input, such as colour, spatial frequency or velocity, are also responsible for retaining those representations after stimulus offset (Magnussen, 2000; Pasternak & Greenlee, 2005).

In a study of velocity memory, Magnussen and Greenlee (1992) presented participants with two gratings moving at different velocities. The duration of the delay between the first and second velocity was systematically varied (e.g. Figure 1.2B). It was found that discrimination thresholds did not increase when the delay was increased from 1 to 30 seconds. This indicates that representations of the original velocity had not decayed within 30 seconds. They also found that the presentation of a distractor grating during the delay period increased discrimination thresholds, despite participants attempting to ignore it. The greater the difference between the to-be-remembered velocity and the distractor velocity, the more performance was impaired. This finding was interpreted as evidence for a lateral inhibitory model, in which populations of neurons responsible for detecting and encoding different velocities are linked by inhibitory connections. The presentation of a distractor velocity would have resulted in inhibition of the first presentation; hence performance in the discrimination task was impaired.

The velocity of a moving sinusoidal grating is a function of both the rate at which the light and dark bars cross a particular point in space (temporal frequency) and the distance between the bars (spatial frequency). In a recent exploration of the perceptual memory model, McKeefry et al. (2007) repeated Magnussen and Greenlee's experiment, but varied the masker gratings spatial frequency, temporal frequency or velocity. It was found that only the latter manipulation increased discrimination thresholds. This provides further support for the perceptual memory model, and suggests that velocity information is retained independently of spatial and temporal frequency.

Although the perceptual memory account of velocity storage is rarely discussed alongside the SPEM control system, these frameworks are not mutually exclusive. To explore this possibility, Wells and Barnes (1998) presented participants with sequences of same-velocity targets spaced by intervals ranging from 1.8 to 7.2 seconds. It was found that ASPEM velocity reduced with longer intervals, suggesting that velocity representations decay within 7.2 seconds. However, in a later study by Barnes and Chakraborti (2002), participants were presented with up to 5 closely spaced trials before a long interval (7.2 or 14.4 seconds) and ASPEM velocity was maintained after 14.4

seconds. It seems that when velocity representations are fully encoded by repeat presentations, the duration of the velocity memory is equivalent to that found by Magnussen and Greenlee (1992). This finding is consistent with the idea that a common velocity memory system could underpin delayed discrimination performance and ASPEM control.

## 1.5 Storage of the motion after-effect

The kind of stimuli used in delayed discrimination tasks have also been used to explore storage of the motion after effect (Figure 1.2C). After viewing a moving stimulus for a prolonged period (an adapting stimuli), a static stimulus (the test stimuli), appears to move in the opposite direction. This is known as the static motion after effect (sMAE). Alternatively, an adapting stimulus may distort the perceived direction of a moving test stimulus (the dynamic motion after-effect). Increasing the duration of the dark interval between the adapting and test stimuli has little effect on the MAE perception. This suggests that the MAE can be stored (Mather, Pavan, Campana, & Casco, 2008).

The relationship between MAE storage and velocity memory is unclear. However, both phenomena are probably controlled by the same neural regions. As discussed above, velocity memory could be mediated by the visual association areas responsible for velocity perception (Pasternak & Greenlee, 2005). An important region for velocity perception, (and thus, hypothetically, velocity memory) is area MT (Medial Temporal, Perrone & Thiele, 2001; Zihl, Voncramon, & Mai, 1983), and Theoret et al. (2002) found that Transcranial Magnetic Stimulation (TMS) disruption of MT during the delay reduced MAE perception. It can be concluded that MT is involved in both velocity memory and MAE storage.

It has also been found that the MAE interferes with SPEM. If participants attempt to follow a dynamic test stimulus with their eyes, pursuit can be biased in the direction of an orthogonal (90°) adapting stimuli. This occurs whether there is a dark interval between adapting and test stimuli or not (Watamaniuk & Heinen, 2007). This pattern of interference indicates considerable overlap between MAE storage, velocity memory and SPEM control.

## 1.6 Short and long-term velocity memory

The work discussed so far has mostly investigated short-term velocity memory, which is relatively accurate but sensitive to disruption. However, it is possible that various forms of semantic knowledge include a different kind of velocity memory. For example, someone's concept of 'rocket' may incorporate the idea 'moves upwards at a very high velocity' (Reed & Vinson, 1996). In support of this, Zago, McIntyre, Senot and Lacquaniti (2008) reviewed evidence that a lifetime of experience with gravity causes people to assume acceleration when observing downward motion (see also Hubbard, 2006). Moreover, implicit knowledge of biological motion kinematics has been found to influence perception of simulated hand motion (Pozzo, Papaxanthis, Petit, Schweighofer, & Stucchi, 2006). Finally, fMRI studies show that motion sensitive area MT is activated by *static* images which imply movement (Kourtzi & Kanwisher, 2000; Senior, Ward, & David, 2002). These findings demonstrate that the brain can build up a representation of an object's typical motion characteristics, and these associations influence actions and judgements.

## 1.7 Motion extrapolation

It seems that a common velocity memory system is involved in guiding SPEMs, controlling hand movements and making delayed velocity discrimination judgements. In this section, it is argued that the common velocity memory system is also involved in estimating the current position of occluded moving objects. This operation is known as motion extrapolation. In a typical laboratory based motion extrapolation task, participants watch a horizontally moving object disappear behind an occluder, and press a button when they judge the occluded target to have reach a particular point (e.g. Rosenbaum, 1975 , and see Figure 1.2D).

Previously, motion extrapolation has been discussed as part of the literature on *time-to-contact estimation* (TTC estimation). There is a wide body of research exploring the forms of information involved in TTC estimation. With regard to lateral motion (across the observers visual field rather than approaching the observer), TTC is specified by the ratio of the 1) degrees of visual angle subtended by the gap between object and its destination, to 2) the rate of change of visual angle. This can be formalized as:

$$\mathbf{TTC(t) = \theta/(\Delta\theta/\Delta t)}$$

Where $\theta$ is the angle subtended by the object-destination gap at time t, $\Delta\theta$ is the change in the angle, and $\Delta t$ is change in time (e.g. Regan & Gray, 2000). TTC at any given time has traditionally been denoted by the symbol '$\tau$' (pronounced 'tau'), and the idea that sensitivity to tau is required for TTC estimation is known as the 'tau hypothesis' (Tresilian, 1999). It has been suggested that animals are directly sensitive to $\tau$, and can thus estimate TTC *without* prior estimation of velocity or distance. Although the TTC literature has been dominated by the $\tau$ hypothesis, the idea in its original form has now been widely discredited (Hecht & Savelsburgh, 2004). For example, the work of Patricia DeLucia over the last 20 years has highlighted the variety of information involved in TTC judgements. She argues that although optic information like $\tau$ may be used in some circumstances, other forms of information are involved in TTC estimation even when these cues give information which is not in agreement with TTC as specified by $\tau$ (for review see DeLucia, 2004).

Tresilian (1995) argued that task parameters may influence TTC judgments in important ways which were not previously recognized. For example, when intercepting a visible object $\tau$ is available throughout the entire operation. In this scenario, performance could be explained by participants responding when $\tau$ reaches a critical threshold. However, in motion extrapolation tasks TTC information is not directly available at the time when the judgement is reported. Tresilian (1995) suggested that for motion extrapolation tasks, TTC may be calculated prior to occlusion, and then this duration could be stored and counted down, in order guide response initiation.

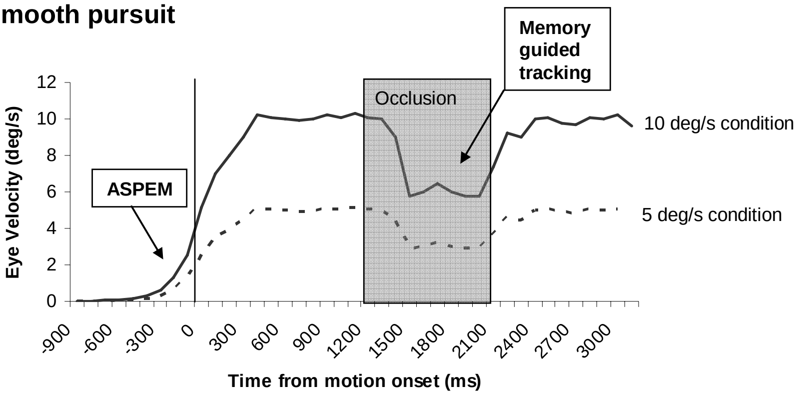
However, since Tresilian's account was published much work has indicated that motion extrapolation involves visuospatial tracking rather than timing. For example, motion extrapolation accuracy is impaired by moving distractor stimuli during the occlusion period (Lyon & Waag, 1995) and the presentation of occluded motion interferes with concurrent visual discrimination (DeLucia & Liddell, 1998). These patterns of interference suggest that visuospatial processes are active during motion extrapolation. Furthermore, induction of the MAE in the location of the occluder systematically affects response times (Gilden, Blake, & Hurst, 1995) as does the presentation of landmarks around the occluded target's trajectory (Pylyshyn, 2003). Finally, response latency to dots flashed in the current position of an occluded target is reduced. This again suggests that visuospatial attention is used to track the position of occluded targets during motion extrapolation (de'Sperati & Deubel, 2006).

The precise role of velocity memory or the oculomotor control system in motion extrapolation is uncertain. Nevertheless, there are good reasons to hypothesise a prominent role. According to the influential *pre-motor theory of attention*, shifts in the focus of visuospatial attention are driven by pre-motor eye movement commands (Rizzolatti, Riggio, & Sheliga, 1994). This theory implies that any task which requires visuospatial attention (such as motion extrapolation) necessarily recruits the pre-motor components of the oculomotor control system. Meanwhile, according to the SPEM literature, pre-motor systems are driven by velocity memory during occlusion. It is thus possible that velocity memory dictates the rate at which visuospatial attention shifts during occlusion. Velocity memory could thereby govern motion extrapolation performance. This idea is tested empirically in Chapter 2.

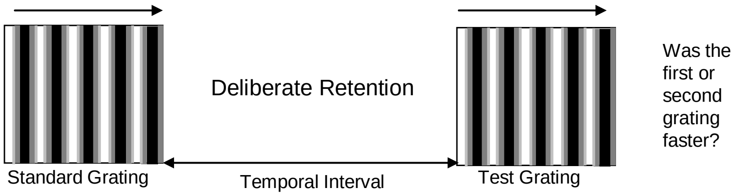
Given this argument, it is interesting that SPEM and motion extrapolation performance are affected by occlusion parameters in the same way. Both are unimpaired during the initial period of occlusion (<100 to 200 ms). After the initial period, SPEM velocity declines (Bennett & Barnes, 2004, 2006) and motion extrapolation accuracy reduces (Benguigui, Broderick, & Ripoll, 2004). This similarity implies overlapping systems. Further support is provided by Wexler and Klam (2001). In this study participants saw a moving target become occluded, and they had to decide whether it was behind or ahead of a specified end point after a certain time. It was found that eye position correlated with judgements; when their eyes were ahead of the end point, participants were more likely to report that the target was ahead of the endpoint, and vice versa. This result was replicated more recently (Jonikaitis, Deubel, & de'Sperati, 2009), again suggesting that eye movements and behavioural judgments on the motion extrapolation task are guided by common mechanisms.

There are two important caveats to this hypothesis. Firstly, as mentioned, these ideas apply to lateral motion extrapolation only. Extrapolation of approaching object motion may involve different mechanisms (Tresilian, 1995). Moreover, the role of head movements in motion extrapolation is not addressed. This is a deliberate simplification, given that head rotation and SPEM are synchronized in many situations (Cecala & Freedman, 2008).

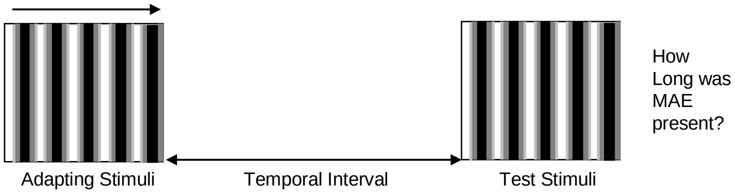
**A: Smooth pursuit**



**B: Delayed velocity discrimination**



**C: Storage of the motion after-effect**



**D: Motion Extrapolation**

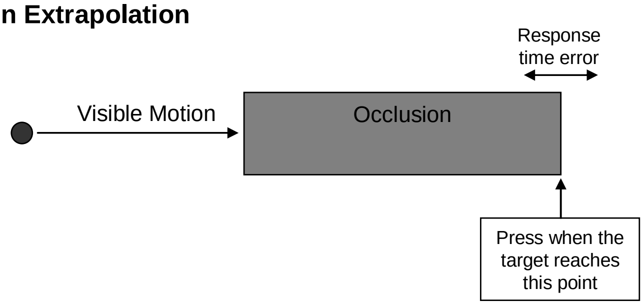


**Figure 1.2: Various tasks which involve velocity memory.** **A**: A prototypical eye velocity vs. time profile from an imaginary experiment in which participants attempted to track a moving target across an occlusion interval with their eyes. **B**: The experimental stimuli from a delayed velocity discrimination task. **C**: Stimuli in a motion after effect storage experiment. **D**: A prototypical motion extrapolation experiment.

## 1.8 The neural basis of velocity memory

According to the accounts discussed so far, an encapsulated 'store' holds velocity representations, and the output from the velocity store guides particular tasks or judgements. In this section, velocity memory is further characterized by exploring its neural basis. Although the conception of velocity memory as a discrete store is a useful heuristic, this depiction should not be taken too literally. As will be described below, there are many anatomically distributed brain regions that code velocity information. These populations may work independently in some contexts, or could work together as a distributed velocity memory system in other contexts.

The neural model of velocity memory described below is influenced by more general theories of working memory (for example, Fuster, 2009), the perceptual memory model (Greenlee, Lang, Mergner, & Seeger, 1995), and work on the role of neural oscillations in cognition (Fries, Nikolic, & Singer, 2007). All these authors generally agree that the brain consists of many anatomically separated populations of specialized or *expert* neurons. These discrete populations are involved in perceiving certain stimulus dimensions or producing specific motor responses. For example, in the occipital lobes, there are anatomically separate populations of neurons sensitive to a particular colour, spatial frequency or orientation. In the frontal lobes, discrete populations of neurons code for specific motor outputs, such as an eye or limb movement.

Given this, we can ask which neural populations are sensitive to velocity (abbreviations are decoded in Box 1). In the primate brain, velocity sensitive neurons are found in the primary visual cortex. Signals from V1 are integrated in the motion sensitive areas MT (Born & Bradley, 2005) and V3A (McKeefry, Burton, Vakrou, Barrett, & Morland, 2008). It is known that MT neurons code velocity information (Perrone & Thiele, 2001) and that bilateral lesions covering the MT/MST complex result in *akineoptosia*, (defined as a failure to perceive motion within the normal range, Zihl et al., 1983). MST neurons are sensitive to eye and head velocity as well as visual velocity

**Box 1: Abbreviations:**
ACC: Anterior Cingulate Cortex
DLPFC: Dorsolateral Pre Frontal Cortex
FEFs: Frontal Eye Fields
IPS: Intraparietal Sulcus
MT: Medial Temporal (AKA V5)
MST: Medial Superior Temporal
SEFs: Supplementary Eye Fields
V1: Primary visual cortex
V3: An extrastriate visual region

signals. This suggests that they combine retinal and extraretinal velocity information (Ilg, 2008; Ilg & Thier, 2003; Thier & Ilg, 2005). This pathway forms the early stages of the dorsal visual processing stream (Milner & Goodale, 2008). The smooth pursuit regions of the FEFs code eye movement velocity. FEF efferents then project to the horizontal and vertical pursuit related motor regions in the brainstem and cerebellum, and these synapse with primary oculomotor neurons in the Abducens Nuclei (Buttner & Buttner-Ennever, 2006; Thier & Ilg, 2005).

It can be seen that many 'sensory' and 'motor' velocity regions are present in the brain. Therefore during tasks which involve velocity memory, these local velocity experts need to be functionally linked, while other regions may need to be actively excluded from the *temporary coalition* (Jensen, Kaiser, & Lachaux, 2007). Functional linkage between these sensory and motor velocity codes could be achieved as follows: Individual neurons oscillate between periods of high and low depolarization. Neurons only produce action potentials, and are most sensitive to input, when they are highly depolarized. In other words, neurons display rhythmic periods of high and low excitability. Groups of neurons can communicate if their rhythms are synchronized. It is likely that task-relevant populations are linked through synchronization in the *beta* (~15 to 25 Hz) or *gamma* (~30 to 100 Hz) frequency bands (Fries, 2005). Conversely, low frequency alpha oscillations (~6 to 14 Hz) may occupy large regions of cortex which are not task relevant. This is a form of inhibition (Klimesch, Sauseng, & Hanslmayr, 2007).

Given these ideas, it can be hypothesised that velocity memory reflects synchronized oscillatory activity across distributed sensory and motor populations after stimulus offset. Indeed, in other contexts, it has been shown that memory maintenance involves persistent high frequency synchronization in the relevant network and increased alpha activity in irrelevant networks (Jokisch & Jensen, 2007). Therefore, although it makes sense to talk about a common velocity memory system (i.e. mediating a variety of tasks), this system may be distributed over many brain regions, which could be functionally linked together by virtue synchronized oscillations. These velocity sensitive regions could also communicate with other task-relevant populations in the same way.

Other task-relevant populations may be those which control visuospatial attention, such as the IPS. Neurons in the IPS code spatial coordinates in a world centred reference frame (Buneo & Andersen, 2006) and lesions to the right IPS produce hemispatial neglect (Heilman, Watson, & Valenstein, 2002). In fact, the IPS and FEFs are the core of the distributed network called the frontoparietal system (Mesulam, 2002). In the context of a motion extrapolation task, stored velocity representations may guide visuospatial attention networks in the right IPS.

Other research suggests that velocity memory could be related to working memory (Baddeley, 1986), which is a function of DLPFC (Levy & Goldman-Rakic, 2000; Müller & Knight, 2006). In a recent fMRI study, Lencer et al. (2004) found that the bilateral V3a, MT, anterior ventral IPS, the right posterior IPS and the FEFs were all activated while participants tracked visible and occluded motion with their eyes. In fact, with the exception of V3a and MT, activation was actually *greate*r in the occluded condition. There were also additional activations in the right SEFs and the DLPFC during occlusion. This indicates that the same neural systems are involved in tracking visible and occluded targets, but that this pursuit network is enhanced by top-down inputs from the DLPFC during occlusion. Indeed, in a follow up study, Nagel et al. (2006) found that the magnitude of DLPFC activity was inversely proportional to the smoothness of pursuit eye movements. This suggests that the DLPFC is recruited whenever cognitive reconstruction of a target trajectory is required to supplement SPEM. This again implicates the DLPFC in velocity memory. This idea received further support from Ding, Powell and Jiang (2009), who compared pursuit visible and occluded pursuit to fixation, and found that the bilateral DLPFC was *only* activated during occlusion. Another frontal region, the ACC, was also more active during occlusion than visible tracking or fixation. However, unlike the DLPFC, ACC activation was not tightly correlated with FEFs activation, implying a more supervisory role.

Burke and Barnes (2008) conducted an fMRI study which compared pursuit and saccadic oculomotor responses to predictable or randomly timed stimuli. They found that the bilateral DLPFC was more active in predictable conditions (where memory guided anticipatory eye movements occurred) than in random conditions (where visually guided eye movements occurred). This is consistent with the findings of Lencer et al. (2004) and Nagel et al. (2006). It was also found that the right DLPFC was more active during pursuit conditions and the left was more active during saccade conditions. This suggests that the right DLPFC is concerned with memory for velocity and the left with memory for spatial position. Interestingly, Ding et al. (2009) found the right DLPFC was more active than the left during memory guided tracking.

A working hypothesis based on the neurophysiological literature is that coherent oscillatory activity in the distributed velocity memory system is under the executive control of the right DLPFC.

## 1.9 Current work

It can be seen that many separate studies have independently depicted a module which guides smooth pursuit eye movements, delayed velocity discrimination or hand movements. Velocity memory may also have a role in motion extrapolation. Although velocity memory can be described as an encapsulated module, on the neural level, it could involve continued oscillatory activity over several anatomically distributed cortical areas. This thesis aims to further characterize velocity memory, particularly in the context of motion extrapolation tasks.

Chapter 2 reports an investigation into whether the velocity memory and pre-motor components of the oculomotor control system mediate motion extrapolation. In the crucial experiment, two forms of motion extrapolation task were presented (cf DeLucia & Liddell, 1998). The hypothesis that overlapping systems control oculomotion and motion extrapolation gave rise to three specific predictions. First, it was hypothesised that, in both tasks, performance would be impaired under fixation conditions. Second, when eye movements are permitted, eye position during occlusion should be related to judgements. Finally, even when required to fixate, small changes in eye position around fixation (<2°) should be influenced by the movement of the occluded target.

Chapter 3 asked whether longer term velocity information (Section 1.6) is also involved in motion extrapolation. In one experiment the median velocity was 20°/s. Red targets were typically slow (10 to 20°/s) and the Green targets were typically fast (20 to 30°/s). It was predicted that these associations would influence response times. If this is true, then participants should respond later (i.e. as if the target was slower) on the red probe trials and earlier (i.e. as if the target was faster) the green probe trials.

Previous work has shown the subsequently encoded velocity representations may blend together. This phenomenon may influence ASPEM velocity (Poliakoff et al., 2005). It may also influence responses on motion extrapolation tasks (Makin, Poliakoff, Chen, & Stewart, 2008). Chapter 4 revisited the blending effect. Problems with the earlier results are addressed, and new experiments which explore blending across tasks are described. In one experiment, a motion extrapolation task was presented during the delay of a delayed discrimination task. If subsequently encoded velocity representations can blend, and both tasks involve a common velocity memory system, then one might expect systematic interference between them.

In order to characterize velocity memory, it is important to know *when* it becomes involved in a particular task. During motion extrapolation, attentive tracking may be controlled by velocity memory alone after the first 200 ms of occlusion. Makin, Poliakoff and El-Deredy (2009) found evidence for this using electroencephalography (EEG). Event related potentials (ERPs) were recorded during a motion extrapolation task. A specific ERP component was found at around 200 ms post occlusion, irrespective of target velocity or location. This confirms that there is a change in brain activity at this point, as hypothesised. Chapter 5 extends this investigation with an improved paradigm that compares both leftward and rightward motion.

Finally, Chapter 6 investigated the role of *upper alpha* (8-12 Hz) oscillations in motion extrapolation. As described in section 1.8, previous work has shown that 8-12 Hz brain oscillations are important in many of cognitive operations (Klimesch et al., 2007). It is thought that cortical areas can be inhibited by virtue of increase upper alpha activity, while task-relevant networks show considerable desynchronization in these frequency bands. Therefore, when tracking a visible target, there could thus be reduced alpha power in the visual cortex, which would be measured at posterior electrode sites. Other authors have argued that sensory networks may be inhibited via alpha synchronization during working memory maintenance (e.g. Grimault et al., 2009). Therefore alpha synchronization may be expected during occlusion.

In the final Chapter it was concluded that this series of experiments expand significantly on previous work. The results clarify a great deal about the nature of velocity memory, and especially how it functions in the context of motion extrapolation tasks.

# Chapter 2

# The oculomotor control system and motion extrapolation

## 2.1 Introduction

The path of a moving object is often blocked from view, however people are still able to judge the current position of a moving object during such periods of occlusion. This operation is known as motion extrapolation, and is important in real life scenarios such as driving (Horswill, Helman, Ardiles, & Wann, 2005). Motion extrapolation is typically measured in a laboratory by presenting a moving target which travels behind an occluder and asking participants to judge when the occluded target would have reached a particular point. As discussed in Chapter 1, existing research implies a central role for the oculomotor system in motion extrapolation. It is well established that motion extrapolation involves visuospatial attentive tracking (de'Sperati & Deubel, 2006), and that shifts of visuospatial attention are controlled by the oculomotor system, even during fixation (Rizzolatti et al., 1994). Therefore motion extrapolation is likely to be controlled by the oculomotor control system.

Two studies have explored this hypothesis. Peterken Brown and Bowman (1991) found that performance on a motion extrapolation task was similar under free eye movement and fixation instructions (at least in some conditions). More recently, Huber and Krist (2004) also observed similar performance under free eye movement and fixation conditions. In one task, participants saw a ball roll off a horizontal ledge and fall onto a visible landing point. The fall was occluded and they pressed a button at the exact time they thought that the target would hit the landing point. They argued that oculomotor and timed responses are both the product of underlying mental motion imagery. It was concluded that although eye movement patterns may sometimes index mental imagery, *'Physical imagery and not the oculomotor system itself...'* (p. 443) guided the timed responses in this task. Despite this conclusion, the current study revisited the putative role of the oculomotor control system in motion extrapolation.

Experiment 1 employed a form of motion extrapolation task referred to as a Discrimination Task. Participants saw a single visual target travel rightwards, disappear, and then reappear further along its trajectory. The target reappeared either at the correct time, too early or too late. The task was to discriminate correct from incorrect reappearance times with a 2 alternative forced choice button press (2AFC, Figure 2.2). In this task, it is necessary to attentively track the target across the occlusion period in order to discriminate reappearance error (DeLucia & Liddell, 1998). Participants performed two sessions which were identical except that fixation was required in one and free eye movements were allowed in the other. Note that participants were not explicitly asked to track the target with their eyes in the free eye movement condition (although most did so, section 2.3.2). It was decided that explicitly requesting ocular pursuit could artificially elevate the contribution of the oculomotor system to the task, and thereby preclude unbiased assessment of the functioning of this system under normal circumstances.

The hypothesis that the oculomotor system is involved in motion extrapolation gave rise to three specific predictions. First, if the oculomotor system is involved in motion extrapolation, then fixation should impair performance. Huber and Krist (2004) reported that this was not the case, and therefore concluded that motion extrapolation is independent of the oculomotor system. However, Huber and Krist (2004) used falling motion with no opportunity to track the occluded target's trajectory, so these findings do not rule out the possibility performance is affected by fixation in all circumstances, and are thus inconclusive.

Second, when participants are allowed to track the target with their eyes, pursuit should be better when behavioural judgements are accurate and vice versa (cf Wexler & Klam, 2001). This would be expected if common systems underpinned the ocular tracking and behaviourally reported judgements.

Third, even in the fixation condition, eye position should relate to the position of the occluded targets. The function of small eye movements which always occur during fixation has been widely discussed. One possibility is that the low amplitude saccadic intrusions which occur during fixation reflect initiated, but inhibited full-scale eye movements towards attended locations in the visual field. Indeed, there is evidence that the direction of fixational eye movements reflect covert shifts of visuospatial attention (Gowen, Abadi, Poliakoff, Hansen, & Miall, 2007; Laubrock, Engbert, Rolfs, & Kliegl, 2007; Pastukhov & Braun, 2010). If the oculomotor system is covertly active during motion extrapolation, as hypothesised, then fixational eye movements should be influenced by the position of the occluded target.

In Experiment 1 target velocity ranged from 10 to 30°/s. However, there were a high number of tightly controlled *probe trials* which travelled at the median velocity

(20°/s). Probes were systematically preceded by either faster (26°/s) or slower (14°/s) *prime trials*. This design had two advantages. First, it allowed the above hypothesis to be tested on a homogenous set of trials, while maintaining variability in the experiment as a whole. Second, it allowed exploration of an additional hypothesis; that the proportion of probe trials judged 'correct' should vary as a function of prime trial velocity. Indeed, using an identical task, Makin et al. (2008) found that probes which reappeared 150 ms too early were more often misjudged as 'correct' after a fast prime trial (Figure 2.1). This *past history effect* implies that subsequently encoded velocity representations had *blended together*. In the current experiment, this blending effect was investigated under conditions of fixation and free eye movements.

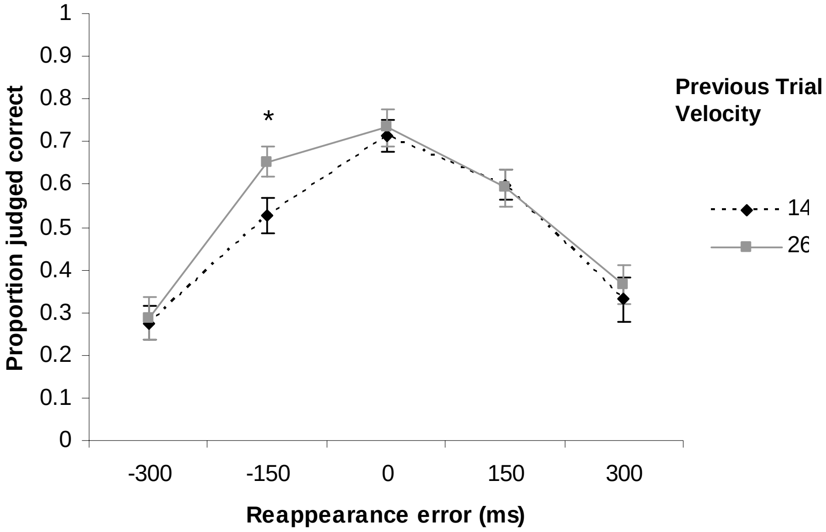


**Figure 2.1: The results of Makin, Poliakoff, Chen and Stewart (2008)**. In this experiment targets disappeared and then reappeared at the correct time, 150 or 300 ms too early or too late. Participants judged whether reappearance was 'correct' or 'incorrect' with a 2AFC button press. If target velocity was remembered as too fast during occlusion then a trial which reappeared too early would be reported as correct, whereas if target velocity was remembered as too slow a trial which reappeared too late would be reported as correct. 20°/s probe trials were preceded by faster (26°/s) or slower (14°/s) primes. The proportion of probes judged correct is plotted as a function of actual reappearance error and prime trial velocity. It can be seen that the proportion of 150 ms early probes judged correct was higher after a fast prime. Negative values reflect early reappearance. * $p$ <0.05.

## 2.2 Experiment 1 method

### 2.2.1 Participants

Thirty two participants (age 20 to 30, 12 male) took part in return for payment (£10) or course credit. As with all experiments reported in this thesis, participants had normal or corrected-to-normal vision and gave written informed consent. The study was given local ethics approval and was conducted in accordance with the 1991 declaration of Helsinki.

### 2.2.2 Apparatus

Participants sat at a table in a dimly lit room, with their head in a chin rest, approximately 75 cm from a 40 X 30 cm CRT monitor which subtended approximately 29.86° of their visual field on the horizontal axis. Visual stimuli were presented using a VISAGE Visual Stimulus Generator (Cambridge Research Systems). This setup was common to all studies reported here. The target was a blue circle of 0.44° in diameter presented approximately at eye level. The target always appeared 13.12° to the left of the screen centre and moved horizontally rightward. This was achieved by presenting the target in a new position on every frame (140 Hz). A symmetrical fixation cross approximately 0.5° wide was presented 2.2° above the target trajectory on all trials. The occluder was the same colour as the background, giving the impression of a target rapidly disappearing behind an invisible curtain. Participants pressed one of two buttons with their right hand on each trial. Eye position was sampled at 50 Hz with an ASL infrared eye tracking system (ASL Eye-Trac 6000). The eye tracker was mounted on the table between the participants and the stimulus monitor (Figure 2.2B). Calibration was achieved by asking participants to look at 1 of 9 points spaced evenly around the target trajectory. This procedure was repeated between blocks of trials.

### 2.2.3 Design

Probe trials were presented in 20 conditions [Eye instruction (fixation, free eye movement) x Prime trial (14, 26°/s) x Reappearance error (-300, -150, 0, 150 or 300 ms)].

### 2.2.4 Procedure

Participants were told that on each trial they would see a blue target move horizontally rightward, disappear, then reappear further along its path and continue moving until it reached the other side of the screen. They were told that on some trials the target would move smoothly through the occlusion period at a constant speed, and to press *button A* if they saw this happen. It was then explained that on other trials the target would reappear 'too late, as if it had stopped briefly during the hidden period', or 'too early as if it had jumped ahead during the hidden period'. They were instructed to press *button B* if they saw either of these non-smooth passages through occlusion.

At the start of each trial, a 200 ms audio cue (300 Hz) was presented. After this, the static target was presented for 200 ms to indicate the start point at the far left of the screen. The target was then blanked for 400 ms, before it reappeared moving horizontally rightward. These events at the beginning of each trial were based on previous work by Barnes and colleagues (e.g. Poliakoff et al., 2005), and were designed to make the onset of motion as spatially and temporally predictable as possible. This design improved the participant's comfort with the task, and facilitated tracking of the visible object. On all trials, the target trajectory was 26.25º long, and was symmetrical around the horizontal centre of the screen. The first visible motion period was always 5.95º in length. This was followed by an occlusion period, which ranged from 5.77 to 11.72º. Reappearance error was produced by adding or subtracting 0, 150 or 300 ms from the occlusion duration, without altering the size of the occluder (Figure 2.2A). The interval between reappearance time of prime trials and the start of the probe trial was always 3500 ms, and was randomized between 3500 and 4500 ms in all other cases. Each participant was first presented with a practice block consisting of 20 trials, with the same range of velocities and reappearance errors as in the experiment proper.

Participants then completed 336 trials, 160 of which were prime-probe pairs. The 80 probes all travelled at a velocity of 20°/s, half were preceded by 14°/s primes and half by 26°/s primes. Primes always reappeared at the correct time. This feature was designed to minimize interactions between response type and velocity which could otherwise complicate the past history analysis (Makin et al., 2008). Probes were presented 8 times at each of the 5 levels of reappearance error and prime velocity. On probe trials, the first period of visible motion always lasted 300 ms. Each probe trial had one of four levels of occluded distance, 6.77, 7.77, 9.74 or 10.73° presented in a pseudorandom order, counterbalanced across reappearance error, prime velocity, and prime trial occlusion duration. On probe trials that appeared at the correct time, this corresponded to hidden durations of 338, 388, 487 and 536 ms. The same 4 occluder sizes were used in the prime trials as the probe trials. In each prime-probe pair, the distance travelled by the occluded target was identical. These parameters were designed to make target velocity the only difference between prime and probe trials.

The remaining 176 trials were filler trials. The filler trials immediately before prime trials always had a velocity of 16, 18, 22 or 24°/s and a reappearance error of +/- 150 ms. The remaining filler trials had velocities of 10, 12, 28 and 30°/s, with each level of reappearance error occurring three times for each velocity, and velocities of 16, 18, 22 and 24°/s with reappearance errors of 0 or +/- 300 ms. The number of filler trials separating prime probe pairs was either 2 or 3. The average velocity of these ranged between 16 and 24°/s and the average reappearance error was between 150 and -150 ms. Occluder size was randomized on a trial by trial basis in the filler trials. These parameters were designed to prevent overall differences in the group of trials before a probe confounding the effect of prime velocity, while producing a great deal of variability in the visual stimulus.

The fixation condition involved an identical task and presentation, except that the participants were instructed to fixate on the cross. Participants completed the free eye movement and fixation sessions either in the same session or on separate days. Half the participants performed the fixation session first. Each session was divided into eight blocks, and the eye tracker calibration was checked between each block.

### 2.2.5 Analysis

All analyses reported in this thesis adhered to certain common stages, unless stated. When measuring behaviourally reported judgements, the mean value from each condition and participant was obtained. Most analysis involved repeated measures ANOVAs, applied to participant level data. Prior to analysis, a small proportion of data points > 2.5 SD from the condition mean were replaced with the next most extreme value (Makin et al., 2008). It should be noted that this was a conservative approach to outlier removal; it results in the smallest possible change to the distribution of values in a condition. Another alternative, of course, would be to retain outliers, but this has the cost of making condition means less representative. A minority of variables broke the normality assumption according to the Kolmogorov-Smirnov and/or Shapiro-Wilk tests of normality. ANOVA analysis was used despite this. This is not unprecedented, nor is it considered by all statisticians to compromise claims about statistical significance (Glass, Peckham, & Sanders, 1972). This decision was based on the fact that normalization procedures (e.g. log transformation) did not always have the effect of producing normally distributed data, and that non-parametric tests nearly always confirmed the results of ANOVAs. The Greenhouse-Geisser correction factor was applied when the sphericity assumption was violated and significant effects were followed up with paired samples t-tests (uncorrected for multiple comparisons).

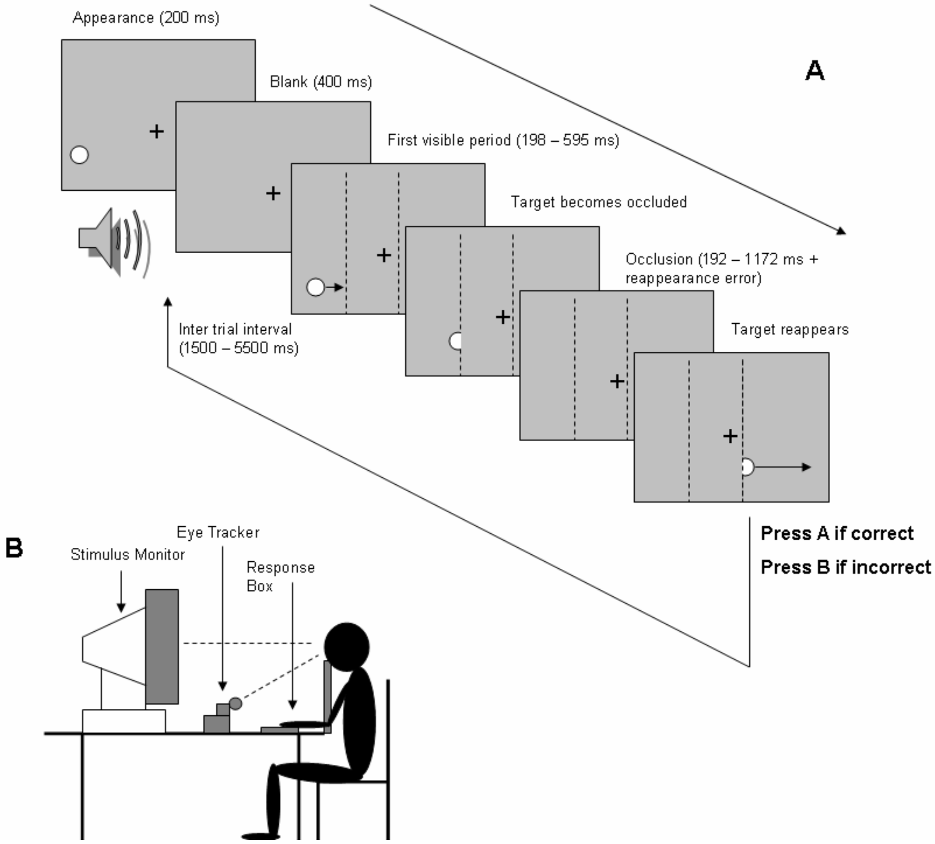


**Figure 2.2: The events of a single trial of Experiment 1**. **A:** Participants saw a target appear, then travel horizontally rightward. The target the disappeared and reappeared further along its path. Reappearance error was 0, 150 or 300 ms too early or too late. The task was to discriminate correct from incorrect reappearance. Vertical dashed lines were not present in the experiment, but indicated the dimensions of the invisible occluder **B:** The experimental set up.

## 2.3 Experiment 1 results

### 2.3.1 Behavioural responses

#### 2.3.1.1 Fixation vs. free viewing

The first hypothesis was that performance would differ on Fixation and Free viewing trials. The proportion of ‘correct’ judgements at each of the 5 levels of reappearance error was analysed as a function of eye movement instruction with two factor repeated measures ANOVA [eye instruction (fixation, free eye movement) x reappearance error (-300, -150, 0, 150 and 300 ms)]. Trials were not excluded due to eye movement profiles to ensure that differences between free eye movement and fixation conditions were not confounded by power. That is, removing trials from the fixation condition could produce apparent performance impairments in the fixation condition due to inferior signal to noise ratio.

The effect of Reappearance Error was highly significant ($F$ (4, 124) = 55.693, $p < 0.001$). A significant quadratic trend explained a high proportion of the variance in the proportion of ‘correct’ judgments ($F$ (1, 31) = 221.0644, $p < 0.001$, partial $\eta^2 = 0.877$). This confirmed that participants could discriminate reappearance error. There was no overall difference between the fixation and free eye movement conditions ($F$ (1, 31) <1, NS), but there was a significant interaction between Reappearance Error and Eye Movement Instruction ($F$ (2.565, 79.50) = 6.575, $p = 0.001$). This was because a greater proportion of -300 ms reappearance trials were erroneously reported as ‘correct’ in the fixation condition ($t$ (31) = -3.364, $p = 0.002$), but a greater proportion of correct reappearance trials were recognised as correct in the free eye movement condition ($t(31) = 4.034$, $p < 0.001$). Comparisons between fixation and eye movement conditions at the other levels of Reappearance Error did not reach significance ($t$ (31) < 1.123, $p > 0.274$, Figure 2.3).

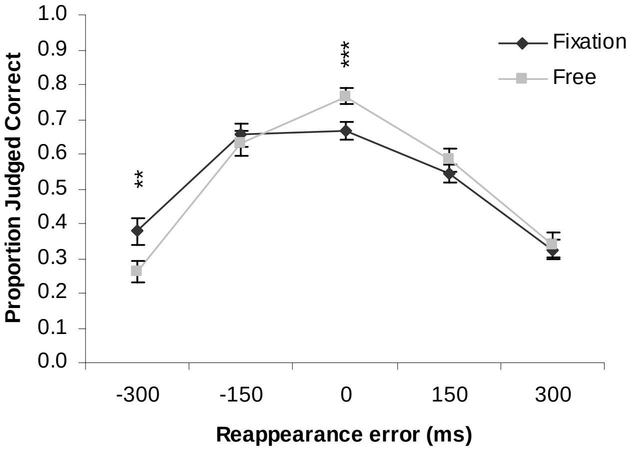


**Figure 2.3: Performance in free eye movement and fixation conditions**. The proportion of trials judged to have reappeared at the correct time is shown as a function of Eye Movement Instruction and Reappearance Error. Negative values reflect early reappearance. Error bars = +/- 1 S.E.M. ** p < 0.01, *** p < 0.001

### 2.3.1.2 Probe trials

It was hypothesised that judgements on probe trials should be influenced by the velocity of preceding prime trials. For each participant, the proportion of 20°/s probe trials judged to have reappeared at the 'correct' time in each condition was measured. These values were then standardized according to each participant's mean proportion of 'correct' responses across all probe trials (Gilden et al., 1995). Trials where participants broke fixation on either the probe or preceding prime trial were excluded (15%). Fixation was judged to have been broken if eye position deviated by more than 2° from the median eye position during the relevant interval (following Kerzel, 2002). Data was then analysed with a 3 factor repeated measures ANOVA [2 eye movement instruction (free, fixation) x 2 (prime velocity (slow, fast) x 5 reappearance error (-300, -150, 0, 150 300 ms)].

There was a main effect of Reappearance Error (*F* (2.219, 68.799) = 50.953, $p < 0.001$). The quadratic trend in this was highly significant, and explained over 89% of the variance in the proportion of correct judgments (*F* (1, 31) = 252.759, $p < 0.001$, partial $\eta^2 = 0.891$). This confirmed that the participants could successfully discriminate reappearance error on the probe trials (Figure 2.4).

There was no main effect of Prime Velocity, and Prime Velocity did not interact with any other factor (*F*, (1, 31) <1, NS). There was no significant effects involving Prime

Velocity when the 5 levels of Reappearance Error were analysed separately (*F* (1, 31) < 1.942, *p* > 0.172). Therefore the blending effect found by Makin et al. (2008) was not replicated.

However, there was a main effect of Eye Movement Instruction (*F* (1, 31) = 6.397, *p* = 0.017), and an Eye Movement Instruction by Reappearance Error interaction (*F* (2.894, 89.725) = 3.155, *p* = 0.03). This was because there were significantly more erroneous 'correct' responses when participants were fixating in the -300 and -150 ms early reappearance error conditions (*F* (1,31) > 7.410, *p* < 0.012), but no effect of Eye Movement Instruction at the other levels of Reappearance Error (*F* (1,31) < 1, NS).

### 2.3.2 Eye movements

Eye position profiles from the probe trials are shown in Figure 2.5. It can be seen that, in general, fixation was maintained well, and participants tracked the target with their eyes in the free eye movement condition. It is noteworthy that eye position fell behind target position at around 200 ms post occlusion. This is consistent with previous work (e.g. Bennett & Barnes, 2004).

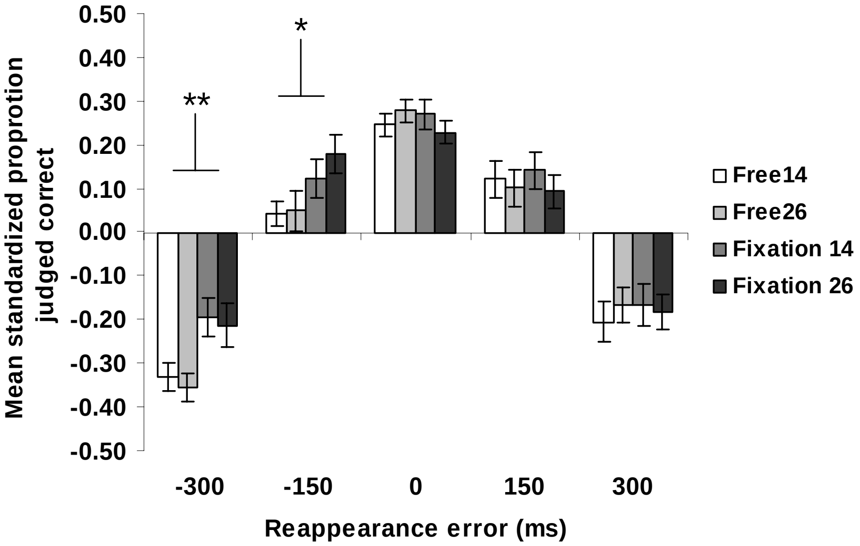


**Figure 2.4: Probe trial analysis.** The mean standardized proportion of trials judged to have reappeared at the correct time as a function of reappearance error, prime velocity and eye movement instruction. Negative values correspond to early reappearance. Error bars = +/- 1 S.E.M. ** p < 0.01, * p < 0.05.

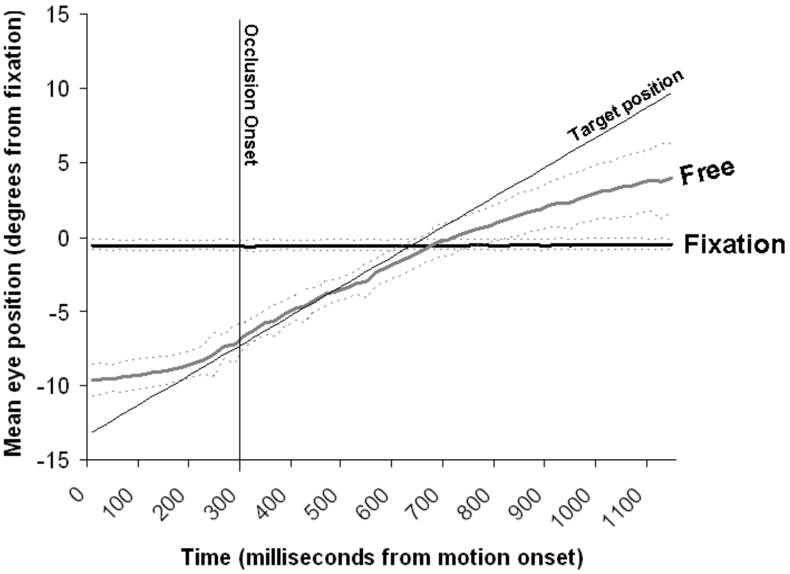


**Figure 2.5: Eye movement profiles.** Grand average eye position on the probe trials is shown as a function of time from motion onset and eye movement instruction. Dotted lines = +/- 1 SD.

### 2.3.2.1 Free eye movement condition

If eye movements and judgements are guided by common representations, there should be a systematic relationship between ocular tracking accuracy and performance accuracy. To explore this, pursuit accuracy was measured on the 20°/s probe trials which reappeared on time, 150 ms too early or too late. The correlation between eye position and target position during the first 260 ms of occlusion was measured (this interval was chosen as tracking cannot reflect responses to target reappearance). Higher correlation coefficients reflect better ocular pursuit. Trials were excluded from this analysis if the correlation coefficient was < 0.75, or if no behavioural response was recorded (12.3%). The vast majority of trials were had stronger correlations than this, so these trials were atypical and would make results less representative.

In the early and late reappearance trials, it was predicted that the 50% of trials with poorer pursuit would have more erroneous 'correct' responses that the 50% of trials with superior pursuit. This was the case in the early trials (126 vs. 137 mistaken 'correct' responses) but this difference was not significant ($\chi^2 = 0.476$, $p$ =0.468). In the late trials, there was no indication of any effect (134 vs. 137 mistaken 'correct' responses). In the on time reappearance trials, it was predicted that there would be more ‘correct’ responses on the 50% of trials with superior pursuit. This was true, but not significantly so (165 vs. 182 ‘correct’ responses; $\chi^2$ = 0.832, p = 0.368).

### 2.3.2.2 Fixation condition

This analysis explored the hypothesis that low amplitude eye movements during fixation are influenced by occluded motion. The 14 and 26°/s trials of the fixation condition were used. These trials were chosen because there was no reappearance error, and thus they provided the maximum number of viable trials per participant. Trials where eye position deviated more than 2° from median eye position were excluded (8.36% of the 14°/s trials, 6.02% of the 26°/s trials). Each participant’s average eye position profile was standardized against their mean value, and then a grand average profile was produced.

Beginning with the 14°/s condition, grand average eye position becomes more leftward as the target approaches the occlusion period. Eye position then seems to reflect the rightward motion of the target across occlusion (Figure 2.6A). To explore this, the relationship between Time and grand average eye position during the period 200 ms after occlusion to 100 ms after the earliest reappearance was analysed with linear regression. This interval was chosen for analysis because the influence of visible motion is presumably minimal. Time explained 24.3% of the variance in average eye position ($r^2$ = 0.243). This slope of the regression line was significantly greater than zero ($F$ (1, 19) = 5.763, $p$ = 0.027). In the 26°/s condition the time vs. average eye position profile is similar (Figure 2.6B). The positive relationship during the occlusion period was again apparent ($r^2$ = 0.140) although this was not significant, presumably because fewer data points were available ($F$ (1, 8) = 1.138, $p$ = 0.322).

The patterns shown in Figure 2.6 were not significant when repeated measures ANOVA was applied to the participant level data. This was presumably because there is a great deal of variation in eye position as it oscillates around the fixation cross. An additional level of data reduction (average across participants) is thus required to bring out the influence of occluded target motion.

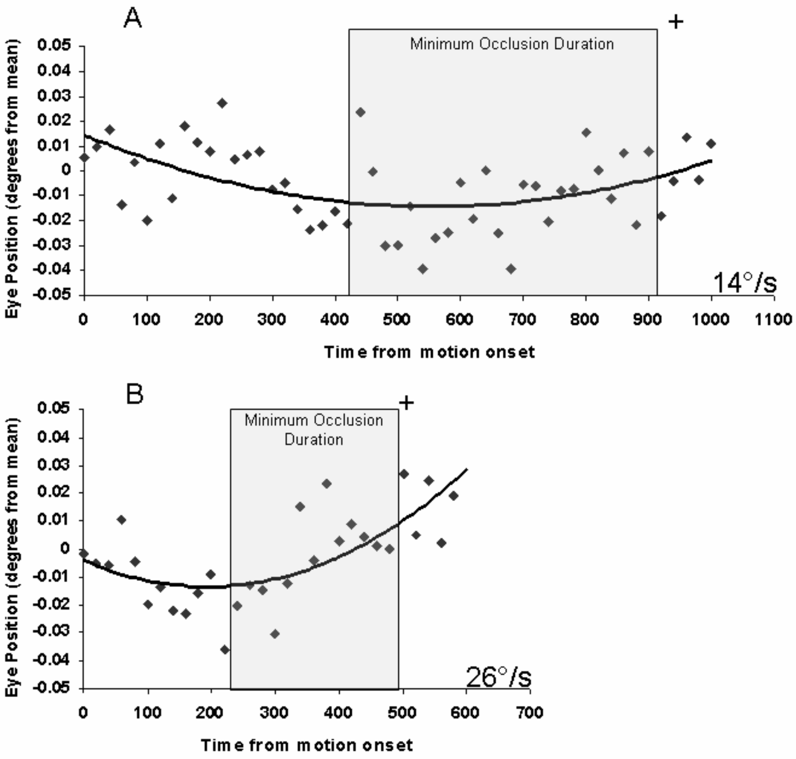


**Figure 2.6: Fixational eye movements**. **A:** The relationship between grand average eye position and time in the 14°/s trials. **B:** equivalent data from the 26°/s trials. The minimum occlusion duration is shown in grey. '+' represents the time the target reaches fixation.

## 2.4 Experiment 1 discussion

In Experiment 1 participants observed a target moving rightward, disappear, and then reappear further along its path. There were 5 levels of reappearance error (-300, -150, 0, 150 or 300 ms). Participants judged whether the targets reappeared at the correct time or not. The task was carried out twice; once with no eye movement instructions, and once when fixation was required. The aim of Experiment 1 was to test the theory that common velocity memory and pre-motor systems control ocular pursuit and behaviourally reported judgments about occluded target position. This theory was tested with three specific predictions.

### 2.4.1 Fixation vs. free viewing

The first prediction was confirmed. Performance was better in the free eye movement condition than the fixation condition. In both the probe trials and the whole data set, early reappearance was less frequently identified in the fixation conditions. It is possible that, during fixation, stored velocity information used to perform the task was based on retinal and pre-motor velocity signals alone, without the aid of encoded efference copy velocity signals (see section 2.9). Alternatively, the act of executing eye movements may help drive visuospatial attention to the occluded targets location. Either way, the result supports the idea that the components of the oculomotor control system guide behavioural judgements about occluded motion.

Nevertheless, one could ask why eye movement instructions influenced detection of early reappearance, but did not alter performance on trials that reappeared too late? In fact, comparable asymmetry was a feature of the past history effect recorded by Makin et al. (2008, see Figure 2.1). It seems that the performance on Discrimination Tasks is more sensitive to experimental manipulations on early reappearance trials. This could be because the accuracy of attentive tracking decays as a function of occlusion duration (Lyon & Waag, 1995; Vaina & Giulianini, 2004), and therefore subtle influences could be masked on the late reappearance trials (where occlusion duration is necessarily longer).

### 2.4.2 Ocular and behavioural performance

The second hypothesis was that superior ocular tracking would coincide with accurate judgements. In some conditions, the data was descriptively consistent with this hypothesis: On trials which reappeared too early, poorer ocular tracking was associated a greater number of mistaken ‘correct’ judgements. Conversely, in the trials that reappeared on-time, better tracking was associated with more ‘correct’ judgements. However, these effects did not approach statistical significance, possibly due to inadequate power. In Experiment 2 this problem was overcome.

### 2.4.3 Fixational eye movements

The third prediction was that eye position during the fixation condition should be influenced by covert tracking of the occluded target. The hypothesis was supported. In the 14°/s trials there was a positive correlation between grand average eye position and time during occlusion. A similar pattern was also evident in the 26°/s trials (although this did not reach significance). This result is consistent with the hypothesis that pre-motor components of the oculomotor control system are excited during motion extrapolation, even if participants are fixating.

When the whole trial duration is considered rather than the occlusion period alone, it can be seen that the grand average eye position moved *left* as the target approaches the fovea. Eye position was most leftward around occlusion onset and then moved right across the occlusion period. This could be explained by attraction to visible target on the left of fixation, (which may increase as the target approaches the fovea), then the attractive target disappearing, facilitating rightward shift back towards the fixation cross. However, it could be argued that the slope of the eye position-time relationship during occlusion indicates covert tracking, rather than just reduced leftward attraction. Reduced leftward attraction would produce a sudden rightward jump when target disappearance is cortically registered, but a clear slope was found.

Another possibility is that fixational eye movements were influenced by expectation of reappearance on the right of fixation. In Experiment 2, the same fixational eye movement analysis was performed on two tasks, one without expectation of reappearance. This disentangled the roles of covert tracking and expectation of reappearance on fixational eye movements.

### 2.4.4 Past history effects

In addition, it was hypothesised that judgements would be affected by the velocity of previous trials. However, this past history effect was not observed. Performance was not modulated by the velocity of the previous trial, either in the fixation or free eye movement conditions. In previous work with identical parameters (Makin et al., 2008), participants were more likely to erroneously report a probe trial which reappeared 150 ms too early as 'correct' after a fast prime trial (Figure 2.1). This was taken as evidence for blending between subsequently encoded velocity representations. Why this result was not replicated is unclear, however, distortions of subjective velocity produced by previous presentations are likely to be small, and may not be detected by the relatively insensitive Discrimination Task. Alternatively, the representation of the previous trial could have decayed during the 3500 ms ITI, although this would not explain the difference between the current results and those of Makin et al. (2008), who used the same ITI. In Experiment 2 ITI was manipulated to investigate this possibility.

## 2.5 Experiment 2

In Experiment 2 two tasks were presented. The first was a Discrimination Task which was similar to Experiment 1. In the second task the target travelled behind a visible rectangular occluder, and did not reappear on the other side. Participants had to press a button at the exact time they thought that the occluded moving target reached the right hand edge of the occluder (Figure 2.7). This was referred to as a *Production Task*. The Discrimination and Production Tasks were based on the same template and many of the stimulus parameters were matched. Both tasks were completed under fixation and free eye movement conditions by the same participants.

Experiment 2 was designed to test the same hypotheses as Experiment 1. As with Experiment 1, performance was expected to be superior in free eye movement than fixation condition. The results of the Discrimination Task should be the same as those of Experiment 1 in this respect. In the Production Task, the effect of fixation could manifest in various ways: For example, *Response time error* (bias towards early or late responses), *Absolute error* (response time error, ignoring the direction of the error) or *Variable error* (the spread of response time errors across the trials) could all be elevated in the fixation condition.

In the Discrimination Task, ocular tracking accuracy was again expected to correlate with superior performance, as in Experiment 1. In Experiment 2 there were a greater number of probe trials available for analysis, and probe trial characteristics were more homogenous. There was only one level of occluder size (8.75°), and 2 levels of reappearance error (-150 and + 150 ms). This increased the number of trials suitable for analysis and thereby improved statistical power. In the Production Task, it was hypothesised that response time and the time that the eye reaches the end of the occluder would be correlated. This would be expected if eye movements and responses are both controlled by the same underlying mechanisms (cf Jonikaitis et al., 2009).

Third, it was predicted that eye position during fixation would again reflect covert target tracking. Unlike Experiment 1, this analysis was conducted on the 20°/s probe trials, where trial parameters were tightly controlled. Whereas participants were expecting reappearance in Discrimination Task, there was no expectation of reappearance in the Production Task. Therefore, in the Production Task, any systematic effect of occluded motion on fixational eye movements could not be explained by the expectation of reappearance.

More generally, it should be noted that Discrimination Tasks *necessitate* attentive tracking. The only way to judge reappearance error is to track the target across the occlusion interval, then estimate the discrepancy between extrapolated target position and target reappearance position (DeLucia & Liddell, 1998). Conversely the Production Task could be theoretically carried out *without* attentive tracking. Instead, one could calculate 'time to contact' information prior to occlusion, then count down this temporal representation during occlusion in order to initiate response initiation at the right time (Tresilian, 1995, and see section 1.5). DeLucia and Liddell (1998) refer to this strategy as 'cognitive clocking'. Experiment 2 further explored the relationship between these tasks.

As with Experiment 1, it was also predicted that judgments should be influenced by the velocity of the previous trial. This was not found in Experiment 1, possibly because velocity representations decayed during the 3500 ms ITI. Experiment 2 again involved 20°/s probe trials immediately after 14 or 26°/s prime trials, but included 2 levels of ITI duration between prime and probe trials (1500 and 5500 ms). It was hypothesised that the effect of the previous trial would only manifest in the short ITI conditions. In the Discrimination Task, fast prime trials could result in more early reappearance probes being judged 'correct', while slow prime trials could result in more late reappearance trials being reported 'correct'. In the Production Task, probe trial response time could be earlier after a fast prime and vice versa. In fact, the Production Task might be more likely than the Discrimination Task to detect past history effects, as it provides a continuous dependent variable.

## 2.6 Experiment 2 method

### 2.6.1 Participants and apparatus

32 Participants (age 18 to 37, 10 Male) were involved. Participants received £20 or course credit. The apparatus was the same as that used in Experiment 1.

### 2.6.2 Discrimination Task

#### 2.6.2.1 Design

20°/s probe trials were presented in 16 conditions [eye movement instruction (free, fixation) x reappearance error (early, late) x prime velocity (slow, fast) x ITI duration (1500, 5500)].

#### 2.6.2.2 Procedure

The task was similar to Experiment 1 (Figure 2.2). Again participants saw a blue target disappear and reappear further along its path. The range of target velocities, occluder sizes, occluder durations and task instructions was the also the same. Reappearance error was again at one five levels (-300, -150, 0 150 or 300 ms), and again the visible period was always 5.95° long.

80 of the trials were probe trials. Probes travelled at 20°/s. Unlike Experiment 1, probe occluder size was always 8.75° and the probes reappeared either 150 ms too early or 150 ms too late. Probe trials were preceded by prime trials. Half of the prime trials moved at 14°/s and half moved at 26°/s. Prime trial occluder size was set at one of 5 levels; from 5.83 to 11.67° in 1.46° increments. Prime trials always reappeared at the correct time. This resulted in 5 levels of 14°/s prime trial occlusion duration (416 to 833 ms in 104 ms increments), and 5 levels of 26°/s occlusion duration (224 to 448 ms in 56 ms increments). The duration between the time of reappearance in prime trials and the onset probe trials (ITI) was either 1500 or 5500 ms (2 seconds either side of the occlusion duration in Experiment 1). Prime trial characteristics were fully crossed with probe trial types.

The remaining 180 trials were filler trials. Ten fillers moved at the extreme velocities of 10, 12, 28 and 30°/s, and had an equal number of reappearance errors of 300 or -300 ms. 40 filler trials travelled at 18 and 22°/s (with reappearance errors of -150, 0 or 150; 8 correct), and 24 trials travelled at 16 and 24°/s (with equal numbers of reappearance errors of -300 or 300). The occluder size and therefore duration was randomized in filler trials. Minimum occluder size was 5.77°/s and maximum occluder size was 11.72°/s. The filler trials immediately before prime trials were controlled. Velocity was never outside the 16 to 24°/s range, and 16, 18 22 and 24°/s trials were balanced across ITI and prime conditions. There were 2 to 3 fillers between each prime probe pair. The average velocity of the fillers was always between 16 and 24°/s the average reappearance error was always between -150 and 150 ms. With the exception of the prime trials, ITI was randomized between 2100 and 4900 on a trial by trial basis. Note that this produced a mean ITI negligibly different from the centre of the overall ITI range.

Before the experiment began, participants completed a 20 trial practice block. There were 2 repeats of 12, 14, 16, 18, 20, 22, 24, 26 and 28°/s trials, and single 10 and 30°/s presentations. 4 practice trials occurred with each level of reappearance error. All other parameters were randomized in the practice block.

### 2.6.3 Production Task

#### 2.6.3.1 Design

20°/s probe trials were presented in 8 conditions [eye movement instruction (free, fixation) x prime velocity (slow, fast) x ITI duration (1500, 5500)].

#### 2.6.3.2 Procedure

The set up was similar to that of the Discrimination Task. The key difference was that the occluder was a now visible grey box, and the target rarely reappeared on the other side. The participants had to press a single button at the exact time that they thought the target would reach the right hand edge of the box (Figure 2.7). The sequence of trials, occluder sizes and ITI durations were designed to be identical to those of the Discrimination Task. All the practice trials reappeared on the right of the occluder so participants could become familiar with the task. Also, an additional 8 reappearing trials were included in the experiment itself to retain interest in the task (1 trial per block, 20°/s).

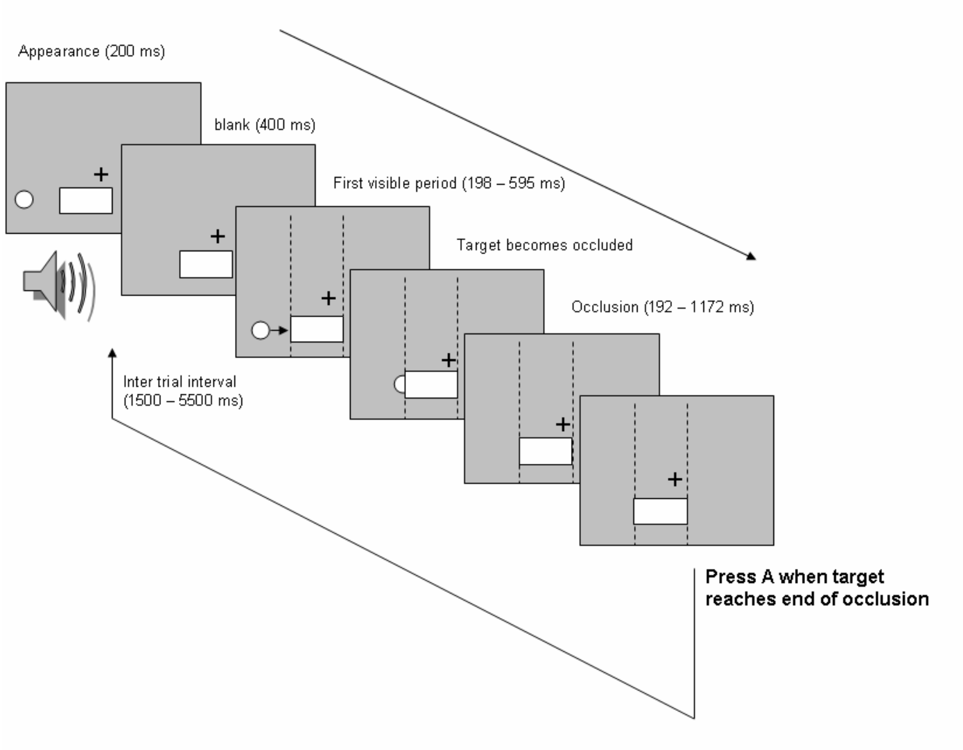


**Figure 2.7: A single trial of the Production Task**. The target moved behind a white rectangular occluder. Participants pressed the button at the exact time they thought it had reached the right hand side of the occluder. All parameters were matched to the Discrimination Task, except there was no reappearance and thus no reappearance error.

### 2.6.4 Analysis

Analysis of the Discrimination Task followed the general principles outlined above (Section 2.2.5). In the Production Task, response time error [time of would be reappearance – response time], and subjective velocity [actual velocity x (occlusion duration/(occlusion duration - error))] were measured on every trial (cf Gilden et al., 1995; Rosenbaum, 1975). When analysing error, a small proportion of trials where response error was > 1000 ms were excluded. When analysing subjective velocity, trials where subjective velocity was > 100°/s or negative were excluded. Such data is unlikely to reflect genuine responses. Fixation was defined as above (Section 2.3.1.2).

## 2.7 Experiment 2 results

### 2.7.1 Behavioural responses

#### 2.7.1.1 Fixation vs. free viewing

As with Experiment 1, it was hypothesised that performance would differ under free viewing and fixation instructions. In the Discrimination Task, the proportion of trials that each participant judged 'correct' was analysed as a function of Reappearance Error (-300, -150, 0, 150 and 300) and Eye Movement Instruction (Free, Fixation) with a repeated measures ANOVA[1]. Results were similar to Experiment 1: there was a significant main effect of Reappearance Error ($F$ (1.791, 55.506) = 17.994, $p$ <0.001). The quadratic trend in the data was significant and explained most of the variance ($F$ (1, 31) = 96.589, $p <$ 0.001, partial $\eta^2 = 0.757$, Figure 2.8A) indicating that participants could perform the task. There was also a main effect of Eye Movement Instruction ($F$ (1, 31) = 6.661, $p = 0.015$) and an Eye Movement Instruction by Reappearance Error interaction ($F$ (2.868, 88.919) = 6.654, $p = 0.001$). Participants were more likely to erroneously report 300 ms early reappearances as 'correct' in the fixation condition ($t$ (31) = 3.955, $p$ <0.001). A similar effect was borderline significant in the 150 ms early reappearance condition ($t$ (31) = 2.020, $p = 0.052$). In the correct reappearance condition, however, participants were marginally more likely to respond 'correct' when free eye movements were permitted ($t$ (31) = -1.872, $p = 0.071$). These results suggest that participants remembered velocities as faster when required to fixate, leading to more early reappearance trials being erroneously reported as correct.

In the Production Task, performance was measured in two ways. First, subjective velocity was analysed. Subjective velocity reflects the velocity the participant judged the occluded target to be travelling, as inferred from their response time. Mean subjective velocity was explored as a function of Target Velocity (10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30°/s) and Eye Movement Instruction (Free, Fixation) with a repeated measures ANOVA. There was a main effect of Target Velocity ($F$ (2.009, 62.284) = 448.090, $p <$ 0.001). A significant linear effect explained most the variance ($F$ (1, 31) = 678.186, $p$ <0.001, partial $\eta = 0.956$). There was also a main effect of Eye Movement Instruction ($F$ (1, 31) = 12.253, $p = 0.001$) and an Eye Movement Instruction x Target Velocity interaction ($F$ (3.066, 95.036) = 10.371, $p < 0.001$). It can be seen in Figure 2.8B that the slope of the relationship between target and subjective velocity is steeper in the fixation condition. Post hoc paired samples t tests show that subjective velocity was higher in the fixation condition at the top five levels of target velocity (*t* (31) > 2.379, *p* < 0.025), and at 18°/s (*t* (31) = 2.104, *p* = 0.044).

Second, Variable Error (i.e. standard deviation), Range and Inter-Quartile Range (IQR) of response time error in all trials was calculated for each participant to provide a metric of performance accuracy (Tresilian, 1995)[2]. Mean response time error and absolute error (i.e. Mean error ignoring the sign) were also explored. Although there were no significant differences in mean error or absolute error, Variable error, IQR and Range were all significantly greater in the fixation condition. It was also found that all performance metrics in the fixation and free eye movement conditions were correlated (Table 2.1). For Range and IQR comparisons, non-parametric tests were used because variables violated the normality assumption.

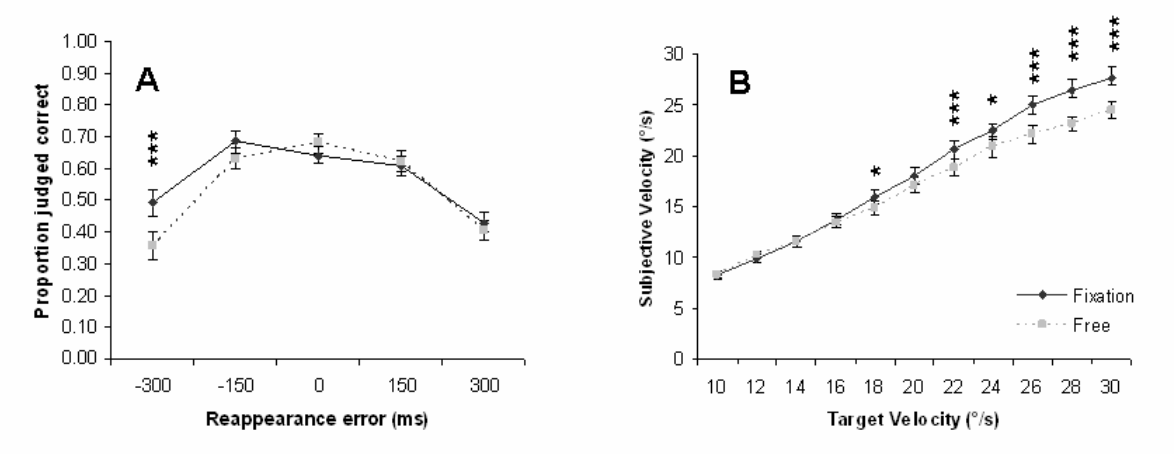


**Figure 2.8: Performance in the Discrimination Task. A:** Mean proportion of trials judged to have reappeared at the correct time is shown as a function of Eye Movement Instruction and Reappearance Error. Negative values reflect early reappearance. **B: Subjective Velocity in the Production Task.** Mean subjective velocity is plotted as a function of target velocity in the free eye movement and fixation conditions. Error bars = +/- 1 S.E.M. ** $p < 0.01$, *** $p < 0.001$.

**1:** As with Experiment 1, every trial was used in this analysis to avoid differences in power that would be produced by removing trials in the fixation condition on which fixation had been broken.

**2:** Before these metrics were calculated, missing data points were replaced with the participants mean response time. This ensured that differences between conditions could not be explained by different numbers of trials in each condition.

|  | Fixation |  | Free |  |  |  |
|---|---|---|---|---|---|---|
|  | M | SD | M | SD | *p* (difference) | *p* (correlation) |
| Mean error | -117.61 | 115.93 | -138.98 | 118.48 | 0.153 | <0.001*** |
| Absolute error | 137.43 | 90.67 | 153.69 | 97.94 | 0.271 | <0.001*** |
| Variable error | 165.68 | 39.41 | 136.57 | 33.69 | <0.001*** | 0.001** |
| IQR | 189.56 | 47.07 | 166.05 | 51.94 | 0.017* | 0.011* |
| Range | 1099.18 | 296.89 | 967.01 | 267.03 | 0.026* | 0.018* |

**Table 2.1**: **Performance in the Production Task.** Average error, Absolute Error, Variable Error, IQR and Range of response times (ms) were measured for each participant in the fixation and free eye movement conditions. Results of statistical comparisons are shown. Negative mean error values reflect later responses here.

### 2.7.1.2 Probe trials

It was predicted that performance in the 20°/s probe trials would be influenced by the velocity of the immediately preceding trial. Trials were excluded from the fixation condition if fixation was broken on either that probe trials or the immediately preceding prime trial (9.5% for Discrimination Task, 13.5% for Production Task).

In the Discrimination Task, the proportion of 20°/s probe trials judged to have reappeared at the correct time in each condition was calculated. As with Experiment 1, each participant's data was then recalculated as a deviation from the overall proportion of probe trials judged 'correct'. The long and short ITI conditions were analysed with separate repeated measures ANOVAs [Eye movement instruction (free, fixation) X Reappearance error (early, late) X Prime velocity (fast, slow)]. In the short ITI condition, participants were significantly more likely to report 'correct' reappearance after a fast prime ($F$ (1, 31) = 6.132, $p$ = 0.019). This did not interact with any other factor ($F$ (1, 31) < 3.276, $p$ > 0.079). In the Long ITI condition, there were no significant effects ($F$ (1, 31) < 2.659, $p$ > 0.112). This suggests that the effect of prime velocity was enhanced in the short ITI condition (Table 2.2).

In the Production Task, mean standardized response time error (error – average error across all probe trials) in the short and long ITI conditions was analysed with separate repeated measures ANOVAs [Eye movement instruction (free, fixation) X Prime velocity (slow, fast)]. In the long ITI condition, there were no significant effects ($F$ (1, 31)

< 1.962, $p > 0.170$), however in the short ITI condition, there was a borderline significant effect of Prime Velocity ($F(1, 31) = 3.970$, $p = 0.055$). There was no main effect of Eye Movement Instruction and no Prime Velocity x Eye Movement Instruction interaction ($F(1, 31) < 1.555$, $p > 0.221$). Paired samples *t* tests confirm that participants responded significantly earlier after a fast prime in the free eye movement condition ($t(31) = 2.307$, $p = 0.028$). This replicated the blending effect reported by Makin et al. (2008). However the equivalent blending effect was not significant in the fixation condition ($t(31) = 1.232$, $p = 0.227$, Figure 2.9). Finally, participants who were strongly influenced by prime velocity in the free eye movement condition were also affected by prime velocity in the fixation condition ($r = 0.368$, $p = 0.038$), and, in the fixation condition, participants whose response times were more variable showed a greater blending effect ($r = 0.465$, $p = 0.007$).

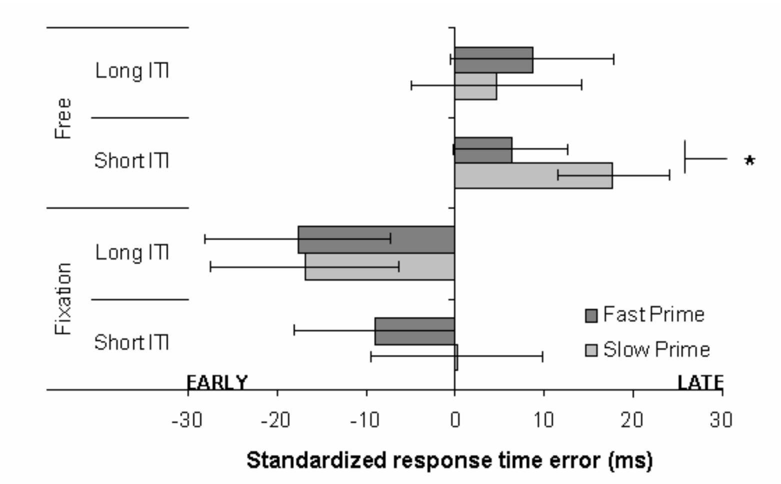


**Figure 2.9: Past history analysis in Production Task.** Mean standardized response time error in the 20°/s probe trials as a function of Eye Movement Instruction, ITI duration and Prime Velocity. Greater values correspond to later responses. Error bars = +/- 1 S.E.M. * $p < 0.05$.

|  |  | Fixation |  | Free Eye Movement |  |
|---|---|---|---|---|---|
|  |  | Slow Prime | Fast Prime | Slow Prime | Fast Prime |
| **Short ITI** | Early | 0.03 | 0.09 | 0.00 | -0.02 |
|  | Late | -0.08 | 0.01 | -0.04 | 0.00 |
| **Long ITI** | Early | 0.03 | 0.02 | -0.02 | -0.01 |
|  | Late | 0.00 | 0.04 | -0.02 | -0.02 |

**Table 2.2: Past history analysis in the Discrimination Task.** Mean standardized proportion of 20°/s probe trials judged to have reappeared at the correct time are shown as a function of ITI, Reappearance error, Eye Movement Instruction and Prime Velocity**.**

### 2.7.2 Eye movements

Eye movements on the 20°/s probe trials are shown in Figure 2.10. Plots depict grand average eye position over time. It is clear that participants complied with the task instructions, only following the target when permitted. It is also noteworthy that average eye position moved away from target position after approximately 200 ms of occlusion in the free eye movement conditions. In the Discrimination Task, eye position fell behind target position at this point. However, in the Production Task, eye position moved ahead of target position to the end of the occluder (see inset).

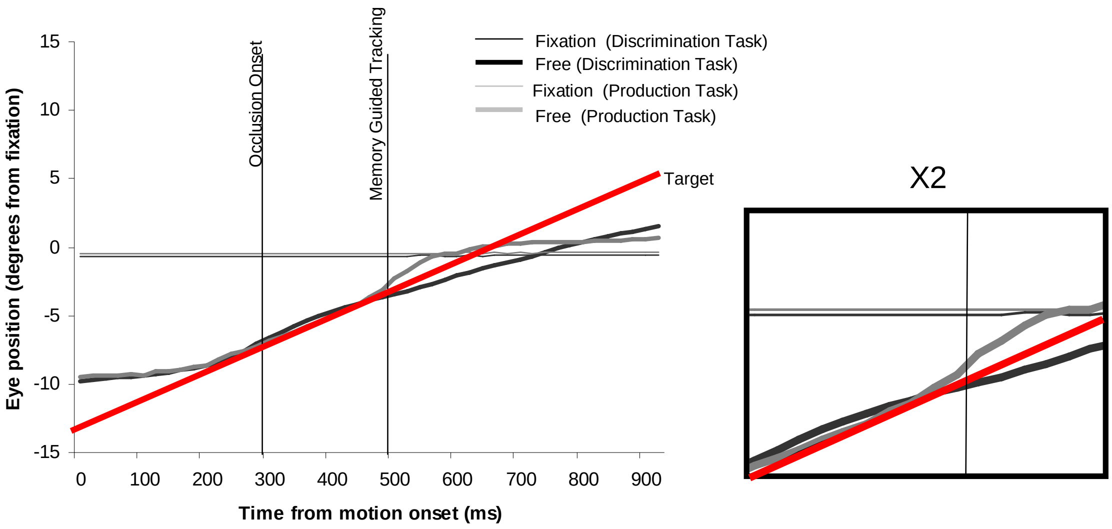


**Figure 2.10: Eye movement profiles.** Mean eye position as a function of time from motion onset in free eye movement and fixation conditions of both tasks. Vertical lines depict occlusion onset and the (putative) onset of memory-guided tracking 200 ms post occlusion. The inset focuses on eye movements around this point.

#### 2.7.2.1 Free eye movement condition

In the free eye movement condition of the Discrimination Task, participants usually tracked the target across the occluder with their eyes (Figure 2.10). It was predicted that participants would be better at discriminating reappearance error on trials where ocular pursuit was superior. On probe trials, reappearance was always 150 ms too early or too late, and never at the right time. Therefore, poor tracking should correspond to increased instances of mistaken 'correct reappearance' judgements. The correlation between eye position and target position during the first 360 ms of occlusion was calculated on each probe trial, as an index of ocular tracking performance. Trials were excluded according to the same criteria as Experiment 1 (11.49%). A median split was carried out, with the prediction that the 50% of trials with poorer tracking should have more instances of participants mistakenly reporting 'correct' than the 50% of trials with better ocular tracking. On the early reappearance trials this hypothesis was confirmed (Poorer Tracking = 380, Better Tracking = 315, $\chi^2 = 6.079$, $p = 0.014$). However, on the late reappearance trials, the opposite pattern was unexpectedly found. That is, in the 50% of trials with good tracking, there were significantly more erroneous 'correct' reports (Poorer Tracking = 325, Better Tracking = 390, $\chi^2 = 5.909$, $p = 0.015$).

In the free eye movement condition of the Production Task, participants typically moved their eyes ahead of the occluded target and fixated the end of the occluder (Figure 2.10). The change in eye position was calculated between every sample during the occlusion period (22 samples across the ~440 ms of occlusion). For each trial, the time of the sample with the largest rightward displacement was identified (Jump time). Trials were excluded if the largest displacement was negative or zero (<1%). The correlation between jump time and response time was measured for each participant. If there is a positive relationship between these variables, then the average Spearman's Rho coefficient across all participants should be greater than zero. This was found to be the case (Mean Coefficient = 0.154, SD = 0.144, $t$ (31) = 6.037, $p$ <0.001). This means that when the eyes moved towards the end of the occluder early, response time was early, and vice versa.

### 2.7.2.2 Fixation condition

As with Experiment 1 it was predicted that low amplitude eye movements during fixation would be affected by occluded motion. Analysis was conducted on the 20°/s probes in which fixation was maintained (8.152% and 10.65% of trials were excluded in the Discrimination and Production Tasks respectively). Data was treated in the same was as in Experiment 1. It can be seen in Figure 2.11 that mean eye position moved rightwards as the target moved rightwards. This pattern seems to continue throughout the occlusion period. To confirm this, time points from 200 ms post occlusion to 100ms after the minimum occlusion duration were analysed using an ANOVA [2 Task (Discrimination, Production) x 10 Time (200 to 380 ms post occlusion)]. There was a main effect of Time ($F$ (4.427, 137.232) = 3.808, $p = 0.004$; linear contrast, $F$ (1, 31) = 6.664, $p = 0.015$, partial $\eta^2 = 0.177$). However, there was no overall difference between the tasks and no Task x Time interaction ($F$ (1, 31) < 2.033, $p > 0.163$).

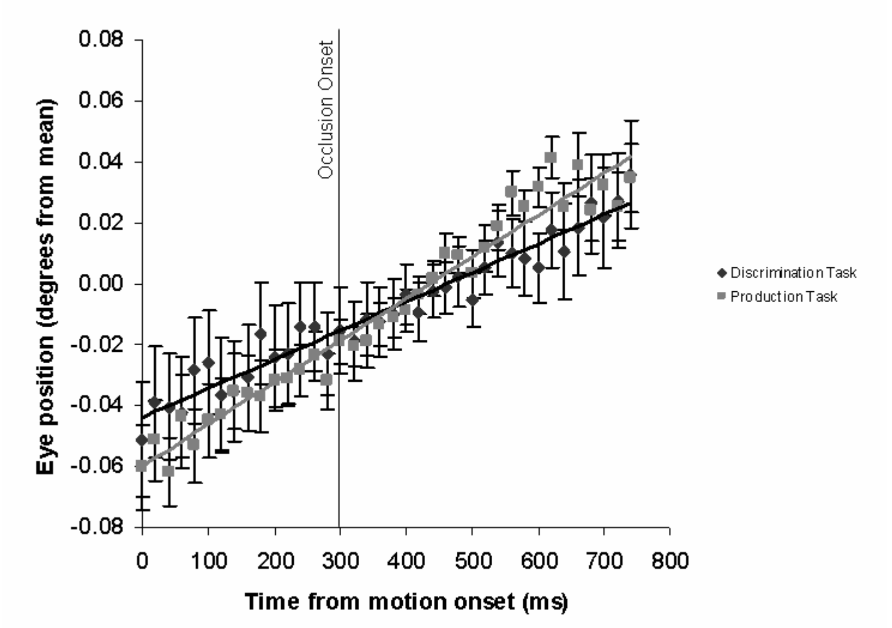


**Figure 2.11: Fixational eye movements both tasks.** The graph plots the relationship between average standardized eye position and time**.** Error bars = + / - 1 S.E.M.

## 2.8 Experiment 2 discussion

Experiment 2 comprised two tasks. The Discrimination Task resembled Experiment 1. Participants saw a target move rightwards, disappear, and then reappear at the correct time, too early or too late. Participants had to discriminate correct from incorrect reappearance. In the Production Task, the target disappeared behind a visible occluder and did not reappear. Participants attempted to press at the exact time the target reached the right hand edge of the occluder. The Discrimination and Production Tasks were conducted under conditions of fixation and free eye movements. It was theorised that all tasks and conditions would employ the velocity memory and pre-motor components of eye movement control system. This theory produced three specific predictions, which are discussed in turn in the following sections, before the secondary aim of investigating past history effects in motion extrapolation is addressed.

### 2.8.1 Fixation vs. free viewing

The prediction that fixation would affect motion extrapolation was supported. In the Discrimination Task, targets which reappeared 300 ms early were erroneously reported as ‘correct’ more often. There were also marginal differences between conditions when the target reappeared 150 ms too early or on-time, but not for late reappearances. This difference could have been masked by noise as occlusion duration increased,(as discussed above). In the Production Task, subjective velocity (i.e. stored velocity as inferred from response time, see method) was usually less than actual velocity because participants typically responded too late (cf Benguigui et al., 2004). Nevertheless, all participants showed a clear linear relationship between subjective and actual velocity, and the slope of this relationship was significantly steeper in the fixation condition. The difference in slopes was probably a consequence of the fact that the subjective velocity metric was more sensitive to response time error when occlusion duration was short, and that occlusion was shorter on the faster trials (see method)

Across all trials in the Production Task, variable error was also significantly greater in the fixation conditions. This contrasts with Benguigui and Bennett (2010), who found no effect of fixation on variable error in a less powerful between participants design.

The current results also challenge previous claims that fixation does not modulate motion extrapolation performance (Huber & Krist, 2004; Peterken et al., 1991).

Another feature of the Production Task was that participants who responded later, or less consistently, in the free eye movement condition also did so in the fixation condition. These correlations support the assertion that the same velocity memory and pre-motor systems are involved in guiding performance, irrespective of fixation demands. It can therefore be concluded that performance differences between fixation and free viewing conditions can be explained by the presence or absence of extraretinal velocity signals, and not to a fundamental change to the neurocognitive mechanisms employed.

### 2.8.2 Ocular and behavioural performance

In the Discrimination Task, participants usually tracked the target with their eyes when they were able to do so. It was hypothesised that more accurate ocular tracking during occlusion would be associated with more accurate judgements. In the early reappearance trials, this hypothesis was confirmed: performance was better in the 50% of trials with superior ocular pursuit. This suggests that common mechanisms guide ocular pursuit and behavioural responses (cf Wexler & Klam, 2001). However, in the late reappearance trials, the opposite effect was found; performance was worse in the 50% of trials with superior pursuit. There is no simple explanation for this and it is difficult to interpret because when a trial is judged to be ‘incorrect’ it is impossible to gauge whether the participant thought the target was early or late. However, this puzzling result still indicates that there was a relationship between ocular pursuit and behavioural judgements.

In the Production Task, eye position did not drop behind target position during occlusion, but instead moved ahead of the occluded target to the end of the occluder. In most participants, there was a positive relationship between the time when the maximum forward eye displacement occurred in the trial and response time, suggesting common processing for ocular and behavioural outputs. It is also interesting that this forward shift in eye position in the Production Task occurred, on average, at around the same time that eye position fell *behind* target position in the Discrimination Task (~ 200 ms post occlusion). This represents the point where occlusion is cortically registered and pure memory guided pursuit takes over from visually guided tracking (Bennett & Barnes, 2004; Makin, Poliakoff et al., 2009).

### 2.8.3 Fixational eye movements

The results of the fixational eye movement analysis were similar to those of Experiment 1, except that there was a clear linear relationship between grand average eye position and target position throughout, not just during occlusion. This effect was much stronger in Experiment 2, and the analysis in Experiment 2 should be considered more robust than that of Experiment 1 as approximately twice as many trials were involved. This result can only be explained in terms of covert oculomotor activation. The results indicate that, despite fixation, the pre-motor drive module is active because it is required for accurate behavioural responses. Discharge from this module is received by lower level ocular pursuit systems, even though they are inhibited by the fixation command. This produces rightward shift in mean eye position that can be abstracted from noise if one averages across a high number of trials. It is also noteworthy that fixational eye movements were comparable in the Discrimination and Production tasks. This implies similar covert activity of ocular pursuit systems, even though the task could be performed using temporal information, as described above. Furthermore, this similarity also confirms that the fixational eye movement pattern cannot be solely attributed to expectation of reappearance.

This data can be related to other work on fixational eye movements. Small saccadic eye movements, known as microsaccades, always occur during fixation (Abadi and Gowen, 2004). Microsaccade direction may reliably index the direction of covert visuospatial attention (Abadi & Gowen, 2004; Gowen et al., 2007; Laubrock et al., 2007). It is not possible to ascertain the role of microsaccades in this data, as the eye tracker lacked the resolution to detect them. In a recent study Pastukhov and Braun (2010) found that microsaccades indexed the direction of visuospatial attention with near 100% reliability, but only during a short period just after stimulus onset when their occurrence is particularly rare. This finding suggests that microsaccades would not contribute much to changes in grand average eye position over a long period. Instead, the pattern reported here may be produced by low amplitude ocular drift from the left to the right. Future studies with high resolution eye tracking could reveal the pattern of microsaccades during motion extrapolation.

### 2.8.4 Past history effects

Makin et al. (2008) found past history effects in both Production and Discrimination Tasks. This result was not replicated in the Discrimination Task of Experiment 2. Instead, participants were more likely to report correct reappearance after a fast prime, irrespective of actual reappearance error. This result cannot be easily interpreted. However, this effect was more pronounced when ITI was short, suggesting that the prime trial representation decayed during the long ITI.

In the Production Task, when ITI was short (1500 ms), participants responded earlier after a fast prime trial than a slow prime trial. This replicates the blending effect found by Makin et al. (2008). The findings also reveal additional characteristics of the velocity memory system. First, although the blending pattern only reached significance in the free eye movement condition, a similar pattern was seen in the fixation condition and the level of effect correlated between the conditions. This indicates that the effect reflects blending between representations at a level where retinal and extraretinal velocity signals are integrated. Second, in the fixation condition, the blending effect was stronger for participants whose response times were more variable, indicating that the influence of a previously encoded velocity was less for participants who are able to represent the current velocity more accurately. Third, the fact that there was no blending effect when the ITI was long (5500 ms), indicated that the velocity representation encoded on the previous trial may have decayed within the longer ITI duration.

## 2.9 General discussion

In Experiment 2, where methods were more developed, most of the predictions relating to the overlap between motion extrapolation and the oculomotor system were partially or fully upheld. In both tasks, performance was affected by fixation and when fixating, eye position nevertheless shifted with occluded target position. In the Production Task, there was a systematic relationship between eye movements and judgment parameters. In the Discrimination Task there was some evidence for an equivalent relationship. Thus the empirical evidence here provides a strong argument that oculomotor control systems are involved in motion extrapolation.

These findings are consistent with the influential premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987). According to this theory, shifts of spatial attention are produced by sensorimotor networks that guide responses to external locations. Attention and motor planning are not distinct cognitive modules; we shift attention to a spatial location by planning an action aimed at that location, even if the planned action is never executed (Eimer, Van Velzen, Gherri, & Press, 2007). In primates, pre-motor systems which control eye movements are likely to be particularly important in shifting visuospatial attention (Rizzolatti et al., 1994). The premotor theory of attention implies that if motion extrapolation involves visuospatial attention, it necessarily involves the oculomotor control system. It should be noted that most work on the premotor theory of attention has explored the link between saccade control and covert attentive shifts. However, there may also be a strong link between SPEM control and covert attentive tracking (cf Ohlendorf, Kimmig, Glauche, & Haller, 2007). In the context of motion extrapolation, pre-motor drive could produce a continuous sweep of visuospatial attention across successive target locations.

Although the results implicate oculomotor control in motion extrapolation, other processes may still be relevant. In some circumstances, people may use time-to-contact information rather than visuospatial tracking, such as when intercepting occluded approach motion (Tresilian, 1995). However, time-to-contact information is probably of marginal significance during extrapolation of lateral motion. In addition, when making higher-level verbal judgments about moving targets, Huber and Krist (2004) provide evidence that propositional knowledge, such as ‘naive physics’ can inform motion extrapolation. Another possible mechanism proposed by Huber and Krist (2004) is mental imagery. They conclude that although eye movements may provide a measure of underlying mental imagery, the oculomotor system is not functionally involved. This conclusion relied on the finding that fixation does not affect performance, which is challenged by the current results. In addition, the hypothesis that motion extrapolation is guided by a continuous shifting of visuospatial attention to external target locations means that mental motion imagery is not necessary (cf Pylyshyn, 2003).

Figure 2.12 depicts a model of motion extrapolation incorporating the oculomotor control system. In fact, this model is simply an expansion of the model of SPEM shown in section 1.2 in Chapter 1: velocity memory and pre-motor components of SPEM control are now responsible for guiding judgments on motion extrapolation tasks as well as eye movements. Although, the effector systems are different, the velocity memory and pre-motor systems (which are typically viewed as part of SPEM control) could be common to both output channels.

The model presented in Figure 2.12 is partially inspired by neurophysiological data. SPEM control systems have been well studied in the macaque brain. The negative feedback loop 'begins' with areas V1 and the MT/MST complex, which code retinal velocity signals (Born & Bradley, 2005). These retinal velocity signals stimulate pre-motor drive, which is located in the smooth pursuit regions of the FEFs (Barborica & Ferrera, 2003). Brainstem and cerebellar populations are innervated by FEF inputs, and drive SPEM directly. During fixation, these low level areas are inhibited by fixation neurons in the superior coliculus (Buttner & Buttner-Ennever, 2006)[3].

In this model, pre-motor drive from the FEFs guides spatial attention to target locations, as well as driving eye movements. Target location may be coded by neurons in the IPS, which is tightly connected to the FEFs. These regions are the core of the *frontoparietal system* which mediates spatial attention (Mesulam, 2002). One possibility is that pre-motor signals drive visuospatial attention to specific points on a *world-centred* spatial representation in the IPS (Gottlieb, Balan, Oristaglio, & Schneider, 2009). That is, target position is coded not in relation to the observer's eye or head, but in relation to other objects in the world (such as the screen edge or occluder). Of course, during fixation, eye, head and world centred spatial maps would be aligned. Conversely, when participants tracked the target with eye movements, only head or world centred coordinates usefully index target position. It is also significant that the IPS guides *multimodal* responses to spatial locations (Buneo & Andersen, 2006). This is relevant for motion extrapolation tasks, because representations of the target moving through space may be independent of the effector used to report judgements about target location.

As described in Chapter 1, velocity memory can be modelled as a distinct cognitive module. However, it is probable that velocity memory reflects persistent neural activity in distributed neural populations which code velocity. These velocity-sensitive neurons could be primarily sensory (e.g. MT) or motor (e.g. FEF). During occlusion, ongoing activity in these neural populations could be facilitated by top down excitation from the DLPFC (Müller & Knight, 2006). This is supported by an fMRI study from Lencer et al. (2004), who found a common network was active during visible or occluded tracking, but additional activation of the DLPFC during occlusion (see also Burke & Barnes, 2008; Ding et al., 2009; Nagel et al., 2006).

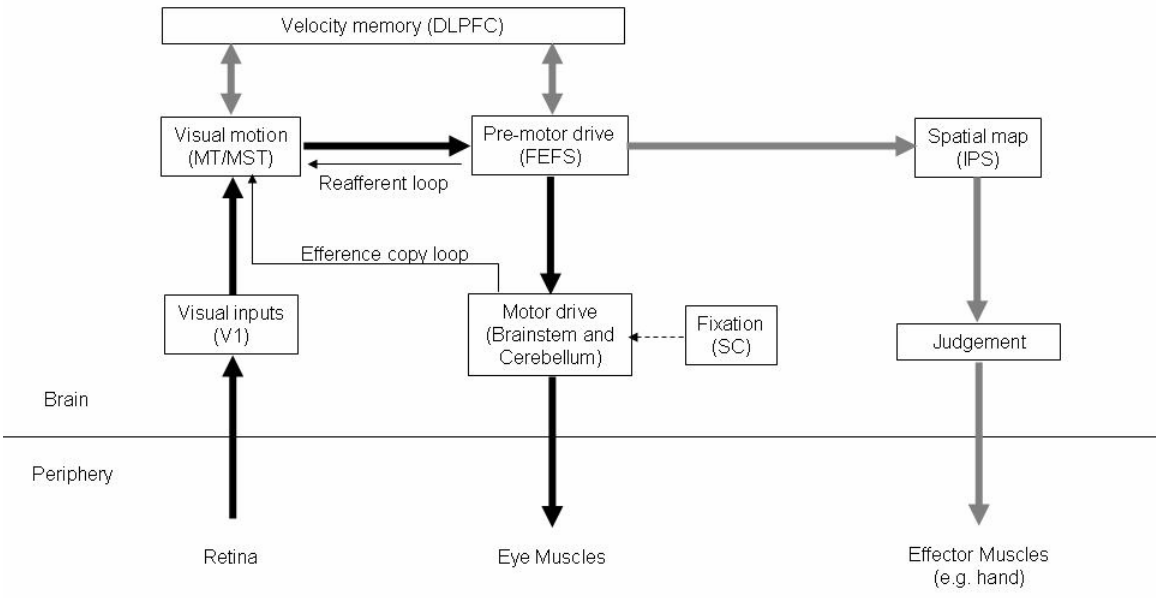


**Figure 2.12: Model of motion extrapolation.** The basis of this model is the oculomotor control system shown in Figure 2.1 of the previous chapter. During motion extrapolation, pre-motor eye movement commands shift visuospatial attention to successive locations on a spatial map. The putative neural correlates of these operations are shown in parenthesis (MT = Medial Temporal, MST = Medial Superior Temporal, IPS = Intraparietal Sulcus, DLPFC = Dorsolateral Prefrontal Cortex, SC = Superior Coliculus).

**3:** The Reafferent loops for predictive pursuit may, on a neural level, constitute projections from pre-motor FEF regions to in the MST. Meanwhile, efference copy loops may project from the low level brainstem populations to MST. This is supported by the finding that some MST cells are sensitive to eye velocity as well as target velocity, so they must process extraretinal velocity signals (Ilg, Schumann, & Thier, 2004).

In summary, this work tested the hypothesis that common velocity memory and pre-motor systems guide both eye movements and judgments about occluded moving objects. This idea was supported by the finding that judgments were less accurate during fixation than when participants were free to move their eyes, that eye position during occlusion was related to behavioural responses, and that eye position correlated with occluded target position during fixation. This work suggests there is an overlap between systems guiding the eye movements and motion extrapolation judgements, whether fixation is required or not, and whether the judgement task demands attentive tracking (Discrimination Task) or not (Production Task).

A secondary aim of these experiments was to investigate the influence of previously seen velocities on motion extrapolation. Makin et al. (2008) found that participants responded as if probe trials were faster after fast primes and vice versa. In this chapter this blending effect was explored in more depth by manipulating the inter-trial interval and eye movement instructions. The effect was observed in the short ITI conditions of the Production Task only. In Chapters 3 and 4 past history effects are explored in more detail.

# Chapter 3

# Short and long term influences on velocity memory

## 3.1 Introduction

In the last chapter it was found that response time error on a motion extrapolation task was influenced by the velocity of the previous trial (referred to as the 'prime trial'). In the Production Task, participants saw a small target move behind an occluder, and had to press a button at the exact time they thought that it had reached the other side. When the duration between one trial and the next was short, they typically responded earlier after a fast prime trial than a slow prime trial. This past history effect replicates the results of Makin et al. (2008). In this chapter, other influences on the common velocity memory system are explored, and their interaction with the past history effect is investigated.

As mentioned in Section 1.6 (Chapter 1), prototypical object-motion characteristics could constitute an additional influence on velocity memory. For example, it is likely that the distributed semantic representation of a rocket would incorporate the schema 'moves very fast'. This kind of longer term knowledge could also influence perception of moving objects (Reed & Vinson, 1996). In support of this, Zago, McIntyre, Senot and Lacquaniti (2008) reviewed evidence that a lifetime of experience with gravity causes people to assume acceleration when observing downward motion (see also Hubbard, 2006). Moreover, implicit knowledge of biological motion kinematics has been found to influence extrapolation of simulated hand motion (Pozzo et al., 2006), and fMRI studies show that motion sensitive area MT is activated by *static* images which imply movement (Kourtzi & Kanwisher, 2000; Senior et al., 2002). These findings demonstrate that the brain builds up representations of the typical patterns of motion associated with particular objects or events. These associations are used in addition to other systems when guiding action or making judgements about moving objects.

In Experiment 3, the influence of typical object velocity on motion extrapolation was explored. The task was similar to the Production Task outlined in the previous chapter. Small circular targets travelled rightwards and disappeared behind a rectangular occluder, and participants had to respond by pressing a button at the exact time they judged the target to have reached the other side. The targets were red, blue or green. Probe targets travelled at 20º/s, and were either red or green. All other probe trial characteristics were matched. The green probes were the slowest of all green targets, which travelled at speeds ranging from 20 to 30º/s. Conversely, red probes were the fastest of all red targets, which travelled at velocities ranging from 10 to 20º/s. It was predicted that participants would respond earlier on green probe trials (where target colour was associated with the faster velocities) and later on red probe trials (where colour was associated with slower movement). Such a result would demonstrate that motion extrapolation is influenced by long term velocity information for the first time.

## 3.2 Experiment 3 method

### 3.2.1 Participants

12 participants (9 female, ages 21-30) took part.

### 3.2.2 Apparatus

The stimulus presentation hardware was identical to that described in Chapter 2. The target was red, blue or green and always appeared 11.67º to the left of the screen centre and moved horizontally rightward at velocities ranging from 10 to 30º/s. The occluder was grey, 3.65º in height and between 2.89 and 17.59º in length[1]. The background was black. The position of the left edge of the occluder was randomised between 2.92 and 4.37º from screen centre on a trial by trial basis. The target path was aligned with the centre of the occluder. Participants rested their preferred hand on a button box and responded by pressing down with their index finger. Eye movements were not monitored in any experiment reported in this chapter, and no eye movement instructions were given. This has an obvious benefit in terms of efficient data collection, but is also desirable in that it mimics real life motion extrapolation scenarios as much as possible.

### 3.2.3 Procedure

Participants were instructed to press the button at the exact time that they thought the target should reappear from behind the occluder. They were told to respond as accurately as they could on each trial, but that red targets were generally slower, blue targets were usually of a medium velocity and green targets were generally faster. Participants were not asked to fixate and no eye movement instructions were given.

The events at the beginning of the trial, prior to motion onset, were identical to that described in Chapter 2 (Figure 3.1A). The moving target was visible for the first 7.30 to

8.75º of its trajectory before disappearing behind the occluder. This meant that the duration of the visible target motion ranged from 243 to 875 ms, depending on velocity. The occlusion duration (from occlusion onset to the time of would be reappearance) was randomized between 277 and 477 ms in 50 ms increments. The range of occlusion durations was identical for each velocity. The next trial began 6.1 s after the start of the previous trial. If no response was detected, a 200 ms higher frequency beep (450 Hz) was presented at the end of the trial.

First, a 22 trial practice block was presented, with velocities ranging from 10 - 30º/s in 2º/s increments (2 trials at each level). As with the experiment proper, red targets were slower (10 - 20 º/s), blue targets were of medium velocities (14 - 26 º/s) and green targets were fastest (20 - 30º/s). All practice trials reappeared on the right of the occluder so that participants could become familiar with the task.

In the main experiment, 3 different coloured targets were presented with different velocity ranges. The number of trials associated with each colour and velocity is shown in Figure 3.1B. The trials immediately before the probe trials were always blue and their velocity was balanced across probe conditions (Makin et al., 2008). At most, 5 trials with the same colour and 3 with the same velocity were presented consecutively.

A small number of the targets (8.9%) reappeared on the right of the occluder in order to maintain interest in the task. The 10, 12, 28 and 30º/s targets each reappeared 3 times, all other velocities reappeared 4 times (1 red, 1 green and 2 blue) except the 20º/s trials, which never reappeared.

**1** Experiment 3 was designed in 2005, prior to others in the thesis, so some stimulus parameters are different from those in other Experiments. This experiment has been accepted for publication where some of the present material is reproduced (Makin, Stewart, & Poliakoff, 2009).

### 3.2.4 Analysis

Standardized Response time error was calculated as described in Chapter 2, with the addition that a small number of outliers (> 2.5 SD from probe mean) were removed from the individual subject's data sets. This change was included so all data in this Chapter was treated equivalently: data sets in Experiment 4 and 5 (see later) included more large RT errors (500 to 1000 ms), and thus an additional outlier removal step was appropriate. Subjective velocity was calculated as before.

## 3.3 Experiment 3 results

Standardized response time error on the red and green probe trials was compared. There was a significant effect of target colour ($t$ (11) = 2.948, $p = 0.013$), reflecting the fact that participants tended to respond earlier (as if the occluded target was moving faster) when the target was green than when the target was red (Figure 3.1C). Subjective velocity was also analysed to assess whether participants were accurately performing the task. In all colour conditions there was a strong linear relationship between real velocity and subjective velocity. In the red trials, this was revealed by a significant linear contrast ($F$ (1, 11) = 114.440, $p$ <0.001), which explained 91.2% of the variance in subjective velocity (Partial $\eta^2 = 0.912$). Similar results were obtained in the green trials (Linear contrast; $F$ (1, 11) = 209.404, $p < 0.001$, Partial $\eta^2 = 0.950$, Figure 3.1C).

### 3.3.1 Control experiment

It was noted that the effect of colour-velocity relationship on response time could have been confounded by target luminance (the green targets were slightly brighter than the red ones). Therefore 12 additional participants were tested (8 females, age 22-28) with the colour-velocity relationship reversed, so red targets were faster and green targets were slower. Probe trial error from both experiments was analysed with a mixed ANOVA [(Association (fast, slow) x colour (green, red)]. There was a main effect of association ($F$ (1, 22) = 4.882, $p = 0.038$), which did not interact with colour ($F$ (1, 22) <1, NS), indicating that response times were significantly earlier when the target was associated with fast movement, irrespective of the target colour or luminance.

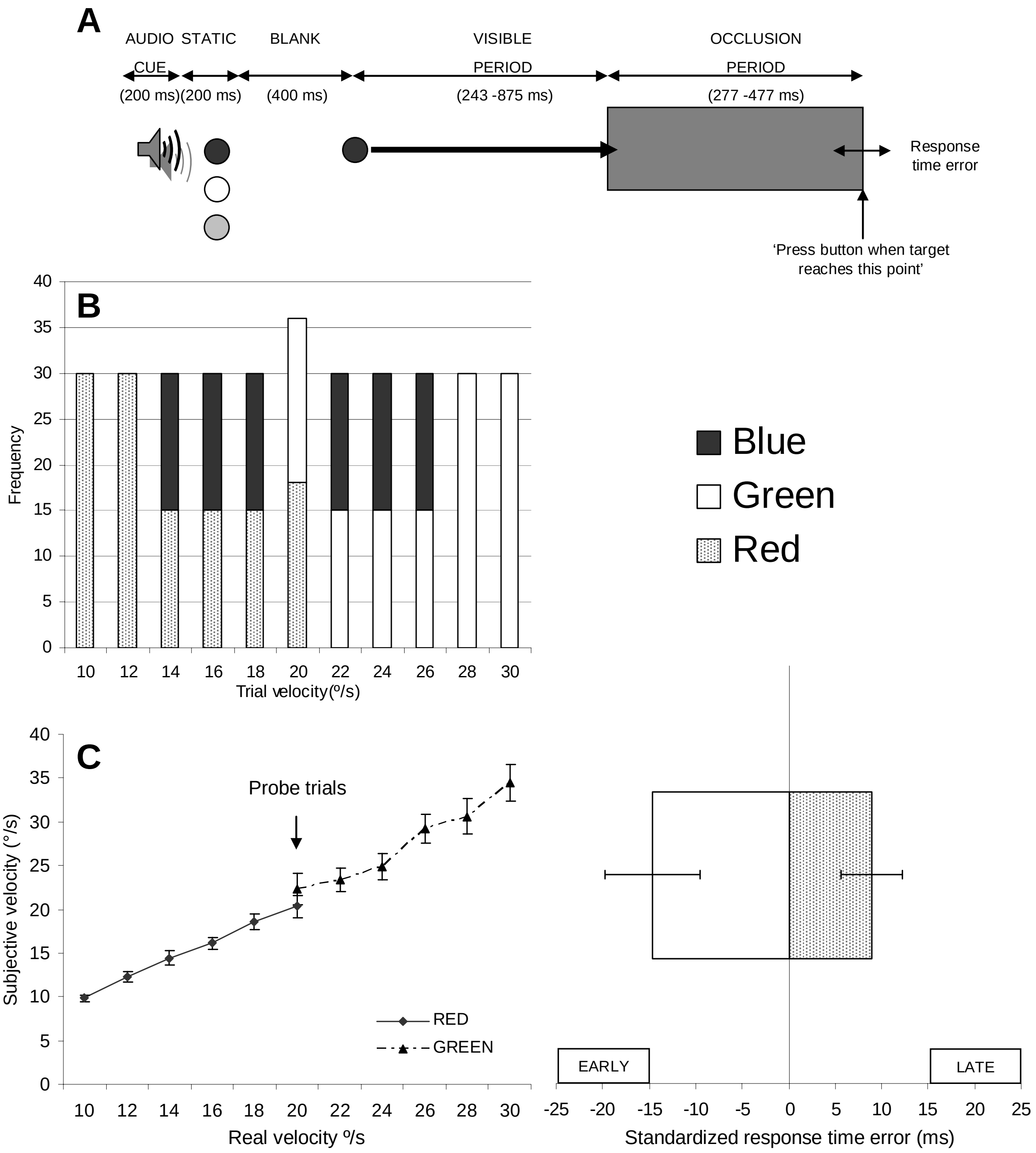


**Figure 3.1: Results of Experiment 3. A**: The sequence of events on an individual trial. **B**: The number of trials presented with each velocity and colour. Red and green probe trials travelled at then median velocity presented (20°/s) although red trials were usually slower and green faster. **C (Left panel): Subjective velocity analysis**. Subjective velocity is shown as a function of real velocity in the red and green trials. **C** (**Right panel): Probe trial error.** The horizontal scale reflects response time error as a deviation from the average response time error on both red and green probes. Negative values indicated that participants responded too early. Error bars = +/- 1 S.E.M.

### 3.4 Experiment 3 discussion

In Experiment 3, a motion extrapolation task was presented in which the colour of the target was associated with its typical velocity. Participants were able to perform the task well: there was a strong linear relationship between subjective velocity and actual velocity. Despite good performance, participants tended to respond earlier early on 20°/s green trials and later on 20°/s red trials. That is, as if the green targets were travelling faster than the red targets. As green targets were typically faster then red ones, this indicates that motion extrapolation was influenced by longer-duration information about the typical velocity of the different coloured targets.

It was noted that the green targets were slightly brighter than the red targets and perceived velocity may increase with luminance (Blakemore & Snowden, 1999). This could have produced the observed effect. Thus, an additional control experiment was carried out in which the colour-velocity relationship reversed, so red targets were faster and green targets were slower. This time, participants responded earlier on the red probe trials, suggesting the effect cannot be attributed to luminance.

One remaining question about Experiment 3 concerns the interplay between the colour velocity association effect and the past history effect described in Chapter 2. Although the velocity of the previous trial was controlled in Experiment 3, there were not enough repeats of each condition to investigate any potential interactions between the typical object velocity effect and the past history effect. If these effects multiply, it would indicate that a stored velocity representation can be distorted by several influences simultaneously. Experiments 4 and 5 investigated this possibility.

There are three other unresolved issues with Experiment 3. First, as discussed in section 1.5 (Chapter 1), when the occluder is visible, responses may be guided by temporal information (DeLucia & Liddell, 1998; Tresilian, 1995). Although there is good evidence that motion extrapolation relies on visuospatial tracking of the occluded target (de'Sperati & Deubel, 2006; DeLucia, 2004), one cannot be completely sure that the paradigm was measuring distortions of velocity memory rather than temporal representations.

Second, it is possible that the interpretation of task instructions, rather than representations of typical motion characteristics, were responsible for the results. Participants were told before the task began that one of the coloured targets would usually move faster, and another would usually move slower. This may have made the colour velocity relationship more apparent, or introduced a demand characteristic whereby participants believed they were supposed to respond as if targets of a particular colour were going faster than they really were.

Third, it is possible that semantic associations with the particular colours could have been responsible for the effects. Green targets could have been associated with green traffic lights (meaning GO), and red targets with red traffic lights (meaning STOP). This could have influenced response times. Indeed, when the colour velocity relationship was reversed, the effect was slightly, (but not significantly) attenuated. This means that the role of associations acquired inside and outside of the lab cannot be distinguished. These possibilities are also addressed in Experiments 4 and 5.

### 3.5 Experiment 4

Before tackling the interplay between long and short term influences on velocity memory, a new motion extrapolation task was developed in which response time could not be computed prior to occlusion. In Experiment 4, a small circular target was seen moving rightwards, as with previous experiments. It then disappeared, as if moving behind an invisible occluder. At the point of disappearance, a vertical ‘endline’ appeared further along the occluded targets path. Participants had to respond by pressing a button at the exact time they thought the occluded target would have reached the endline (Figure 3.2). This task captured the advantages of Discrimination and Production Tasks: It was impossible to compute response time a priori (because the endline only appeared after occlusion), but nevertheless, a continuous measure of performance was available.

Experiment 4 asked whether past history effects could be obtained with the new *Appearing Endpoint* task. All targets were blue. As usual, 20º/s probe trials were preceded by 14 or 26º/s primes. It was predicted that participants responded earlier after faster prime trials than slower prime trials. The interval between prime and probe trials was short (2200 ms). Although this was a little longer than the 1500 ms ‘short ITI’ used in the Chapter 2, pilot work indicated that this change increased comfort with the task.

### 3.6 Experiment 4 method

#### 3.6.1 Participants

24 Participants (age 20 to 31, 9 male) were involved

#### 3.6.2 Apparatus

The apparatus was similar to Experiment 3, apart from a few changes to the stimuli described below.

#### 3.6.3 Design

20°/s probe trials were presented in two conditions (Prime velocity 14º/s or 26º/s).

#### 3.6.4 Procedure

On each trial, participants saw the target move from left to right. It disappeared behind an invisible occluder. At the point of occlusion onset a vertical green 'endline' appeared at the end of the invisible occluder. Participants were instructed to imagine the target continuing on its path after occlusion, and then press the button at the exact time they thought the target had reached the endline. There was no fixation cross, and no eye movement instructions were given.

The sequence of events prior to motion onset was identical to Experiment 3, except the target appeared 13.12° from screen centre, before reappearing travelling horizontally rightward at a velocity ranging from 10 - 30º/s. The moving target was visible as it travelled across 8.66º towards the screen centre. The duration of the visible period ranged from 300 ms to 866 ms[2]. The target then disappeared behind an invisible occluder. The horizontal size of the occluder ranged from 5.77º to 11.72º. This resulted in minimum and maximum occlusion durations of and 192 and 1172 ms. The green endline was 3.65 º tall and 0.14º wide. The endline was centred on the targets path. The endline was visible from occlusion onset to 1000 ms after the target would have reached the end of its trajectory. Figure 3.2A schematizes the experimental parameters.

There were 376 trials in total. 80 of these were probe trials, which travelled at 20º/s. Half the probe trials were preceded by slower (14º/s) prime trials, half by faster (26º/s) prime trials. The occluder size on the probe trials was 8.75º and thus probe occlusion duration was always 437 ms. The occluder size on the prime trials was 1 of 5 levels, ranging from 5.83 to 11.67° in 1.46° increments. This resulted in 5 occlusion durations on the 14°/s prime trials (416 to 834 ms in 104 ms interval) and another 5 on the 26°/s prime trials (224 to 448 ms in 56 ms intervals)[3].

The velocity of the trials before the primes (N-2 trials) was also controlled. Velocity ranged from 16 - 24°/s, and both probe conditions were preceded by an equal distribution of N-2 Velocities. There were 2-5 filler trials in between each prime-probe-pair. The average velocity on these filler trials was always 16 – 24°/s. Occluder size was randomized on a trial by trial basis on all trials except the prime and probes. The interval between time when the occluded target touched the endline in the prime trials and the onset of the probe trials was always 2200 ms. On all other trials this interval was randomized between 2800 and 5600 ms.

Before the experiment began, participants completed a practice block of 11 trials. This included 1 trial at each velocity between 10 - 30°/s in 2°/s increments. The occlusion duration was randomized in the practice block, and the practice trials were presented in a random order. The experiment proper was broken into eight blocks of 43-50 trials. The blocks were presented in one of four orders, dictated by a Latin square. The order in clusters of prime probe and filler trials were presented was then reversed within each block, and another 4 block orders were produced. Three participants completed each block order.

### 3.6.5 Analysis

Standardized response time error on the probe trials was obtained and treated in the same way as Experiment 3, with the exception that trials where participants responded within the first 100 ms of occlusion were excluded. These responses could not be visually guided and thus cannot have reflected a genuine attempt to press when the target reached the endline. Subjective velocity was also obtained and treated in the usual way, but again trials where participants pressed within the first 100 ms of occlusion were excluded.

### 3.7 Experiment 4 results

Standardized error on the probe trials was influenced by the velocity of the prime trials. Participants responded later after a slower prime trial than a faster prime trial ($t$ (23) = 2.373 $p$ = 0.026, Figure 3.2B). There were significant positive correlations between subjective velocity and actual velocity in each participant's data set ($r > 0.677$, $p < 0.026$). This suggests that subjects were performing the Appearing Endpoint Task with a reasonable degree of accuracy. Moreover, there was a very strong linear relationship between mean subjective velocity and actual velocity. This was revealed by linear contrast ($F$ (1, 23) = 140.751, $p < 0.001$, partial $\eta = 0.860$; Figure 3.2C).

### 3.8 Experiment 4 discussion

In Experiment 4 a new form of motion extrapolation task was presented. Participants observed a moving target travel rightwards and become occluded. At the same time, an endline appeared further along the occluded target's trajectory. Participants attempted to press a button when the occluded target reached the endline. As predicted, response time on probe trials was influenced by the velocity of previous prime trials. After a fast prime, participants responded earlier, as if the current trial was faster. Conversely, after a slow previous trial, participants responded later, as if the current trial was slower. This blending effect replicates the results of Makin et al. (2008) and the Production Task from Chapter 2, in a new task which cannot be performed using a 'clocking strategy' (cf DeLucia & Liddell, 1998; Tresilian, 1995). Given the success of Experiment 4, Experiment 5 was conducted to assess the interaction between the short-term blending effect and the long-term effect of colour-velocity associations.

**2** A longer visible period was selected based on pilot work which showed that this manipulation improved participants comfort with the more difficult Appearing Endpoint task.

**3:** Unfortunately, a programming error resulted in five (12.5%) of the 26°/s primes having a random occluder size (5.77º to 11.72º). This would not have made much difference to the median occlusion duration. Probes following these primes were included in the main analysis, but excluding these trials did not alter results. This was also true of Experiment 5.

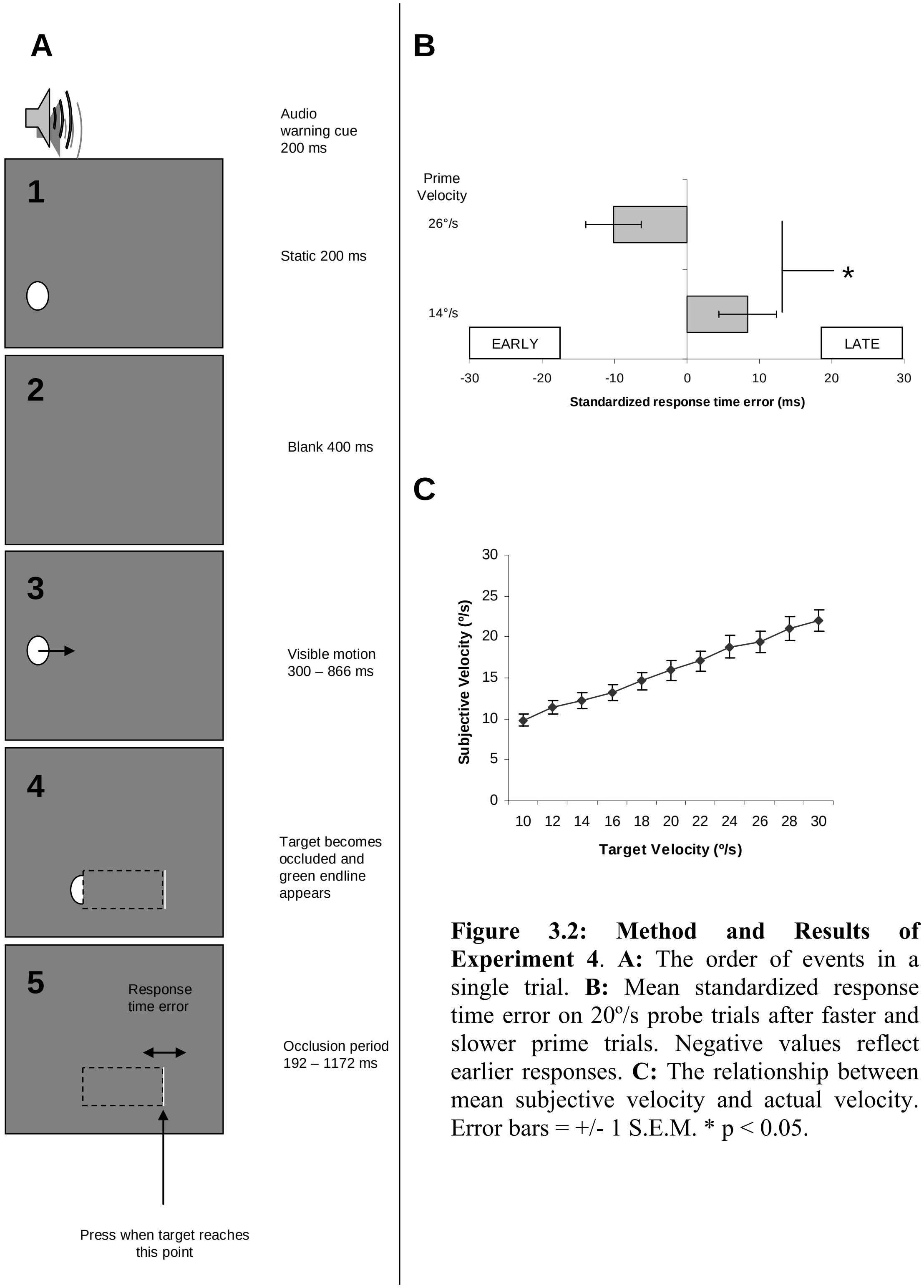


**Figure 3.2: Method and Results of Experiment 4**. **A:** The order of events in a single trial. **B:** Mean standardized response time error on 20º/s probe trials after faster and slower prime trials. Negative values reflect earlier responses. **C:** The relationship between mean subjective velocity and actual velocity. Error bars = +/- 1 S.E.M. * $p < 0.05$.

### 3.9 Experiment 5

In Experiment 5 the interaction between the blending effect and colour-velocity associations on the Appearing Endpoint Task was investigated. Experiment 5 also compared participants who were either aware or naïve of the colour-velocity relationship. In addition, purple or orange targets were used rather than semantically loaded red and green. The sequence and spatial parameters of the trials were the same as those of Experiment 4. However, the half the probes trials were of the colour associated with the faster velocity set (20-30º/s) and half were of the slower velocity set (10-20º/s). Prime trials were always blue (which was associated with medium velocity set, 14-26º/s).

Response Time Error, Absolute Error and Variable Error in the probe trials were compared with equivalent metrics from the free eye movement condition of the Production Task of Experiment 2. This comparison was validated by the fact that there were the same number of 20°/s probe trials (80), and the probe trial parameters were the same in terms of occluder size (8.75°) and duration (437 ms). These comparisons facilitate discussion about the mechanisms involved in different forms of motion extrapolation task.

### 3.10 Experiment 5 method

#### 3.10.1 Participants

32 Participants (age 19 to 37, 6 Male) were involved.

#### 3.10.2 Apparatus

The apparatus was identical to that used in Experiment 4, except that the target was now 1 of 3 colours (orange, blue or purple).

#### 3.10.3 Design

Probe trials were presented in 4 within-participant conditions [2 Prime velocity (14 º/s, 26º/s) X 2 Association (fast, slow)] and 4 between-participant conditions [Colour associated with fast trials (orange, purple) X Experiment instruction (explicit colour-velocity relationship, implicit colour-velocity relationship)]. Table 3.1 clarifies the design.

**Table 3.1: The design of Experiment 5**

| PRIME VELOCITY | 14 | 26 | 14 | 26 | 14 | 26 | 14 | 26 | 14 | 26 | 14 | 26 | 14 | 26 | 14 | 26 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ASSOCIATION | Fast | | Slow | | Fast | | Slow | | Fast | | Slow | | Fast | | Slow | |
| COLOUR OF FAST TRIALS | Orange | | | | Purple | | | | Orange | | | | Purple | | | |
| INSTRUCTION | Participants told about the colour-velocity relationship | | | | | | | | Participants NOT told about the colour-velocity relationship | | | | | | | |

### 3.10.4 Procedure

The spatial and temporal parameters of the trials were identical those used in Experiment 4. The same sequence of trials and velocities were used. However, the colour of the targets was manipulated so that the faster targets (20 to 30º/s) were associated with one colour (orange or purple), and slower targets (10 to 20º/s) were associated with the other colour. Half the 20º/s probe trials targets were the colour associated with the faster velocity; half were colour associated with the slower velocity. Blue targets travelled at mid range velocities (14 to 26 º/s). The prime trials were always blue. Prime trial velocity and the Association factors were balanced to produce 4 within-participant probe conditions.

Half the participants were informed about the relationship between colour and velocity in the written experiment instructions. This was then repeated in verbal instructions. The other half was not informed about the colour velocity relationship. For half the participants in the explicit and implicit instructions groups, the orange targets were faster and the purple targets slower. For the other participants this relationship was reversed, so purple targets were slower and orange faster. The exact distribution of velocities and colours are shown in Figure 3.3.

The practice block consisted of 11 trials. Again this included one trial at each velocity from 10 and 30º/s, in 2º/s increments. Targets travelling at the 6 most extreme velocities matched the colour-velocity relationship in the experiment proper.

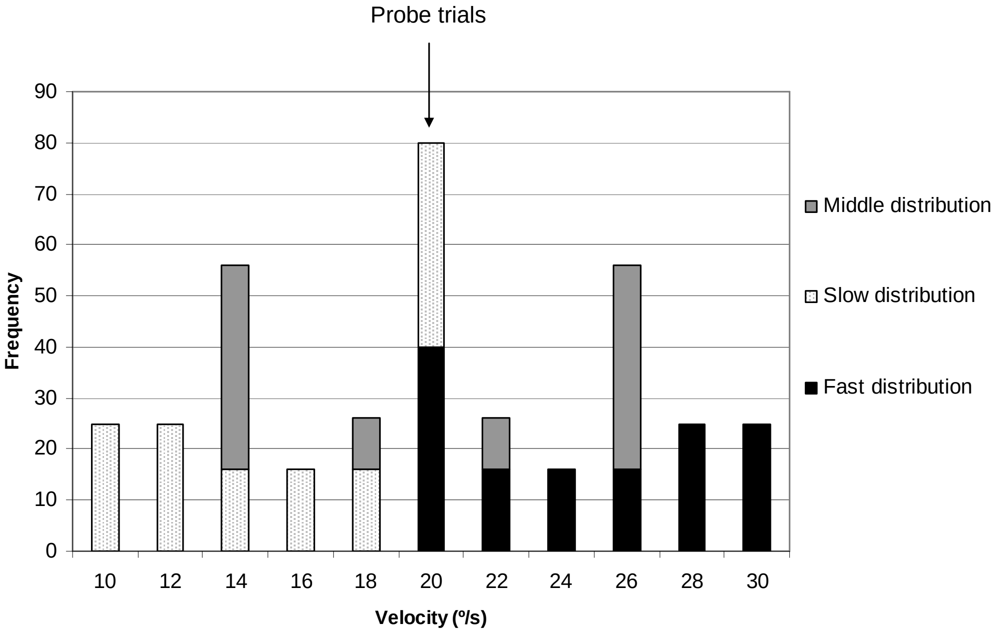


**Figure 3.3: The distribution of trials associated with the different coloured targets**.

### 3.10.5 Analysis

Pre processing was identical to Experiment 4. However, for Experiment 5, response time error, absolute error and variable error were compared with the same metrics from the Short ITI, Free viewing condition of the Production Task of Experiment 2. Missing data points were replaced by the mean value. It would be undesirable if apparent task differences were attributable to different outlier removal procedures, so for this analysis, all data followed the outlier removal procedures of Experiment 2 (in practice, results were not changed by this decision). Non-parametric Mann Witney U tests were used when variables violated the normality assumption.

## 3.11 Experiment 5 results

Standardized error in the 20 °/s probe trials was explored with a 4 factor mixed methods ANOVA. There were two within-subject factors [2 Prime velocity (fast, slow) X 2 Association (fast colour, slow colour)] and two between subjects factors [Colour of fast trials (purple, orange) x 2 Instruction (implicit colour-velocity relationship, explicit colour-velocity relationship)].

The 4 factor ANOVA revealed a main effect of Prime Velocity. As with Experiment 4, participants responded earlier after the fast prime trials than the slow prime trials ($F$ (1, 28) = 10.027, $p = 0.004$). This blending effect was modulated by other factors ($F$ (1, 28) > 5.157, $p < 0.032$). These interactions were produced by the fact that a significant blending effect was present in every condition except when the probe target colour was associated with slower velocities, and participants were explicitly told about the colour velocity relationship ($p < 0.05$, Figure 3.4A).

The 4 factor ANOVA did not find a main effect of Association ($F$ 1, 28) <1, NS) and the effect of Association was not altered by whether participants were made aware of the colour-velocity relationship at the start of the experiment or not ($F$ (1, 28) < 1, NS). However, there was an Association x Colour of fast trials interaction ($F$ (1, 28) = 5.647, $p = 0.025$). This was because there the predicted pattern occurred when orange targets were fast, but the opposite pattern occurred when the purple targets were fast. However, neither of these patterns was significant when analysed alone ($F$ (1, 14) < 3.369, $p > 0.086$), so the interaction is difficult to interpret.

As with Experiment 4, there was a significant positive correlation between mean subjective velocity and actual velocity in every participant's data set ($r > 0.854$, $p < 0.002$). The linear relationship between target velocity and subjective velocity explained 81.4% of variance ($F$ (1, 31) = 135.429, $p < 0.001$, partial $\eta^2 = 0.814$ Figure 3.4B).

Finally, Average response time error, variable error and absolute error were obtained from the 32 participants. These metrics were compared to equivalent data from the short ITI, free eye movement condition of the Production Task of Experiment 2 (see Chapter 2). In Experiment 5 participants responded later, were more variable and had higher absolute error ($p < 0.001$, Figure 3.4C).

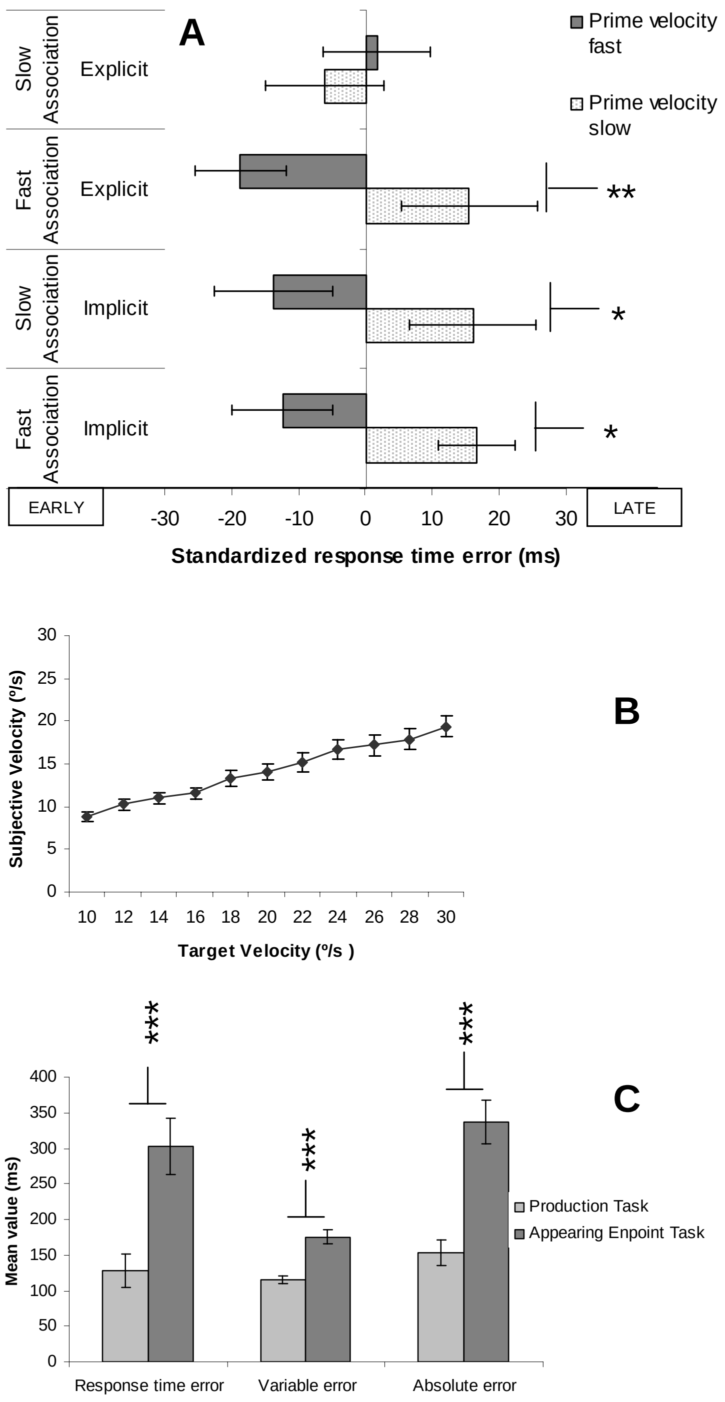


**Figure 3.4: Results of Experiment 5**. **A:** mean standardized response time error on 20 °/s probe trials after faster and slower prime trials, as a function of probe trial colour (slow distribution or fast distribution) and experiment instruction (implicit or explicit colour velocity relationship) **B:** relationship between mean subjective velocity and actual velocity. **C:** Response time error, Variable error and Absolute error in probe trials of Experiment 5 and the Production Task from Experiment 2. Error bars = +/- 1 S.E.M. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Positive values reflect late response time errors in C.

### 3.12 Experiment 5 discussion

The results of Experiment 5 showed a clear past history effect, replicating the findings of Experiment 4. Again participants responded as if probe trials were faster after fast primes and vice versa, suggesting that subsequently encoded velocities can blend. Performance in Experiment 5 was less accurate than in the simpler Production Task of Experiment 2 (reported in Chapter 2). This is unsurprising given that attentive tracking would have been disrupted by the sudden presentation of the endline further along the targets path. Indeed, participants were typically responding too late. One possibility is that the participants spent some time shifting attention to the endline when it appeared, and then back to target position, before continuing to track the occluded target. On the fast trials the constant time needed to shift attention to the endline constituted a greater proportion of the occlusion duration; hence subjective velocity is relatively decreased on the faster trials (Figure 5B).

There was no main effect of target colour, even when participants were told about the colour-velocity relationship. Therefore the results of Experiment 3 were not replicated. Instead, a trend towards the expected pattern was found, but only when orange targets were associated with faster motion. This effect should not be over-interpreted, but it implies that some colour-velocity relationships are learned more readily than others. For example, it is conceivable that warm colours and fast motion are perceived as compatible characteristics, and this subjective compatibility facilitated association.

Another unexpected finding was that the past history effect was attenuated when the probe target colour was associated with the slow distribution, but only when participants were explicitly told about the colour-velocity relationship. How can this pattern be explained? It could be that the appearance of a the ‘slow’ coloured target at the beginning of the trial indicated that there was going to be enough time to process the appearance of the endline and track the occluded target precisely. Irrelevant representations from the previous trial could thus be inhibited. Conversely, when the colour cue predicts a fast target, participants may have anticipated high task demands, and rely on more general representations which are biased towards the most recently seen velocity. When they are told about the colour velocity relationship, these differences may be more pronounced.

## 3.13 General discussion

This Chapter reports three motion extrapolation experiments which were designed to explore the effect of typical object velocity on motion extrapolation and to assess whether this effect interacts with the past history effect recorded in earlier work.

Experiment 3 explored the effect of typical object velocity on motion extrapolation. Participants saw a small target move rightward and disappear behind a visible rectangular occluder. They attempted to press a button at the exact time they thought the target had reached the right hand edge of the occluder. Targets travelling at velocities between 10 and 30°/s were presented in 3 different colours. One colour was usually associated with the faster velocities (20 to 30°/s) and one with the slower velocities (10 to 20°/s). It was found that on the 20°/s probe trials of the colour associated with the slow movement, participants responded later than the 20°/s trials of the colour associated with the fast movement. This suggests that representations of typical object velocity influence timed responses to occluded targets.

This result adds to previous evidence for a role of long-term typical motion representations in perception. As mentioned in the introduction, the initiation time of interceptive actions is influenced by internal models of gravity (Zago et al., 2008). ‘Cognitive gravity’ may also influence perception of the final position of a moving target (Hubbard, 2006). These results both suggest that well-encoded information about the typical behaviour of moving objects can distort judgements. Implicit knowledge of the kinematics of biological motion has also been shown to influence extrapolation of simulated hand movements (Pozzo et al., 2006). This again suggests that knowledge about typical motion can supplement recent perceptual input. The current work expands on these studies by demonstrating an influence of typical object velocity in motion extrapolation. In this case, the short term velocity memory used to guide motion extrapolation may be distorted by learned colour-velocity associations. The work also differs from these studies in that associations were learned within the experiment itself, rather through a life-time of experience.

Recent neurophysiological work has explored the association of colour and motion in the Macaque monkey. de Hemptinne, Lefevre and Missal (2008) found that coloured cues which predicted the direction of upcoming motion produced direction-specific firing in the supplementary eye fields (SEFs). This suggests that the SEF encodes colour-motion associations (Ackerley, Wild, & Makin, 2008). The SEFs are tightly connected to the FEFs, which are likely to mediate tracking during occlusion (Barborica & Ferrera, 2003). This neural architecture is consistent with the finding that colour-velocity association interferes with motion extrapolation performance.

Experiments 4 and 5 explored the interaction between the typical object velocity effect and the past history effect. A new motion extrapolation task was designed, in which occlusion duration could not be calculated a priori (DeLucia & Liddell, 1998). In Experiments 4 and 5, the past history effect was replicated, but no influence of colour-velocity association was found. Therefore the only clear theoretical advance made by Experiments 4 and 5 is increased confidence that the shorter term past history effect is due by interference between successively encoded velocity representations rather than temporal representations.

It is theoretically possible that the long term typical velocity effect found in Experiment 3 or past history effect found in Experiments 4 and 5 could be masked by poor performance on the probe trials (floor effect) or very good performance on the probe trials (ceiling effect). Analysis of the past history effect suggests that it is more pronounced when performance is less accurate. As discussed, participants may actively inhibit previously encoded velocity representations, or refresh their processing systems to a greater degree when they are performing well. Conversely, the longer term influence of typical object velocity disappeared in the more difficult Appearing Endpoint Task, implying a ceiling effect.

Typical velocity effects probably reflect fairly permanent modulation of connectivity between velocity and colour sensitive neural populations (cf Hubbard, 2006; Senior et al., 2002). On the other hand, the short term past history effect probably involves temporary increases in the excitability of very recently seen velocity codes. Indeed, Makin et al. (2008) found a far more robust effect of the most recently observed (N-1) prime trial than the trial before that (N-2). Given these differences, it is perhaps unsurprising that short and long term effects on velocity memory would be differentially sensitive to floor and ceiling effects.

There are at least two alternative explanations for the absence of typical object velocity effects in Experiment 5. First, as it could have been that participants were using temporal representation to guide response initiation in Experiment 3, and colour – time-to-contact associations produced the effect. This is implausible given the volume of work suggesting that such Production Tasks involved visuospatial attentive tracking rather than cognitive timing, even when timing strategies are theoretically available (see Chapter 2). Another possibility is that the semantic relevance of the red and green targets enhanced association between colour and velocity processing in Experiment 3. When orange and purple targets were used in Experiment 5, the effect disappeared.

In summary, these Experiments demonstrate two related influences on velocity memory. First, long term learning of typical object velocities can distort the velocity representations used in motion extrapolation. Second, recently seen velocities can also distort velocity memory. Both effects are in the same direction – a history of processing faster targets results in participants judging the current targets to be faster. However, the effects may be differentially sensitive to task difficultly, and only the short term blending effect was reliably replicated.

# Chapter 4

# The past history effect revisited

## 4.1 Introduction

Several studies have measured the interplay between subsequently encoded velocities. For example, Magnussen and Greenlee (1992) presented a *delayed velocity discrimination task* which comprised a *standard* moving grating, then a ten second interval, and finally a *test* grating. The task was to judge whether the standard or test grating was faster. During the interval, a ‘masker’ velocity was presented. Discrimination performance was impaired when the masker velocity differed from the standard velocity. This suggests that stored velocity representations can be disrupted by new velocity input, and that the same velocity sensitive neurons in the visual cortex are responsible for both velocity perception and velocity memory (McKeefry et al., 2007; Pasternak & Greenlee, 2005).

Kerzel (2001) presented another delayed velocity discrimination task. In this study, single moving dots were used as standard and test stimuli. Participants judged whether standard and test velocities were the same or different. During the interval, fast or slow hand movements were produced. Fast hand movements led to the first velocity being perceived as faster and vice versa. This suggests that visual and manual velocity representations can *blend together*, and that that velocity inputs from a different modalities share a common memory resource.

Comparable velocity blending also influences anticipatory smooth pursuit eye movements (ASPEM). Poliakoff, Collins and Barnes (2005) found that ASPEM velocity was influenced by the velocity of previous trials, even though they were not relevant to the task. These authors concluded that stored velocity representations which guide ASPEMs comprised a blend of recently seen velocities (see also Jarrett & Barnes, 2002).

In Chapters 2 and 3, it was found that motion extrapolation is also influenced by previously seen velocities. Participants usually responded as if the probe trial was faster after a fast prime trial and vice versa. This could again be due to blending of subsequently encoded velocity information (Makin et al., 2008). It seems that delayed velocity discrimination, ASPEM velocity, and motion extrapolation are all affected by velocity blending. This implies that a common velocity memory system is involved in all these tasks.

However, the blending effects found in Chapters 2 and 3 could also be explained by participants generalizing response times from prime to probe trials. The interval from trial start to response time was, on average, longer in slow prime trials than the fast primes. If participants tended to reproduce the overall trial duration from one trial to the next, it would lead to the observed pattern. Reanalysis of previous results suggest that response time generalization was indeed a major influence on motion extrapolation. To explore this, the fast and slow prime conditions were analysed separately. In both cases, participants responded later on probe trials when they had responded later on prime trials and vice versa (see Appendix 1). Furthermore, in Appendix 2, additional experimental data is reported which found that the blending effect on motion extrapolation disappeared when the overall duration of prime and probe trials were matched.

The above analyses suggest that the response time generalization cannot be ruled out. However, there are still two published demonstrations which cannot be explained in this way. Makin et al. (2008) and Lyon and Waag (1995) both report compatible blending effects in motion extrapolation where overall trial duration was not a confound. In these Discrimination Tasks participants produced *non-speeded* 2AFC judgments about occluded target position (DeLucia & Liddell, 1998), so response time generalization cannot explain these results. Nevertheless, the results of Makin et al.'s (2008) Discrimination Task were not replicated in four additional experiments with very similar parameters (Chapter 2), although this could be because Discrimination Tasks are relatively insensitive to small subtle influences. At any rate, demonstrations of velocity bending in motion extrapolation remain inconclusive.

The current study was designed to address two questions. First, the question of whether motion extrapolation is influenced by blending of subsequently encoded velocities is revisited. Second, does motion extrapolation involve the same velocity memory system as delayed discrimination? Each trial involved a delayed velocity discrimination task. The standard grating travelled rightwards at 10, 14 and 18°/s. The test was 30% faster or slower than the standard. There was a 10 second delay between standard and test, and participants judged whether the standard or test grating was faster (Figure 4.1). Signal Detection Analysis was used to measure discrimination accuracy (d') and bias towards a particular decision (standard faster or test faster, C). In Experiment 6, a motion extrapolation task was presented during the delay. This was similar to the

Production Task in Experiment 2, except that the target moved at velocities of 12 or 16°/s. The range of velocities was chosen to make the grating motion appear as clear as possible.

If motion extrapolation is influenced by previously seen velocities, and delayed discrimination and motion extrapolation involve a common velocity store, response times on the motion extrapolation task should be influenced by the velocity of the standard grating. More specifically, participants should respond later when retaining a slow standard, and earlier when retaining a fast standard. Meanwhile, slow motion extrapolation velocities should bias participants towards reporting that the first grating was slower but fast motion extrapolation velocities should bias participants towards reporting the first grating was faster.

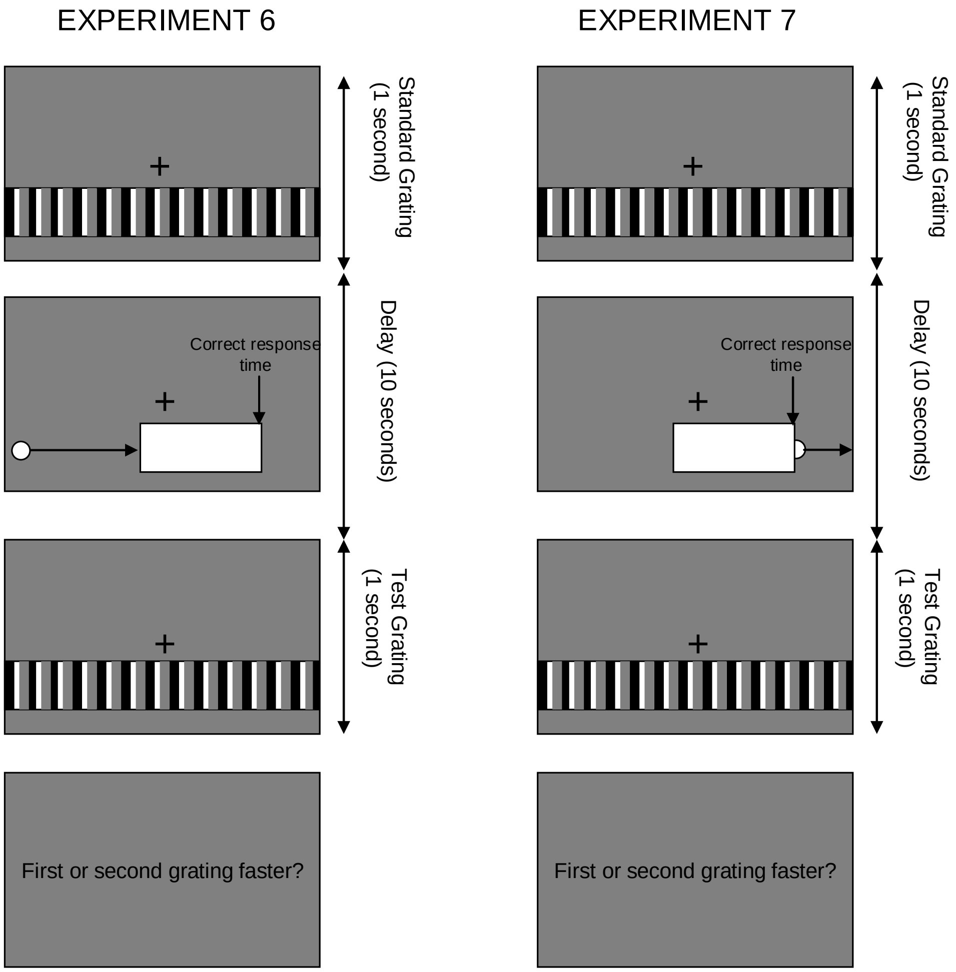


**Figure 4.1**: **The trial structure in Experiments 6 and 7.**

## 4.2 Experiment 6 method

### 4.2.1 Participants

24 participants (age 18 to 28, 5 male) were involved.

### 4.2.2 Apparatus

The same hardware was used as in previous experiments. Sinusoidal gratings were 3.65° high with a spatial frequency of 1 cycle per degree. The width of the grating was the same as the width of the screen. Grating velocity ranged between 8 and 21.6°/s. In the motion extrapolation task, the target was a small blue disk (0.44° in diameter) and the occluder was a grey box (5.77 – 11.72° wide, 3.65° high). The target path went through the centre of the occluder. Target velocity ranged from 12 to 16°/s. A fixation cross was presented at the centre of the screen. The motion extrapolations task and sinusoidal gratings were centred 5.83° below the fixation point. The top of the grating was ~4° from fixation (Campana, Pavan, & Casco, 2008). On the grating discrimination task, participants entered choices with a computer keyboard using their left hand. Responses on the motion extrapolation task were made by pressing a button on a button box with the right hand.

A fixation cross was presented in the centre of the screen throughout trial. Fixation was monitored with a 50 Hz ASL eye tracker. No trials were excluded due to eye movement criteria because it was not fundamental to the experiment. However, eye position was monitored in real time by the experimenter to ensure that, in general, participants complied with fixation instructions.

### 4.2.3 Design

Delayed discrimination performance was measured in 12 different conditions [Standard grating velocity (10, 14 or 18°/s) X Test grating velocity (Faster or slower than the standard grating) X Motion extrapolation task velocity (12 or 16 °/s)]. Each condition was repeated four times.

Performance on the motion extrapolation task was measured in 6 different conditions [Velocity (12, 16°/s) X Previous standard velocity (10, 14 or 18°/s)]. Each motion extrapolation condition was repeated 8 times.

### 4.2.4 Procedure

Participants pressed a button to begin each trial, which consisted of a standard grating, motion extrapolation task and a test grating. The participant had two tasks: They had to respond by pressing a button at the exact time they thought the target would reappear in the motion extrapolation task, they then had to judge whether the sample or test grating was fastest by pressing one of two keys on a computer keyboard. This judgment was made in a non-speeded fashion after the presentation of the test grating (Figure 4.1).

There was a 300 ms pause between participants beginning the trial and the onset of the sample grating, which lasted 1 second. The interval between sample and test grating was always 10 seconds (McKeefry et al., 2007), and included the motion extrapolation task, which began 1 second after the end of the sample grating. The test grating also lasted 1 second. Participants were prompted to enter their judgement 1 second after the end of the test grating. The gratings and the target in the motion extrapolation task all moved rightwards, and the stimuli involved in these tasks both occurred in the same retinal locations (assuming fixation was maintained).

Experiment 6 had 60 trials in total. On the 48 experiment trials, sample velocity was 10, 14 or 18°/s, the target on the motion extrapolation task moved at 12 or 16°/s and the test grating velocity was 30% faster or slower than the sample. Every combination of these parameters was used to give 12 conditions, which were presented 4 times each. The other 12 trials were filler trials, in which the velocity of the sample and test gratings was randomized between 10 and 18°/s and the motion extrapolation task was 10, 14 or 18°/s. On the filler trials, each motion extrapolation velocity was presented 4 times. This preserved the mean motion extrapolation velocity of 14°/s, and resulted in a mean sample grating velocity negligibly different from 14°/s. On every motion extrapolation presentation, the visible period was 8.87° long, resulting in durations ranging from 429 ms of 887 ms. Occluder size was randomized between 8.74 and 11.67° on every trial, resulting in minimum and maximum occlusion durations of 485 ms and 1167 ms.

The trials were presented in 4 different random sequences. The order of trials in these blocks was then reversed to produce another 4 trial sequences, and 3 participants were presented with each sequence. Before the experiment began, there was a 12 trial practice block, which included 1 repeat of every combination of sample grating velocity

(10, 14 and 18°/s), motion extrapolation velocity (12, 16°/s) and test grating velocity (30% faster or slower than sample).

## 4.3 Experiment 6 results

### 4.3.1 Motion extrapolation

Mean standardized response time errors were analyzed with a two factor repeated measures ANOVA [Motion extrapolation velocity (12, 16°/s) x standard grating velocity (10, 14, 18°/s)]. This analysis revealed a main effect of motion extrapolation velocity. The participants responded later in the 12°/s than the 16°/s trials ($F$ (1, 23) = 11.986, $p$ =0.002). There was no main effect of standard velocity ($F$ (2, 46) = 2.064, $p$ = 0.139), but there was a marginally significant interaction effect ($F$ (2, 46) = 3.076, $p$ = 0.056). To further explore this, one factor sub ANOVAs [standard velocity (10, 14, 18°/s)] were applied to the 12 and 16°/s motion extrapolation conditions. In the 12°/s condition, there was no effect of standard velocity ($F$ (2, 46) < 1, NS), while in the 16°/s extrapolation condition, this effect was significant ($F$ (2, 46) = 5.301, $p$ = 0.009). This was largely because participants responded earlier after a 14°/s standard than a 10°/s standard ($t$ (23) = 3.110, $p$ = 0.005, Figure 4.2).

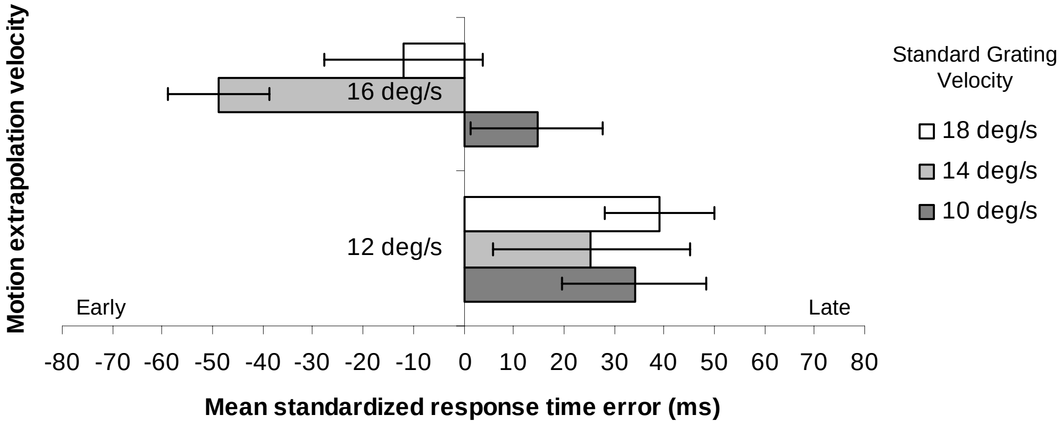


**Figure 4.2: Motion extrapolation task results**: Standardized response time is shown as a function of target velocity and standard grating velocity. Error bars = +/- 1 S.E.M.

### 4.3.2 Delayed velocity discrimination

Sensitivity to the difference between the standard and test gratings was explored with signal detection analysis (Green & Swets, 1966). For each participant, sensitivity (d') and bias (C) metrics were calculated. The metrics were compared between conditions where motion extrapolation was 12 or 16°/s. Differences between conditions were then explored with paired samples *t* tests, or Wilcoxon Signed Ranks tests if the assumption of normality was violated.

Participants were very sensitive to the difference between standard and test gratings. Average d' was greater than zero (chance level) in both conditions ($p < 0.001$, binomial test). In fact, sensitivity was greater in the fast motion extrapolation condition (average d' 2.03 vs. 2.34, $p = 0.015$).

In the 12°/s motion extrapolation condition, participants were biased towards reporting that the standard was slower (average C = -0.143), while in the 16°/s motion extrapolation condition, they were slightly inclined towards reporting that the standard grating was faster (average C = 0.054). This difference between these conditions was significant ($p = 0.009$).

## 4.4 Experiment 6 discussion

In Experiment 6, a delayed velocity discrimination task was presented, with a motion extrapolation task during the delay period. It was predicted that responses on the motion extrapolation would be later after a slow standard grating than a fast standard grating, but this pattern was not found. However, the velocity of the standard grating did affect performance on the motion extrapolation task in a different way; compared to all other conditions, participants responded very early on 16°/s motion extrapolation trials after a 14°/s standard grating. There was also a significant effect of motion extrapolation velocity itself, with relatively early responses on the 16°/s trials and later responses on the 12°/s trials. It seems that the difference in velocity in these conditions was *subjectively magnified*. One possibility is that this phenomenon partially masked the influence of the standard gratings. In future experiments, it may be a simpler to use probe trials with a single velocity in order to overcome these range effects.

The results of the delayed discrimination task were as expected. When motion extrapolation velocity was slow, participants were biased towards judging the standard velocity as slower, and when motion extrapolation was fast, they were more likely to report the standard as faster. These results demonstrate velocity blending across tasks, and thereby suggest that a common velocity store underpins delayed discrimination and motion extrapolation.

However, this result cannot distinguish the contribution from different components of the motion extrapolation task: It could be that observing visible motion distorted the representations of the standard velocity. Alternatively, the effect could have been produced specifically by memory-guided tracking during occlusion. Finally, some other difference between the 12 and 16°/s motion extrapolation trials, like trial duration or average response time, could have been responsible for the observed results. Experiment 7 was designed to disentangle these possibilities.

### 4.5 Experiment 7

In Experiment 7, the delayed velocity discrimination task was replicated. However, the motion extrapolation task was changed. Now the target emerged at the right of the occluder, and was not visible before occlusion. The task was to press a button as soon as the target emerged from the occluder. In this task, button presses occurred around the same time as Experiment 6. Participants saw the same visible velocities, but did not engage in occluded target tracking (Figure 4.1). If the effect in Experiment 6 was attributable to the visible velocity signals, it should be present again in Experiment 7.

### 4.6 Experiment 7 method

A different set of 24 participants (age 20 to 33, 5 male) took part. The apparatus, design and procedure was identical to Experiment 6, with the exception that the target was seen to emerge on the right of the occluder and was not visible before hand. Participants were instructed to press as soon as the saw the target emerge from the occluder (Figure 4.1).

### 4.7 Experiment 7 results

Performance on the delayed discrimination task was obtained in exactly the same way as in Experiment 6. Sensitivity (d') across both experiments was explored with mixed methods ANOVA [Distractor Velocity (12, 16°) X Experiment (Motion Extrapolation, Visible Motion)].

There was no overall difference between d' scores in Experiments 6 and 7 ($F$ (1, 46) < 1, N.S). However, there was a main effect of Distractor Velocity on sensitivity ($F$ (1, 46) = 8.634, $p$ = 0.005). This was because participants were more sensitive to the difference between standard and test gratings whenever the Distractor Velocity was fast. The effect of Distractor velocity on d' was similar in both Experiments reported in this Chapter ($F$ (1, 46) < 1 N.S, Figure 4.3A).

In both experiments, participants were biased towards reporting the first grating as slower after a slow distractor and faster after a fast distractor (main effect of Distractor Velocity, $F$ (1, 46) = 15.895, $p$ < 0.001, interaction $F$ (1, 46) < 1, N.S). An overall difference between experiments was also apparent, with greater bias towards reporting the first grating as faster in Experiment 7, but this difference did not reach significance (F (1, 46) = 2.495, p = 0.121 Figure 4.3B).

### 4.8 Experiment 7 discussion

Performance on the delayed velocity discrimination task in Experiment 7 resembled Experiment 6. Again participants were more sensitive after a fast distractor, and were more likely to report the first grating as slower after a slow distractor and vice versa. This suggests that the blending effect in Experiment 6 was not produced by tracking occluded targets, but simply by viewing moving distractors.

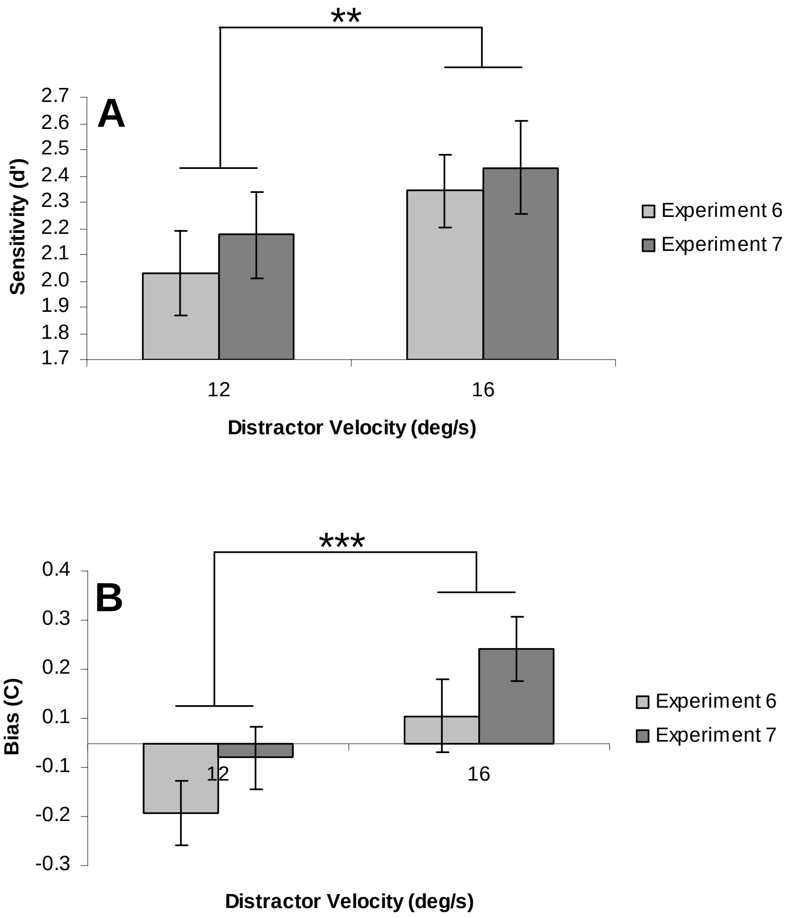


**Figure 4.3: Delayed discrimination task results: A:** Sensitivity (d') as a function of distractor velocity and experiment. **B:** Response bias (C) as a function of distractor velocity and experiment. Negative values indicate a bias towards reporting the standard grating as slower, positive values indicate a bias towards reporting standard as faster. (**$p <$ 0.01, *** $p < 0.001$).

## 4.9 General discussion

In Chapters 2 and 3 it was reported that responses on motion extrapolation tasks were influenced by the velocity of previous trials. The pattern of interference suggests that subsequently encoded velocity representations blend together. Other measurements of velocity memory, such as delayed discrimination performance (Kerzel, 2001; McKeefry et al., 2007) and ASPEM velocity (Poliakoff et al., 2005), also reveal a comparable velocity blending effect. This similarity indicates that a common velocity memory system (in which subsequently encoded representation blend together) controls all these operations. However, it is possible that the apparent blending effect in motion extrapolation tasks could be produced by response time generalization (Appendices 1 and 2).

Experiment 6 was designed to measure the effect of velocity blending on motion extrapolation once the response time generalization confound was removed. It also asked whether delayed discrimination and motion extrapolation involved the same velocity memory system. The results were interesting, but possibly raise more questions than they answer. It was found that motion extrapolation was influenced by the velocity of the standard grating, but this effect interacted with stimulus parameters in a complex way: participants responded significantly later on the 12°/s than the 16°/s motion extrapolation trials, and an influence of standard velocity only appeared in the fast trials. It seems that the range of velocities presented can influence response times as much as any experimental manipulation, and these range effects partially or wholly mask effects of interest. As mentioned in section 4.4, the use of a single probe trial velocity could be a more successful approach in future.

Conversely, there was a much clearer effect of motion extrapolation velocity on delayed discrimination. Participants remembered the standard grating as slower when the motion extrapolation task was slow and vice versa. This is consistent with the velocity blending account, and also suggests the tasks involve common resources.

A similar effect was found in Experiment 7, even though there was no requirement to attend to the distractor velocity. Of course, participants may have encoded distractor velocity spontaneously, and this is made more likely because they had to respond to its appearance by pressing a button. It is also possible that participants imagined the target travelling behind the occluder before it appeared on the right hand side (e.g. Assad & Maunsell, 1995). It is not possible to assess the relative contribution of these processes. However, taken together, these results indicate that the moving dot stimuli used throughout this thesis are processed by the same systems which retain grating velocity information in delayed discrimination tasks. This is consistent with the ideas described in Chapter 1.

Did the distractors in Experiments 6 and 7 blend with *stored* representations of the standard grating (as suggested), or distort *perception* of the subsequent test grating? Indeed, the obtained results could be explained if participants perceived the test grating as faster after a slow distractor and vice versa. This could be referred to as a *contrasting effect* (Makin et al. 2008). However, there are two reasons for adopting the original blending interpretation: First, the velocity blending effect has been found in other experiments. Second, Kerzel (2001) addressed this issue directly by comparing a conventional experiment where the distractor was presented between the standard and test velocities, to a novel experiment where it presented *before* both the standard. Results suggested that the distractor velocity blended with the standard velocity in both experiments. This result is inconsistent with the idea that distractor velocities contrast with the subsequent presentation.

It was also found that delayed discrimination performance was better on trials with a fast distractor. This was not predicted. One tentative explanation could be that fast distractors had shorter durations, and thus disruption of the standard velocity trace was reduced. It is also possible that fast distractors were attention grabbing or cortically arousing, and would have improved performance on *any* concurrently presented task. A third possible explanation is that the faster distractor reduced the subjective duration of the delay between standard and test gratings, and thereby reduced memory decay. Indeed, it is known that subjective time passes more quickly when viewing moving stimuli, and that this effect is enhanced with faster velocities (Kanai, Paffen, Hogendoorn, & Verstraten, 2006).

In summary, the work in this chapter addressed two questions. First, the studies asked whether motion extrapolation is influenced by the velocity blending effect after response time generalization confounds are removed. There was some evidence for this, but the effect interacted with other stimulus parameters. Second, it was asked whether delayed discrimination and motion extrapolation employ the same velocity memory system. Evidence for this hypothesis was stronger. It was found that the velocity of moving targets biased in delayed discrimination judgments, irrespective of whether target velocity was crucial for performance or not. This suggests that the moving dot stimuli activate the velocity memory system which mediates delayed discrimination, as proposed in Chapter 1.

# Chapter 5

# Changes in event related potentials during motion extrapolation

## 5.1 Introduction

Previous work has established that people track occluded targets with visuospatial attention during motion extrapolation tasks (de'Sperati & Deubel, 2006). In Chapter 1, it was argued that any task which involves visuospatial attention necessarily involves the oculomotor control system, even if participants fixate (Eimer et al., 2007). In Chapter 2, it was suggested that judgments about occluded target position are driven by the velocity memory and pre-motor components of the SPEM control network, even during fixation. This chapter describes an EEG experiment, (Experiment 8) which was designed to explore covert tracking of visible and occluded targets.

In the model outlined in Chapter 2, covert attentive tracking of visible motion is guided by retinal and extraretinal velocity signals (Churchland, Chou, & Lisberger, 2003). However, when the target becomes occluded, attentive tracking is guided by velocity memory alone (Bennett & Barnes, 2006a). In this model, the same pre-motor systems fix visuospatial attention on the moving target, irrespective of whether the target is visible or not. However, the rate at which the ‘spotlight’ of attention moves (cf Posner, 1980) is controlled by visual velocity signals when the target is visible, but stored velocity signals when the target is occluded.

It was also hypothesised that the switch to memory guided tracking occurs around 200 ms post occlusion. Indeed, until this point SPEM and judgments about target position are similar to when moving targets are visible (G. R. Barnes & Collins, 2008; Benguigui et al., 2004; Pola & Wyatt, 1997). However, SPEM and judgement accuracy both decline after this initial period (Vaina & Giulianini, 2004). This implies a switch to different cognitive mechanisms.

Makin, Poliakoff and El-Deredy (2009) used the Event Related Potential (ERP) technique to investigate covert tracking of visible and occluded targets. In this work, we recorded ERPs during two tasks. During the Visible Task, a small moving target travelled rightwards at 12 or 20°/s. During the Occluded Task, identical targets became occluded for at least 500 ms mid trajectory.

In both tasks, a positive ERP developed in the right occipital-parietal electrode cluster. This positivity was probably generated by brain systems engaged in covert attentive tracking. In the Visible task, amplitude peaked after the moving target passed fixation. This suggests that attentive tracking was primarily driven by visual inputs. In the Occluded Task, the development of this ERP was clearly affected by occlusion onset, and scalp activity diverged from the Visible Task around 200 ms post occlusion. This change could reflect the switch to memory-guided tracking at this point (Figure 5.1).

Although the results of Makin et al. (2009) provide good preliminary evidence for the model of motion extrapolation, there are many remaining questions. For example, the targets always moved rightwards, and we found right lateralized ERPs. This could be because visuospatial attention is a right hemisphere function (Lencer et al., 2004; Mesulam, 2002). However, other ERPs linked to visuospatial attention are lateralized according to the direction of the attentive shift (Eimer & Driver, 2001), therefore the topography of the location and occlusion related ERPs may differ if target moved leftward. In this chapter, the experiment conducted by Makin et al. (2009) was extended by comparing leftward and rightward motion conditions, and several other potential confounds were also addressed.

In our original experiment, the Visible and Occluded Tasks required different motor responses. In the Visible Task, occasional *oddball* trials were presented in which target velocity doubled for 100 ms at an unpredictable point. Participants had to press a button as soon as they saw an oddball, but no motor response was required in the absence of an oddball. The Occluded Task was similar to the Discrimination Task of Experiment 2 (Chapter 2). Targets reappeared at either the correct time or 300 ms too late, and participants pressed one button for correct reappearance, and another for late reappearance. Therefore, unlike the Visible Task, a motor response was required on every trial. Moreover, in both tasks, participants made right handed responses. Thus asymmetrical motor response preparation could have contributed to the lateralized ERPs (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). Although Makin et al. (2009) presented analysis which argued against this, the role of motor preparation remains uncertain.

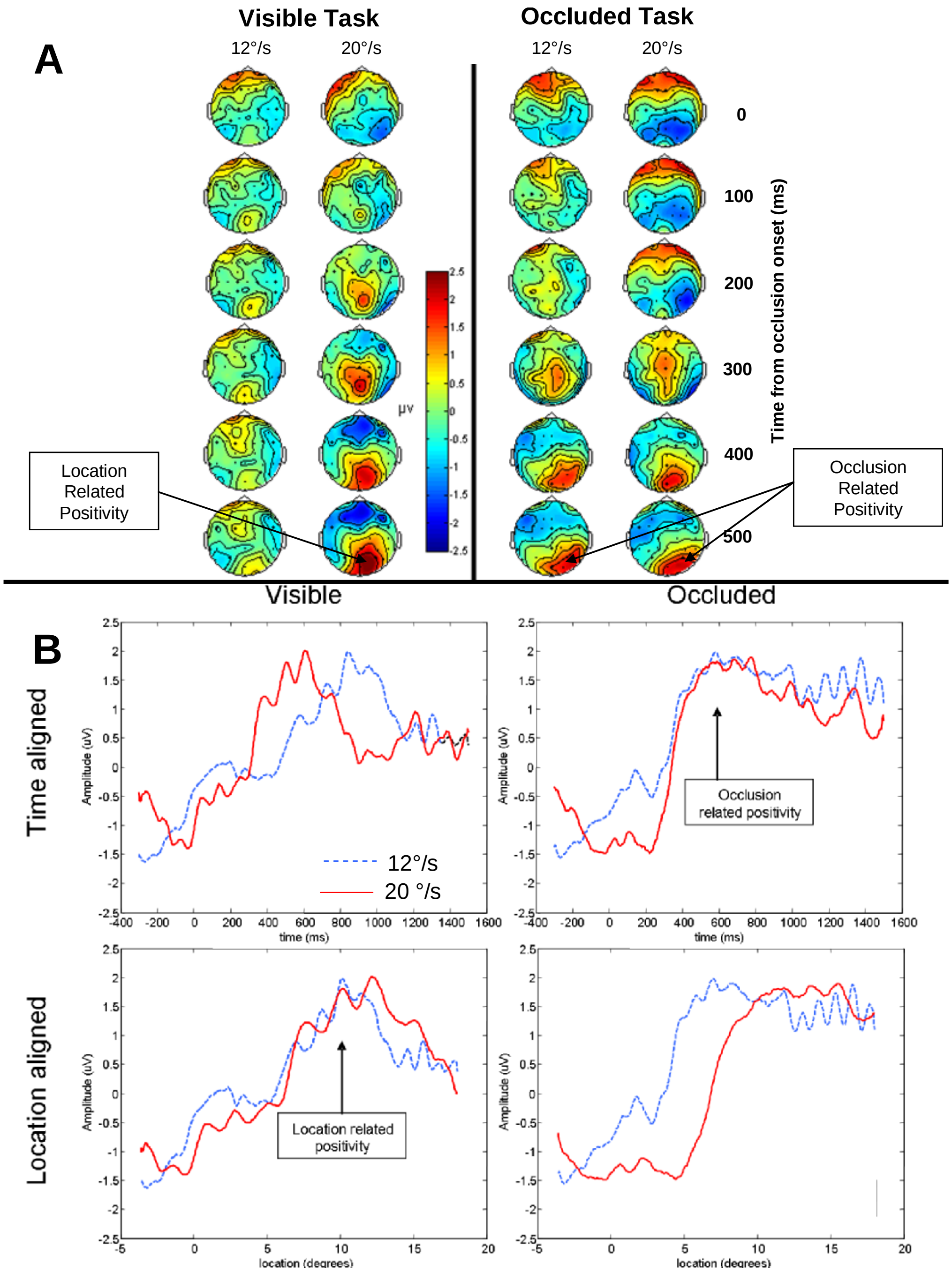


**Figure 5.1: Results of Makin, Poliakoff and El-Deredy (2009)**. **A:** scalp topographies from the first 500 ms of the *occlusion period from* the Occluded Task, or from equivalent period in the Visible Task. The left columns show data from the 12 and 20°/s conditions of the Visible Task. It can be seen that a posterior, right lateralized positivity has emerged during the 20°/s condition, but not yet in the 12°/s condition. This is the Location Related Positivity. The right columns show data from the Occluded Task. Here the positivity emerges in both tasks at a fixed point post occlusion, irrespective of target location or velocity. This is the Occlusion Related Positivity. **B:** Event Related Potentials **(**ERPs) from the right posterior electrode cluster in the Visible and Occluded Tasks (left and right columns). Amplitude in the 12 and 20°/s is plotted as a function of Time (Top row) or Location (Bottom row). Location and Occlusion Related ERPs are labelled throughout.

In the current work (Experiment 8), these confounds were eliminated. In both tasks, participants waited until the motion had finished before pressing buttons. In the Visible Task, a visual prompt then required them to report 'oddball' or 'no oddball' by pressing with either their left or right hand. In the Occluded Task, participants again waited until the display had finished, but then report 'on-time' or 'late' reappearance in the same way. Importantly, the hand which corresponded to a particular judgement was not known until the response screen appeared. Therefore no systematic, asymmetrical motor preparation could develop during stimulus presentation (cf Murray et al., 2004).

Makin et al. (2009) required participants to fixate while they tracked the moving targets covertly, and we used the horizontal electro-oculogram (HEOG) to monitor fixation. Trials with excessive eye movements were excluded. However, it is possible that some eye movements still contaminated the data. In the current work, we used an eye tracker to assess the quality of fixation in each trial. This ensured that ERPs cannot be produced by participants breaking fixation.

Two further improvements on our earlier study were also made. Originally there were 40 trials in each condition of the Visible Tracking Task, but 80 in the Occluded Tracking Task. In the current experiment, there were 60 trials in every condition. Second, in our original experiment, participants did not fixate before stimulus onset, possibly resulting in a noisy baseline. In the current study, participants fixated for 1200 ms before stimulus onset.

Finally, this experiment allowed further exploration of fixational eye movements. Experiment 2 demonstrated a positive relationship between grand average eye position and target position. The presence of this relationship implies covert activation of the oculomotor control system during motion extrapolation. However, the targets always moved rightwards in Experiment 2. This result should be replicated when the targets move leftwards. This would confirm the effect was produced by participants covertly tracking (rather than some general tendency to make small eye movements to the right as the trial progressed). The current experiment also allowed direct comparison of fixational eye movements during visible and occluded tracking.

## 5.2 Experiment 8 method

### 5.2.1 Participants

20 participants (4 male, aged 18-29, all right handed) were involved.

### 5.2.2 Apparatus

The same stimulus presentation hardware was utilized again. The target travelled at 12 or 20º/s. The target was static in its start position for 600 ms before moving horizontally leftwards or rightwards. The target was not blanked prior to motion onset and there was no audio warning cue. This differs from other experiments in this Thesis. These changes were designed to prevent evoked potentials overlapping with motion related activity. A white target was chosen (rather than blue) to maximise visual salience and for consistency with Makin et al. (2009).

Continuous EEG was recorded using Synamps (Neuroscan Inc) from 61 AgCl extended 10-20 scalp electrodes relative to a CZ reference, and subsequently average referenced offline. Vertical and horizontal electro-oculograms were recorded with separate electrodes placed above and below the left eye and on the outer canthi of both eyes respectively. Impedance was kept below 5KΩ throughout and EEG was sampled at 500 HZ. Bandpass filters were set at 0.01 Hz - 100Hz. This set up was identical to that used by Makin et al (2009). The eye tracker and calibration procedure were identical to that described in Chapter 2.

### 5.2.3 Visible Task procedure

In the Visible Task, targets were presented in four conditions [(12 or 20º/s) X (leftward or rightward motion)]. There were 60 repeats of each condition. The experiment was broken into 6 blocks, with 10 repeats of each condition per block. The trials in each block were presented in a pseudo-random order, with no more than 3 repeats of a single condition presented sequentially. Each block contained 8 oddballs, giving 48 oddballs in total (16.7%, the same proportion as Makin et al. 2009). Half the participants did the blocks in reverse order.

The visual stimuli on the rightward trials were identical to those used by Makin et al. (2009). On each trial the target remained static 1.8° from either the left or right hand edge of the screen for 600 ms. It then moved rightward for 26.25° on a path centred on the fixation point. Motion duration was 1312 ms in the 20°/s conditions, and 2187ms in the 12°/s condition. The velocity change oddball could occur at any point during the central 17.5° of the target's path. This corresponds to durations of 875 ms in the 20°/s condition and 1458 ms in the 12°/s conditions. The velocity changed oddball involved the target velocity doubling in speed for 100 ms. After the target reached the end of its trajectory, there was a 300 ms pause and the response screen appeared. The leftward trials were a mirror image of the rightward trials (Figure 5.2).

The response screen consisted of the words 'NORMAL' and 'ODDBALL' presented to the left and right of screen centre. Participants rested their index fingers on the 'A' and 'L' buttons of a keyboard. The position of the words indicated which button corresponded to which judgment. The hand used to report each judgement was balanced across conditions. This design prevented asymmetric motor response preparation during the visual motion (e.g. Murray, 2004). Participants could take as long as they liked to respond. There was then a 1.2 second pause before the next trial, during which participants fixated.

Before the experiment, participants completed a practice block of 16 trials consisting of 4 oddballs (one repeat of each condition) and 12 normal trials (3 repeats of each condition), with an equal number of left and right hand responses.

### 5.2.4 Occluded Task procedure

In the Occluded Task targets were presented in four basic conditions: [(12 or 20º/s) X (leftward or rightward motion)]. There were 60 repeats of each condition. Again the visual stimuli in the rightward trials of this experiment were identical to those used by Makin et al. (2009). As with the Visible Task, the target remained static 1.8° from the edge of the screen for 600 ms. It the moved rightward across 26.25°. The path of the moving target was centred on the fixation point. The first 5.95° of target motion was visible. The corresponded to a duration of 300 ms in the 20°/s condition and 500 ms in the 12°/s conditions. There were 5 different occluder sizes, ranging from 10.21 to 13.71° in 0.875° increments. This produced 5 occlusion durations for the on-time 12°/s targets (850 to 1142 ms) and 5 occlusion durations for the on-time 20°/s targets (510 to 685 ms). For late reappearance trials, the target reappeared in the same positions as the on-time reappearance trials, but 300 ms too late (see Chapter 2). After reappearance, the target travelled to the end of its path (thus for on-time trials, motion duration was identical to the Visible Task). There was then a 300 ms pause before the response screen appeared. The leftward trials were a mirror image of the rightward trials (Figure 5.2).

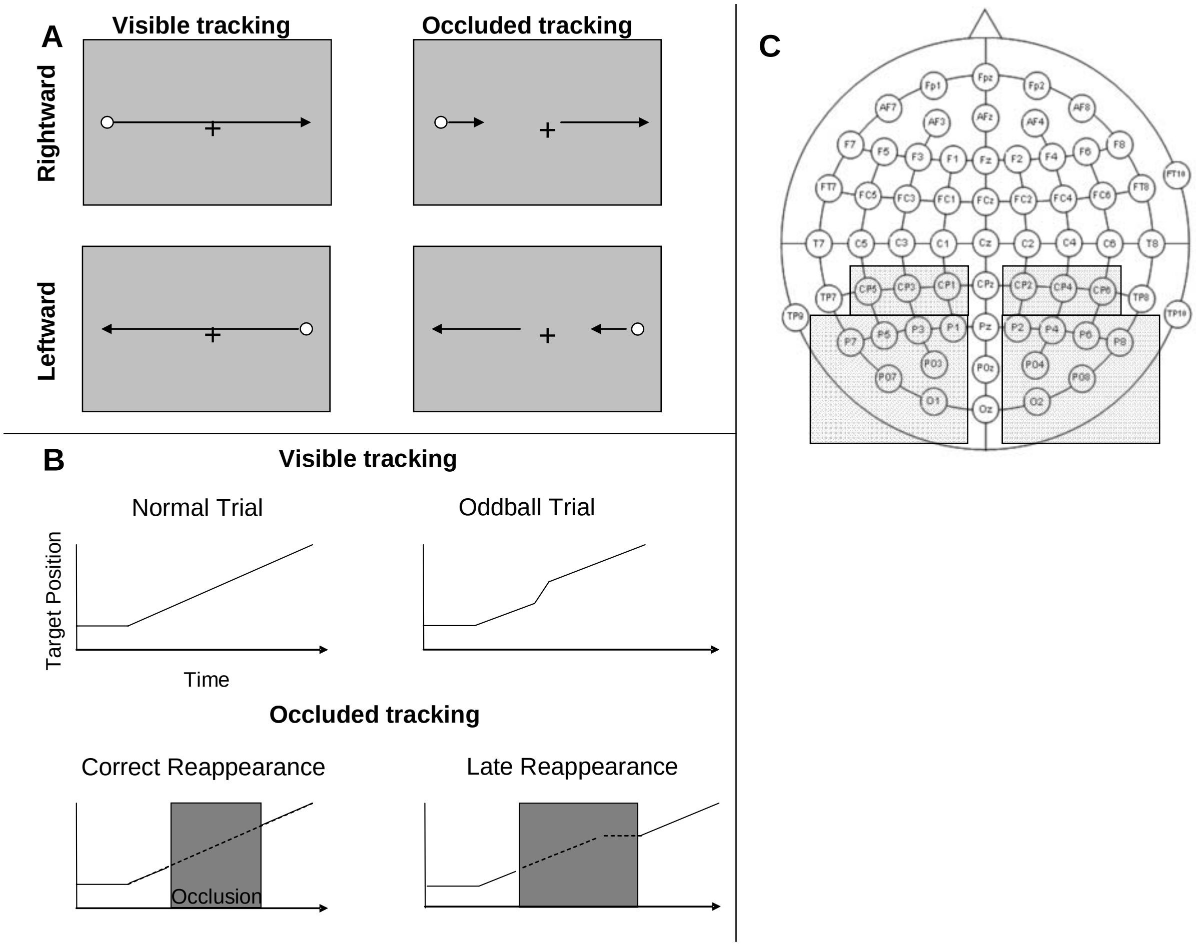


**Figure 5.2: The visual stimulus. A:** Diagram of the basic tasks. **B:** Upper panels: Schematic of the target position vs. time in the Visible Task. Lower panels: schematic of target position vs. time in the Occluded Task. **C:** The layout of scalp electrodes. Grey shaded regions show the left and right clusters which were used for all analysis.

The response screen was designed to be as similar as possible to the Visible Task. It displayed the words ‘ONTIME’ and ‘LATE’ to the left and right of screen centre. Responses were again made with ‘A’ and ‘L’ keys on a computer keyboard and the position of the words indicated which button corresponded to which judgement. Response hand was counterbalanced across conditions and responses were unspeeded. After the response screen, there was 1.2 seconds of fixation before the static target appeared for the next trial.

Like the Visible Task, the Occluded Task was split into 6 blocks. Over two blocks, each possible trial type occurred once (2 speed X 2 direction X 2 reappearance error X 2 response hand X 5 occluder size). Half the participants completed the blocks in the reverse order. The practice block again consisted of 16 trials with balanced stimulus parameters.

### 5.2.5 Analysis of behavioural data

Signal detection analysis was used to assess participants' performance in the Visible Task (Green & Swets, 1966). In the Occluded Task, the proportion of trials judged to have reappeared on-time was analysed as a function of actual reappearance error (on-time, late), movement direction (left, right), and speed (12, 20°/s) with a repeated measures ANOVA. The pre-processing conventions outlined in Chapter 2 were applied (Section 2.2.5).

### 5.2.6 Analysis of EEG data

Pre-processing of the EEG data was designed to be as similar as possible to that of Makin et al. (2009). Artefacts in the EEG data resulting from eye blinks, saccades, and mains interference were removed using Independent Components Analysis (ICA, Jung et al., 2000). Between 1 and 8 components were removed from each block (median = 4). Data was then segmented into epochs from -400 ms to 3092 ms around target onset. Epochs were baseline corrected relative to a pre-target onset period of 200 ms.

Epochs with high HEOG activity were excluded from analysis. High HEOG activity was identified by amplitude exceeding 70 μv at electrodes AF7 or AF8, or by a correlation of > 0.75 between AF7/AF8 and the horizontal electro-oculogram during the first 1700 ms. Two participants with <50 of trials remaining after this treatment were excluded from further analysis. The number of trials included was high, and approximately equal in both tasks (Visible Task, M = 86.51%, SD 12.52%, Occluded Task, M = 84.97%, SD 14.02%, $t$ (17) = 0.475, $p$ = 0.641).

To explore the patterns of ERP activity during visible and occluded tasks, sequences of topographic maps of scalp activity were produced (Praamstra, Boutsen, & Humphreys, 2005), using grand average voltage at each electrode. Inspection of the sequential topographies showed interesting ERP patterns in two clusters of electrodes, which were explored statistically (P2, P4, P6, P8, PO4, P08, O2, CP2, CP4 and CP6 and their left sided homologues, see Figure 5.2C). Effects were explored with repeated measures ANOVAs. Paired t tests were used to explore significant interactions. Data points always comprised the average amplitude over a 40 ms window centred on the stated time point.

### 5.2.7 Analysis of eye position data

Eye position data was used to confirm that participants did not break fixation during the trials included in the EEG. Eye position data was also used to investigate fixational eye movements (Abadi & Gowen, 2004). Eye position vs. time profiles were produced as described Chapter 2 (Section 2.3.2.2). Again Trials where horizontal eye position deviated more than 2° from median eye position were excluded from this analysis (5.046%).

## 5.3 Experiment 8 Results

### 5.3.1Visible Task

#### 5.3.1.1 Behavioural results

Signal detection analysis revealed that all participants were sensitive to the velocity change oddballs in every condition (Average d' > 0, t (17) >7.357, *p* <0.001, one sample t test). Sensitivity values (d') were compared with 2 factor repeated measures ANOVA [Speed (12, 20°/s) X Direction (left, right)]. There were no main effects (*F* (1, 17) < 1, NS), but there was a significant Speed X Direction interaction (*F* (1, 17) = 13.886, *p* = 0.002). This was because participants were equally sensitive to velocity change oddballs in both speed conditions when the target moved rightward (*t* (17) = -0.991, *p* = 0.336), but were more sensitive in the 12°/s condition than the 20°/s condition when the target moved leftward (*t* (17) = 2.775, *p* = 0.013, Figure 5.3A). The participants responded cautiously in all four conditions, with a bias towards reporting that no velocity change oddball occurred, whether or not an oddball had been presented (Average C > 0, *t* (17) > 5.082, *p* < 0.001, one sample t test). Next response bias values were analysed with repeated measures ANOVA [Speed (12, 20°/s) X Direction (left, right)], but this revealed no main effects or interactions ($F$ (1, 17) < 2.495, $p$ > 0.132, Figure 5.3B).

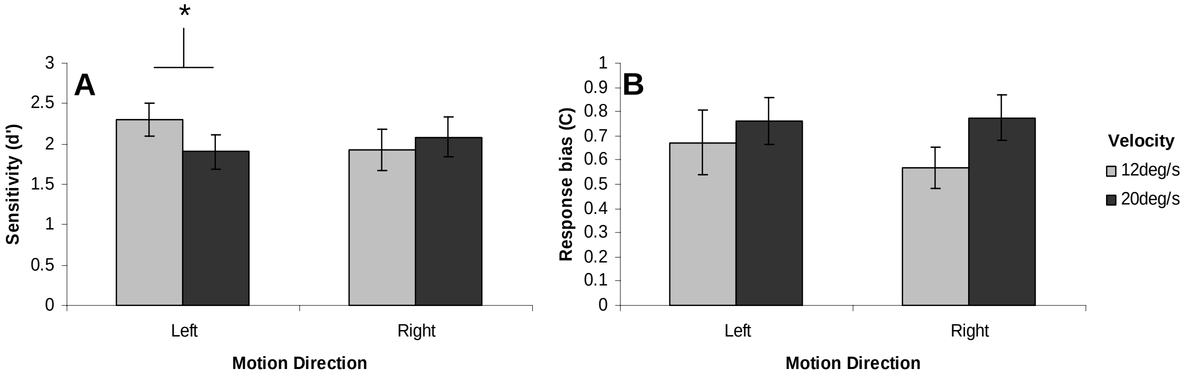


**Figure 5.3: Performance in the Visible Task. A:** Sensitivity (d') to velocity change oddballs. Zero indicates random responding. **B:** Response Bias. Positive values indicate bias towards reporting 'no oddball'. * $p < 0.05$.

### 5.3.1.2 EEG results

Sequences of grand average topographic maps were produced in order to visualize ERP patterns in the Visible Task. Topographic plots were produced at 200 ms intervals in four conditions (12, 20°/s X leftward, rightward). Topographic maps in the 12 and 20°/s conditions are laid out as a function of time in Figure 5.4.

There a several important patterns in Figure 5.4. First, a posterior positive potential developed in all conditions. This component was lateralized according to the direction of target motion. When the target moved leftward, the posterior positivity moved from right to left electrode sites. When the target moved rightwards, the posterior positivity shifted in the opposite direction. In both motion direction conditions, amplitude increased after the target passed the centre of the screen. The component also became more anterior towards the end of the trial.

In both speed conditions, the component became lateralized after the target passed the centre of the screen. The lateralization thus occurred *later* in the 12°/s than the 20°/s condition. The ERPs in the rightward motion conditions are similar to those found by

Makin et al. (2009). However, this data expands on the findings of Makin et al. (2009) by showing an equivalent *left lateralized* ERP when the target moved leftwards.

There are also some differences between these results and those of Makin et al. (2009). The amplitude of the posterior positivity was greater; it was spread over more electrodes, and had a more anterior focus. More significantly, the lateralization of the posterior positivity was tightly time locked to the point where the target passed the fixation cross. The component shifted focus from central posterior electrodes to lateralized electrodes at around 200 ms after the target crossed fixation (Figure 5.4). This pattern gave the general appearance of a topographic focus shifting as a function of target location. Indeed, Makin et al (2009) described it as the ‘Location Related Positivity’. However the effect is largely explained by ERPs *time locked* to the target switching visual hemifield. ERP topography at other times during the trial was not so closely related to target location. This ERP may be more accurately described as the *Hemifield Switch Positivity* (HSP) rather than the ‘Location Related Positivity’.

These patterns are evident in Figure 5.5A. Here amplitude in the *left electrode cluster* is shown for the *leftward motion condition* and amplitude in the *right electrode cluster* is shown for the *rightward motion condition*. It can be seen that there was a clear HSP in all conditions, which peaked around 240 – 260 ms after the target passed screen centre. The latency of the HSP is exemplified in Figure 5.5B, which is realigned and baseline corrected to the period 200 ms before the target reached screen centre**.** This demonstrates that the HSP latency is linked to the target crossing fixation.

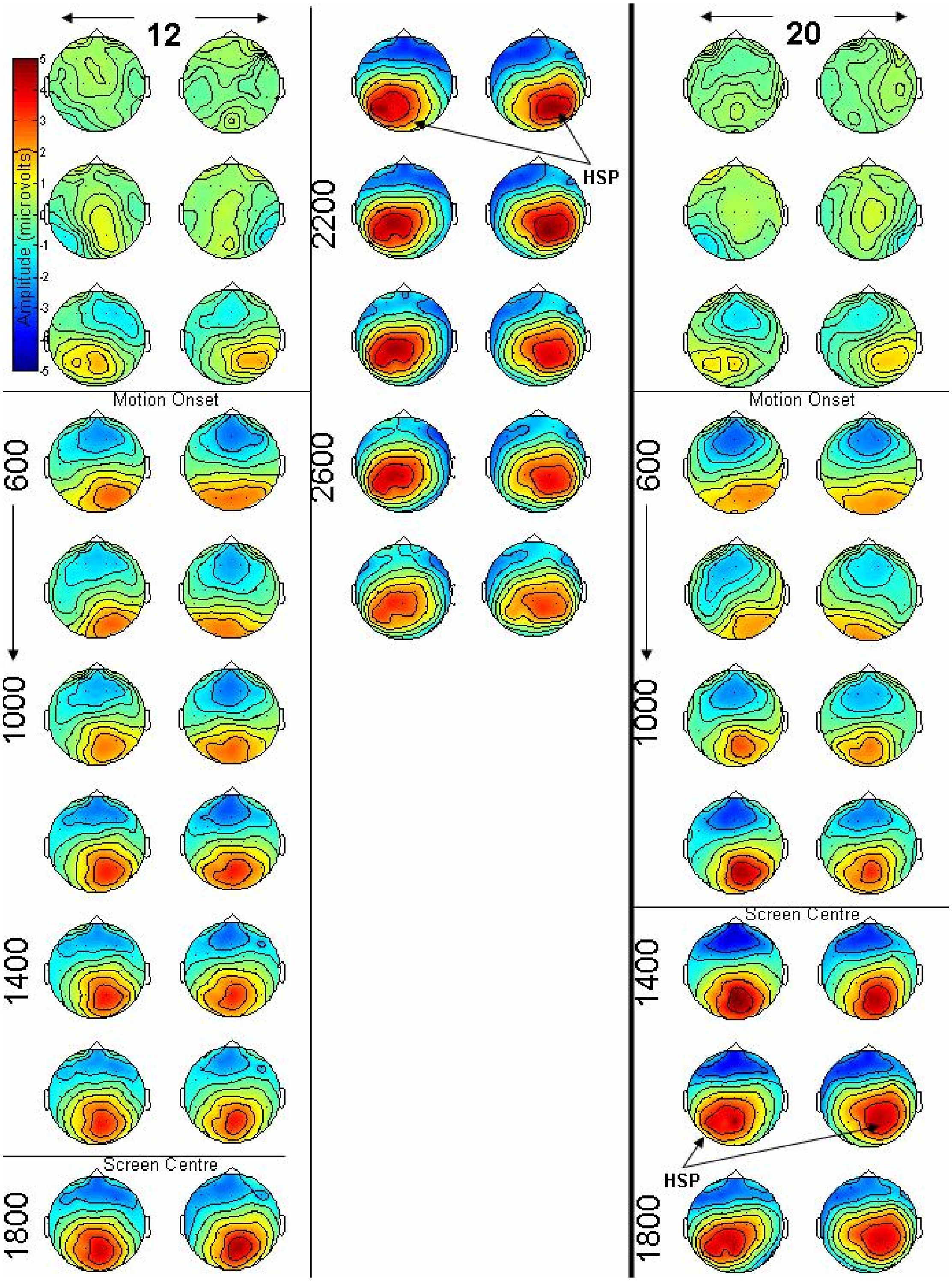


**Figure 5.4**: **Sequential topographies from the Visible Task**. Data from the 12°/s trials are shown on the left of the figure (and continue in the middle column). Data from the 20°/s trials are shown on the right side of the thick black vertical line. Leftward and Rightward motion conditions are placed adjacently. Each row represents a 200 ms interval. Maps show average amplitude from a 40 ms window around the stated point. Horizontal lines indicate the approximate time motion began and the target reached screen centre HSP = Hemifield Switch Positivity.

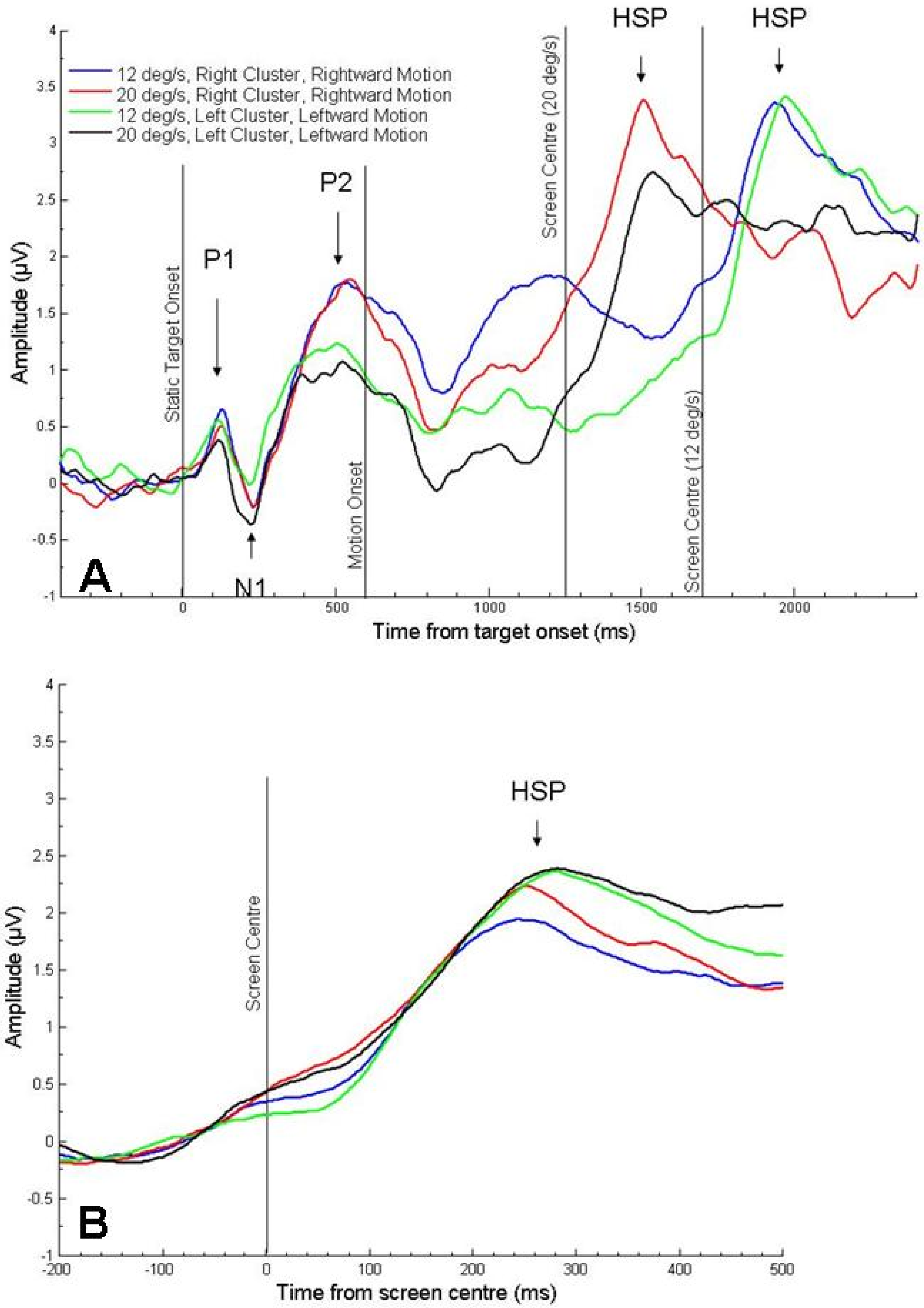


**Figure 5.5: Event related potentials in the Visible Task**. **A:** Event Related Potentials (ERPs) from the leftward motion ERPs are recorded from left sided posterior electrodes, rightward motion ERPs are recorded from right sided homologues. Vertical Lines illustrate events during the trial. P1, N1, P2 and Hemifield Switch Positivity (HSP) components are labelled. Plots baseline corrected to a 200 ms pre-stimulus interval. **B:** The HSP wave realigned to screen the time the target passes fixation, and baseline corrected to a 200 ms interval before this point. All plots are smoothed with a 20 Hz filter.

The characteristics of the HSP were confirmed statistically. Amplitude was measured at every 100 ms interval during the first 1300 ms of motion. Separate two-factor repeated measures ANOVAs [2 Speed (12°/s, 20°/s) X 14 Time (0:1300 ms after motion onset)] were applied to the left cluster- leftward motion and to the right cluster- rightward motion conditions.

In the left cluster, leftward motion analysis, there were significant main effects of Speed and Time ($F$ (1, 17) > 5.942, $p < 0.033$), and a significant Speed X Time interaction ($F$ (4.950, 84.155) = 11.504, $p < 0.001$). This was because amplitude was significantly higher in the 20°/s condition at all time points from 800 to 1200 ms after motion onset ($p < 0.018$), while there was no amplitude difference at the other time points ($p > 0.065$, Figure 5.6A).

In the right cluster, rightward motion analysis, there was no effect of Speed ($F$ (1, 17) < 1, N.S), but there was a main effect of Time ($F$ (1.953, 33.201) = 5.858, $p = 0.007$), and a significant Speed X Time interaction ($F$ (4.148, 70.519) = 11.453, $p < 0.001$). This was because amplitude was higher in the 12°/s condition at 400, 500, 600 and 1300 ms post motion onset ($p < 0.047$), but higher in the 20°/s condition at 800, 900 and 1000 ms post motion onset ($p < 0.031$, Figure 5.6B).

The latency of the HSP was also explored by measuring the time point when amplitude was 50% of the maximum (Luck, 2005). Measurements were obtained from all but two participants, who were excluded because they did not show an HSP in every condition. Data from the remaining participants was explored with 2 factor repeated measures ANOVA [2 Direction, (leftward, rightward) X 2 Speed (12, 20°/s)].

This analysis found a strong main effect of Speed ($F$ (1, 15) = 795.090, $p < 0.001$; 12°/s, M = 1839.5, 20°/s, M = 1408.3). There was no main effect of Direction and no Direction X Speed interaction ($F$ (1, 15) < 1, NS). Next, the same data was standardized as a deviation from the time the target passed fixation. Analysis of standardized data found no effect of Speed ($F$ (1, 15) < 1, N.S, 12°/s, M = 146.0, 20°/s, M = 152.3). This indicates that HSP was indeed time-locked to the point when target crossed fixation.

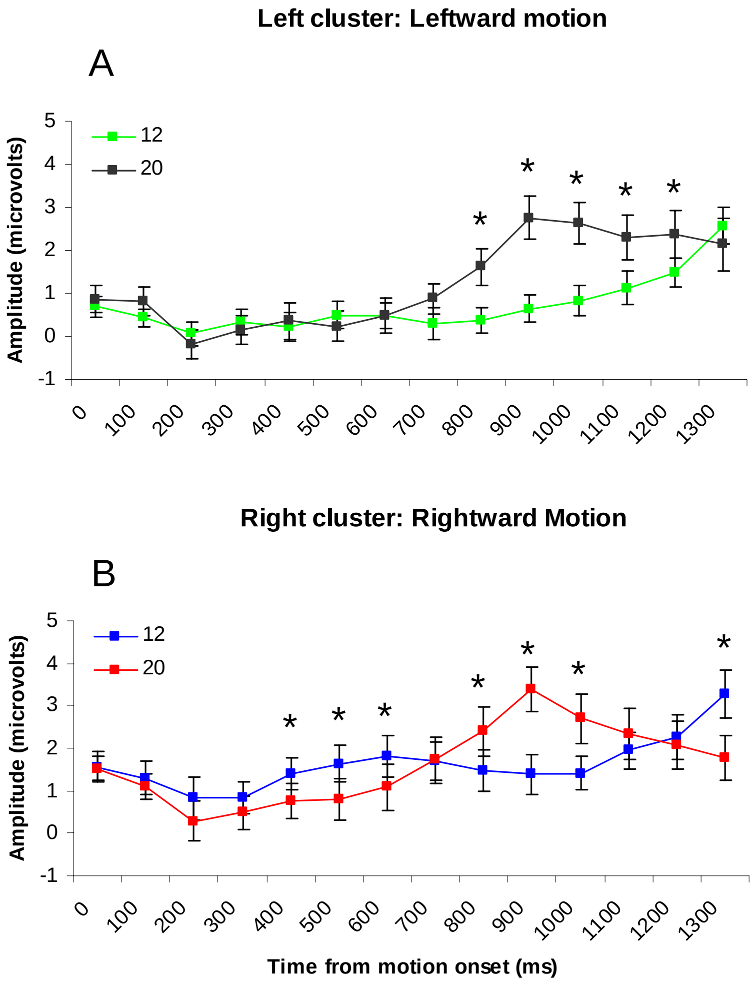


**Figure 5.6: Results of the Visible Task**. **A:** Left cluster, leftward Motion data. **B:** Right cluster, rightward motion data. Amplitude is shown as a function of time and speed. Zero refers to motion onset. * $p < 0.05$. Error bars = +/- 1 S.E.M.

### 5.3.2 Occluded Task

#### 5.3.2.1 Behavioural results

The proportion of trials judged to have reappeared ‘on-time’ was analysed as a function of Reappearance error (on-time, late), Speed (12, 20°/s) and Direction (left, right) with repeated measures ANOVA. Participants were more likely to report on-time reappearance when the target had indeed reappeared on-time ($F$ (1, 17) = 264.12, $p < 0.001$). This confirms that they were performing accurately. There was no main effect of direction ($F$ (1, 17) = 1.034, p = 0.323), but participants were more likely to report on-time reappearance in the 20°/s condition (*F* (1, 17) = 13.433, *p* = 0.002). There was also a Direction X Speed interaction (*F* (1, 17) = 5.567, *p* = 0.031). This was because participants made more on-time reappearance when the target was going left in the 20°/s trials (*F* (1, 17) = 4.812, *p* = 0.042), but not in the 12°/s trials (*F* (1, 17) < 1, NS, Figure 5.7).

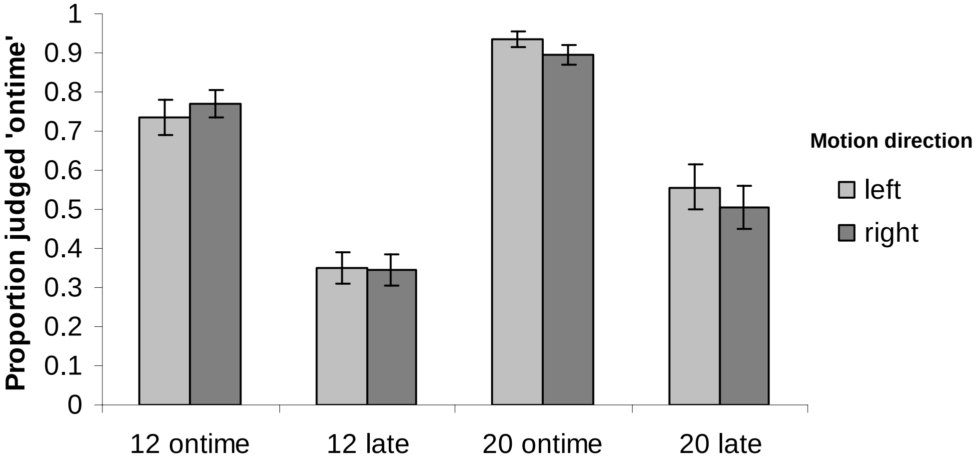


**Figure 5.7: Performance in the Occluded Task**. The proportion of trials judged ‘on time’ is shown as a function of speed, reappearance error and direction. Error Bars = +/- 1 S.E.M.

### 5.3.2.2 EEG results

Sequential topographic maps are shown in Figure 5.8. The development of posterior positive ERPs was generally similar to the Visible Task. ERPs were lateralized according to motion direction. However, the time-course of this component was different to the Visible Task. In the Visible Task, lateralized positivity peaked ~250 ms after the target passed fixation. Conversely, in the Occluded Task, the posterior positivity became focused on central electrodes around 200 ms after occlusion in all conditions. This was followed by a lateralized positive component, emerging ~260 ms post occlusion. The latency of these components was not modulated by speed or by how close the target was to the fixation point.

The ERPs associated with rightward motion resembled the occlusion related ERPs found by Makin et al. (2009). However, in this experiment, the topographic focus was more spread across hemispheres and was more anterior. The occlusion-related ERPs were lateralized according to motion direction, but lateralization was less pronounced than in the Visible Task. This is again different from the findings of Makin et al. (2009), where lateralization was equivalent in both tasks.

This experiment also demonstrated another significant feature of the occlusion-related ERP. Makin et al. (2009) described this component as the 'Occlusion Related Positivity'. However, occlusion related ERPs recorded in lateralized clusters included both a small *negative* and then a large positive deflection. These components can be more accurately termed the *Occlusion Related Deflection* (ORD), rather than 'Occlusion Related Positivity'.

The latency of the ORD is demonstrated in Figure 5.9A. These plots depict ERPs in the left cluster for leftward motion conditions, and ERPs in the right electrode clusters for rightward motion conditions. Until occlusion, these ERP waveforms were like those of the Visible Tracking Task. However, there was a small negative deflection at ~180 ms post occlusion, and then a large positive deflection at ~260 ms post occlusion. ORD latency is very similar in all conditions. This is made clear by Figure 5.9B, where the ORDs are realigned and baseline corrected to the period 200 ms prior to occlusion.

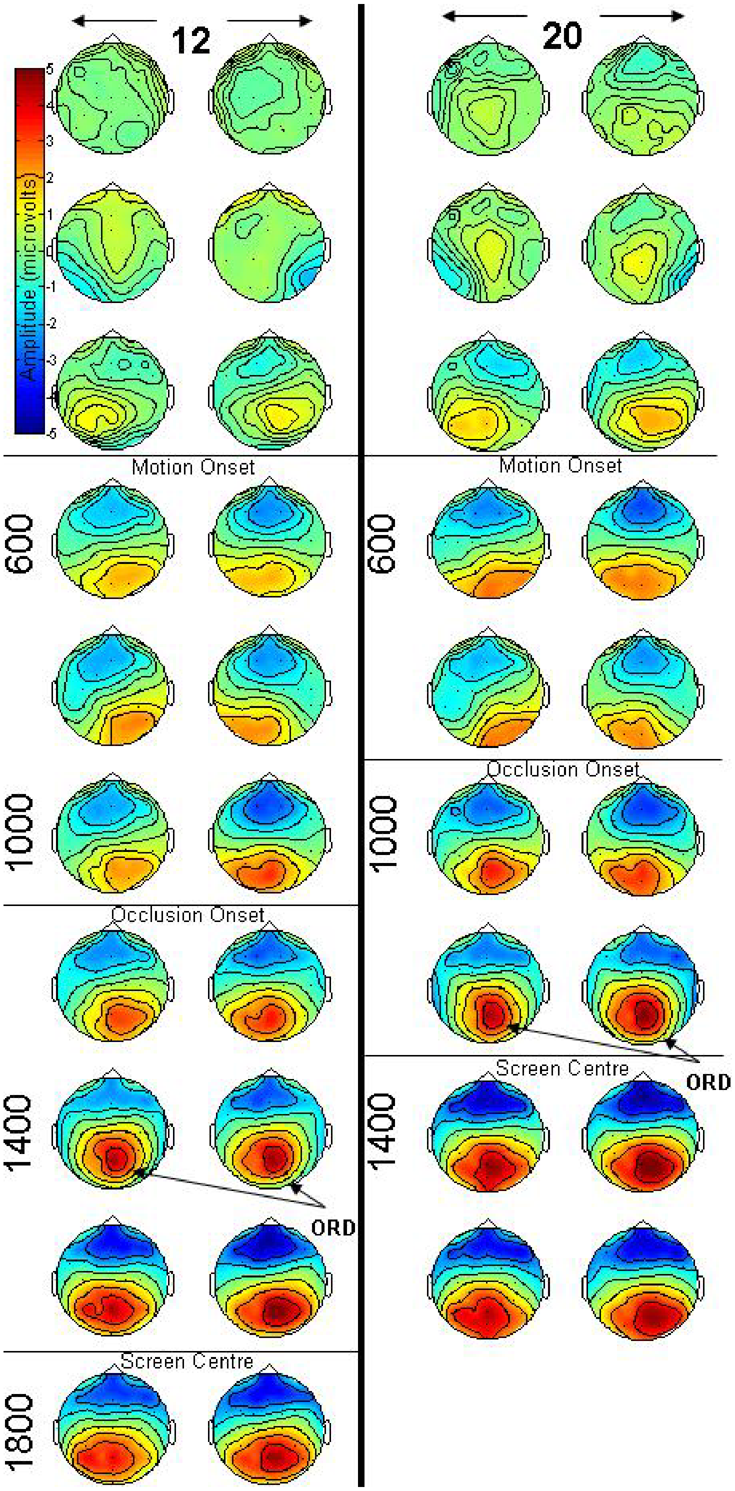


**Figure 5.8**: **Sequential Topographies from the Occluded Task**. Data from the 12°/s trials are shown on the left of the figure, data from the 20°/s trials are shown on the right side. Leftward and Rightward motion conditions are placed adjacently. Each row represents a 200 ms interval. Horizontal lines indicated the approximate onset of motion, occlusion and the time the target reaches screen centre. ORD = Occlusion Related Deflection.

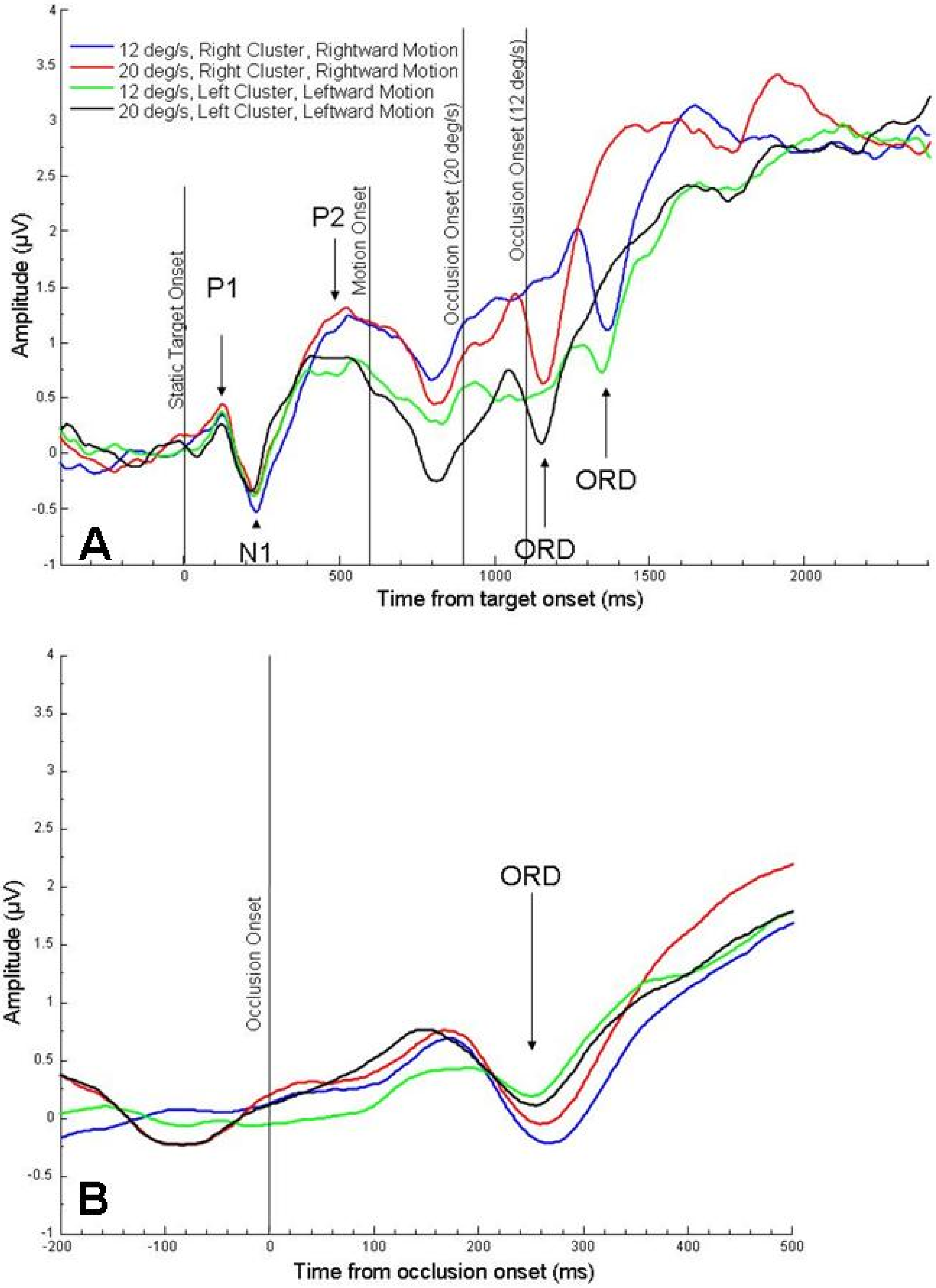


**Figure 5.9: Event related potentials in the Occluded Task**. **A:** Event Related Potentials (ERPs) from the leftward motion ERPs are recorded from left sided posterior electrodes, rightward motion ERPs are recorded from right sided homologues. Vertical Lines illustrate events during the trial. P1, N1, P2 and ORD components are labelled. Plots are baseline corrected to a 200 ms pre stimulus interval. **B:** ORD waves realigned to occlusion onset and baseline corrected to a 200 ms pre-occlusion interval. All plots are smoothed with a 20 Hz filter.

Characteristics of the ORD were confirmed statistically. First, amplitude was compared between the 12 and 20°/s conditions at various time points. In order to analyse the ORD, amplitudes from 0 to 500 ms post occlusion in 100 ms intervals were obtained. This corresponds to the minimum occlusion duration. Separate two factor repeated measures ANOVAs [Speed (12, 20°/s) X Time (0: 500 ms post occlusion)] were applied to the left cluster-leftward motion and right cluster-rightward motion conditions.

In the left cluster-leftward motion analysis there was a main effect of Time (*F* (2.388, 40.601) = 16.897, *p* < 0.001). However there was no amplitude difference between the 12 and 20°/s conditions and no Time X Speed interaction (*F* (5, 85) < 1.850, *p* > 0.113, Figure 5.10A). Results from the right cluster- right motion analysis were very similar. There was again an effect of Time (*F* (2.027, 34.461) = 23.800, *p* < 0.001), but no amplitude difference between speeds and no Time X Speed interaction (*F* (5, 85) < 1. N.S, Figure 5.10B).

Next the time point of when the positive component of the ORD reached 50% of peak amplitude was measured in each participant. Two participants did not show clear ORDs in all conditions, and were excluded (these were not the same two participants who were without the HSP). Data was analysed as a function of Direction (Left, Right) and Speed (12°/s, 20°/s) with repeated measures ANOVA. As expected, 50% of peak amplitude occurred earlier in the 20°/s condition because the target reached occlusion earlier (*F* (1, 15) = 218.102, *p* < 0.001; 12°/s, M = 1455.3, 20°/s, M = 1251.7). There was no effect of Direction and no interaction (*F* (1, 15) < 1, N.S.). Next, 50% peak time was measured as a deviation from occlusion onset, and then reanalysed as above. This eliminated the effect of Speed (*F* (1, 15) < 1, N.S., 12°/s, M = 355.3, 20°/s, M = 351.7), confirming that the ORD was time locked to occlusion onset in all conditions.

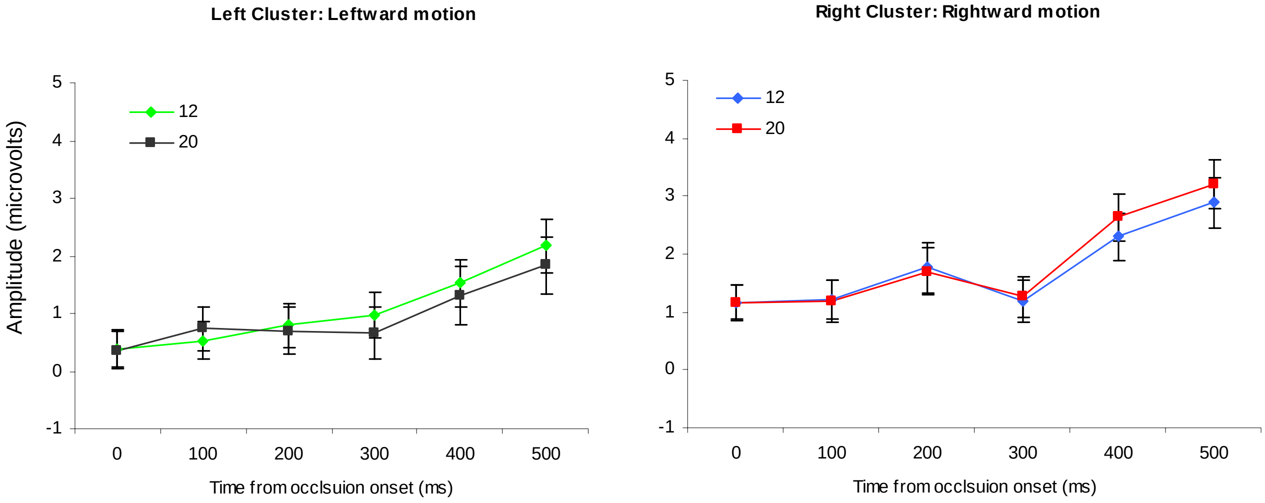


**Figure 5.10**: **Results of the Occluded Task**. **A:** Left cluster, leftward motion data. **B:** Right cluster, rightward motion data. Amplitude is shown as a function of time and speed. Zero refers to occlusion onset. Error bars = +/- 1 S.E.M.

### 5.3.3Visible and Occluded Tasks compared

The above analyses suggest that ERP waveforms were similar in the Visible and Occluded Tasks until motion onset. In the Visible Task, there was a specific *HSP* component when the target passed fixation. Conversely, in the Occluded Task, there was a unique *ORD* component when the target entered occlusion. In this section statistical analysis addresses the similarities and differences between the tasks.

Both tasks began with identical intervals during which target was static for 600 milliseconds. Presentation of the static visual target produced a Visual Evoked Potential (VEP) in the contralateral hemifield. VEPs can be seen in Figure 5.5A for the Visible Task and Figure 5.9A for the Occluded Task. The P1 and N1 components of the VEP were similar in all conditions. This was confirmed by analysis of amplitude as a function of Task (Visible, Occluded), hemisphere (left, right), speed (12, 20°/s) and Time (0, 100, 200 ms from target onset) with repeated measures ANOVA. There was a main effect of Time ($F$ (2.239, 38.414) = 14.596, $p < 0.001$), but no other effects or interactions ($F$ (1, 17) < 2.814, p > 0.111). The consistency of VEPs provides confidence in the quality of EEG data.

In the Visible Task, a HSP waveform peaked around 250 ms after the target passed fixation (Figure 5.5A). This component did not occur during the Occluded Task (Figure

5.9A). In order to confirm that the HSP was unique to the Visible Task, amplitude was measured at the time points over which HSP occurred. These time points were 1700-2300 ms post target onset in the 12°/s condition, and 1200 – 1800 ms in the 20°/s condition (in 100 ms intervals). Next, amplitude was measured at identical time points in the Occluded Task. Four separate Task X Time repeated measures ANOVAs were used to analyse each speed and direction condition. Both ANOVAs for the 12°/s conditions found significant interactions ($F$ (1.886, 32.063) > 4.107, $p < 0.029$). This confirms that the HSD waveform was unique to the Visible Task. In the 20°/s condition, the time of the HSD partially overlapped with the ORD, so there were no Task X Time interactions ($F$ (3.717, 63.195) < 2.330, $p > 0.07$).

In the Occluded Task, the ORD wave began ~180 ms post occlusion. This component appears unique to the Occluded Task (compare Figure 5.5A and 9A). To confirm this, the data used in the original analysis of the ORD was compared to data from identical time points in the Visible Task. Four separate Task X Time repeated measures ANOVAs were used to analyse each condition. In the 12°/s conditions there were Task X Time interactions ($F$ (2.665, 45.306) > 7.077, $p < 0.002$). This suggests that the ORD waveforms were indeed unique to the Occluded Task. In the 20°/s conditions, there were no Task X Time interactions ($F$ (2.753, 46.793) < 1.245, $p > 0.303$). This was because the HSP and ORD occur at similar times in the 20°/s trials.

### 5.3.4 Statistical topography analysis

The topographic distribution of HSD and positive component of the ORD showed some similarities, but also some differences. Both were lateralized according to the direction of motion. However, this was more pronounced for the HSD. These patterns were confirmed statistically. Time points corresponding to the peak of the HSD were chosen for Visible Task analysis. In the Occluded Task, ORD had a clear onset, but no clear peak. Therefore the time the point 100 ms after minimum occlusion duration was used. At this time, ERPs are likely to reflect occluded target tracking, and the positive component of the ORD was at, or near, maximum. Scalp maps from these time points are show in Figure 5.11.

Statistical topographic analysis was based on the approach of McCarthy and Wood (1985). Amplitude values in each condition and electrode were then normalized by 1:

obtaining the amplitude at each electrode and subtracting minimum amplitude at any electrode, 2) subtracting the maximum amplitude at any electrode from the minimum amplitude at any electrode, and 3) dividing the result of 1 by the result of 2. This technique is designed to remove amplitude differences between conditions that would otherwise bias topographic analysis. Statistical analysis focused on the P3 and P4 electrodes, which provided a representative recording of the ERPs of interest (this was because inclusion of too many levels in the factor 'Electrode' makes it impossible to measure sphericity, and because it can lead to spurious electrode by condition interactions which do not reflect robust patterns in the data).

Normalized amplitudes in the 12 and 20°/s trials of the Visible Task and the Occluded Task were analysed with four separate repeated measures ANOVAs [(Direction, (leftward, rightward) x electrode (P3, P4)]. In the Visible Task, there were significant Direction X Electrode interactions ($F$ (1, 17) > 22.744, $p < 0.001$). In the Occluded Task, There was a significant Direction X Electrode interaction in the 12°/s ($F$ (1, 17) = 13.010, $p = 0.002$), but not the 20°/s condition ($F$ (1, 17) = 1.893, $p = 0.187$). This analysis confirms the patterns in Figure 5.11.

It should be pointed out that the validity of statistical topographic analysis has been questioned by Luck (2005). He rightly argues that, although this procedure normalizes the range of amplitudes across different topographic plots, it does not completely eliminate the contribution of amplitude differences to Condition X Electrode interactions. However, this criticism may be less relevant to the current analysis because the ERP amplitudes in the chosen electrodes where very similar across conditions prior to normalization.

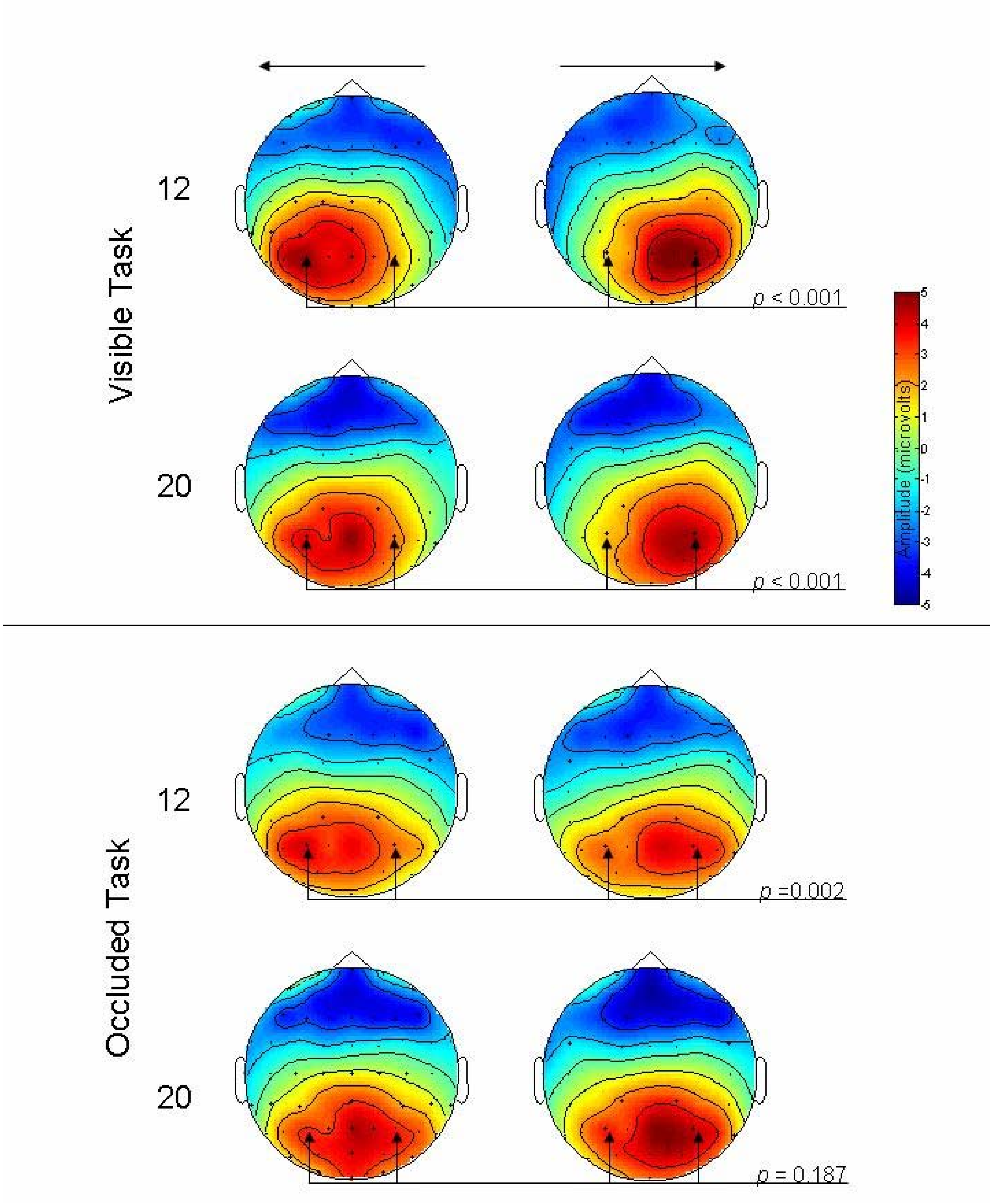


**Figure 5.11: Topographic analysis of the Hemifield Switch Positivity and Occlusion Related Deflection.** Grand average topographic maps at the peak of the Hemifield Switch Positivity and Occlusion Related Deflection waveforms are shown in all conditions. The significance of the Direction X Electrode interaction at the P3 and P4 electrodes is also included (see text).

### 5.3.5 Fixation quality

Participants were required to fixate throughout all trials. Eye movement artefacts were removed from the raw EEG data with ICA, and trials with activity indicative of eye movements were excluded. These methods removed high voltage electrophysiological artefacts produced by oculomotor muscles or movement of the retinal dipole. However, ICA does not eliminate *cortical activity* resulting from the visual effects of eye movements, and the exclusion criteria were not foolproof. Therefore it remains possible that unwanted eye movements could have contributed to the pattern of ERPs seen here (Rugg & Coles, 1995).

To address this possibility, EEG data was compared with eye position data acquired from an eye tracker. Grand-average eye position hardly moved during any condition, so participants were generally fixating very well. However, there were a small number of trials included in the EEG analysis where participants broke fixation. The prevalence of eye movements around the time of important ERPs was thus explored. As with previous analysis, eye movements were identified by eye position deviating by more than 2° from the median eye position (Kerzel, 2002). Samples where the eye tracker lost signal were also conservatively defined as breaks of fixation. Deviations during the 300 ms preceding ERP peaks in the Visible Task and Occluded Task were of particular interest. These intervals comprised 16 time points. For each participant, condition and time point, the number of trials contaminated by an eye movement was measured.

Consider that a participant's ERPs were produced by averaging across all valid trials in each condition. In the Visible Task there were thus 72 ERPs in total [18 (participant) X 4 (conditions)]. How many of these ERPs were produced by averaging over a trial which was contaminated by an eye movement? Approximately 49% of ERPs were not contaminated by any eye movements at all. When ERPs were contaminated, only a very small proportion of contributing trials were affected. For the worst participant, time point and condition, the maximum proportion of trials contaminated by an eye movement in a particular direction was 8.8%. The mean value was 0.99%. Moreover, there was no hint of a positive correlation between the participants' contamination level and their ERP amplitude (Spearman's Rho Coefficient $< 0.035$, $p > 0.446$, one tailed). This suggests that ERPs in the Visible Task do not reflect unwanted eye movements.

In the Occluded Task, 68% of ERPs were totally uncontaminated. The maximum proportion of trials contaminated by a leftward or rightward eye movement was 8.82% (M = 0.21%). Again there was no relationship between contamination and ERP amplitude (Spearman's Rho Coefficient < 0.247, *p* > 0.162, one tailed). This suggests that ERPs in the Occluded Task were not caused by breaks of fixation.

### 5.3.6 Fixational eye movements

The analysis described in this section demonstrated that fixational eye movements were systematically related to stimulus parameters, replicating the fixational eye movement effects reported in Chapter 2. Moreover, fixational eye movements occurred around the time of the ERPs, suggesting the two phenomena are linked.

For this analysis, all trials where fixation was broken were excluded. Each participant's eye position data was averaged across all valid trials and then standardized against the mean value. Figure 5.12 shows changes in standardized eye position in both tasks. Beginning with the Visible Task, it can be seen that eye position shifts around the time the target passed fixation. The direction of the shift is dictated by motion direction: Eye position shifts leftwards when the target moves left and rightwards when the target moves right. This happens later in the 12°/s condition than the 20°/s condition. In the Occluded Task, patterns were similar. However, this shift began around 200 ms post occlusion, and is not so tightly related to the target reaching fixation.

Separate Direction X Time repeated measures ANOVAs were each speed and task condition separately. These ANOVAs explored time points sampled every 100 ms (See Chapter 2, section 2.3.2.2). The time points used in a particular ANOVA were chosen to capture the cross over effect between leftward and rightward motion conditions (Figure 5.12). The impressions in Figure 5.12 were confirmed by Direction X Time interactions in all analyses (*F* (1.749, 29.733) > 4.045, *p* < 0.034).

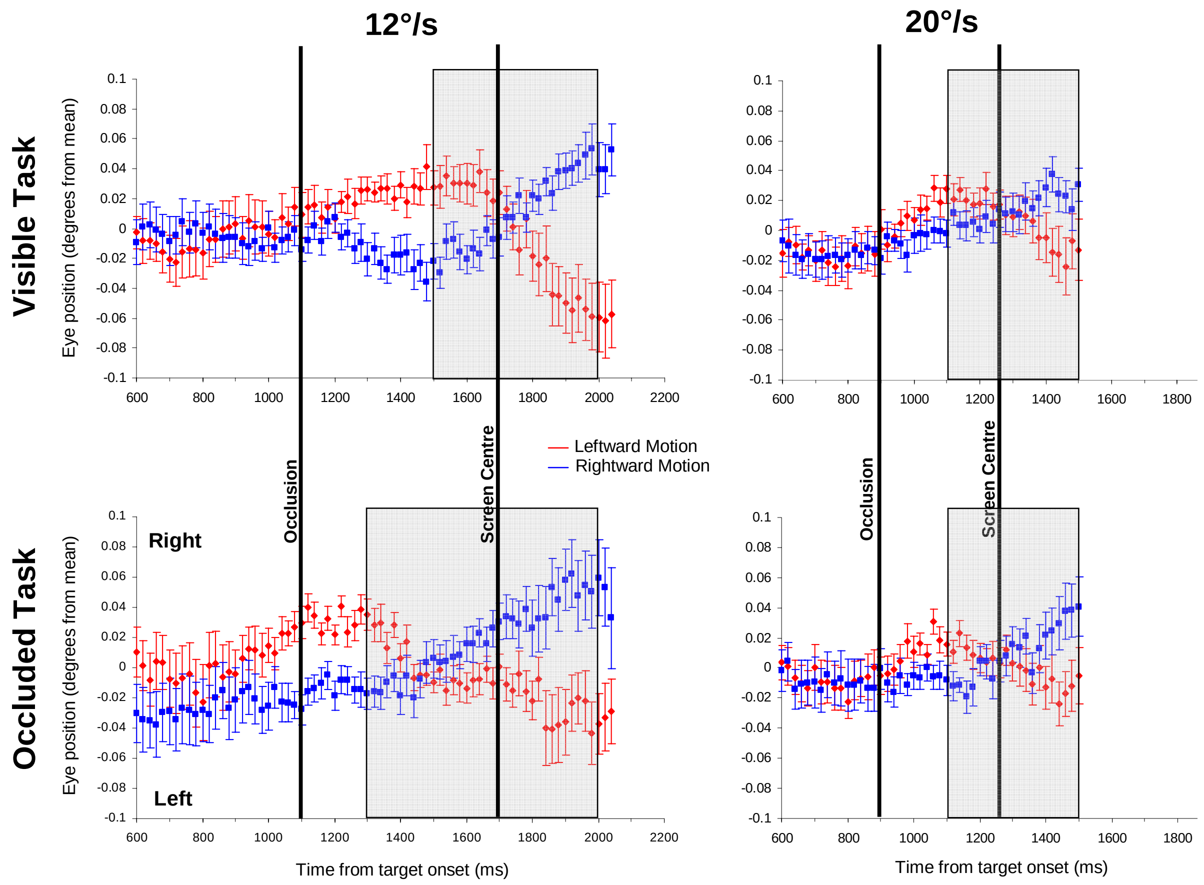


**Figure 5.12: Fixational eye movements.** Standardized eye position is shown as a function of time in the 12 and 20°/s conditions of the Visible and Occluded tasks. Grey boxes delineate the analysed period (see text). Error Bars = +/- 1 S.E.M.

## 5.4 Experiment 8 discussion

### 5.4.1 Behavioural performance

In this experiment, two tasks were completed by the same participants. In both tasks participants observed a moving dot while they fixated. In the Visible Task the target remained visible throughout, and participants attempted to detect rare velocity change oddballs. Participants were sensitive to the oddballs in every condition, implying that they were tracking the targets covertly. They were also unlikely to perceive an oddball when none was present, which is important because it suggests the ERPs recorded were not produced by misperception of non-existent oddballs. In the Occluded Task, the target travelled behind an invisible occluder, then reappeared at the correct time or 300 ms too late. Participants were far more likely to report on-time reappearance when this was the appropriate response. This suggests they were covertly tracking the occluded moving targets (DeLucia & Liddell, 1998).

There was no overall difference between leftward and rightward motion conditions in either task. However, there were some Direction X Speed interactions. In the Visible Task, this largely produced by slightly greater sensitivity to oddballs in the 12°/s leftward condition than any other condition. In the Occluded Task, the interaction was produced by a greater frequency of on-time reappearance reports in the 20°/s leftward condition. In both these interactions arose from fairly small differences and cannot be easily interpreted.

### 5.4.2 ERPs

Both tasks produced a positive potential at posterior electrode sites. This component always moved across the scalp, but the direction of the topographic shift depended on the target direction. When the target moved rightwards, the positivity shifted from the right to left hemisphere electrode sites. Conversely, when the target moved leftwards, the positivity moved leftwards. The component always reached peak amplitude in the second half of the trial. This pattern is schematized in Figure 5.13.

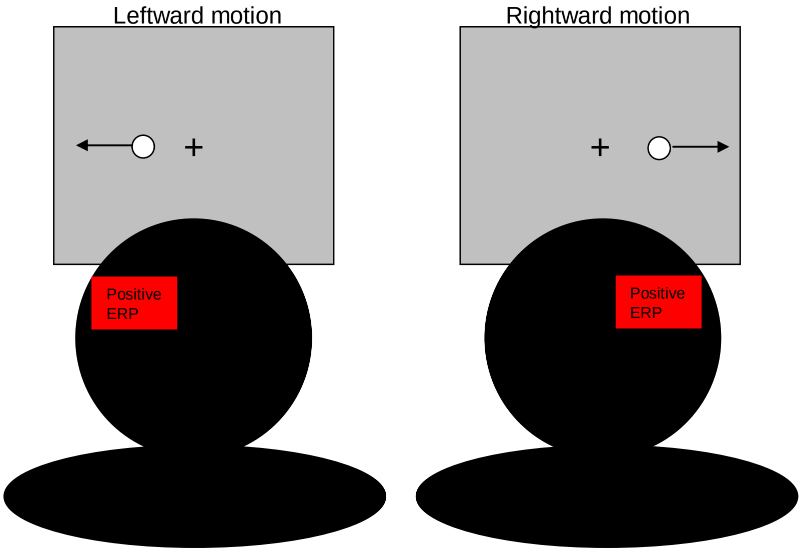


**Figure 5.13: Schematic ERP distribution in the second half of the leftward and rightward motion trials.** The drawing depicts participants looking at the leftward and rightward moving targets, and the pattern of ERPs recorded from posterior electrodes.

This is a significant extension of our earlier results, which showed right lateralized ERPs with rightward motion only (Figure 5.1). The current experiment conclusively demonstrated that these ERPs are not invariably right sided. This resembles other ERPs produced by covert shifts of visuospatial attention,  for example, the Anterior Directing Attention Negativity (ADAN) and Late Directing Attention Positivity (LDAP) are both lateralized according to the direction of covert attentive shifts (Eimer & Driver, 2001; Eimer et al., 2007). The ERPs recorded in this experiment can also be compared with another component found by Praamstra et al. (2005), who recorded a positive ERP component ipsilateral to the direction of covert attention.

Before examining task differences, it is worth considering the general pattern. It is likely that the posterior positivity was produced by cognitive processing of the moving targets. It is superficially tempting to interpret the ERP shift as a series of VEPs produced by the visual target sequentially exciting neural populations in the primary visual cortex. This cannot be true, because the ERP observed here was *ipsilateral* to visual target position and VEPs are maximal in the *contralateral* hemisphere. Instead, the locus of the posterior positivity could depend on the relative balance of activity left and right hemisphere frontoparietal networks. These networks are known to mediate visuospatial attention and were probably *bilaterally* activated in all experimental conditions (Lencer et al., 2004). However the relative excitation of each hemisphere could depend on the current orientation of visuospatial attention (McKeefry et al., 2008; Mesulam, 2002), and ERP distribution could reflect this.

The morphology of the HSP and ORD waves are compatible with this account. In the Visible Task, one would expect a pronounced hemispheric rearrangement after the target passes fixation, hence the HSP. Likewise, the ORD could be produced by a relatively sudden top down input to both hemispheres after the initial period of occlusion, (producing a centralized positivity), and then increasing activity in a one hemisphere as participants attempt to track the occluded target across the meridian (producing a lateralized positivity).

It is also possible that the initial part of the ORD reflects changes in visual cortex activation produced by the disappearance of the moving target. Indeed, it is morphologically similar to the ERP produced by motion onset (Figure 5.9).  However, it is unlikely that the continued topographic shift of the posterior positivity would be produced by a visual offset alone, and may thus reflect covert tracking of the occluded target (See section 7.2 in Chapter 7 for further discussion).

The ORD can be further understood in light of earlier work by Lencer et al. (2004). As discussed in Chapter 2, these authors recorded the BOLD response while participants tracked visible and occluded motion. In both tasks, common activity was found throughout the bilateral frontoparietal network. Moreover, there were additional activations of the DLPFC during occlusion. The DLPFC is known to play a role in working memory (Levy & Goldman-Rakic, 2000) and velocity memory (Burke & Barnes, 2008). This indicates that attentive tracking is supplemented by velocity memory during occlusion. The current experiment suggests that the switch to memory-guided tracking begins around 200 ms post occlusion.

. In summary, this ERP data, like that of Makin et al. (2009), supports the model of motion extrapolation shown in Chapter 2. According to this model, pre-motor signals drive visuospatial attention to particular spatial locations, even during fixation (cf Rizzolatti et al., 1994), and the same pre-motor systems control visible and occluded target tracking. This hypothesis was supported by the fact that ERP topography was similar in both tasks. Furthermore, according to the model, memory guided tracking takes over from visually guided tracking after the initial period of occlusion. This hypothesis was supported by the appearance of the ORD at around 200 ms post occlusion.

Although the ERPs were comparable with those recorded by Makin et al. (2009), there were some minor differences. For example, lateralization was less pronounced in this experiment. This could be because of differences with the manual response paradigm. In our earlier study, participants sometimes pressed a button during the trial itself, and they always used their right hand. In the current experiment, participants made a button press response *after* each trial, and response hand was unknown during the visual presentation. This design precluded asymmetrical motor preparation during the trials (Murray et al., 2004). ERPs could have been more bilateral in the current experiment because motor response confounds were eliminated.

There is second explanation for the decreased lateralization. It could be that each trial excited representations of previously seen trials (Chapter 3). In our earlier EEG experiment, all trials moved rightwards, so participants would only remember rightward motion. Conversely, in the current experiment, representation of both leftward and rightward motion would be re-activated. The fact that ORD was less lateralized than the HSD fits this hypothesis: It could be that stored velocity representations played a greater role in the Occluded Task, so the reactivation of older representations was enhanced.

### 5.4.3 Eye movements

In this experiment an eye tracker was used to monitor fixation. This allowed confirmation that the ERPs were not produced by large eye movements. The number of trials where participants moved their eyes during the ERPs was minimal, and there was no correlation between the number of times participants broke fixation and ERP amplitude. This increases confidence that the ERPs recorded by Makin et al. (2009) were also free from unwanted eye movements.

In Experiment 2 (Chapter 2), it was found that grand average eye position was influenced by target motion, even during fixation. In the current experiment, eye position moved leftwards when the target moved leftwards and vice versa. It could be that this fixational eye movements were produced by *dynamic conflict* between fixation commands and the SPEM control system, which was engaging with the moving targets (cf Pastukhov & Braun, 2010). The fact that comparable effects were found during the visible and occluded tracking implies similar covert oculomotor activity was involved in both cases.

Moreover, comparison of fixational eye movements and ERPs suggested that both were produced by the same underlying brain activity: In the Visible Task, the most important shift in mean eye position was time locked to the point when the target reached screen centre, just like the HSP. In the Occluded Tracking Task, the shift in mean eye position occurred around 200 ms after occlusion onset, irrespective of target speed. This is similar to the ORD. These similarities suggest that ERPs and fixational eye movements may both index common neurocognitive events. It is possible that they are both measures of covert activity in the eye movement control system.

Another possibility is that fixational eye movements could have caused the ERPs directly. Dimigen et al. (2009) found that small eye movements, known as microsaccades, produce cortically generated, positive, ERPs ipsilateral to the direction of the eye movement. Microsaccades aimed toward the moving targets would produce an ERP similar to HSP and ORD. It is impossible to ascertain the role of microsaccades in this experiment directly, as the eye tracker lacked the necessary resolution. However, if fixational eye movements caused the ERPs, then participants who show a clear shift in mean eye position would have higher ERPs. In order to explore this, the linear relationship between mean eye position and time was quantified in all participants. This size of participant's fixational eye movement effect was compared with the amplitude of their HSP and ORD waveforms. There was no significant positive correlation between the magnitude of the fixational eye movement effect and ERP amplitude in any condition (Spearman's Rho Coefficient, $< 0.35$, $p > 0.084$, one tailed). This suggests that the ERPs were not actually caused by fixational eye movements. Instead, ERPs and fixational eye movements could both result from covert tracking.

### 5.4.4 Conclusions

In summary, this experiment indicates that similar neural regions mediate visible and occluded target tracking, but that occluded target tracking may be guided by velocity memory alone after ~200 ms. This work also expands on the findings of Makin et al. (2009) by demonstrating that lateralized ERPs are dependent on the direction of motion, and cannot be attributed to motor preparation or large eye movements. Finally, small, fixational eye movements and ERPs were both related to stimulus parameters in a comparable way. This is exactly what would be expected if the ERPs reflect covert activity of the oculomotor control system. In the next Chapter, this EEG data is analysed in the frequency domain to assess the role of 8-12 Hz oscillations in visible and occluded tracking.

# Chapter 6

# Changes in upper alpha ERD and ERS during motion extrapolation

## 6.1 Introduction

As described in the introduction, the brain is comprised of many discrete populations of specialized neurons, sensitive to particular stimulus dimensions (e.g. velocity). These populations rhythmically oscillate between periods of high and low excitability. Task relevant populations may oscillate at higher frequencies, in the *beta* (15 – 25 Hz) and *gamma* (30 to 100 Hz) ranges (Fries, 2005). Populations not involved in a task may oscillate at lower *alpha* frequencies (6 to 14 Hz, Pfurtscheller & Lopes da Silva, 1999). In this chapter the EEG data reported in Chapter 5 are reanalysed in the frequency domain. Rhythmic oscillations in scalp recorded potentials were measured. These scalp oscillations are instructive because they are thought to be a reflection of rhythmic brain activity.

In this work, *upper alpha* oscillations were investigated. The upper alpha frequency band is not defined consistently, and peak frequency can vary between individuals. Here activity in the 8-12 Hz range was prominent, so upper alpha is defined as such. This encompasses most definitions of upper alpha (Klimesch et al., 2007).

There have been numerous investigations into the functional role of upper alpha oscillations (for review see Klimesch et al., 2007). It is thought that *Event Related Synchronization* (ERS) in the upper alpha band reflects top-down inhibition of cortical networks. Conversely, *Event Related Desynchronization* (ERD) reflects cortical activation. During a cognitive task, ERD is usually recorded in task-relevant networks while ERS is recorded in task-irrelevant networks. For example, preparation of a motor response produces ERD in central electrodes contralateral to the active limb and ERS in ipsilateral central electrode sites (Pfurtscheller & Neuper, 1997). This *centre-excitation-surround–inhibition* architecture amplifies important processes and suppresses interference. It is also thought that maintenance of information in working memory produces ERS. The topographic distribution of this ERS is linked to the contents of working memory and hemifield of presentation (Jokisch & Jensen, 2007), while amplitude may be a function of memory load (Grimault et al., 2009). It is now generally agreed that ERS and ERD in the upper alpha frequency bands are important mechanisms of cognitive control (Jensen et al., 2007; Pfurtscheller & Lopes da Silva, 1999).

This Chapter describes patterns of 8-12 Hz ERD and ERS recorded during Experiment 8 (see Chapter 5). In the Visible Task, the moving target presumably excited visual processing areas in the occipital lobes. It is therefore likely that ~10Hz ERD will be evident in posterior electrode clusters. Given its visual origins, this component may be influenced by the location of the target as it moved across hemifields, and it may become maximal around the time the target reached the fovea. Conversely, ERS could necessary maintaining velocity representations when the target becomes occluded. It was therefore predicted that ~10 Hz power in posterior electrodes would be relatively higher during occlusion than during equivalent periods in the Visible Task.

## 6.2 Analysis

The raw EEG data was identical to that used to analyse ERPs in the previous chapter. The same validation procedures apply, and the same trials were excluded. Frequency power from 6 to 14 Hz (in 0.5 Hz increments) was calculated relative to a 100 ms pre-stimulus baseline. Oscillations are often *time locked* to a stimulus, but not *phase locked*, and may thus be removed by averaging across trials. For this reason, oscillations do not appear in ERP plots in Chapter 5. For this analysis, it was therefore necessary to compute the *power* on a trial by trial basis before averaging. On each trial, power at a chosen frequency was obtained by multiplying the raw data by an idealized *wavelet* (a waveform of the chosen frequency). The more the raw data around the time point resembles the wavelet, the higher the power at that time point. The wavelet was then shifted to the next time point, until it reached the end of the epoch. This operation produced a vector specifying power as a function of time. Finally, these vectors are averaged within and then across participants. Because power was measured in microvolts, the measure depended to some extent on the characteristics of chosen wavelet (Roach & Mathalon, 2008).

As with ERPs, power had scalp topography: that is, power was higher in some electrodes than others. Sequential topographies were produced to get an impression of which frequency bands show systematic changes and the scalp distribution of these changes. In light of this, statistical analysis focused 8-12 Hz power in left and right posterior electrode clusters (O2, PO8, P2, P4, P6 and P8 and left sided homologues, see Chapter 5 Figure 5.2).

## 6.3 Results

### 6.3.1 Visible Task

Sequences of topographic maps from the leftward, rightward, 12 and 20°/s conditions of the Visible Task are shown in Figure 6.1. Topographic maps represent grand average 8-12 Hz activity at each electrode. As with all analyses and figures, activity is averaged over a 40 ms window around the stated point and is measured as a deviation from a 100 ms pre-stimulus baseline.

There are several important patterns here. Beginning with the 12°/s trials, there was an *asymmetry* between the leftward and rightward motion conditions. During the first half of the leftward trials, there was contralateral ERD at posterior electrodes, and ipsilateral ERS at posterior/central electrodes. During first half of rightward trials, there was contralateral ERD, *but no ipsilateral ERS* (Figure 6.8). After the target passed fixation, ERD became bilateral and more pronounced in both direction conditions. In the 20°/s trials, the same pattern was found. However, the sequence of events happened more quickly in the 20°/s condition. This suggests that the pattern was a reflection of target location.

Figure 6.2 shows time-frequency spectrograms from the left and right posterior electrode clusters. In all conditions, there was clear ERD in the 8-12 Hz range after the target passed fixation. This occurred later in the 12°/s than the 20°/s condition. In the right cluster-leftward motion plots, ERS can be seen during the first part of the trial. No equivalent is apparent in other cases. Finally, it can be seen that, in the 20°/s conditions, low frequencies were amplified after the trial was over. This effect also occurred in the 12°/s conditions, but cannot be seen here due to limits of the X axis.

These patterns were confirmed statistically. Separate repeated measures ANOVAs (Speed X Time) were used to explore mean 8-12 Hz power for each cluster and both direction conditions. As with the ERP analysis in Chapter 5, data at 100 ms intervals from motion onset to the end of the shortest trial was used.

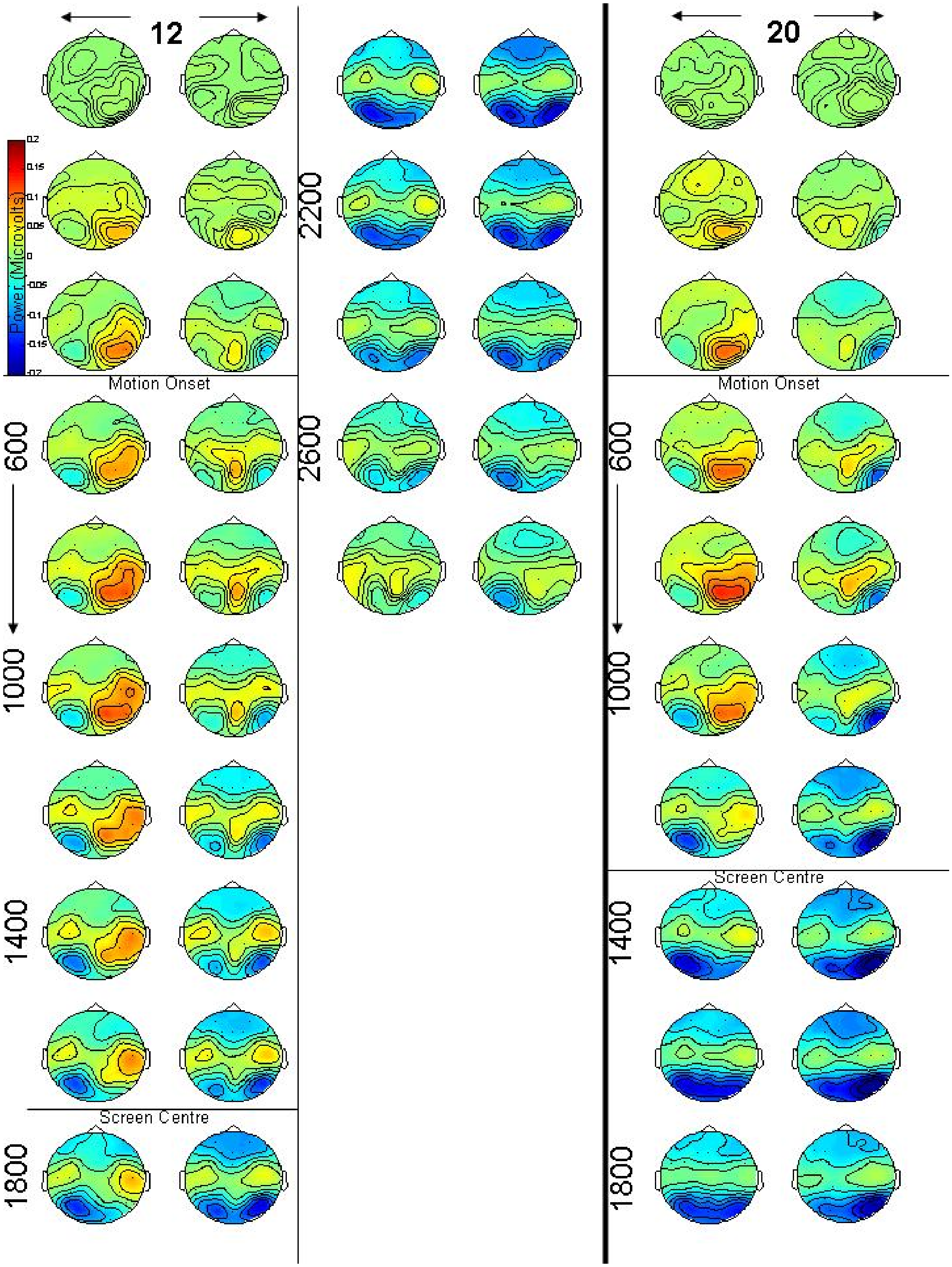


**Figure 6.1: Grand-average topographic maps of 8-12 Hz power in the Visible Task**. The layout of the data matches Figure 5.4 from the previous chapter (again the 12°/s condition continues in the middle column). Blue indicates ERD (putative neural excitation), while red indicates ERS (putative neural inhibition).

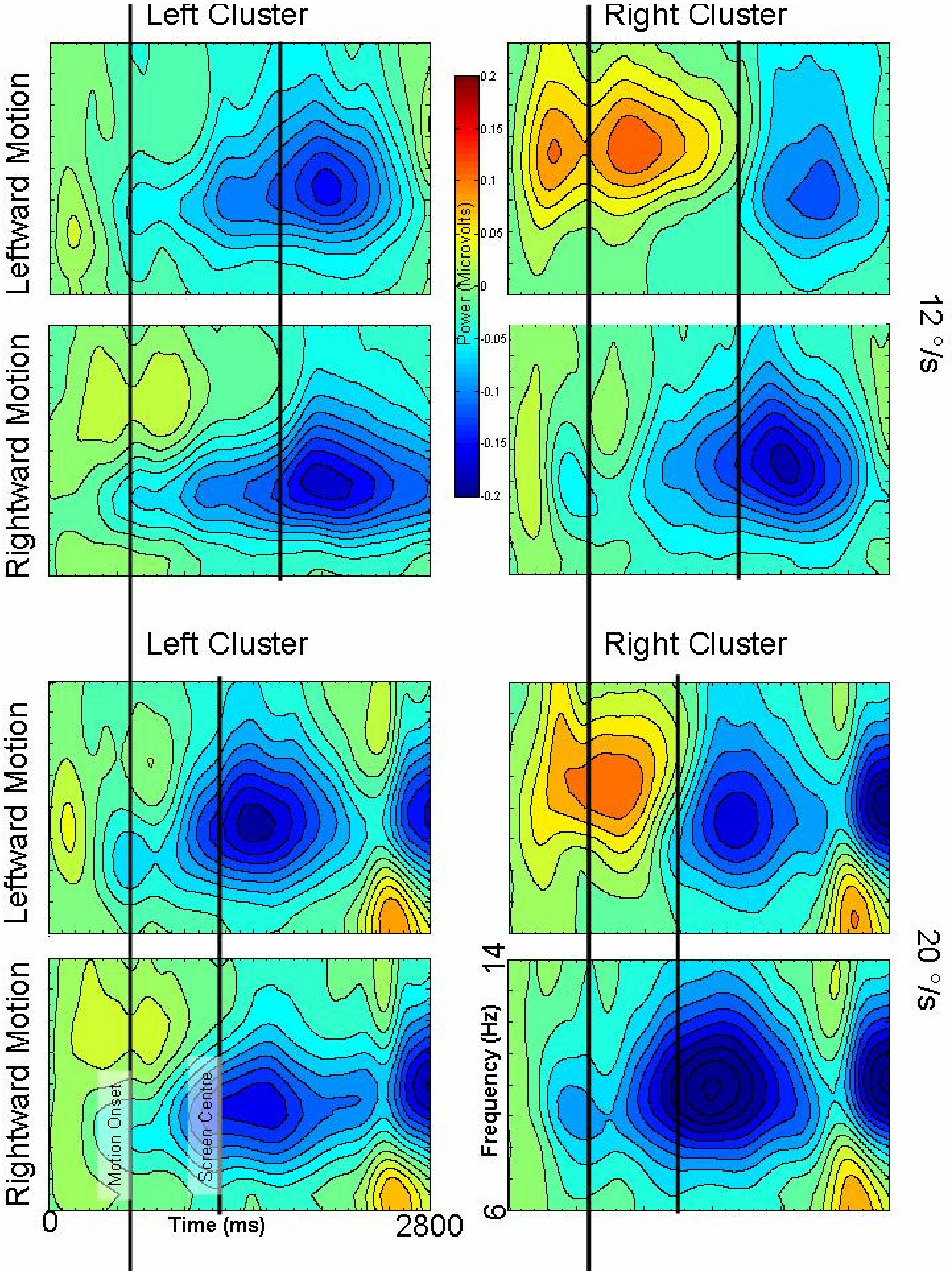


**Figure 6.2**: **Grand average time-frequency plots from the Visible Task**. Blank lines indicate motion onset and the point where the target reaches screen centre. Blue indicates ERD (putative neural excitation), while red indicates ERS (putative neural inhibition).

Nearly every variable broke the normality assumption according to the Kolmogorov-Smirnov test ($p < 0.05$). One reason for this was that three atypical participants showed consistent above-baseline 8-12 Hz activity throughout. This differed from the ERP analysis in Chapter 5, where nearly all variables were normally distributed. Although ANOVA is robust to violation of the normality assumption (Glass et al., 1972), non-parametric tests were used to corroborate significant effects and follow up interactions (Friedman's ANOVA and Wilcoxon Signed Ranks Tests).

In the *left cluster, leftward motion analysis* (Figure 6.3A), power did not differ between the 12 and 20°/s conditions ($F$, $(1, 17) = 2.613$, $p = 0.124$). However, power changed with Time ($F\ (1.557, 26.469) = 11.931$, $p < 0.001$). Non-parametric Freidman's ANOVA confirmed the effect of Time in both speed conditions ($p < 0.001$). The Time by Speed interaction was also significant ($F\ (1.928, 32.781) = 6.184$, $p = 0.006$). This was because power was greater in the 12°/s condition at 500, 700, 800 900 and 1000 ms post motion onset ($p < 0.036$, Wilcoxon Signed Ranks Tests).

In the *left cluster, rightward motion* analysis (Figure 6.3B), there was again no overall difference between speeds ($F\ (1, 17) = 1.189$, $p = 0.291$), a main effect of Time ($F\ (1.241, 21.089) = 6.212$, $p = 0.016$), and a Speed X Time interaction ($F\ (2.463, 41.872) = 4.379$, $p = 0.013$). Non-parametric tests indicated that the effect of Time was significant in both speed conditions ($p <0.001$). The interaction was explained by greater power in the 12°/s condition from 400 to 1000 ms post motion onset ($p < 0.049$).

In the *right cluster, leftward motion analysis* (Figure 6.3C), both main effects and the interaction were significant ($F\ (1, 17) > 5.950$, $p < 0.027$). The main effects were corroborated with non-parametric tests ($p < 0.019$). The interaction was explained by significantly greater power in the 12°/s at time points from 600 to 1300 ms post motion onset ($p < 0.044$).

Finally, in the *right cluster, rightward motion* analysis (Figure 6.3D), both main effects ($F\ (1, 17) > 9.527$, $p < 0.008$) and the interaction ($F\ (2.493, 42.386) = 5.850$, $p = 0.003$) were significant. The main effects were replicated with non-parametric analysis ($p < 0.005$). Power was greater in the in the 12°/s condition from 0 to 1100 ms post motion onset ($p < 0.029$).

Another approach was also used to establish windows of significant ERD and ERS. Non-parametric chi square tests were used to assess whether more than 50% of participants were above or below baseline power at each time point ($p < 0.05$). It was found that this criterion was reached at earlier time point in the 20°/s trials (Figure 6.3). In the Right Cluster- Leftward Motion analysis, there was significant ERS early in the trial (Figure 6.3C).

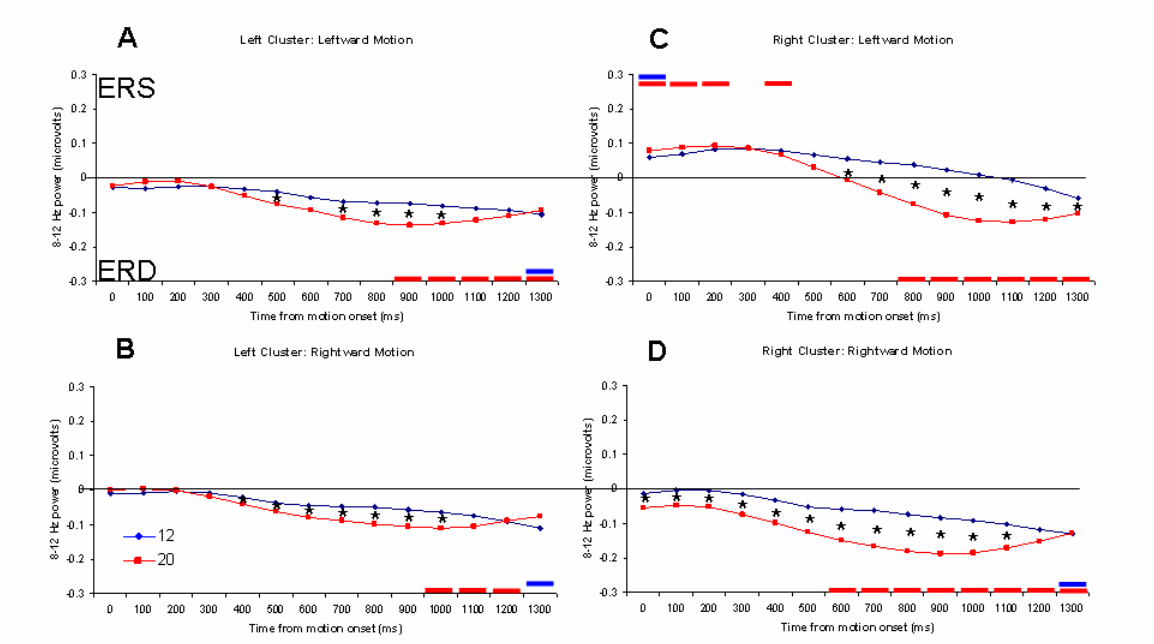


**Figure 6.3: Results of the Visible Task.** Each plot shows a particular combination of electrode cluster and motion direction. Data in each plot is shown as a function of time and speed. * = significant difference between 12 and 20°/s conditions. Thick Blue horizontal bars indicate intervals with significant deviation from baseline in the 12°/s condition. Thick Red bars show the same information for the 20°/s condition (Chi squared test, $p < 0.05$).

### 6.3.2 Occluded Task

Sequences of Topographic maps from the leftward, rightward, 12 and 20°/s conditions are shown in Figure 6.4. In 12°/s condition the patterns were similar to the Visible Task until the onset of occlusion. When the target travels leftward, there was contralateral ERD and ipsilateral ERS at posterior electrode clusters. When the target travels rightwards, there was contralateral ERD but no ipsilateral ERS. After Occlusion onset, this topographic distribution of alpha activity was relatively stable. The ipsilateral ERS in the leftward motion condition decreased, but remained present throughout occlusion. This is different to the Visible Task. During the same period of the Visible Task, ERD amplitude increased and became more bilateral, and ERS disappeared.

In the 20°/s condition patterns were similar to the 12°/s condition. However, the ipsilateral ERS in the leftward motion trials reduced earlier. This was presumably because occlusion began earlier when the target moved faster. The distribution of upper alpha activity was stable during the occlusion period. This is similar to the 12°/s condition, but differs from the Visible Task, where ERD became bilateral and ERS disappeared over these time points.

The same patterns can be seen in the time-frequency plots in Figure 6.5. These were produced from the same left and right posterior electrode clusters as in the Visible Task. Compared to the Visible Task, there was a conspicuous absence of ERD in all conditions. The ipsilateral ERS in leftward motion conditions were still evident. However, the patterns present at the beginning of occlusion did not change much throughout the minimum occlusion duration (although ERS appears to reduce in amplitude during occlusion, and then possibly increase afterwards).

These patterns were confirmed statistically. Analysis focused on the 8-12 Hz activity during the minimum occlusion period (0 to 500 ms post occlusion in 100 ms increments). As with the Visible Task, power was analysed as a function of Time and Speed with separate repeated measures ANOVAs for each cluster and direction separately. Again most variables violated the normality assumption according to the Kolmogorov-Smirnov test, so non-parametric tests were used to corroborate important findings. Chi square tests were again used to assess intervals of significant ERD and ERS, however there were no significant differences from baseline at any analysed interval ($p > 0.058$).

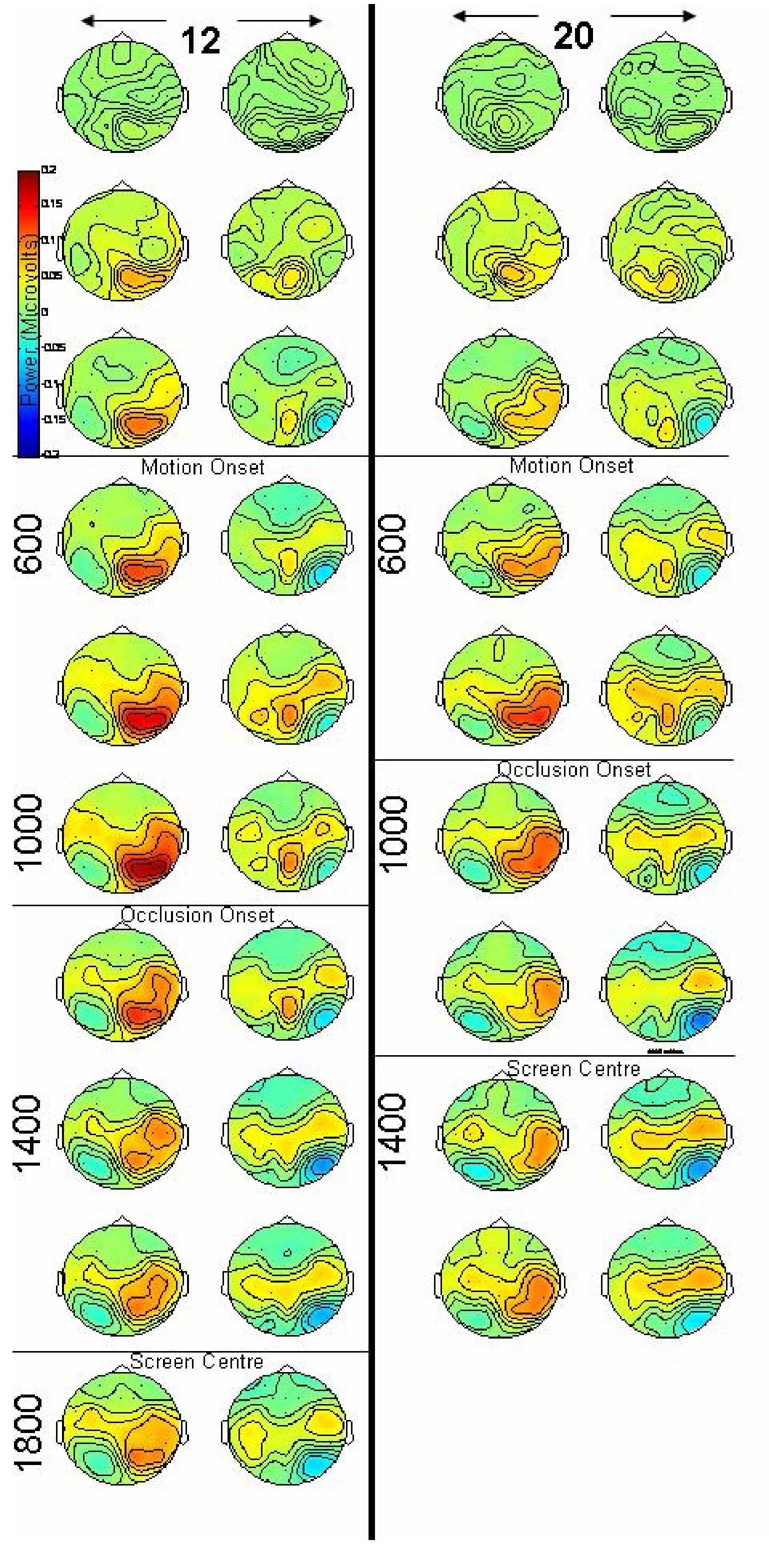


**Figure 6.4: Grand-average topographic maps of 8-12 Hz power in the Occluded Task**. Layout matches Figure 5.8. Blue indicates ERD (putative neural excitation), while red indicates ERS (putative neural inhibition).

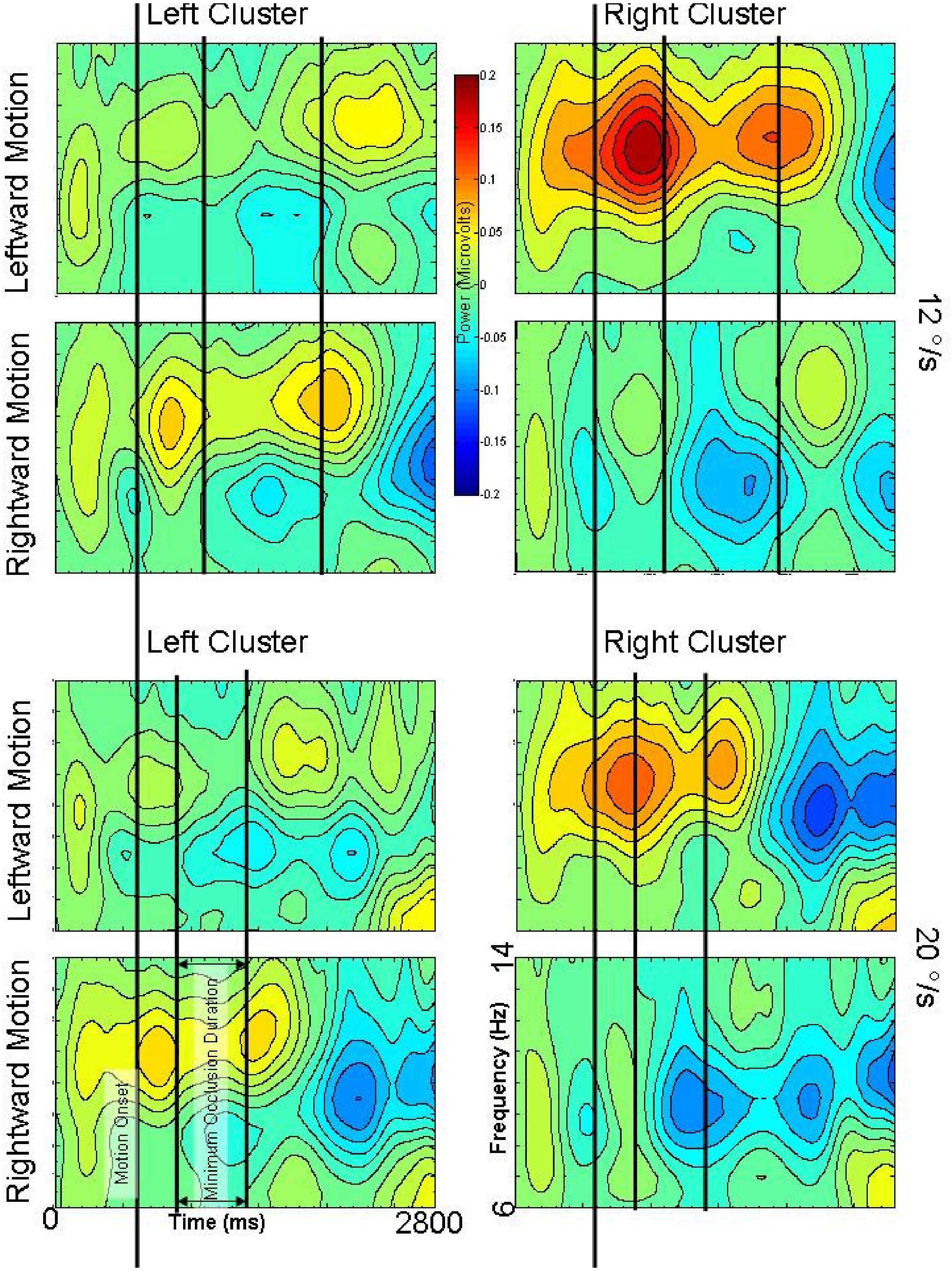


**Figure 6.5**: **Grand average time-frequency plots from the Occluded Task**. Black lines indicate motion onset, the start and end of the minimum occlusion duration. Blue indicates ERD (putative neural excitation), while red indicates ERS (putative neural inhibition).

In the *Left Cluster, Left Motion analysis* (Figure 6.6A), there was no power difference between 12 and 20°/s conditions ($F$ (1, 17) < 1, NS). There was a main effect of Time ($F$ (1.985, 33.741) = 5.978, $p$ = 0.006). This was confirmed with non-parametric Friedman's ANOVA ($p$ < 0.034). In the *Left Cluster, Right Motion* Analysis there were no effects ($F$ (1.368, 23.253) < 2.080, $p$ > 0.157, Figure 6.6B).

In the *Right Cluster-Left Motion analysis* (Figure 6.6C), there was no main effect of Speed ($F$ (1, 17) < 1, N.S). However there was a main effect of Time ($F$ (1.248, 21.221) = 10.840, $p$ = 0.002). This was corroborated with Freidman's ANOVAs ($p$ < 0.001). There was no Speed X Time interaction ($F$ (2.175, 36.968) < 1, N.S).

In the *Right Cluster, Right Motion Analysis* (Figure 6.6D), results were similar. There was an effect of Time ($F$ (1.686, 28.663) = 13.494, $p$ < 0.001), which was evident with non-parametric ANOVAs ($p$ < 0.001). There was no effect of Speed or interaction ($F$ (1.455, 24.730) < 1, N.S). Note that Figure 6.6 is plotted on the same scale as Figure 6.3 to facilitate comparison between Visible Task and Occluded Task.

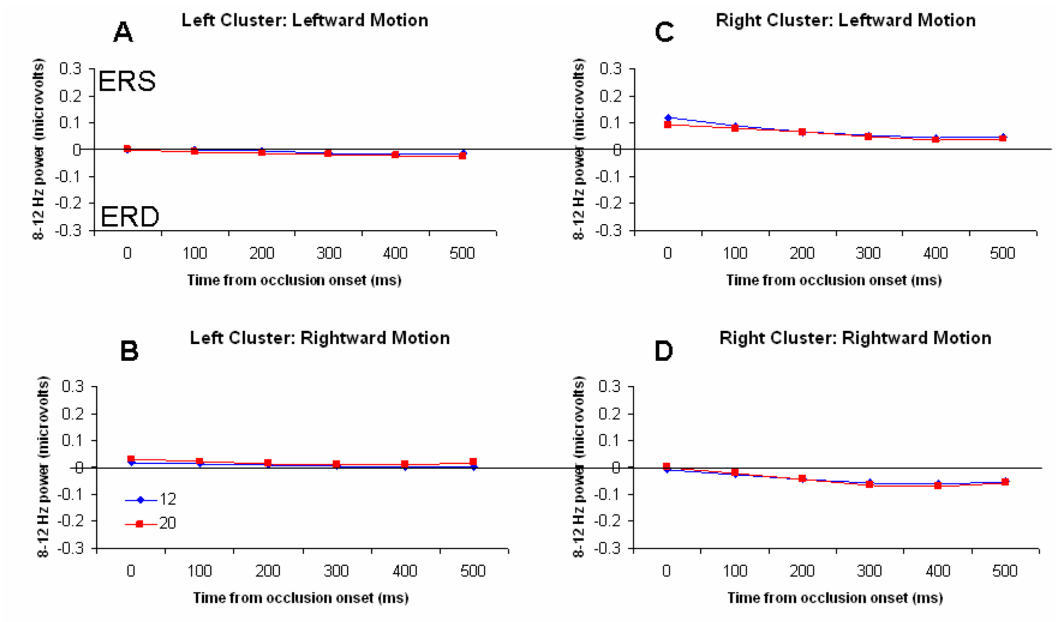


**Figure 6.6: Results of the Occluded Task**. Alpha power is shown as a function of time and speed for every combination of electrode cluster and motion conditions.

### 6.3.3 Visible and Occluded Tasks compared

The above analysis suggests that the patterns of upper alpha were different in the Visible Task and Occluded Task, but only after occlusion onset. In order to establish that there were no differences between the tasks prior to occlusion onset, the period from 100 ms post target onset to the beginning of occlusion was analysed. Again samples were taken at 100 ms intervals. This comprised 10 and 8 data points in the 12 and 20°/s conditions respectively. Separate Task X Time repeated measures ANOVAs were applied to each cluster, speed and direction condition. There were no effects in any analysis ($F$ (1, 17) < 3.993, $p > 0.062$). Non-parametric tests confirmed that there were no overall amplitude differences between the Visible Task and Occluded Tasks ($p > 0.057$). This is to be expected, given that the Visible Task and Occluded Task presentations were identical prior to occlusion onset.

In the Visible Task, the posterior ERD became bilateral around the time that the target passed fixation. Conversely, in the Occluded Task, this effect was not pronounced, so upper alpha power was relatively higher during occlusion. Here these impressions are confirmed statistically. Since 8-12 Hz power did not always change as a function of time during occlusion, time was not included as a factor. Instead, 8-12 Hz power was measured in the left and right clusters at the final 100 ms interval of the minimum occlusion duration. This was 800 ms post occlusion onset in then 12°/s trials and 500 ms post occlusion in the 20°/s trials. Equivalent data was obtained from the Visible Task.

12 and 20°/s conditions were analysed separately with 3 factor repeated measures ANOVAs [Task (Visible, Occluded) x Electrode cluster, (left, right) X Motion direction (leftward, rightward]. It was necessary to analyse speed conditions separately because data was taken from different time points in the 12 and 20°/s conditions. Again, all variables violated the normality assumption, so non-parametric post hoc tests were used. There was a main effect of task in both 12 and 20°/s conditions ($F$ (1, 17) > 7.588, $p < 0.015$), because power was significantly greater in the Occluded Task in all sub conditions ($p < 0.021$, Figure 6.7). Other effects were also present, but these confirmed the patterns described above, so are not discussed here.

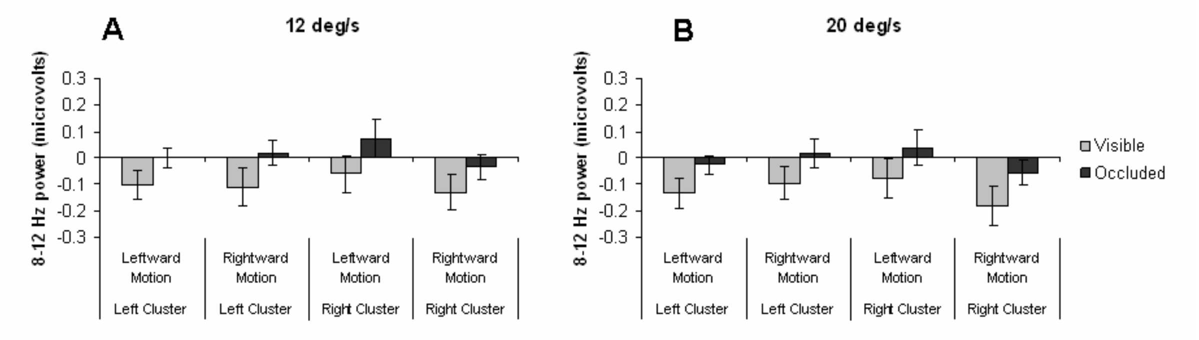


**Figure 6.7: Visible and Occluded Tasks compared.** Graphs depict mean 8-12 Hz power at the end of the minimum occlusion period of the Occluded Task, or equivalent point from the Visible Task. **A:** Data in the 12°/s condition. **B:** Data from the 20°/s condition. Power is measured as a deviation from pre-stimulus baseline. Error bars = +/- 1 S.E.M.

## 6.4 Discussion

The results clearly demonstrate that changes in ~10 Hz brain activity are associated with visible and occluded target tracking. The patterns found here are consistent with well-established models of the frontoparietal attentive network, and with ideas about the functional significance ERD and ERS in the ~10 Hz frequency band. In this section, patterns in the data will be described and interpreted.

### 6.4.1 Visible Task

It is thought that the brain mechanisms which guide visuospatial attention to external locations are asymmetrical. The right parietal lobe is involved in directing attention to both left and right areas of space, while the left parietal lobe is involved with directing attention to the right hemifield only (Mesulam, 1999). Evidence for this comes from neuropsychological studies investigating patients with hemispatial neglect, which more often follows right hemisphere lesions (Heilman et al., 2002), and from neuroimaging studies, which have shown a propensity of right hemisphere activations during visuospatial manipulation tasks (J. Barnes et al., 2000).

The distribution of alpha activity in the Visible Task was also asymmetrical. Consider the first period of target motion, which is schematized in Figure 6.8. When the target travelled leftwards, attention was directed to the *right* visual field during this early part of the trial. This early period was characterised by contralateral (left sided) ERD and ipsilateral (right sided) ERS at posterior electrodes. When the target travelled rightwards, attention was directed to the *left* visual field during the first part of the trial. This resulted in contralateral (right sided) ERD, but not ipsilateral (left sided) ERS. As mentioned in the introduction, upper alpha ERD is thought to reflect cortical excitation, while ERS is thought to reflect top-down inhibition. It thus seems that when attention is focused on the right visual field, the relevant contralateral visual networks are excited, and the irrelevant ipsilateral visual networks are inhibited. However, when attention is aimed at left visual field, the contralateral visual system is excited, but the ipsilateral visual system is not inhibited. This finding is consistent with the idea that more neural mechanisms are involved in directing attention to the right hemifield than the left hemifield (Mesulam, 2002).

When the target approached and crossed fixation, bilateral ERD was present in posterior clusters, and bilateral ERS was present in central clusters. This is the classic alpha response to centrally presented visual stimuli (Klimesch et al., 2007). This response probably reflects additional excitation of bilateral visual cortices as the target crossed the fovea. After fixation, bilateral ERD was attenuated.

It should be noted that the time course of posterior ERD in the Visible Task is very similar to the Hemifield Switch Positivity (HSP) described in the previous chapter. The HSP was also linked to the time when the target passed fixation, and thus peaked earlier in the 20°/s trials. Moreover, fixational eye movements were also related to stimulus parameters in a comparable way. These similarities suggest that all three metrics reflect common neurocognitive processes, although the exact relationship between them is, as yet, unknown.

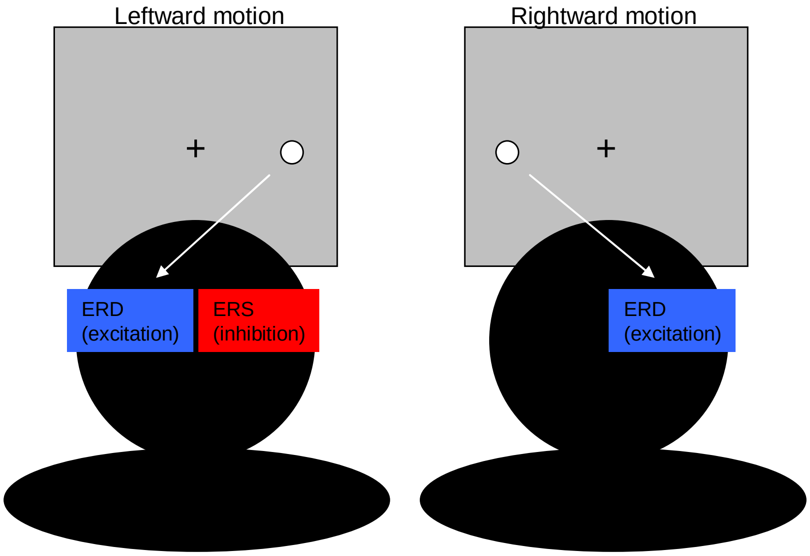


**Figure 6.8: Schematic of the events in the first half of leftward and rightward motion trials**. The drawing depicts participants looking at left and rightward trials and the pattern of ERD and ERS recorded from posterior electrodes.

### 6.4.2 Occluded Task

During the period before occlusion, upper alpha activity in the Occluded Task did not differ statistically from upper alpha activity in the Visible Task. This is unsurprising, given that presentations were identical until occlusion. As with the early portion of the Visible Task, attention to the right visual field was associated with contralateral excitation and ipsilateral inhibition. Attention to the left visual field was associated with contralateral excitation only (Figure 6.8). The fact that this pattern occurred in both tasks confirms its reliability.

The distribution of alpha activity at the onset of occlusion persisted throughout the occlusion interval (although in some conditions, power was reduced slightly). Conversely, alpha distributions evolved substantially over the same period in the Visible Task.

The large bilateral ERD in Visible Task was not apparent in the Occluded Task. In other words, compared to the Visible Task, there was an increase in 8-12 Hz power during occlusion. This could reflect effortful maintenance of target representations. Indeed in other contexts, ERS has been associated with working memory maintenance (Jokisch & Jensen, 2007), and it has been suggested that ERS could inhibit new sensory inputs that would otherwise disrupt the fragile contents of working memory (Grimault et al., 2009). The relative ERS during occlusion could be a manifestation of this phenomenon.

It is thought that ERPs may reflect phase resetting of the alpha rhythm. For example, sensory ERPs generated by the primary visual cortex, such as P1, could reflect stimulus driven changes in the phase of upper alpha oscillations (e.g. Hanslmayr et al., 2005). If there is a functional change in alpha during occlusion, we would expect an ERP time-locked to occlusion onset. The Occlusion Related Deflection (ORD) reported in Chapter 5 fits this category. The ORD could be the manifestation of a change in alpha activity at around 180 ms post occlusion. The timing of alpha phase reset/ORD is consistent with the putative onset of memory guided tracking (Makin et al., 2009).

There is an alternative explanation for the increase in alpha during occlusion. It could be that the absence of visual stimulation resulted in a return to baseline 'resting' brain activity. However, there are four reasons to doubt this. First, all participants could perform the task, so must have been tracking the targets covertly (DeLucia & Liddell, 1998). Second, there was no increase in the lower frequency alpha bands (6-8 Hz), which are associated with rest, during occlusion. An increase in low frequency power *did* happen after the end of the trial, but not during occlusion. Third there was an ERP time locked to occlusion onset, implying a top-down resetting of alpha phase. Finally, the distribution of 8-12 Hz oscillations during occlusion resembled that found immediately before occlusion, and not that found in the inter-trial interval. It thus seems plausible that alpha activity during occlusion reflects active processing of occluded motion.

### 6.4.3 Summary

In summary, these results show that upper alpha oscillations are intimately involved with covert tracking of visible and occluded targets. During visible target tracking, 8-12 Hz oscillations in occipital electrodes were significantly reduced around the time that the target crossed the fovea. This could reflect bottom-up excitation of the visual cortex. During occluded target tracking, however, there was no comparable desynchronization. Alpha activity during occlusion could reflect inhibition of sensory input in order to maintain an internal representation of target motion. Finally, the patterns of ERD and ERS were related to stimulus parameters in the same way as the ERPs and fixational eye movements reported in Chapter 5. The interplay between these phenomena is unknown. However, it is probable they were all produced by the brain mechanisms which control covert tracking, and thus they all give insights into the nature of these mechanisms.

# Chapter 7

# General Discussion

## 7.1 Introduction

This thesis attempted to characterize the human faculty for storing velocity information. When characterizing *any* putative information processing module, there are at least three pitfalls to be avoided:

1) Exploring the module with an impoverished subset of experimental paradigms and thereby underemphasizing the heterogeneity of its applications.
2) Rigidly categorizing the module as 'sensory', 'cognitive' or 'motor'.
3) Associating the module with a single anatomical location in the brain.

These approaches can be useful within certain, limited contexts, but can also impede a broader understanding. In Chapter 1 an integrated account of velocity memory was presented, and these pitfalls were deliberately avoided. It was argued that velocity memory can be described meaningfully as sensory, motor *and* cognitive. Furthermore, it was suggested that velocity memory does not have a single anatomical locus, and that it is employed in many tasks which are rarely considered together.

The current model of velocity memory is as follows: The core neural components are the MT/MST complex and the FEFs (Figure 7.1). The MT/MST complex codes the velocity of moving visual targets, and comprises the *sensory side* of the network. The smooth pursuit regions of the FEFs code the velocity of SPEMs, and are thus on the *motor side* of the network (Thier & Ilg, 2005). These sensory and motor velocity codes are tightly linked, and it is not clear where the dividing line between 'sensory' and 'motor' should be drawn (cf Dennett, 1991). To blur this distinction further, area MST receives feed-forward 'motor' information about eye movements via reafferent and efference copy loops (Ilg, 2008). During smooth pursuit, it is likely that MT/MST and FEFs are functionally coupled through synchronized, high frequency oscillations in the beta or gamma bands (cf Fries, 2005). On a neural level, velocity memory could reflect continued synchronization in this network after stimulus offset. Finally, it is likely velocity information is stored more accurately if this is an explicit task demand (e.g. Pola & Wyatt, 1997). This effort may be a function of the DLPFC, which could facilitate ongoing oscillatory activity in the distributed velocity memory system when necessary (cf Levy & Goldman-Rakic, 2000; Müller & Knight, 2006).

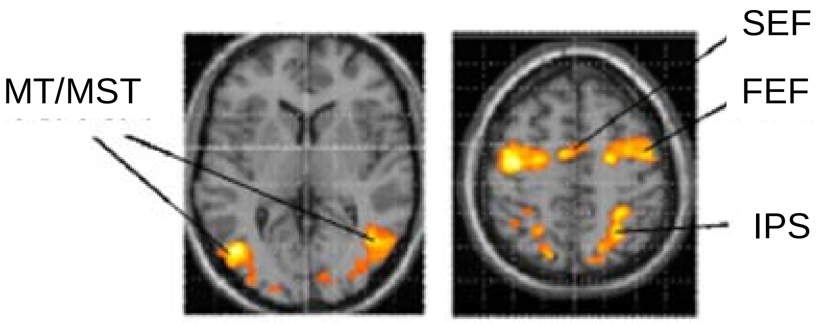


**Figure 7.1**: **The brain regions involved in ocular pursuit of a visible moving target compared to static fixation** (adapted from Kimmig et al., 2008).

While the distributed velocity memory system is important for controlling SPEM, it can be flexibly recruited in any number of contexts. For example, the same distributed velocity memory system could mediate delayed discrimination (Magnussen & Greenlee, 1992). Of course, the system would need to be coupled to the effectors involved in reporting the judgement in this case. Likewise, if the task is to produce a hand movement at a remembered velocity (G. R. Barnes & Marsden, 2002), the velocity store would need to be temporarily linked to manual motor systems rather than (or in addition to) oculomotor systems. The important point is that, although the tasks differ, a common velocity memory system is involved in all cases.

In this final chapter, the function of velocity memory in various contexts is described, and experimental evidence from the previous chapters is drawn together. The function of velocity memory over different timescales is considered. The review begins by looking at the role of velocity memory during single motion extrapolation trials. Next, discussion turns to the past history effect, whereby velocity information is retained from one trial to the next. Finally, various forms of long-term velocity memory are considered.

### 7.2 Velocity memory in motion extrapolation

The neurocognitive mechanisms involved in motion extrapolation were discussed in previous chapters. For example, in Chapter 2, it was pointed out that neural populations in the posterior parietal cortex are involved in directing attention to the current position of moving targets, and for programming the motor responses which are dependent upon target location. Evidence comes from previous research, which has shown that some IPS neurons fire when a task-relevant object is in a particular location, independently of current gaze direction (Gottlieb et al., 2009), and that IPS populations are a part of pragmatic motor maps, the function of which is to produce *actions* aimed at the encoded locations (Buneo & Andersen, 2006). Moreover, several neuroimaging studies have found that the IPS is equally active during both visible and occluded motion (e.g. Olson, Gatenby, Leung, Skudlarski, & Gore, 2004), so IPS networks seem absolutely central to controlling responses on motion extrapolation tasks.

While some FEF efferents synapse with oculomotor neurons in the brainstem, others project to the IPS. The FEFs and IPS are the core of a visuospatial attention network known as the *frontoparietal system* (Mesulam, 2002). This neural architecture is consistent with the pre-motor theory of attention, which envisages a tight relationship between oculomotor control and spatial attention (Rizzolatti et al., 1994). In Chapter 2, it was argued that, during motion extrapolation, velocity memory could communicate with the frontoparietal system in order to shift visuospatial attention and/or eye movements at the *appropriate rate* (cf Wexler & Klam, 2001).

The novel empirical work in Chapter 2 validates this model. In Experiment 2, two forms of motion extrapolation task were presented under free eye movement and fixation conditions. In both tasks, performance was impaired by fixation. This challenges previous null results (Huber & Krist, 2004) and suggests that the oculomotor control system *is* involved in making judgements about occluded target position. Moreover, when eye movements were permitted, ocular tracking and behavioural judgements were systematically related. This is again consistent with the idea that common mechanisms control ocular and behavioural outputs. Finally, even in the fixation condition, small changes in eye position were related to the position of the occluded target. This strongly implies that the oculomotor system was covertly active, despite fixation.

According to the model of motion extrapolation presented in Chapter 2, identical frontoparietal mechanisms focus visuospatial attention on moving targets whether they are visible or occluded. The only difference is that the rate at which visuospatial attention moves is partially controlled by visual velocity signals when the target is visible, while, after occlusion, tracking is guided purely by stored velocity signals. It is likely that the switch to pure memory-guided tracking occurs at around 200 ms post occlusion (Benguigui et al., 2004; Bennett & Barnes, 2004).

The pattern of ERPs found in Experiment 8 (Chapter 5) supports these ideas. Participants covertly tracked moving targets while fixating. In the Visible Task, moving targets remained visible throughout, while in the Occluded Task, targets became occluded mid trajectory. In both tasks, there was a positive ERP component which shifted from left to right posterior electrode sites, or vice versa, depending on the direction of motion. The scalp distribution of this component was similar in both tasks, suggesting that the same neural generators were involved. The shift in topographic focus was possibly produced by a systematic change in the balance between left and right hemisphere networks as the target crossed fixation. In the Visible Task, this ERP was thus labelled the Hemifield Switch Positivity (HSP). In the occluded task, the component became centralized at 200 ms post occlusion. The latency of this Occlusion Related Deflection (ORD) is consistent with a shift to memory guided tracking at this point (see also Makin, Poliakoff et al., 2009).

A major methodological improvement in this study was the use of an eye tracker to monitor fixation. This confirmed that fixation was maintained successfully on the majority of trials. The eye tracker also allowed exploration of fixational eye movements. While Experiment 2 demonstrated that grand average eye position shifted rightwards as the target moved rightwards, Experiment 8 found that the reverse was also true. This confirms the fixational eye movements are indeed related to visible and occluded tracking.

An important feature of the fixational eye movements in Experiment 8 was their similarity with ERPs. In the Visible Task, the shift in mean eye position occurred around the time that the target reached fixation (like the HSP). In the Occluded Task, the shift in mean eye position occurred around 200 ms post occlusion (like the ORD). This suggests that fixational eye movements and ERPs were measures of the same neurocognitive activity, as hypothesised. However, it also raises the possibility that small eye movements actually produced the ERPs (Dimigen et al., 2009). According to this account, the HSP and ORD would only be indirect measures of attentive tracking, mediated via small eye movements. However, this alternative account predicts that participants with more fixational eye movements should show larger ERPs, and this was not the case.

In summary, the results in this thesis suggest that tracking of visible and occluded targets is mediated by the premotor components of the oculomotor system, even during fixation. This was supported by the results of Experiment 2, which showed overlap between ocular and behaviour responses. It is also likely that the premotor systems could be guided by extraretinal and retinal velocity signals when the target is visible, but by stored velocity signals alone after the initial period of occlusion. This part of the model was supported by the pattern of ERPs in Experiment 8.

The current account of motion extrapolation could be supported and expanded with additional experiments. For example, further EEG experiments are necessary to establish that the ORD was not simply produced by visual target disappearance or by expectation of reappearance after occlusion. It would be useful to contrast the Occluded Task with two other tasks: In one, the participants would not track the target during occlusion, but passively view the same presentation. If covert tracking of the occluded target generates the ORD, this component would disappear in such a task, where covert attentive tracking is absent. In a second task, participants could still attempt to track the target during occlusion, but it would only rarely appear on the other side. In this task, there would be no expectation of reappearance, but the ORD should remain because tracking of the occluded target is still a feature of the task. Moreover, the role of head movements in motion extrapolation was not assessed here, but head movements are important in real life target tracking. It would be interesting to see if motion extrapolation performance improved when head movements were encouraged. Another possibility would be to explore the contribution of different brain regions to motion extrapolation by disrupting them with Transcranial Magnetic Stimulation (TMS) during occlusion. In fact, this project is currently underway at Bradford University, in collaboration with Declan McKeefry.

Finally, it can be noted that object position is only one aspect of the physical world that can change at a particular rate. Other examples include changes in the pitch of a sound, changes in stimulus colour or shape. People could perceive the rate at which these attributes morph between states, and extrapolate the change across ‘occlusion periods’ at the correct rate. Perhaps all forms of extrapolation involve some kind of velocity memory? Future investigations could look at correlations between performances on a variety of extrapolation tasks. A positive result would imply that a common velocity memory system guided all forms of extrapolation.

### 7.2.1 Neural oscillations in motion extrapolation

As mentioned in section 7.1, discrete neural populations distributed around the brain often enter temporary coalitions capable of representing multidimensional information. Populations involved in the temporary coalition are functionally linked if their oscillations are synchronized in the beta or gamma frequencies (Fries, 2005). In the context of motion extrapolation, neural populations which store velocity (MT and the FEFs) may be functionally linked with populations that guide visuospatial attention (IPS) by high frequency synchronization. This hypothesis is supported by the finding that the strength of the motion signal in MT is proportional to gamma power (Siegel, Donner, Oostenveld, Fries, & Engel, 2007). Furthermore, one study has reported gamma synchronization between frontal and right parietal sources during mental object rotation (Bhattacharya, Petsche, Feldmann, & Rescher, 2001). It seems likely that motion extrapolation, like many other tasks, is mediated by high frequency synchronization.

However, high frequency synchronization may only be one side of the coin. Low frequency alpha oscillations (~6 to 14 Hz) tend to dominate in networks where high frequency oscillations are absent, and vice versa. It is thought that synchronization in the alpha frequency bands reflects a form of top down inhibition, and desynchronization reflects a form of excitation (Pfurtscheller & Lopes da Silva, 1999). In Chapter 6, upper alpha oscillations (8 to 12 Hz) were measured during visible and occluded tracking. In the Visible Task, upper alpha activity in bilateral posterior electrode clusters desynchronized around the time the target passed fixation. This was presumably caused by bottom-up excitation of the visual cortex. In the occlusion period of the Occluded Task, there was significantly greater alpha power than at equivalent periods in the Visible Task. This could reflect top down inhibition of visual inputs in order to protect stored velocity representations from disruption (cf Grimault et al., 2009; Klimesch et al., 2007). It is possible that this top down inhibition is a function of the DLPFC, which is known to be more active during occlusion (Lencer et al., 2004). This hypothesis requires further corroboration, but collectively the data presented in Chapter 6 confirms the relevance of oscillatory activity in motion extrapolation.

In future work this analysis could be expanded by measuring other frequency bands. For example, distinct patterns of beta and gamma activity could appear during occlusion. Moreover, it would be possible to test the predictions about the functional significance of alpha during occlusion. It was hypothesised that this may reflect top-down inhibition of potentially disruptive visual inputs. If so, one would expect the phase of frontal alpha activity to precede the phase of posterior alpha activity (cf Hanslmayr et al., 2005). Finally, it would be interesting to use source localization techniques to identify the brain regions responsible for scalp recorded oscillations. It can be predicted that regions of the frontoparietal network would be identified (cf Bhattacharya et al., 2001).

### 7.3 Velocity representations from previous trials

Makin et al. (2008) found that motion extrapolation is influenced by the velocity of previous trials. This past history effect suggests that, as well as mediating performance on current trials, velocity representations could persist from one trial to the next. This could be an important feature of the velocity memory system and therefore the current work rigorously investigated past history effects. In Experiments 2, 4 and 5 it was found participants responded earlier on 20°/s probe trials after a fast prime trial and vice versa. The direction of this past history effect suggests that subsequently encoded velocity representations may blend together.

However, it is possible that observed results could be mediated by *response time generalization* rather than velocity blending. In the experiments where the blending effect was recorded, fast prime trials lasted less time than slower ones. This design means that the effect could be produced if participants responded at the same time-after-trial-onset that they had responded on the prime trial. Further analysis showed the response time generalization occurred in these experiments (Appendix 1), while the blending effect disappeared in a control experiment where the trial duration confound was eliminated (Appendix 2). It should be noted that velocity blending was recorded in the Discrimination Tasks of Makin et al. (2008) and Lyon and Waag (1995). In these experiments participants made non-speeded judgements about occluded target location, so response time generalization cannot explain these results. However, considering all data together, it can be concluded that motion extrapolation tasks are probably not the best tool for measuring past history effects. Part of the problem (already recognized by Makin et al., 2008), arises from the fact that it is impossible to match all spatial and temporal parameters of trials which travel at different velocities.

It can nevertheless be concluded that velocity blending exists, and that it can be measured with other tasks. Indeed, in Chapter 4, velocity blending was observed in a delayed velocity discrimination task. In two experiments participants had to compare Standard and Test velocities which were separated by a 10 second delay. It was found that the presentation of a moving target during the delay systematically influenced discrimination. When the target was fast, participants remembered the standard velocity as faster and vice versa. This effect was found whether participants actively processed the target velocity or not (see also Kerzel, 2001; Magnussen & Greenlee, 1992; McKeefry et al., 2007).

Given that many sensory and motor systems can store velocity information, one might ask *where* the blending effect occurs. The perceptual memory model emphasises the role of low level visual areas, like MT, in velocity storage (Pasternak and Greenlee, 2005), so perhaps the blending effect reflects interference between subsequently encoded velocity representations in MT? There are two relevant strands of evidence here. First, comparable blending effects are found when participants are fixating and free to track targets with their eyes. This suggests that the blending can occur between extraretinal velocity signals, while area MT is thought to process retinal velocity information only (Newsome et al., 1988). Second, in previous delayed velocity discrimination experiments, the *speed* of masker stimuli presented between the standard and test gratings affects judgements, but its *direction* was inconsequential. This implies speed and direction information can be dissociated in the brain, and blending occurs between speed representations (cf Matthews, Luber, Qian, & Lisanby, 2001; Matthews & Qian, 1999). Conversely, MT neurons respond maximally to particular combinations speed and direction (Perrone & Thiele, 2001). These considerations imply that the blending effect is not solely produced by interference in area MT.

In fact, Experiments 6 and 7 were designed as a foundation for future investigations in the role of MT in velocity memory. Cells in area MT are sensitive to velocities > 8°/s, have relatively small receptive fields (Born & Bradley, 2005), are arranged retinotopically, and code the contralateral visual field (McKeefry et al., 2008). Conversely cells in the upstream area MST are not retinotopically organized and have much larger receptive fields (Campana et al., 2008). If velocity representations are retained in MT, then the influence of moving distractors would disappear when they were presented in a different spatial location to the standard velocity. In Experiments 6 and 7 stimuli were presented 4° below fixation. In future experiments, distractors could be presented 4° above fixation, with gratings 4° below fixation. If this manipulation abolishes the blending effect, it would demonstrate a primary role for MT in velocity memory.

### 7.4 Visuomotor, procedural and semantic forms of velocity memory

Magnussen and Greenlee (1992) found that stored velocity representations were fragile and can be disrupted by incoming motion information (see also Experiments 6 and 7, and McKeefry et al., 2007). Conversely, Vidoni et al. (2009) found that well encoded sequences of eye and hand movements were still evident after a three day break, during which participants continued with their disruptive daily lives. It is possible that these studies tap different forms of velocity memory. Magnussen and Greenlee (1992) suggest that the velocity of a moving grating must be held in a visual code. Conversely, in Vidoni et al.'s study, sequences of actions could have been extremely well learned, resulting in far more robust *procedural memory* for effector velocities (Figure 7.2). The velocity memory system described above is more akin to the 'visual code' suggested by Magnussen and Greenlee (1992), although pre-motor velocity signals could be more important than these authors suggest (cf Chakraborti et al., 2002).

It is also likely that velocity information can be associated with other visual features. In Chapter 3, another motion extrapolation task was reported in which participants learned that red targets usually travelled slowly, and green targets usually travelled quickly. This knowledge influenced performance, indicating that object-velocity associations can influence motion extrapolation. One contributing brain area may have been the SEFs (Figure 7.1). In a study by de Hemptinne et al. (2008), monkeys learned colour cues which predicted the direction of upcoming motion. Some SEF neurons fired when presented with the cue, indicating that they mediated colour-motion associations. These neurons are upstream of the FEF populations, which have a more direct motor function (Ackerley et al., 2008). The model of motion extrapolation shown in Chapter 2 can be expanded to include the SEFs (Figure 7.2). It is conceivable that these associations in the SEFs are the foundation of how we learn the typical movement characteristics of everyday objects.

Indeed, over time, typical movement characteristics may become a part of semantic knowledge. For example, our semantic representation of a rocket may include the node 'very fast' while our semantic representation of a snail would include the node 'very slow' (Reed & Vinson, 1996). An important strand of neuroimaging research has explored the neural basis of these representations. In the year 2000, two fMRI studies found that area MT was more active when viewing static images that implied motion, (e.g. a cup in mid air falling off a shelf) compared to matched, static images which did not imply motion (e.g. a cup placed safely on a shelf, Kourtzi & Kanwisher, 2000; Senior et al., 2000). These results were intriguing because MT is renowned for low-level motion perception, rather than high-level interpretation. Although recent magnetoencephalograhic data indicates that this MT activation is caused by feedback connections from frontal regions (Fawcett, Hillebrand, & Singh, 2007), area MT may function as a node representing 'motion' in semantic networks that give meaning to still photographic images (Senior et al., 2002). While it is possible that MT activation could be an epiphenomenal by-product of representations supported by other networks, a representational role for MT is consistent with accounts of *embodied cognition* (in which perceptual and motor networks are responsible for coding even the most abstract ideas, Barsalou, 1999). This idea is also included in Figure 7.2.

Finally, it is thought that dissociable brain mechanisms process the distinctive patterns of motion produced by moving animals and humans (Baker, Keysers, Jellema, Wicker, & Perrett, 2001; Billino, Bremmer, & Gegenfurtner, 2008). Memory for biological motion could arise from learning the stereotypical visual motion patterns produced by animals. However, motor simulation could also be important for interpreting biological motion (e.g. Cross, Hamilton, & Grafton, 2006). Biological motion processing networks are probably connected to the systems discussed here, but this is beyond the scope of the current work.

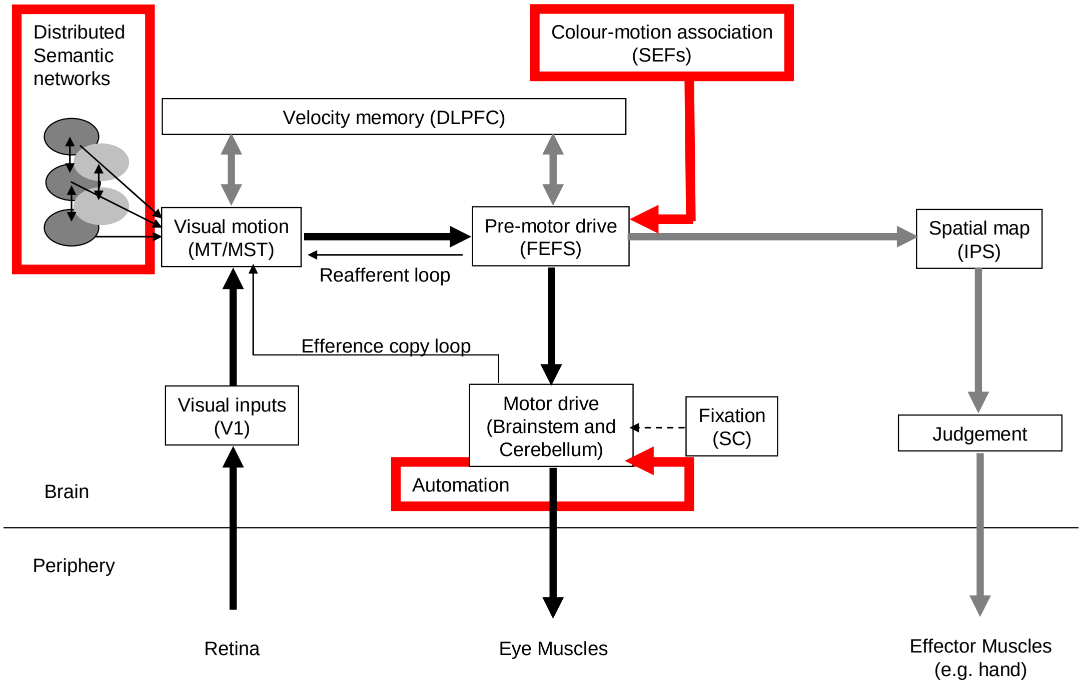


**Figure 7.2: Additional velocity memory systems.** The network of brain areas involved in motion extrapolation is shown (this is identical to Figure 2.11, Chapter 2). However, research suggests three elaborations (shown in red): First, it is likely that the sequences of particular eye and hand movement velocities can be automated and retained for a long period. This is probably a function of the cerebellum. Second, associations between objects and their typical motion characteristics may be mediated by the SEFs. The SEFs could pass this information to the FEFs in order to influence behaviour. Thirdly, MT/MST may function as a 'motion' node in distributed semantic networks which represent complex ideas.

## 7.5 Summary

This chapter attempted to bring together the account of velocity memory provided by previous chapters of this thesis. Based on previous literature and current results, the following possibilities were proposed:

1) Velocity memory can be described as persistent high frequency synchronization across a network of sensory and motor populations which represent velocity. During storage, potentially disruptive visual input may be inhibited via lower frequency oscillations. Indeed, in Chapter 6 it was found that ~10 Hz oscillations were more apparent over the visual cortex during velocity retention.

2) This velocity memory system is best known for its role in controlling SPEM, but may be involved in many other tasks, including motion extrapolation. Chapter 2 provided evidence that the common systems control eye movements and motion extrapolation judgements, and that the oculomotor control system is covertly active during fixation.

3) During the visible period of motion extrapolation tasks, attentive tracking may be guided by retinal and extraretinal velocity information, but after the first 200 ms of occlusion, pure memory-guided tracking takes over. In Chapter 5, specific ERPs components were recorded which index this change.

4) Subsequently encoded velocity representations can blend together. This blending effect may not be measured reliably with motion extrapolation tasks, but is evident in other paradigms (see Chapter 4)

5) At least two other forms of 'velocity memory' are identifiable. First, the speed of effector movements may be automated if actions repeated many times. This is a form of procedural velocity memory. Second, semantic knowledge of objects may include representations their typical motion characteristics. This information is presumably acquired though a process of association between velocity information and other stimulus features. Indeed, Chapter 3 describes evidence for colour-velocity association. These two forms of velocity memory are distinct, but overlap with the common velocity memory system described here (Figure 7.2).

In conclusion, this thesis draws together several disparate strands of literature about velocity memory. In light of this synthesis, velocity memory can be described as persistent functional coupling between populations of velocity sensitive neurons after moving stimuli disappear. This velocity memory system can be employed during a variety of different judgments and behaviours. In particular, theoretical work on eye movements, delayed discrimination and motion extrapolation could benefit from this account of velocity memory.

# Appendix 1

To assess whether probe trial response time was indeed influenced by prime trial response time in Experiment 2 (Production Task, Free viewing, Short ITI condition), the correlation between prime and probe response times was obtained from each participant (Spearman's Rho). Correlations were obtained in the fast and slow prime trials separately. If probe responses are not influence by prime duration, as previously assumed, then the average coefficient should approximate zero. However, the distribution of correlation coefficients was centered above zero in both conditions (Figure 1A and B). This was confirmed by highly significant one sample t tests ($t$ (31) = 5.879, $p < 0.001$; $t$ (31) = 11.090, $p < 0.001$). The same was pattern was found in the Experiment 4. Again the mean Spearman's Rho coefficient was significantly greater than zero in both fast and slow prime conditions ($t$ (23) = 4.057, $p < 0.001$; $t$ (23) = 4.833, $p < 0.001$, Figure 2C and D). Finally, this pattern was evident in Experiment 5 as well (slow primes, $t$ (31) = 4.685, $p < 0.001$; fast primes $t$ (31) = 5.681, $p < 0.001$, Figure 2E and F). The clear presence of response time generalization in the all experiments where the blending effect was reported casts doubt on the original explanation.

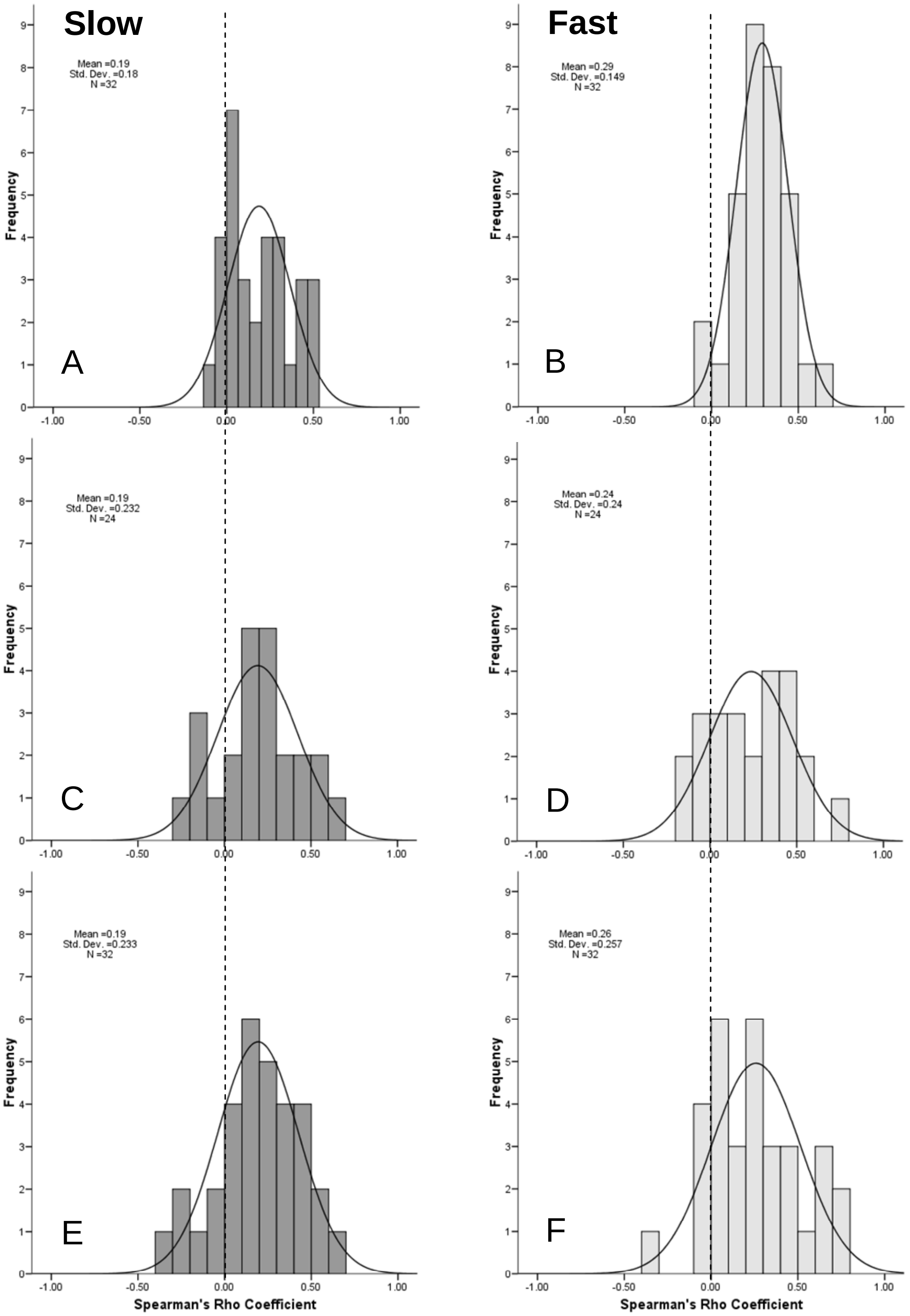


**Figure 8.1: Distribution of correlation coefficients between prime and probe trial response times.** Left column shows data from slow prime conditions. The right column shows data from fast prime conditions. Top row show (A and B) show data from the Production Task. The middle row (C and D) shows data from the Appearing Endpoint Experiment. The bottom row (E and F) show data from the Coloured Target Appearing Endpoint Experiment. If response time generalization was absent, the distributions would be centred on zero (none were, $p < 0.001$).

# Appendix 2

## Time and displacement control experiment

In order assess whether the blending effect could be accounted for by response time generalization, another motion extrapolation experiment was conducted. Again 20°/s probe trials were preceded by 14 or 26°/s prime trials. In one condition (the *Displacement Control* condition, Figure 3A) the size of the prime and probe visible and occluded periods was always the same. In the Displacement Control condition, response time generalization could potentially account for the past history effects. In the other condition (*Time Control* condition, Figure 3B) the overall trial duration on prime and probe trials was always identical. This was achieved by manipulating the size of the visible and occluded periods. In the Time Controlled condition, response time generalization could not explain any past history effects. In this experiment, the trial before the primes (N-2) also travelled at 14 or 26°/s (balanced across conditions) but analysis collapses across this factor for brevity[1].

## Method

### Participants

30 participants aged 19 - 30 (10 male) took part.

### Apparatus

The apparatus used was similar to in previously described experiments, except occluder length and position varied according to the condition. In addition, the start point was randomized trial-by-trial between 400 and 450 pixels to the left of the centre.

### Design

The participants received the 20º/s probe target 40 times in total. It was preceded 10 times by every combination of prime trials: N-1 (14º/s, 26º/s) x N-2 (14º/s, 26º/s). For 5 presentations, they were visible and occluded over the same distance as the probe (Displacement Control condition; Figure 1A) and for the other 5 presentations the prime trials were visible and occluded for the same length of time as the probe (Time Control condition; Figure 1B).

### Procedure

Participants attempted to respond at the exact time they thought the target had reached the right hand edge of the occluder. The trial onset sequence (i.e. target appearance and audio cue) was the same other experiments in this thesis.

Participants were first presented with a practice block consisting of 22 trials with velocities ranging from 10 to 26º/s[2]. The target always reappeared during practice. 248 trials were then presented. 120 of these were experimental prime-prime-probe trials: the probe velocity (20º/s) was presented 40 times, preceded 5 times by every combination of Time Control prime trials (40 presentations) and 5 times by every combination of Displacement Control prime trials (40 presentations). In the Time Control condition, the visible and occluded *durations* were equal within every prime-prime-probe group. In the Displacement Control condition, the visible and occluded *distance*s were equal within each prime-prime-probe group. In the Time Control trials, the 5 repeats of each combination were associated with different occlusion durations (337, 387, 437, 487 and 537 ms) but the visible duration was always 300 ms. In the Displacement Control trials, the 5 repeats of each group of experimental trials were associated with different occluder sizes, (6.77, 7.76, 8.75, 9.76, and 10.73°) but the visible portion was always 5.95°.

The remaining 128 trials were filler trials which separated the experimental trials. There were eight different filler trial velocities, (10, 12, 16, 18, 22, 24, 28 and 30 º/s) each of which was presented on 16 occasions. For half of the fillers, the displacements were selected such that the occlusion duration varied randomly between 287 and 587 ms and had a visible duration which varied randomly between 200 and 400 ms. For the other half of the filler trials, displacement was randomly selected between 5.77 and 11.72° and visible displacement was selected randomly between 3.96 and 7.93°. This meant that across the experiment, the velocity of the filler trials was neither systematically related to either displacement or duration. The filler trials were distributed randomly and there were always at least 3 filler trials between every group of prime and probe trials. For 4 of the filler trials at each velocity, the target reappeared (although never on a trial immediately preceding a prime trial). Overall, the target reappeared on 13% of trials.

In the experimental trials, the interval between the reappearance time of one trial and the start of the next trial was always 3500 ms (i.e. for the gap between the N-2 and the

N-1 and the N-1 and the probe). All other inter-trial intervals were randomized between 3500 and 4500 ms.

The eight combinations of prime-prime-probe trials were presented in 5 blocks (of 49-50 trials) in a pseudorandom order separated by filler trials (see above). All 8 different sets of prime-prime-probe trials were presented once before they were repeated. Chance order effects that might be produced by the filler trials were again minimized by reversing the order of prime-prime-probe trials and producing another 5 blocks. Half the participants completed the original set of blocks and half completed the reversed blocks, with the order of block presentation being dictated by a Latin square. Each of the 10 possible block sets (forward/reverse x 5 possible block orders) was used 3 times.

### Results

Standardized response time error was analyzed as a function of 2 within participant factors [Control (time, displacement) x Prime velocity (fast, slow)] with repeated measures ANOVA. Results are shown in Figure 1C. There was no main effect of Control ($F$ (1, 29) = 1.545, $p$ = 0.224) or Prime velocity ($F$ (1, 29) = 3.042, $p$ = 0.092). However, there was a significant interaction between these factors ($F$ (1, 29) = 9.259, $p$ = 0.005). This interaction was caused by a significant blending effect in the Displacement Control condition (where participants responded earlier after a fast prime ($t$ (29) = 3.263, $p$ = 0.003) but no effect in the Time Control condition ($t$ (29) = 1.163, $p$ = 0.254).

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**1** This experiment was completed in 2006, prior to the others reported in the thesis, but was originally analyzed with a different emphasis.

**2:** It would have been preferable to have the same distribution of velocities during practice as the main experiment. This design was admittedly sub optimal, but is unlikely to have made an important difference.

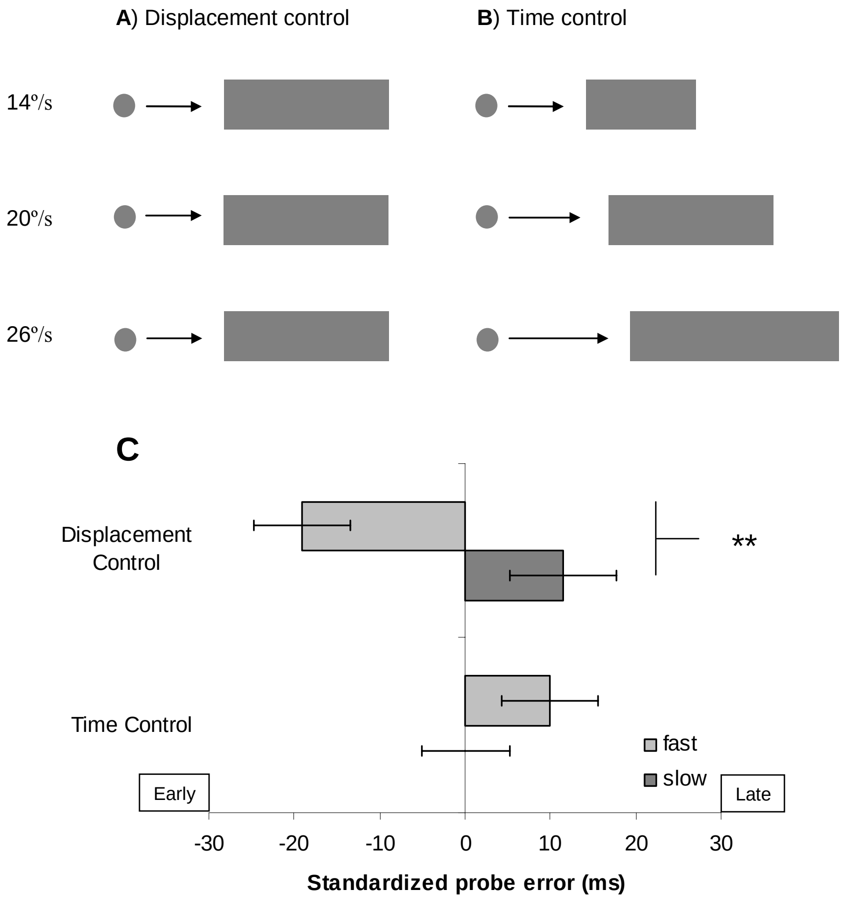

**Figure 9.1: Method and Results.** **A:** In the Displacement Control condition, targets of different velocities all traverse the same visible and occluded displacement and thus the duration of the trial is proportional to its velocity. **B:** In the Time Control condition, all experimental trials last the same length of time. This is achieved by manipulating the length of the visible portion and the occluder, according to the target velocity. **C:** Mean standardized probe error is shown as a function of condition and prime velocity. Error bars = +/- 1 S.E.M. ** $p < 0.01$.

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