A Journey Through Time and Space: The Spatiotemporal Profile of Attention Relative to Saccade and Reach

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ABSTRACT

In an interactive environment, we use a multitude of eye and hand movements to gather information about our surroundings, and to act upon what we see. While these are the eventual, overt behaviours that we observe, there are countless hidden neural processes guiding where we move our eyes and hands. This thesis will examine one such of these processes: visual attention. Visual attention has been shown to produce perceptual benefits, such as an increase in contrast sensitivity, at the attended location, and there is evidence that before an eye or hand movement is made, attention shifts to the location of that upcoming movement target. This thesis aimed to comprehensively map the spatiotemporal profile of attention when reaches and saccades were being planned and executed, in order to compare how attention shifts when different types of movements are being made.

The first experiment mapped the spatiotemporal profile of attention relative to a reach alone. Results of this study showed that when a reach alone is being planned, there is a broad spatial allocation of attention across the visual field, while the temporal profile shows a slight increase before the onset of a reach, with a dramatic drop in performance once the hand is in flight. The second experiment compared the spatiotemporal profile of attention for saccades alone, and saccades with a concurrent reach. These results, in contrast showed a large increase in performance before the start of a movement, and a plateau of performance during the movement itself. The third experiment aimed to explore how attention may differ depending on where a probed location is situated relative to the direction of a movement, and to compare how this may change across different movement effectors. Results showed that the profile of attention differed depending on both movement effector and whether the probe appeared in line with or orthogonal to the direction of a movement. These results also suggest that attention spreads differently when a saccade is being made, irrespective of whether a reach is being conducted or not.

Overall, the results of this thesis showed three main effects: the spatiotemporal profile of attention is different when a saccade is being made compared to a reach alone; attentional facilitation at the location of a probe is different depending on where the probe is located, relative to the direction of movement; and this profile of attention varies depending on the type of movement being enacted. Additional results also suggest that attention may act in a dual facilitatory/inhibitory manner, depending on the movement effector. Taken together, these results provide evidence that different types of movement planning may require different levels of attentional guidance, and also provide evidence that pre-movement attention may be a flexibly allocated resource, depending on the demands of the task, and the movements being enacted.

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ABBREVIATIONS (IN ORDER OF APPEARANCE)

EEG	Electroencephalography
LIP	Lateral intraparietal cortex
2AFC	Two alternative forced choice
FEF	Frontal eye fields
ERP	Event related potential
PPC	Posterior parietal cortex
VAM	Visual Attention Model
SFA	Selection for Action theory
SC	Superior colliculus
fMRI	Functional magnetic resonance imagery
IPS	Intraparietal sulcus
SOA	Stimulus onset asynchrony
RSVP	Rapid serial visual presentation
PRR	Parietal reach region
PMC	Premotor cortex
PMv	Ventral part of premotor cortex
MI	Primary motor cortex

SUMMARY OF THESIS

This thesis is comprised of three research chapters in the form of manuscripts prepared for publication, a literature review and a general discussion. The overall aim of the research contained within this thesis is to explore the spatiotemporal profile of visual attention when a saccade and/or reach is being planned and executed. Chapter 2 is a manuscript that has already been published in the *Journal of Vision*. Chapters 3 and 4 are manuscripts that have been prepared for publication. Chapter 5 summarises the results and provides a discussion and comparison of the experimental findings, and the implications for future research.

A note on terminology: unless included in the title of a paper (for example in Chapter 3), the term "pre-movement" will be used to describe pre-motor attention, in order to disambiguate any incidental usage from the "Pre-motor theory of attention" which is also discussed at various points throughout this thesis.

CHAPTER 1: LITERATURE REVIEW

This chapter provides an overview of the current literature surrounding visual attention and the interaction between vision, action and attention. The overview starts with a discussion of visually guided action, and how vision is important for planning movements in a visually rich, interactive world. Subsequently, there is a broader discussion of the problem of target selection in a visually rich environment, and a brief discussion of some of the current theories that explain how people may use salience maps, priority maps, and attention to focus on particular features in a scene. The major part of the literature review focusses on visual attention, and the interaction between attention and action, which is the main focus of this thesis. Finally, there is an outline and discussion of the relationship between attention, eye movements and hand movements, in both psychophysical/behavioural terms and neurophysiological terms.

CHAPTER 2: THE SPATIOTEMPORAL PROFILE OF ATTENTION RELATIVE TO A REACH

This manuscript uses psychophysical techniques to comprehensively map the spatial and temporal profile of visual attention relative to a goal-directed movement alone, without an accompanying saccade. This experiment aimed to determine how attention may shift across the visual field while a hand movement was being planned and executed, which provides an insight into how attention might be used to guide and facilitate manual movements. A novel experimental paradigm was used to measure attentional facilitation at six locations and nine time-points during a reach to a visual target. The main conclusions of this study were that attention increases and then is sustained during the preparation of a reach, and deteriorates as the hand nears the reach end-point. This study also suggests that the spread of attention may differ depending on the target location relative to the direction of the reach.

CHAPTER 3: DISSOCIATING THE PREMOTOR ATTENTIONAL SHIFT FOR SACCADES AND REACHES

This chapter focuses on the spatiotemporal characteristics of visual attention when a concurrent saccade and reach are being made, compared to when a saccade alone is being executed. This study demonstrates how planning a saccade alone compared with planning a saccade and concurrent reach affects when and where attention is allocated, allowing insight into how attention may play a role in saccade and reach planning. The paradigm was a modification of the paradigm used in Chapter 2, to allow for general comparison of results. This study showed that the pre-movement attentional shift happened on a similar timescale when a reach was being planned with a saccade, compared to the saccade alone, and the shape of the function was also similar. This suggests a unified attentional resource guides movements in the presence of a saccade.

CHAPTER 4: THE PROFILE OF ATTENTION DIFFERS AT LOCATIONS ORTHOGONAL TO REACH DIRECTION

This chapter aims to resolve the pattern of results seen in Chapter 2 by exploring the effect of reach direction on the attentional profile at locations either in line with, or orthogonal to the direction of either a reach alone, saccade alone, or a concurrent reach and saccade. The main conclusions suggest that there is a difference in the attentional profile at locations orthogonal to reach direction, and this differs depending on the movement being enacted. Similar results have only before been found when exploring the peri saccadic remapping process. The results also suggest that the spatiotemporal profile of attention is malleable, depending on the paradigms and demands of a task. This experiment also provides further evidence that that some areas of the visual field surrounding a target may be subject to attentional inhibition as well as facilitation.

CHAPTER 5: DISCUSSION

This chapter amalgamates the findings from the three substantive experimental chapters and discusses these results with a comparison to previous research in the area, and in the context of current predominant theories of pre-movement attention. The major crux of this thesis – how enacting different types of movements may affect the spatiotemporal profile of attention – will be discussed in depth, and in particular this section will explore both reasons why the saccade seems to dominate this attentional profile, and why attention accompanying a reach without a saccade follows such a different time-course. Secondary issues that have arisen from the experiments will also be considered, such as the idea of attentional inhibition. These topics will be discussed in terms of both psychophysical evidence, and links will be drawn to possible underlying neurophysiological mechanisms.

1. INTRODUCTION

"Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others…"

- William James, 1890

Visual attention is an important perceptual and neurological process, which is integral to our perception of the world, and also to the way in which we select impending movement targets when we interact with our environment. The concept of attention itself is not a new one: in 1649 Descartes foreshadowed the problems of modern neuroscience by (albeit erroneously) suggesting that attending to a location was achieved by "tilting" the pineal gland toward the object of interest, thus bringing it into attentional focus[1]. The state of attentional theorising remained stagnant from there, and centuries passed before a more formal scientific exploration of attention was conducted, when, in 1871 Helmholtz postulated that attention could be directed to a location without an overt eye movement being made to that location, and suggested that this focal enhancement could happen independent to the current foveal fixation. There was a lull in attentional research until the 1970s however, when the concept of attention was formalised, and modern attentional research started to conduct rigorous tests on how attention is allocated, and what factors might influence this. A key finding by Posner (1980) reintroduced the idea that people can voluntarily enhance perceptual experience at a location by attending to it, and it soon became evident that attention plays an important role in a world which is navigated using vision as our primary sensory modality. In everyday life, we are constantly making eye movements to gather information about the world

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[1] Or as Descartes so eloquently phrased it: "When one would fix his attention some pretty while to consider, or ruminate on one object…"

around us, and make innumerable hand movements to interact with our environment. These hand movements are carefully guided by vision, and it seems that attention plays an invisible, but important, role in the planning and guidance of both of these actions. Attention is, however, a somewhat dynamic and elusive force, and studies trying to determine the spatial and temporal profile of attention when a saccade or reach is being planned are divergent in their conclusions.

This thesis aims therefore to explore one of the most pertinent questions currently surrounding attention, and that is, simply, how attention is linked to the planning and execution of saccades and hand movements over time and space. This problem in itself incorporates many other problems of attention and movement planning in general, such as the role of attention in selecting objects in a scene, the flexible nature of attention, and the neural organisation of attentional, visual and motor pathways. These problems are still subject to some amount of debate, and while there are a number of theories that aim to explain the interconnection between attentional selectivity, action planning and execution, there is as yet no definitive answer as to how these are linked.

Vision and visually guided hand movements are tightly coupled (Land & Hayhoe, 2001; Wilmut, Wann, & Brown, 2006), and attention has been implicated in the planning and execution of both saccades and goal-directed movements (Deubel & Schneider, 1996; Jonikaitis & Deubel, 2011). Enacting a movement, whether it is a saccade or hand movement requires an abundance of neurological processes to ensure the correct location is selected, encoded, and that an accurate motor plan is formed to guide the movement (Desmurget, Pélisson, Rossetti, & Prablanc, 1998). Each of these stages in turn incorporates many cortical connections, and each stage in the process is dependent on the previous stage to ensure the saccade or hand lands accurately and precisely at the target location. Attention, and the perceptual benefits it provides, has been implicated in each of these processes. This thesis will consider each of these problems in a general review of the literature, and aims to draw each disparate body of evidence into a unified view of how attention may play a role in the planning and execution of eye and hand movements.

When reading the following thesis, it should be kept in mind that there is one overarching problem which the three experiments contained herein aim to explore, and that is to determine when, and how, attention shifts when planning and executing saccade and hand movements. Mapping the spatiotemporal profile of attention during eye and hand movements provides an insight into how attention may aid in the planning and guidance of these actions, and also allows us to see how attention may act differently when different types of movements are being planned. While not the main focus of this thesis, related problems such as the possible incorporation of attention into a unified priority map for movement planning, and the possible shared or dissociated nature of the attentional mechanisms underlying eye and hand movements will be also considered in order to situate this work into a broader theoretical framework.

1.1 INTERACTING WITH THE ENVIRONMENT: VISUALLY GUIDED ACTION

In an interactive and dynamic environment, we use vision as our primary sensory modality to tell us where we are in the world, and where other things are relative to us. When we have to actively engage with this environment, for example when making goal directed reaches, visual guidance is paramount for allowing us to do this with accuracy and precision. The consequence of making an inaccurate reach may only be petty if you reach for a cup of tea and knock it over, but under higher risk situations, making an inaccurate reach could result in true harm. Vision provides us with the information we need to make accurate reaches, and indeed when making goal directed movements, these eye and hand movements are tightly coupled. This thesis will therefore start with the basic assumption which underpins the subsequent theoretical and experimental sections: that goal-directed reaches are primarily guided by vision, and these two movements are generally enacted with a complex synchronicity.

1.1.1 VISION IS IMPORTANT FOR ACTION

Eye and hand movements are generally coupled when making goal directed movements. This been shown in both naturalistic studies where participants complete everyday tasks such as making a cup of tea or a sandwich (Land & Hayhoe, 2001; Land, Mennie, & Rusted, 1999), and in more artificial sequential pointing tasks (Wilmut et al., 2006). During these activities, saccades precede hand movements, with the eye moving to the next reach location just before the hand moves there. While it has been suggested that this lead-time is approximately 200 ms (Wilmut et al., 2006), evidence suggests however that eye-hand latencies can vary depending on the demands and timing of the task (Gribble, Everling, Ford, & Mattar, 2002; Ma-Wyatt, Stritzke, & Trommershäuser, 2010; Sailer, Eggert, Ditterich, & Straube, 2000). Even such a normal, every-day sequence of activities such as boiling a kettle requires constant visual monitoring of each event in the manual sequence (Land et al., 1999). Indeed, it has been suggested that this sequence of hand following the eye allows for a feed-forward system of visual information that guides the programming of a hand movement (Wilmut et al., 2006).

There is evidence that the same visual information is used to plan both eye and hand movements (Gegenfurtner & Franz, 2007; Ma-Wyatt & McKee, 2006; Stritzke & Trommershäuser, 2007), and studies have shown that it's difficult to select a new saccade target while a reach is already underway to an existing reach target (Neggers & Bekkering, 2000). This suggests a very tight coupling of eye and hand movements during rapid movements, and further suggests that the mechanisms that are used to select movement targets may be shared, or at least very tightly coupled. Visual precision for the localisation of a target limits pointing precision to the same target (Ma-Wyatt & McKee, 2006; Gegenfurtner & Franz, 2007), suggesting that this same visual information may also be linked with subsequent saccade and reach planning. This raises the question of whether factors such as object salience, and attentional enhancement (factors that affect perception) may therefore play a role in the planning of both saccades and reaches. This coupling of motor plan formation for eye and hand movements has support from numerous neurophysiological studies, and this will be discussed further in section 1.5.3.

Planning and executing a hand movement involves a complex interaction between visual information and proprioceptive feedback from the arm's position. To achieve an accurate goal-directed movement, the brain uses a motor plan that guides the hand throughout the movement (Desmurget, et al., 1998). This motor plan uses a combination of feedback and feedforward information, and while many studies suggest that an action plan is computed prior to the commencement of the reach, the role of visual information throughout the reach is vital for updating the motor plan to ensure ultimate end point accuracy (Desmurget & Grafton, 2000). For example, it has been shown that the brain is able to better estimate target position for an upcoming reach if it can integrate both predicted target location and online sensory feedback, than by using only one of these information sources on its own (Vaziri, Diedrichsen, & Shadmehr, 2006), and that this visual feedback is incorporated into online control of a reaching movement throughout the entirety of the reach (Saunders & Knill, 2003). This reliance on visual information throughout the reach has been demonstrated by studies where the visual feedback of the reach target was cut off during the reach – removing visual feedback during the reach resulted in a decrease in endpoint precision, demonstrating that visual information during the reach, and not only at the outset is an important planning in making an accurate goal directed movement (Ma-Wyatt & McKee, 2007). Indeed, the importance of vision for the completion of a reach was also demonstrated by exploring how restricting the view of the hand and reach target affected overall reach performance. Reach performance can be affected by reducing the quality of visual information available at the outset of the reach (Ma-Wyatt & McKee, 2006), and also by restricting visual information at various time-points throughout the reach (Ma-Wyatt & McKee, 2007). Thus, visual information is important in both the planning stages of the reach, and while the hand is in flight. This reliance on visual information in order to plan, update and execute an accurate hand movement has implications for the effect attention may have on such a process. Perceptual properties of stimuli are so affected by attending to that area, and reaching to a location depends so highly on visual information, and indeed the perception of the reach target, it would be remiss to assume that attention is not implicated in this process.

The next stage in the attentional problem relates to how we actually locate objects in the environment so that we can make a movement there, and ultimately, how attention may also play a role in this initial planning process.

1.2 THE PROBLEM OF FINDING THINGS IN THE ENVIRONMENT – FROM SALIENCE TO PRIORITY MAPS

Making a visually guided movement involves a large amount of planning, especially when this reach is being conducted in a visually rich environment, as it would be in everyday life. At any given time, the visual system is presented with a myriad of information, only a small proportion of which is behaviourally relevant. Our brains must filter out the irrelevant information so only that which is immediately behaviourally relevant comes into our conscious perception. In terms of movements, before a motor plan can be made to any location, that target must be selected, and the visual input must be filtered in order for this selection to occur. This problem of target selection will be discussed later in section 1.6 in the context of potential mechanisms and networks that control attention and target selection, but the basic overview and some models of how this may occur will be outlined first, as an introduction to why we may need attention to aid us in selecting and targeting locations and objects in the environment.

There have been many theories as to how this initial filtering process may work, and the evolution of these theories provides the basis for the current views of attentional selection that underpins this thesis. It is important to understand what factors are influential in determining which parts of a scene we actively perceive, and ultimately, which parts of a scene are important when an eye or hand movement is being planned.

1.2.1 SALIENCE

When considering the problem of how stimuli are filtered into our conscious perception, the primary factors to be considered are the properties of the stimuli themselves. Hence, the concept of stimulus salience has been a predominant theory in determining which parts of a scene are behaviourally relevant for perceptual purposes, and subsequently, which parts of a scene are relevant when attention is being shifted, or a movement planned.

A stimulus is salient if it stands out from its surroundings; that is, if it differs from its surrounds due to a certain low-level attribute, such as luminance, contrast, or colour (Itti & Koch, 2001; Koch & Ullman, 1985). Salience can be described as a 'bottom-up' process, meaning that the intrinsic visual properties of the stimulus are adequate to capture attention, without any 'top-down' cognitive control (Treismann, 1986; Wolfe, 1994). This bottom-up salience is a result of low-level visual processing, and it has been suggested that it is computed early in the visual system. In terms of visual attention, the speed with which attention can be deployed based purely on salience is around 25 to 50 ms (Itti & Koch, 2001). It has been suggested that salience is computed in a pre-attentive manner across the entire visual field. Early visual features such as intensity, colour and contrast are processed by neurons at the first stage of visual processing in a massively parallel manner. This early processing is evidenced by the "pop-out" nature of salient stimuli - for example, a red dot will immediately stand out from an array of green dots.

1.2.2 COMPUTING SALIENCE

Understanding the way in which salience is computed enables a better understanding of the concept of salience itself, and the role is may play in attentional selection and movement planning. The way in which salience is most commonly conceptualised is via the saliency map devised by Itti and Koch (2001) as shown in figure 1.1.

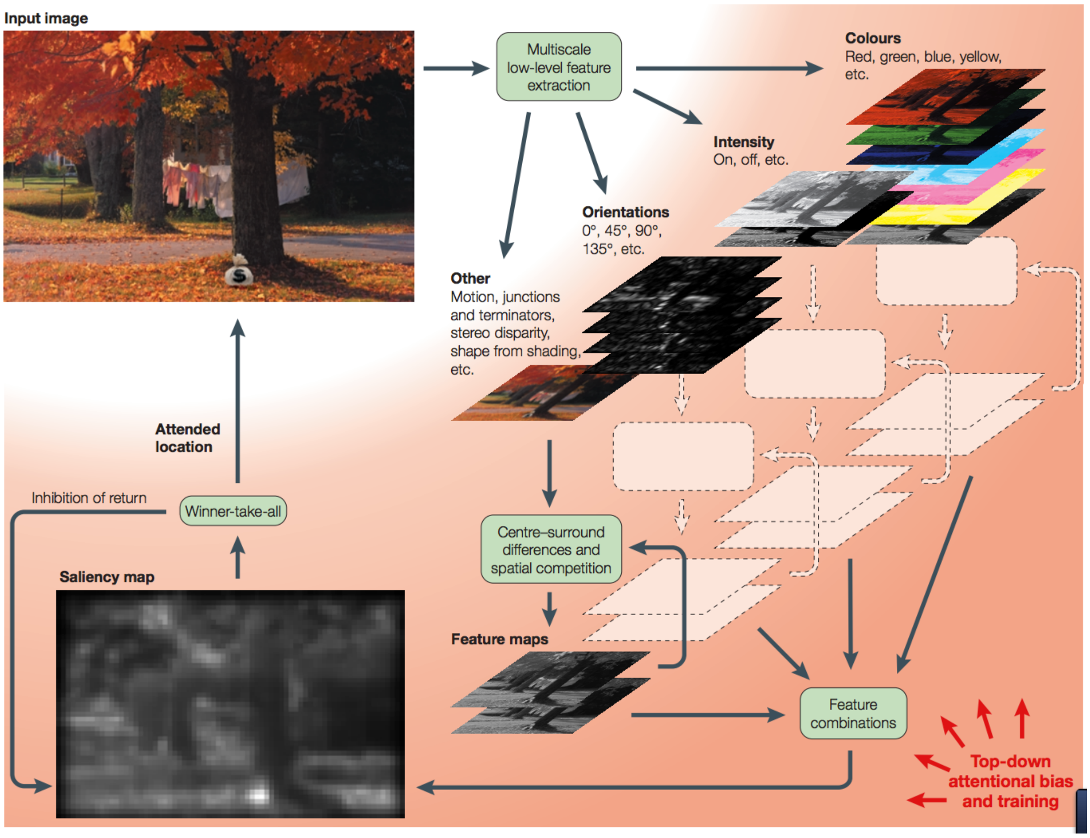

Figure 1.1 - The salience map as conceived by Itti & Koch (2001).

This map describes the way in which features in our environment are evaluated to determine the most salient part of the scene. In computing salience, an image is broken down into low-level features such as colour, intensity and orientation. These feature maps highlight areas which differ from their surrounds, and these stand-out areas are then combined into a saliency map, where the most salient feature is computed in a 'winner take all' fashion, and attention is then directed to that feature. Attention is thus allocated to stimuli in order of decreasing salience (Itti & Koch, 2001). A feature is therefore defined as salient if it wins the competition based on one or more of its visual features. However, the computation of salience is susceptible to top-down attentional bias and training effects, and these influences may affect where attention is ultimately directed (Fecteau & Munoz, 2006). These influences have provided a basis for the criticism of this simple model: for example a simple saliency map account does not take into consideration high-level factors such as behavioural relevance, reward, uncertainty, learning or priors, and while it can explain patterns of attentional capture in simple visual search tasks, it does not so accurately explain patterns of eye-movements in more naturalistic scenes (Tatler, Hayhoe, Land, & Ballard, 2011). These shortcomings have inspired the suggestion of a more comprehensive 'priority map' that will be discussed later.

1.2.3 HOW DOES SALIENCE AFFECT BEHAVIOUR?

So how does salience affect where an individual looks, and where they direct their attention? Ultimately, people want to direct attention to the place in the environment that is the most important for their current goal so that they can carry out that goal under attentional supervision. This goal-related attention can be described as 'top-down.' Contrasting with the bottom-up allocation of gaze, top-down processes direct attention to the part of a scene which is most relevant to the current task. There is a large amount of evidence to suggest that top-down influences are stronger than pure bottom-up processing when attention is directed during a task (Hayhoe, Shrivastava, Mruczek, & Pelz, 2003; Land, 2006; 2009; Rothkopf, Ballard, & Hayhoe, 2007; Triesch, Ballard, Hayhoe, & Sullivan, 2003). However, stimulus salience should not be discounted, as there is equal evidence to suggest that this low-level processing is important when determining where, and how, attention is directed. The evidence for both bottom-up and top-down processing will be outlined henceforth.

1.2.4 TOP-DOWN VS BOTTOM-UP

Many studies have explored the role of top-down control of attention to provide evidence that the conspicuity, or salience, of objects is far less important than their role in a task (Land, 2006), although early studies suggest that task relevance may play a role in where eye movements are directed (Yarbus, 1967). Subsequent studies have explored the relationship between task-demand and stimulus salience by measuring eye movements in natural tasks, finding that the eyes were driven more by the 'script' of the activity than the intrinsic salience of other objects in the scene, (Land et al., 1999), and that it is the task being completed that constrains what objects the gaze system will target (Hayhoe et al., 2003). Indeed, in a virtual reality task, it was seen that participants fixated primarily on task-relevant objects, even when salient distractors were added to the scene (Rothkopf et al., 2007). These studies provide evidence that in an extended, natural task, factors such as task demands may influence where attention is allocated, and additional evidence suggests that only task-relevant information is attended, and much less information is automatically computed by the visual system than was previously thought (Triesch et al., 2003).

In terms of pure salience maps, it has been suggested that these salience map models can account for the attentional allocation for hand movements, with evidence suggesting that initiation latencies of pointing movements during a visual search task are faster for high rather than low contrast stimuli. This suggests that salience can affect both attention and perceptual performance, as well as the guidance of manual pointing movements, and these models can, to some extent, be used to account for this (Zehetleitner, Hegenloh, & Muller, 2011). So, it seems as though there may be an effect of both top down and bottom up processes in determining where attention is directed, and this could also be described as the difference between exogenous and endogenous attention. Indeed, these differences in attention may explain the differences in studies citing either top down or bottom up influences.

Recently it has been argued that stimulus salience plays a vital role in the allocation of attention, and that in fact the initial processing of visual information in the brain is completely stimulus-driven (Theeuwes, 2010). Theeuwes argues that the processing that occurs up to 150 ms after a scene is viewed is based purely on object salience, and only after 150 ms does top-down control have any influence over where attention is directed. This viewpoint is contrary to that of aforementioned studies, which deem top-down processes to be the more influential factor in determining where attention is directed. Neurological evidence however supports this time-line of information processing: a study by Hickey et al. (2009) used EEG to explore the deployment of exogenous (salience-driven) and endogenous (task-driven) attention, and found that attention deployed immediately after stimulus onset was exogenous, and only after a certain delay is attention endogenously driven (Hickey et al., 2009). This dual influence of both top-down and bottom up factors has also been seen in studies showing that saccades with shorter latencies tend to be more salience-driven than those with longer latencies (van Zoest, Donk, & Van der Stigchel, 2012), and it has been suggested that this may reflect the processing of both exogenous and endogenous stimuli. This indicates that stimulus salience may be important for capturing attention immediately after a stimulus is presented, while task-relevant stimuli may only become important later. This however also demonstrates that even both initial salience and bottom up processes and task demands are important for attentional highlighting, so a model of attentional capture based on salience alone is inadequate: a more expansive model is needed to incorporate the effects of both salience and task demand, since both of these factors seem to play an important role in directing attention.

1.2.5 THE PRIORITY MAP

The saliency map of Itti and Koch (2001) allowed for the influences of cognitive bias when computing salience, which suggests that the concept of ‘salience’ may not be an entirely bottom-up process. It has been suggested that a combination of bottom-up and top-down processes determine which is the most ‘interesting’ element of a scene (Masciocchi, Mihalas, Parkhurst, & Niebur, 2009), and indeed it has been suggested that visual input may be processed by a ‘priority map’ rather than a pure saliency map (Fecteau & Munoz, 2006).

This priority map is proposed to integrate both bottom-up and top-down signals to determine the attentional priority of items, which in turn determines how visual attention should be directed - to the item with the highest attentional priority. Navalpakkam and Itti (2002) conceptualised a model of how attention is allocated, incorporating both salient elements of a scene, and cognitive processes such as task demands and working memory demands (see figure 1.2). In this model, the visual system uses the elements of three simultaneous ‘maps’ to determine which part of the scene to direct attention or eye movements to. The salience map is created by extracting the most salient elements of the scene; the task-relevance map is created from the behavioural relevance of individual scene elements, and the attentional guidance map is calculated as the product of both salience and task relevance maps. This model incorporates an ‘agent’ as the bridge between working memory, long term memory and the maps that are being maintained by the visual system. For the purposes of this thesis however, the most relevant element of this model is the interaction between the salience map, task relevance map, and attentional guidance map. This conceptualisation of the interaction between low-level visual stimuli, task relevance and attention may help to explain how and why attention is allocated across the visual field when different motor tasks are being completed, and this interaction between attentional ‘priority’ and movement planning will be discussed further in section 1.6.

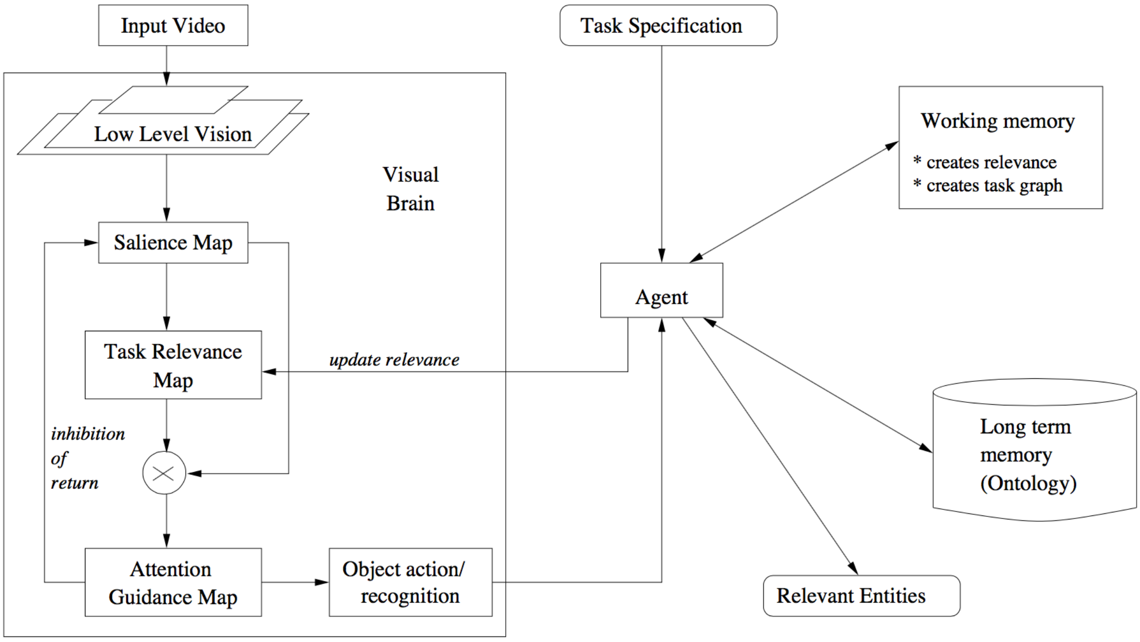

Figure 1.2 – model of how an attentional guidance map may be calculated. The scene is processed by low-level visual processes, before influences such as memory and task demands create an additional "task relevance map" which combines both low-level salience information and task demands to allocate attention in the attentional guidance map. From Navalpakkam & Itti (2002).

The idea of a priority map has been supported by empirical evidence (Bays, Singh-Curry, Gorgoraptis, Driver, & Husain, 2010) showing that when both goal-related and salient distractors were presented simultaneously, participants directed attention to the stimulus with the highest combined priority. In the same study, patients with damage to the posterior parietal cortex were also studied, and their pattern of response suggested that there is a unified representation of top-down and bottom-up signals in the parietal cortex, supporting the notion of a priority map which combines both stimulus and goal related signals. Indeed, it has been argued that the lateral intraparietal area (LIP) of the parietal cortex itself acts as this priority map, integrating top-down and bottom-up signals to create attentional output (Bisley & Goldberg, 2010).

Another recent study investigated the integration of top-down and bottom-up stimuli by comparing the fixations of patients with visual agnosia to those of unimpaired individuals. Visual agnosia is a condition that renders an individual unable to recognise objects, thus essentially depriving them of certain top-down control mechanisms. It was indeed found that this reduction in top-down control meant that patients' eye-movements were directed more often to targets defined by salience alone than ones requiring top-down instructions when compared to healthy controls whose top-down control mechanisms were intact (Foulsham, Barton, Kingstone, Dewhurst, & Underwood, 2009). This suggests that while both top-down and bottom-up influences are important for directing eye-movements, when one of these mechanisms is compromised, the other is weighted more strongly.

This concept of the priority map can be used to explain gaze patterns in the afore-mentioned studies which investigated eye movements in natural environments (Land & Hayhoe, 2001). Land (2009), whilst not referring directly to a priority map, has however described the task-guidance component of as an interaction of a movement sequence as a being guided by a schema system. While the emphasis on this case is on the 'script' of the task (i.e. sequential actions required to make a cup of tea), the idea of an overarching control map that is used to guide eye movements is analogous to the concept of a priority or attentional map controlling this guidance (figure 1.3).

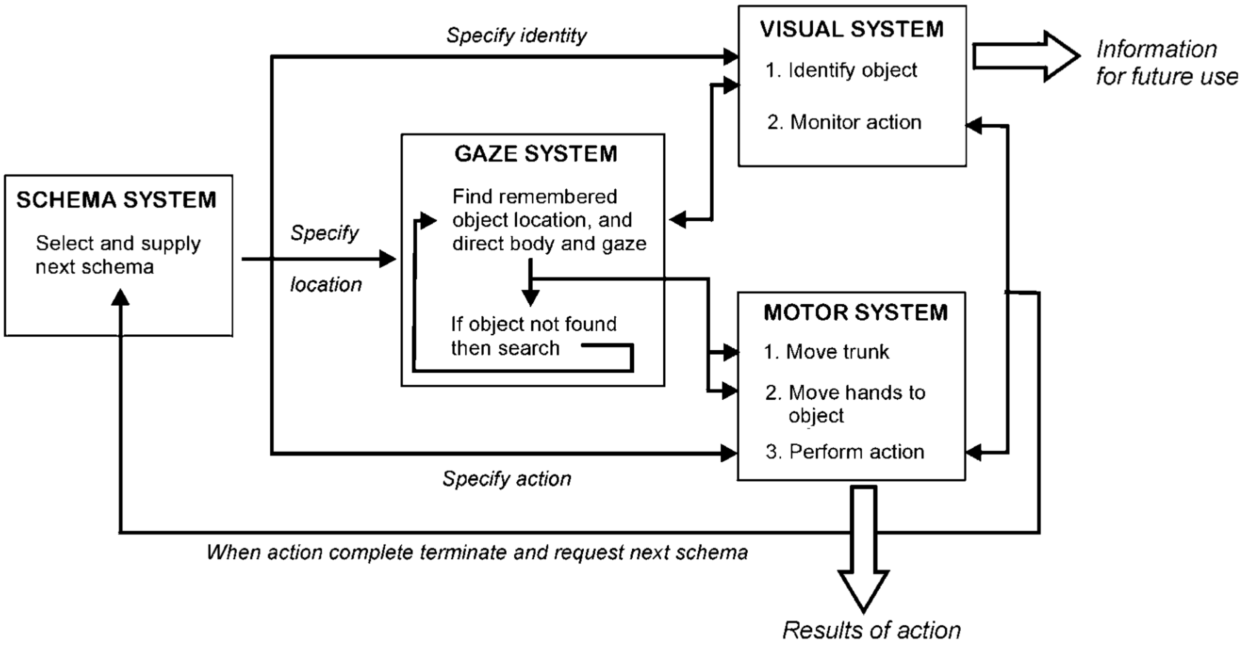

Figure 1.3 – analogous to the concept of a priority map, in this conceptualisation of gaze in natural tasks, the ‘schema system’ uses task information and action scripts to determine where the eyes and hands should be next directed (Land, 2009).

This supports the behavioural evidence that suggests that gaze will generally be directed to the areas of highest behavioural relevance, despite the presence of distractors. This idea of a cohesive priority map has been raised in a number of different contexts, and there is empirical evidence to support the idea that attention and eye movements are controlled by some uniform guidance mechanism that incorporates both top-down behavioural information, and more low-level stimulus features.

So, it seems to be the case that the priority map view is the most parsimonious means of determining how elements are selected in the environment, and while this section provided a brief overview of the reasons why a priority map be behaviourally important, the role of the priority map in integrating attention, eye and hand planning will be further discussed in section 1.6. However, we must first discuss the paramount foundation of this thesis: visual attention.

1.3 VISUAL ATTENTION

The previous section outlined the factors that may determine how an object or location is flagged as being behaviourally relevant. Once this location is chosen, attention can be shifted to that location to either covertly produce a perceptual enhancement without any overt saccade being made, or the location can be attentionally selected as a location to which an upcoming movement will be made. When a movement is being planned to that location, attention then provides additional perceptual benefits that may aid in the process of making a motor plan, and provides ongoing visual guidance for the duration of the movement. This dynamic role of attention during a movement will be further discussed in section 1.4.

1.3.1 ATTENTION ELICITS PERCEPTUAL BENEFITS

Attention can be categorised as either overt attention, where the locus of attention matches the current foveal location, or covert attention, which allows an area in the periphery to be enhanced by the attentional process without making an eye movement (Posner, 1980). While attention can be categorised as either exogenous or endogenous attention, and while there may be differences in the suggested mechanisms underlying these different forms of attention (Lu & Dosher, 2000), a thorough discussion of these issues is beyond the scope of this thesis. Hence, this thesis will focus on endogenous attention, as all experiments utilise cueing paradigms to deliberately direct attention and movements to the required location.

Attending to a location produces a number of perceptual enhancements at that location, such as increased contrast sensitivity and spatial resolution (Carrasco, Ling, & Read, 2004). There is a wealth of psychophysical evidence that supports the claim that attention produces these benefits, and while it is undisputed that indeed attention does enhance perception of a location, there are numerous potential mechanisms by which this occurs, and attention can seemingly act in many ways. The empirical evidence for attentional benefits will be outlined, as well as the psychophysical models used to explain attention, and a brief account of some possible neuronal mechanisms that may explain how attention changes the appearance of an attended location.

There have been numerous studies demonstrating how attention produces perceptual benefits at the attended location (Carrasco, 2011; Carrasco et al., 2004; Carrasco, Talgar, & Cameron, 2001; Palmer, Verghese, & Pavel, 2000), and perhaps one of the most notable of these is the apparent increase in contrast sensitivity which can be seen at the attended location. Studies have shown that attending to a location alters the appearance of objects at that location by increasing contrast sensitivity, and thus apparent contrast (Carrasco et al., 2004; Morrone, Denti, & Spinelli, 2002). In the case of this study, attending to a location changed the perceived contrast of stimuli, allowing observers to perform better in perceptual discrimination tasks. Similarly, using a 2AFC task of contrast sensitivity on tilted gabor patches, Pestilli, Viera & Carrasco (Pestilli, Viera, & Carrasco, 2007) found that performance increased when attending to a location, creating an increase in perceived contrast at that location.

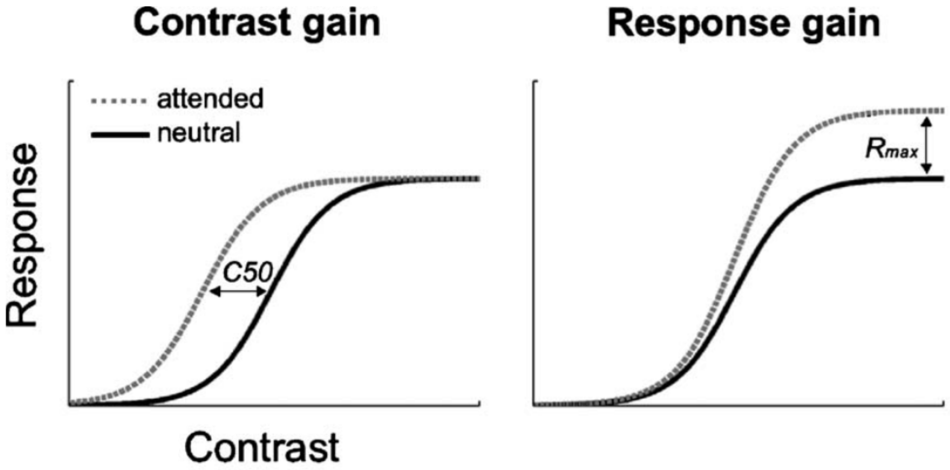

Figure 1.4 – two possible mechanisms of how attention may alter stimulus appearance (from Carrasco, 2011). The left graph shows how contrast gain results in a leftward shift in contrast threshold (C50), while the right graphs shows response gain triggering a change in the slope and asymptote (R_{max}) of the response function.

It has been suggested that attending to a location can increase the amplitude of neural responses and reduce their variability, as well as synchronising the firing of certain neural populations (Cameron, Tai, & Carrasco, 2002; Fries, Reynolds, Rorie, & Desimone, 2001; Carrasco, 2011). Specifically, it has been proposed that two types of gain control mechanisms may be central to the perceived contrast enhancement at an attended area (Sclar, Lennie, & DePriest, 1989a). The first of these mechanisms is contrast gain: this explanation suggests that less contrast is necessary for an "attending" neuron to reach the same response level as a "non-attending" neuron (figure 1.4). An alternative possible mechanism for this attentional enhancement is response gain, which shows an increase in neural firing rate that is proportionate to the intensity of the stimulus. In cases of visual search, it may be the case that this change in gain can also be explained using signal detection theory (Verghese, 2001). This theoretical mechanism has been supported by studies showing that attending to a stimulus in effect increases the visual saliency, or 'effective contrast' of that stimulus (Carrasco et al., 2004; Sclar, Lennie, & DePriest, 1989b).

Indeed, both models have empirical support: for example, Li et al. (2008) found that increased contrast gain could explain attentional enhancement in V1, V2, V3, V3A and V4 neurons as measured by BOLD fMRI activity in those regions, while Ling and Carrasco (2006), using a psychophysical paradigm, noted a leftward threshold shift in the psychometric function of response to the attended compared to non-attended area, suggesting an underlying contrast gain mechanism. Attentional performance patterns reflecting a change in response gain have also been seen. For example, Morrone, Denti & Spinelli (2004) found that a response gain model fits the psychometric functions observed for response to luminance and colour contrast. It may also be the case that a hybrid of both contrast and response gain may account for attentional enhancement: Huang & Dobkins (2005) suggested that contrast gain could account for enhancements in the early stages of visual processing, while response gain accounts for enhancements in the later stages. It could be the case that early visual areas such as V4 and MT show the contrast gain effect (Martınez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000), whereas response gain reflects later (unspecified) stages of processing. Nonetheless, whatever the mechanism may be that underlies attentional facilitation, the functional outcome of both explanations is that stimulus contrast is perceived as being higher when that stimulus is being attended to. However, interestingly (and conversely), this “gain” in neural activity corresponding to the attended area is also accompanied by a reduction of gain of neurons corresponding to surrounding, un-attended areas (Martınez-Trujillo & Treue, 2002). This dual function of attention will be discussed more in section 1.3.3 in relation to the possible pattern of both attentional facilitation and suppression seen in the visual field.

Other stimulus characteristics have also been found to be enhanced by attention, including the finding that attention modulates performance on detection and identification of oriented lines (Blanco & Soto, 2002). This is directly relevant to the experiments in this thesis, as they utilise an oriented line discrimination task. Another interesting perceptual enhancement is the change in spatial resolution that attention elicits, and the proposed underlying mechanisms for this phenomenon. Yesurun and Carrasco (1998) found that spatial resolution in both gap and vernier resolution tasks were enhanced when attention was cued to the stimulus location compared to when it wasn’t. They also found that spatial resolution was enhanced in texture segmentation tasks (Yeshurun & Carrasco, 1998). This evidence shows that attending to a location allows participants to distinguish finer grain details compared to at non-attended locations. They postulated that this finding was evidence that attention affects the spatial filters that may be responsible for the way visual stimuli are processed. These filters increase in size as eccentricity from the retina increases. By shifting attention to the areas in the visual field governed by larger retinal spatial filters, participants’ performance in a fine texture discrimination task increased, possibly due to a decrease in the size of the spatial filters due to the attentional enhancement. This decrease in filter size may be due to a related shrinking of the receptive field around the attended stimulus, allowing finer spatial resolution, thus enhancing the perceptual performance in relation to that stimulus. Attending to a stimulus can also allow the spatial filter to match that of a cued stimulus feature such as orientation (Baldassi & Verghese, 2005). Neurophysiological evidence does indeed support this notion that attention can reshape a receptive field. Anton-Erxleben, Stephan & Treue (2009) found that when attending to a stimulus inside the area of a receptive field of an MT neuron, the receptive field (both surround and centre) shrank toward the attended location. Interestingly, when attending to an area adjacent to the receptive field, the receptive field expanded, suggesting a mechanism that enhances representation of both the attended area and surrounds – see figure 1.5 for further explanation (Anton-Erxleben et al., 2009; Womelsdorf, Anton-Erxleben, & Treue, 2008).

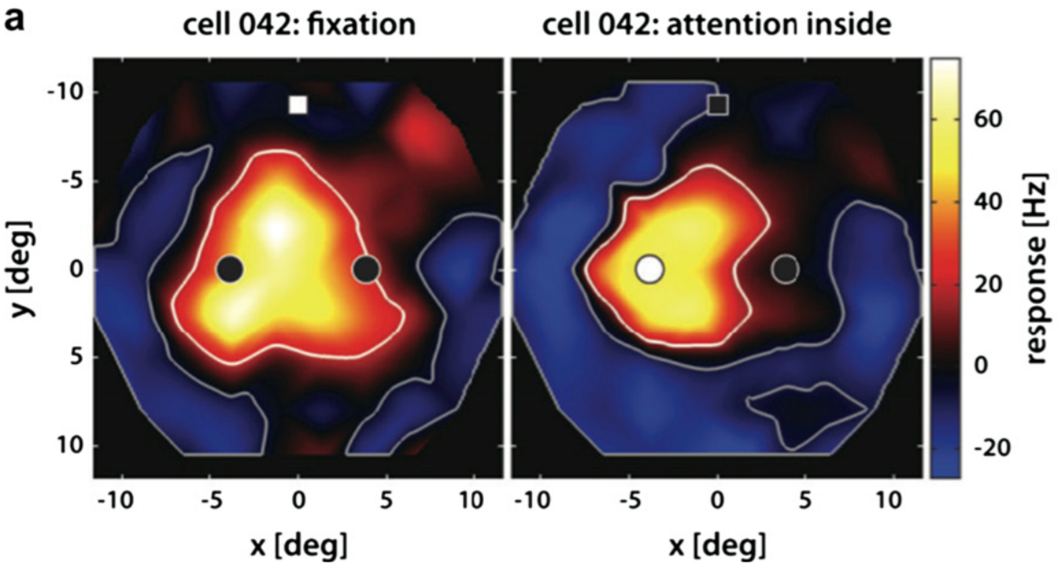

Figure 1.5 – receptive field map of macaque MT neuron (from Anton-Erxleben et al., 2009). The image on the left depicts the receptive field when fixation is on the white square at the top of the image. The image on the left depicts the receptive field when fixation is on the white circle to the left. It can be seen that the receptive field area (outlined in white) has shrunk around the attended target, while the surrounding inhibitory area (outlined in grey) has also shifted, and in this case, expanded.

This idea that attention can cause a neural modulation at locations neighbouring the attended area was also supported by evidence that whilst enhancement in V4 extended to adjacent locations, this spread was asymmetrical, dependent on the particular cell being recorded: some cells had the highest response when attention was directed to the left of the stimulus, others when it was directed to the right, suggesting an interesting spatial interaction between neuronal enhancement and attention (Connor, Preddie, Gallant, & Van Essen, 1997). This means that attention allows certain receptive fields to be flexible, and allows them to transcend their spatial resolution limit, particularly in higher cortical visual areas (Carrasco, 2011).

So in brief, attention elicits a number of perceptual benefits at the attended location, and this can be seen in both the psychophysical and neurophysiological evidence. It is well established that attending to an area enhances perception of that area, even if the mechanisms by which this occurs are not completely understood. Obviously attention is of great behavioural importance in a predominantly visually navigated world: the models of salience maps and priority maps and action schemas described in section 1.2 all share the ultimate goal of describing how people decide to shift their attention to a particular area, with the assumption that that shift will be both visually, and behaviourally beneficial. The next step in the story of attention is to understand what happens when the impending location to be attended is selected: how does attention actually "shift" to this upcoming location?

1.3.2 ATTENTION SHIFTS – THE PROFILE OF COVERT ATTENTION

When attention needs to be directed to a location, we can say that attention "shifts" to that location: essentially this means that a previously unattended location is now receiving a perceptual benefit from attention being directed there. The timeline of this shift is important as it can demonstrate how attention shifts, and at what point attention may be important when a task is being completed. Additionally, the timeline of a covert attentional shift can be compared to that of the pre-movement attention shift for different types of movements: for example, eye and hand movements. Comparing the temporal properties of the attentional shift between these modalities gives an insight into the planning mechanisms that might be utilised when different movements are or aren't being planned, and how attention may play a role in this planning process. The covert attentional shift has a well-documented timeline, and it is important to outline its characteristics: the timeline of attention when no movement is being made provides a solid basis for a comparison with pre-movement attention. Any temporal differences observed can then more readily be attributed to the effects of the motor planning itself. Therefore, this section will look at how attention shifts when there is no action being planned, or in other words, when a location is being attended to covertly.

The temporal properties of covert attention have been studied comprehensively over the last couple of decades (Cheal & Lyon, 1991; for example: Liu, Stevens, & Carrasco, 2007b; Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989), and studies are in general consensus that when directing covert attention to a location, the peak of this attentional shift occurs at around 300 ms after that location is cued (Nakayama & Mackeben, 1989). This build-up of attention occurs from about 100-275 ms after cueing (Muller & Rabbitt, 1989), and the duration of this attentional facilitation can be maintained for a few seconds after the initial attentional peak occurs at around 300-500 ms (Ling & Carrasco, 2006). ERP evidence has shown that activity related to covert attention shifts starts at 160-360 ms in posterior brain regions, before moving to central regions (200-320 ms and 400-560 ms) and then frontal regions (200-520 ms) (Nobre, Sebestyen, & Miniussi, 2000b). This shows that although the attentional shift may start relatively early, regions associated with the orienting of attention are still active for a sustained period, and different regions may become more important in attentional processing at different time points. This is consistent with evidence that the planning and execution of eye and hand movements incorporates an extensive neural network, with different areas responsible for different stages of these movements.

However, there has been some evidence to suggest that the temporal characteristics of covert attention may be somewhat malleable: when observers know when a stimulus is going to appear, they can orient attention to that stimulus at the appropriate time, suggesting that attention can be temporally as well as spatially cued (Coull & Nobre, 1998). Factors such as cue validity can also affect how covert attention is deployed, with observers giving more weight to the information provided by more valid cues (Giordano, McElree, & Carrasco, 2009). The type of cue used also plays a role in the speed of the attentional shift, and manipulating how informative a cue is, or type of cue, can also be seen to affect attentional performance (Kinchla, 1992; Yantis & Jonides, 1990). The properties of a cued stimulus could additionally play a role in how attention is measured – for example, studies suggest that when there is higher uncertainty in a task, say if the contrast of a stimulus is low, or if its location is uncertain, the effects of using a pre-cue in a task are greater than when there is less uncertainty (Cameron et al., 2002), (Pelli, 1985). This shows that while the time-course of covert attention is generally accepted to be around 300 ms after a cue, this is not necessarily always the case, and there are a number of factors that may affect this discrepancy in results, hence it is important to note how different experimental paradigms and task demands may impact measures of attention.

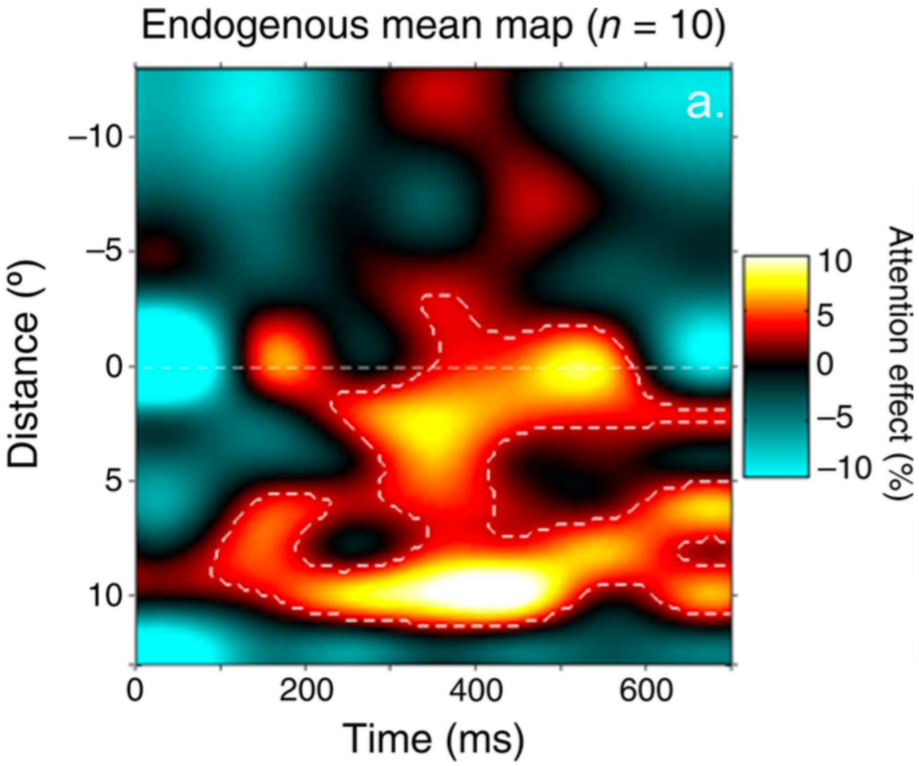

Figure 1.6 – the spatiotemporal properties of the covert attentional shift, from (Koenig-Robert & VanRullen, 2011) . The image shows the attentional shift on the cued side (positive values on the Y axis) compared with the uncued side (negative values on the Y axis), as this changes with time (on the X axis). The characteristics of the attentional shift show both areas of facilitation (red/orange) and inhibition (blue/black).

The spatial profile of covert attention, and its interaction with these temporal characteristics is equally as fraught with methodological concerns which have been seen to affect how attention shifts across the visual field. Early work by Shulman et al. (Shulman, Remington, & McLean, 1979) suggested that attention outward through space from a cue, in an analogue fashion, with reaction times improving at longer stimulus onset asynchronies (SOAs) as eccentricity of a target increased. This model of the attentional shift was however disputed later by Murphy & Erikson (Murphy & Eriksen, 1987), and Ericksen & Webb (Eriksen & Webb, 1989), who found no relationship between the time to shift attention and eccentricity of the attended object. Eriksen & St James (Eriksen & St James, 1986) additionally found that the size of attentional focus can vary depending on whether a pre-cue is used, and that attention is distributed in a more general, uniform manner than previously suggested. Factors such as pre-cues again act as further confounding influences on measuring a consistent spatial profile of covert attention. As will be discussed in greater length in section 1.5.4, experimental factors such as pre-cues, cue length, SOA length and discrimination task paradigm may also affect the measure of attention relative to when a saccade or reach is being made. As with covet attention, these factors may account for discrepancies in the results of measures of pre-movement attention.

More recent work by Koenig-Robert and Van Rullen (2011) has however investigated both the spatial and temporal characteristics of the covert attention shift in a comprehensive manner, for both endogenous and exogenous attention shifts. Endogenous attention showed peak enhancement around 400 ms after the cue, at around 8 to 10 degrees eccentricity from central fixation. The temporal properties of the attentional shift were consistent with previous literature, however this study was particularly interesting as it mapped the spatial shift as well as the temporal shift, showing a number of local peaks and troughs across the visual field, with enhancement seeming to move in an outwards direction from the focal point (see Figure 1.6). This shows that the covert attentional shift is a dynamic spatiotemporal enhancement, and while some areas may show an increase in performance, other locations show a concurrent inhibition in performance. This dynamic pattern of facilitation and inhibition is interesting as it highlights the duality of the attentional orienting process, and suggests that the mechanisms controlling attention might be more complex than just providing enhancement at a single location.

1.3.3 THE SPATIAL PROPERTIES OF ATTENTION – FACILITATION AND INHIBITION

In the previous sections, attention has been discussed as a primarily facilitatory effect, and indeed, attending to an area does provide a perceptual enhancement at that location. However, the way in which attention acts seems to be far more complex than a mere facilitation effect: both psychophysical and neurophysiological studies have recently suggested that attention acts in a dual facilitation/suppression manner. Attention acts to not only enhance areas of interest in the visual field, but also supresses area that are irrelevant: this in effect makes the attended area even more salient compared to the surrounding areas of suppression.

The actual extent of the attentional ‘window’ is as yet unresolved. Some studies have traditionally viewed attentional facilitation as a type of spotlight that highlights small parts of the visual field at a time (Shulman et al., 1979), whilst others view it as a broader, more general enhancement of space (Baldauf & Deubel, 2009; 2010; Gersch, Kowler, Schnitzer, & Dosher, 2009). The previously mentioned study by Koenig-Robert & Van Rullen (2011) showed that generally, during endogenous attention tasks, attention spread from the fixation point across the visual field up to about 8 to 10 degrees eccentricity (see Figure 1.6). Specifically, this study measured contrast sensitivity thresholds at 14 eccentricities from the fixation point at the centre, and 11 SOAs, and interpolated between these points to create a comprehensive map of covert attention across eccentricity and time. The magnitude of the attentional facilitation observed was about 12 % modulation in contrast sensitivity, at 10 degrees from the cue. Additionally, they observed a secondary locus of attentional focus at the central cue location – this suggests that attention can be spread over various spatial foci. They also observed areas of inhibition across the visual field that countered the other areas of attentional facilitation.

This idea of attention producing areas of inhibition as well as facilitation has support from both physiological and psychophysical data. In visual search tasks, it has been found that there was interference for objects located close to the attended item (Bahcall & Kowler, 1999), and that items neighbouring the attentional focus were supressed (Caputo & Guerra, 1998). This suggests that the space closest to the attentional focus may be subject to some form of attentional suppression. Cutzu & Tsotos (2003) conducted a psychophysical experiment to examine the spatial properties of attention surrounding an attended target during a covert attention task. They found that there was an annulus of inhibition directly surrounding the attended location, but performance increased gradually with eccentricity across the visual field. A similar pattern was observed in a magnetoencephalographic study, where recordings of cortical activity suggested that when attending to a stimulus, there is an enhancement at the focus of attention, surrounded by a narrow band of inhibition (Hopf, Boehler, & Luck, 2006). Again, as with the psychophysical study, performance returned to a normal level at further eccentricities. This centre-surround pattern was also exhibited in the FEF, as distractors were suppressed in a search task, with the behaviourally relevant location being enhanced (Schall, Sato, Thompson, Vaughn, & Juan, 2004). This inhibitory pattern was also seen in a task where observers had to attend to a target in a centre/surround stimulus configuration: in this case it was seen that the extent of the attentional window can change, depending on the segmentation properties of the stimulus, with the attentional window decreasing as the segmentation becomes less defined (Kim & Verghese, 2012). It was suggested that this may be due to facilitation at the centre of the target, and suppression of the surrounds – a pattern which reflects the aforementioned work on attentional inhibition.

The dichotomy of attentional facilitation and suppression has also been seen in movement studies, suggesting it might also be a property of pre-motor attention. In a study of reaching sequences, Baldauf, Wolf & Deubel (2006) measured the attentional facilitation at locations between each subsequent movement location. This study found that performance at these ‘between’ locations was greatly reduced compared to performance at the actual reach target (a difference of approximately 30 % performance increase). Further, an ERP paradigm was used to record the neural correlates of attentional facilitation during a similar sequential reach movement task (Baldauf & Deubel, 2009). In this study it was found that when probes were presented at the locations of impending movement locations, the amplitude of the N1 components elicited was higher than when the probes were presented at movement irrelevant locations. Interestingly, the inter-movement locations also elicited a much lower N1 response than the actual movement targets, suggesting again that attention may only select relevant movement goals, and this selection does not spread to surrounding locations. Further psychophysical evidence comes from a letter discrimination task, which found attentional facilitation at the location of an impending saccade, while other locations showed a concurrent suppression of performance (Doré-Mazars, Pouget, & Beauvillain, 2004). Additionally, when sequences of saccades were being made, it was seen that inter-saccade locations were actively supressed relative to locations on the upcoming saccadic path (Gersch, Kowler, & Dosher, 2004). Other studies have shown that performance at the cued saccade target is better than surrounding targets (Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012), and in particular Bahcall & Kowler (1999) investigated the effect of attentional 'interference' between spatially close targets, finding that attentional performance at locations surrounding a cued target was worse the closer these locations were to the target.

This could suggest that attending to a location produces a reduction of processing capacity for surrounding locations, so attending to one location always comes at the attentional expense of another location. This may be because supressing nearby targets reduces interference with the cued target, allowing for better perceptual performance (Shiu & Pashler, 1995). This idea of attending to one target to the attentional determent of another has also been investigated in the context of determining whether the eye or hand carries more attentional weighting in concurrent saccade/reach tasks. For example, some studies found that either the saccade target received attentional facilitation over the reach target (Khan, Song, & McPeek, 2011), while others suggest that attention can be split across both separate reach and saccade targets, without the need for inhibition of one of the targets (Song & Bédard, 2013). These ideas will be discussed further in section 1.5.2., and this general spread of attentional facilitation across the visual field will be discussed further in section 1.4, in relation to both saccades and hand movements.

So, attentional facilitation gives a number of perceptual benefits, and these can be measured using both behavioural and neurophysiological paradigms, and it can be seen that the spatial and temporal properties of attention seem to have a fairly flexible pattern, even when a simple endogenous covert attention task is being conducted. However, in the interactive environment that is our world, attention serves a greater purpose than covertly plucking areas of relevance from the visual field while we stare fixedly at one point, and that purpose is to guide both eye and hand movements.

1.4 ATTENTION AND ACTION

Research has shown that visual attention and eye movements seem to be linked, and studies have certainly demonstrated that a pre-saccadic shift of attention occurs to the location of the impending saccade (Deubel & Schneider, 1996; 2003). Many researchers have argued that the location of the pre-saccadic attentional shift is necessarily linked with the location of the upcoming saccade, and that these cannot be dissociated (Khan et al., 2011; for example: Song & McPeek, 2009; Song & Bédard, 2013) – however, there is evidence to the contrary that suggests that attention and action can be dissociated, depending on the task demands of the perceptual and motor tasks taking place (Blangero et al., 2010; Khan et al., 2009). The research surrounding attention and action can be generally be categorised into studies that support a shared representation for the two actions, and studies that argue that attention and action are separate entities in the brain. A good place to start when exploring the wealth of literature on the subject is with the theories that have been underpinning the general understanding of the area. Once the basic assumptions are understood, it is easy to categorise the empirical findings into one of the two stances, and this is important in understanding the theoretical and experimental paradigms that constitute the greater part of this thesis.

1.4.1 CURRENT THEORIES OF PRE-MOVEMENT ATTENTION

One of the major theoretical questions that attention researchers have been investigating is whether attention for perception and attention for action are driven by the same internal mechanisms, or whether they are completely separate entities.

There are two predominant theories that try to explain this – the more commonly cited Pre-Motor Theory of Attention (Rizzolatti, Riggio, & Sheliga, 1994), and the Visual Attention Model (VAM) (Schneider, 1995).

The Premotor Theory of Attention

First formally expressed in 1994 by Rizzolatti, Riggio and Sheliga, this theory attempts to reconcile the attention that accompanies visual perception, and that which accompanies movements. This theory is based around three main claims:

1. Attentional selection mechanisms are not separated from spatial pragmatic maps used for the perception of a scene. The neural mechanisms controlling attention are no different from these spatial maps.
2. Attentional facilitation is caused by the preparation of visually-guided, goal-directed movements.
3. The particular pragmatic maps that then produce or guide attention are activated according to the requirements of a particular task.

The basic assumption that underpins the premotor theory is that attention for action and attention for perception are inextricably linked (there is no separate attentional resource for perception alone), and that planning of a motor action is both necessary and sufficient for attention to be deployed. There has been much debate about whether the assumptions of this theory are correct, with some proponents providing evidence for the theory, and others heartily disagreeing (see Smith & Schenk, 2012) for review).

It seems to be the case that there are a number of shared mechanisms for perception and action, and while this supports the overall gist of the pre-motor theory, the evidence seems to suggest that the specific cornerstones of the theory are somewhat over-simplified. More recent studies and more precise neurophysiological evidence suggest that the pre-movement attentional system may be far more complex than the theory allows for, and this system in fact integrates information from a large number of interconnected neural circuits (Smith & Schenk, 2012). For example, the postulation that motor activation is functionally equivalent to a shift of attention should mean that the locus of at upcoming movement and the attentional shift should always be coupled. While this is often the case (as will be outlined further in section 1.4.2), it is not necessarily always true, as studies have shown that depending on differing paradigms and task demands, attention can be dissociated from the movement target (Kowler, Anderson, Dosher, & Blaser, 1995; Montagnini & Castet, 2007; Smith & Schenk, 2012). Furthermore, if movement planning really is necessary for a shift in attention, then covert, endogenous shifts of attention should not be possible. While it has been argued that covert attention is merely a 'holding off' of a planned saccades, there is accumulating evidence to rule this out, as studies have shown that patients with oculomotor problems are still able to covertly attend to a location (Gabay, Henik, & Gradstein, 2010; Smith & Schenk, 2012; Smith, Rorden, & Jackson, 2004). The possible mechanisms underlying pre-movement attention, and the evidence about whether they are indeed shared or separate will be discussed further in section 1.5.

VAM and the Selection for Action theory

A different view of the pre-motor attentional shift was proposed by Schneider in 1995, and that is the Visual Attention Model. The critical distinction between this theory and the premotor theory is that VAM, or Selection for Action theories, argues that while there is a link between attention and motor planning, the attentional and perceptual facilitation observed before a movement is not just a result of the movement planning. Rather, it is a requirement that attention shifts to the goal location to encode its spatial position and facilitate movement planning. However, this account suggests that the attentional mechanism that is activated prior to a movement is a completely separate resource that is merely utilised by movement planning systems, and is not otherwise linked to these networks (Schneider, 1995).

The question of which, if any, of these theories is correct is still unresolved, as there is evidence in support of both accounts. Both accounts agree that an attentional shift precedes a a movement is made to a location. However, the controversial issue is whether this attentional shift is caused by, and is undissociable from the motor systems (premotor theory), or whether it is a separate resource hijacked by the motor planning network (VAM).

One issue that neither of these theories attempts to resolve is whether the attentional resources related to eye and hand movements are shared, or whether there are separate resources being used by the different motor effectors. Both the pre-motor theory and VAM discuss eye and hand movements, but the emphasis is generally on saccades, and if hand movements are being made, the general assumption is that saccades are being made to the same target location as the hand movement. The issue of whether or not these attentional faculties are dissociable is one that will be discussed later in section 1.5. However, the theory can have no support without the empirical evidence, so the studies that have shown this pre-movement attentional shift will now be outlined.

1.4.2 PRE-MOVEMENT ATTENTION SHIFT

Although early psychophysical experiments argued against the notion of a pre-movement attentional shift i.e. (Remington, 1980), it is now commonly accepted that attention and saccades seem to be closely linked. Before the enactment of a saccade or hand movement, attentional facilitation increases at the location of the upcoming target. Many studies, utilising different techniques have demonstrated this. For example, contrast discrimination tasks (Rolfs & Carrasco, 2012; White, Rolfs, & Carrasco, 2013), letter identification tasks (Deubel & Schneider, 2003; Doré-Mazars et al., 2004), orientation discrimination tasks (Zhao et al., 2012), and ERP studies (Collins, Heed, & Röder, 2010) have all shown enhanced performance when a movement is being made to the location of the perceptual probe/discrimination task, or when a manual response is being prepared (Eimer, Forster, Velzen, & Prabhu, 2005). Not only this, but there is evidence to suggest that when a saccade is being planned to a location, subjective perceptual experience of visual intensity (as measured by contrast threshold) also increases (Rolfs & Carrasco, 2012), suggesting that movement planning may enhance perception via a number of different pathways, and on many different levels of neural representation. It could be the case that each of these perceptual benefits can be attributed to a different part of the attentional neural network, as attention has been seen to affect activity from lower visual areas such as V1, to higher parietal and temporal areas (Moore, 2006). These neural processing mechanisms will be discussed in detail in section 1.4.6.

Many studies have shown that attention is better at the location of a planned saccade than at movement irrelevant locations. Kowler et al. (1995) used a letter identification task in a circular array of eight letters, to determine whether perceptual performance was better at the location of an upcoming saccade than other locations, and found that perceptual attention could not be entirely dissociated from the saccade goal, even when a perceptual judgement had to be made to another location. Similarly, Deubel & Schneider (1996) used an array of five characters which changed from either an ‘8’ symbol to a ‘3’ or ‘E’ symbol as targets, with other elements in the array changing to ‘2’ or ‘5’ as distractors. They found that letter identification performance was greatest when a saccade was being directed or even merely planned to the location of discrimination performance. When the saccade and perceptual discrimination occur at different locations, performance was greatly diminished. Zhao et al. (2012) also found that perceptual performance was better at the saccade goal than other locations, across differing levels of target contrast, even when there was external noise. Rolfs & Carrasco (2012), Deubel (2008) and Jonikaitis & Deubel (2011) all reported similar results of attentional facilitation at the saccadic endpoint. However, as these studies were primarily investigating the time-course of the pre-saccadic attentional shift, they will be discussed further in section 1.4.3.

This pre-saccadic attentional shift has also been seen in more naturalistic tasks, where free saccades were made around the screen and attention measured in the pauses between saccades (Wilder, Kowler, Schnitzer, Gersch, & Dosher, 2009). This importantly demonstrates that the observed attentional shift is not merely an artefact of artificial experimental manipulations. Interestingly, the link between saccades and attention seems to suggest not only a facilitatory coupling, but also an inhibitory coupling – when participants were instructed not to make a saccade to a location, perceptual performance was suppressed at that location (Dhawan, Deubel, & Jonikaitis, 2013). This provides further support for the notion that attention is an inhibitory as well as facilitatory process, and movement planning may also affect this.

In addition, evidence suggests that preparing a saccade not only facilitates perception at the target location, but actually facilitates the saccade itself, as a study showed that when saccades were made to a cued location, saccade latencies were shorter than when they were uncued (Crawford & Muller, 1992). This pattern of saccade facilitation was also found by Belopolsky & Theeuwes (2009), who observed shorter saccade latencies when a saccade was being planned to a location to which covert attention had previously been directed.

The shape and spread of this pre-saccadic attentional shift is an unresolved issue, and while some studies argue for a single, focussed attentional locus (Song & Nakayama, 2006), others argue for a more distributed generalised attentional enhancement across the visual field (Baldauf & Deubel, 2009; 2010; Gersch, Kowler, Schnitzer, & Dosher, 2009). The spread of the attentional locus, or loci, is also an unresolved issue, as it is unclear whether the enhancement is distinct, or more Gaussian in nature. An ERP study suggested that the attentional 'window' might form a gradient, with the peak response being shown at the saccade target, and strength of responses diminishing with eccentricity from this location (Collins et al., 2010).

It may be the case that the measured spread of attentional enhancement is dependent on the particular task demands of the experimental paradigm – if for example participants are required to make sequences of hand movements (Baldauf

& Deubel, 2009; Gersch et al., 2004; 2009), the attentional facilitation across these behaviourally relevant locations may reflect that. In comparison, if participants are required to only make a single movement, it would make sense that attention would be allocated in the most parsimonious manner, and thus only the one, upcoming, behaviourally relevant location would be selected for attentional enhancement. The pattern of attentional facilitation during sequences of saccades and hand movements will be discussed further in section 1.4.5.

While there is strong evidence that attention does indeed shift to the location of an upcoming reach, there has been speculation about whether this attentional shift is related to target selection, or whether the shift is used to guide the motor plan that is being updated throughout the reach. Research looking at hand trajectories in a target/distractor task saw curved trajectories that aimed first for the distractor, and then for the target (Song & Nakayama, 2006). This suggests that the focus of attention is changing throughout the course of the reach, and the direction of the trajectories reflect this changing focal locus. Examining the temporal profile of attention may provide more insight into how the attentional locus shifts over time, and while the temporal profile alone has been studied (as will be outlined in the next section), the spatiotemporal profile of pre-movement attention has not been explored in any detail. The first experiment in this thesis thus aims to map this spatiotemporal profile, to provide more insight into how the attentional locus might change throughout a reach, and how this might reflect the motor plan both at the outset of the reach, and during the online updating process.

1.4.3 TEMPORAL DYNAMICS – SACCADES

It has been well documented that before making a saccade, there is a shift of attention to the upcoming saccade landing point. It is interesting to compare the temporal dynamics of attention when there is a perceptual task alone to when there is a movement, as this is one way of discerning whether the mechanisms which control the shift may be shared or separate. This in turn can provide evidence for one of the divergent theories on how pre-movement attention is driven. Ultimately however, it is the comparison of the temporal dynamics of pre-saccade and pre-reach attention that is the main focus of this thesis – the timescale of the pre-saccadic shift will be outlined first, followed by the timescale of the pre-reach attentional shift.

There have been numerous studies trying to determine the time-scale of the pre-saccadic attentional shift, however there is some discrepancy in the timing of this shift, which may arise in part from the different paradigms used to measure attention, as will be discussed later in section 1.5.4. Some studies claim the shift accompanying a saccade can happen as early as 50-100 ms after a cue (Deubel, 2008; Rolfs & Carrasco, 2012) (see figure 1.7), and others have found that this shift happens on a slower time-scale, of around 150-200 ms after cue (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Jonikaitis & Deubel, 2011; Montagnini & Castet, 2007).

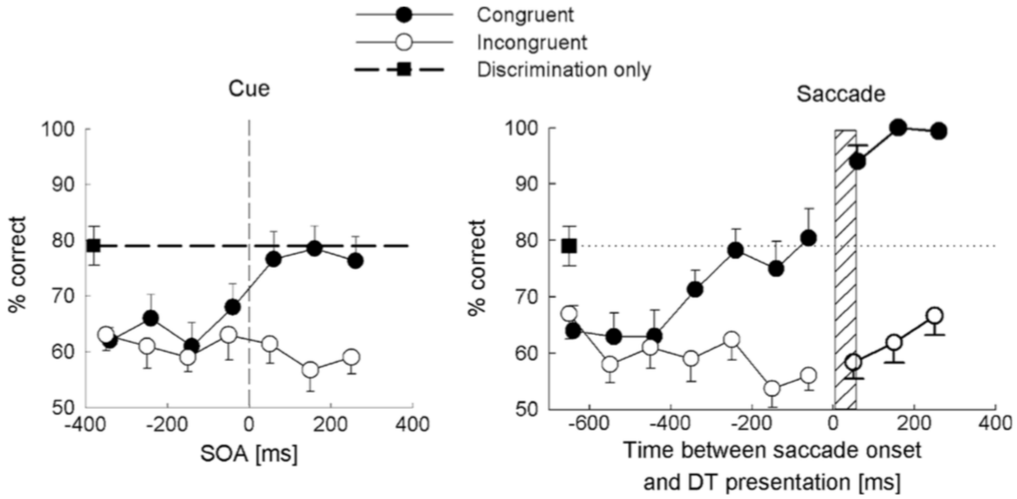

Figure 1.7 – Timeline of pre-saccadic attention from Deubel (2008). This study showed that attention at the saccade location (congruent) was enhanced relative to a movement irrelevant location (incongruent), and this shift starts approximately 100 ms after cue onset (left), or 400 ms before saccade onset (right).

Deubel (2008) measured the attentional shift relative to saccadic onset in a letter discrimination task and found that attention builds up at the saccadic location more so than at other, irrelevant locations, and this shift happens as quickly as 50-100 ms after cue, and approximately 400 ms before a saccade (Figure 1.7). While this study measured performance relative to saccade onset, other studies have measured the attentional shift only relative to cue onset/offset. For example, Castet et al. (2006) found that attention builds up at the saccadic location over a period of 150-200 ms after cue onset. Interestingly, this study found that it was not only the saccade location that showed an attentional facilitation, but locations neighbouring this location also showed a benefit in performance. This shows that the facilitation may not be tightly locked to the saccade target, but may provide a benefit in a broader spread around the target: this contrasts to some previous research in the area, which suggests that attentional enhancement may only be seen at the saccade target (Deubel & Schneider, 1996; 2003; Khan et al., 2011). This evidence that attention may spread beyond the saccade target is interesting, as it suggests that the spatial profile of attention may not necessarily be fixed, and may not be locked to the saccade target, but may be flexible, depending on the particular task being completed.

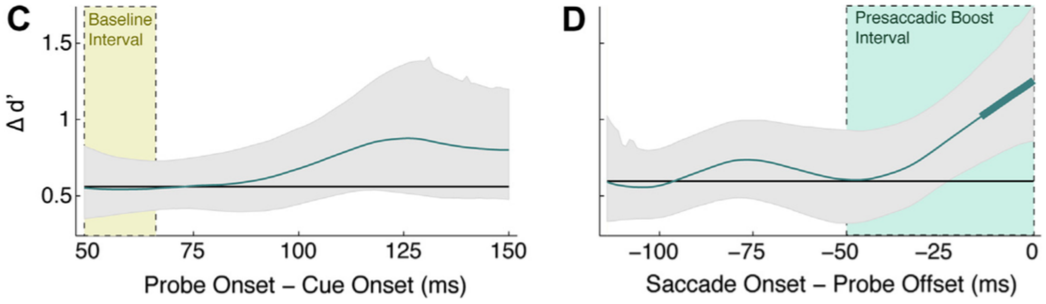

Figure 1.8 – Pre-saccadic attentional shift as measured by White et al. (2013). This study found that pre-saccadic attention peaked around 125 ms after cue onset (left), and built up from around 50 ms before saccade onset (right).

White, Rolfs & Carrasco (2013) found that attention built up at the impending saccade location in the 50 ms before saccade onset (as shown in Figure 1.8). This attentional facilitation was higher at the saccade location than neighbouring non-saccade locations. Similarly, Rolfs & Carrasco (2012) found that attentional facilitation built up from 100 ms before saccade onset on an orientation discrimination task. In this contrast discrimination task, average saccade latency across observers was about 190 ms, and the perceptual enhancement preceded the saccade onset by about 100 ms, showing that the attentional shift occurred quite early in the saccade preparation. Particularly, they found that observers perceived a stimulus to be of higher contrast at the location of the saccade target shortly before the saccade is executed. This is slightly incongruent with studies such as Deubel (2008), which suggests that attention may peak 250 ms before saccade onset (Figure 1.7). These differences may be accounted for by the particular timings of the task – for example the paradigm used by Deubel (2008) included longer SOAs and the mean saccade latency in this case was 259 ms (in comparison to the 190 ms of Rolfs & Carrasco, (2012)). This difference in timescale and saccade latencies may explain why such differences are seen between studies – if the saccade itself is being planned and deployed in a more leisurely fashion, the accompanying attentional deployment may reflect this, and attentional facilitation may act on a similarly slow timescale. This does seem to be the case, with studies reporting shorter saccade latencies also reporting a much more condensed attentional shift (Rolfs & Carrasco, 2012).

It should be noted that this attentional shift accompanying a saccade has a seemingly slower time-course than that of the previously discussed attentional shift elucidated by a covert attention task, which is approximately 300 ms (Cheal & Lyon, 1991; Nakayama & Mackeben, 1989). The difference in timecourse between purely perceptual attention and pre-movement attention could suggest that different mechanisms are responsible for these attentional shifts, or it could be the case that there is an additive effect whereby the additional demands of planning and executing a saccade facilitate the shifting of attention to that location. If the addition of different movements affects how attention is deployed, then the next pertinent question is how enacting a reach may change the temporal profile of attention.

1.4.4 TEMPORAL DYNAMICS - REACHES

The temporal dynamics of the pre-reach attentional shift have also been explored, but to a far lesser extent than that which accompanies a saccade. This pre-reach attentional time-course is important, as it gives insight into how the attentional mechanisms that guide eye and hand movements may be deployed. A comparison of the time-course of both pre-reach and pre-saccade attention can provide insight into how each of these movements might trigger an attentional shift, and how attention may aid in both target selection and online guidance for these different movements. To a lesser extent, it also allows for a general discussion of whether these mechanisms may be independent or shared, as will be explored further in section 1.5.

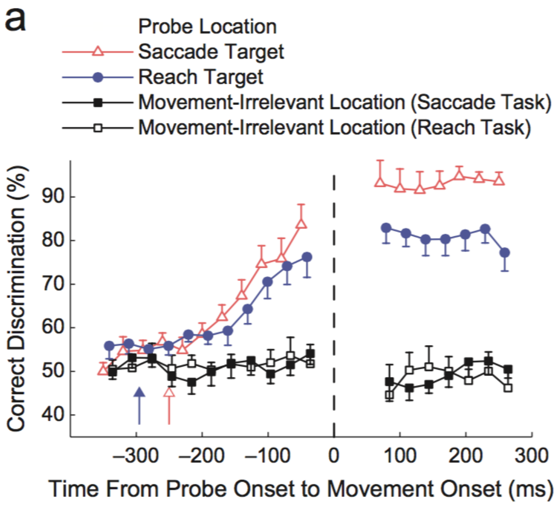

Figure 1.9 – The timeline of pre-movement attention from Jonikaitis & Deubel (2011). This study measured the temporal pattern of attention for a saccade alone (red) and reach alone (blue), and found both to improve from around 150 ms before movement onset.

Jonikaitis & Deubel (2011) measured the temporal dynamics of attention before a saccade alone, reach alone, and a saccade-plus-reach, using a letter discrimination paradigm (see Figure 1.9). They found that attention built up at the target location, with an improvement of around 30 % difference in perceptual discrimination ability at the target compared to an irrelevant location. There was a slight discrepancy in the time-course of the attentional shift with and without a reach – when a saccade alone was being performed, a significant improvement in performance was found around 80 ms after cue onset. When a reach alone was being performed this improvement was seen later, at around 140 ms after cue onset. This suggests that planning both a reach and saccade may involve different mechanisms than planning a reach alone, or alternatively that attention might be deployed differently when different movements are being planned. Rolfs, Lawrence & Carrasco (2013) similarly explored the time-course of attention using an orientation discrimination task, when a reach was being made concurrent to a saccade. In this study a dramatic increase in performance was recorded around 100 ms after cue onset, however it does not provide any insight into whether this shift may be driven by either saccade or reach planning, or indeed both.

It can be seen therefore, that while the attentional shift preceding saccade and reach seem to be on a similar timescale, slight differences have been observed. However, given there is also a difference in measurements of pre-movement attention between studies ostensibly measuring the same effect, it is hard to draw any solid conclusions between paradigms. It may be the case that differences in paradigms may be causing the observed timing differences, which could in turn be reflective of different movement latencies between studies. These differences show again that attention may be quite flexible, and also highlights the importance of conducting a thorough investigation of the spatiotemporal profile of attention, where all variables that may affect this profile of attention are controlled between studies, so that any timing differences observed can be more confidently attributed to the preparation and execution of a particular movement, and not the different temporal aspects of the paradigm itself. These paradigms that have been discussed thus far however have looked at a single saccade or reach alone, which is useful for determining how attention shifts. However, in order to determine how attention functionally aids us in everyday life, these attentional shifts must be examined in the context of sequences of multiple movements.

1.4.5 ATTENTION DURING SEQUENCES OF MOVEMENTS

The pre-movement attentional shift has also been studied in paradigms where the participant is required to make multiple hand movements – by measuring the spatiotemporal characteristics of attention relative to a sequence of movements, we can begin to determine how the attentional shift may change dynamically in scenarios which are more akin to the way we would interact with our environment than studies which look at the attentional shift relative to just a single pointing movement.

Evidence strongly suggests that when making a sequence of hand movements, attention will select upcoming movement locations, and that the extent to which attention facilitates perceptual performance at these locations depends on the order in which the pointing movements are made to these goals. It is contentious however as to whether these sequences of movements are planned in parallel, with every upcoming location being selected equally, or whether locations are selected sequentially, with the amount of attention allocated to a location being directly related to the sequence in which the movements are planned.

Numerous studies have shown that when preparing a sequence of hand movements, the upcoming movement targets all show attentional facilitation. For example, Baldauf and Deubel (2008) found that in a bimanual reaching task, letter discrimination performance was better at the movement goals compared to movement irrelevant locations, for both hand movements, suggesting that the attentional system can facilitate performance at both movement goals in parallel. In sequential manual movement tasks, a similar pattern was found, with all movement relevant locations being selected in parallel, rather than serially (Baldauf & Deubel, 2008). Additionally, when instructed to grasp an object, it was found that the whole action sequence was planned well in advance (Hesse & Deubel, 2010). Gersch et al. (2009) however studied the allocation of attention during the performance of non-repetitive sequences of saccades, and found that it is possible to perform a memorised sequence well without attention highlighting the entire upcoming saccadic path. This pattern was also seen in less complex sequences, with only the next saccadic target in the sequence being highlighted by attention (Gersch et al., 2004). This attentional highlighting of upcoming targets in a sequence was also seen to enhance a number of perceptual features, such as feature discrimination and feature detection, with and without visual noise present (Zhao et al., 2012). This shows that attention can be allocated to multiple targets in parallel. Views on whether the entire upcoming sequence is selected (as in Hesse & Deubel, 2010), or whether one upcoming location is selected at a time (Gersch et al., 2004), seems to differ. A notable difference between these studies is that in the cases of saccade sequences only (Gersch et al., 2004; 2009), only one impending target location is selected, whereas when a manual movement is being planned (Baldauf et al., 2006; Hesse & Deubel, 2010), all locations are selected. This could suggest that planning a series of hand movements requires a broader attentional selection of locations in the visual field than planning saccades alone. It could also be the case that the speed of movements affects how attention is allocated during sequences of movements: the slower the delay between each reach, the less visual attention is allocated to subsequent goals. When a rapid sequence of movements is planned, attention is spread broadly across all upcoming targets – when the movements are slower, these impending targets are not selected (Baldauf, 2011). This suggests again that attention may be flexible, and how it is deployed may depend on factors such as movement latencies. These studies suggest that the scope of attentional facilitation may depend on task demands, and that attention can highlight multiple targets at a time, and actively supress targets that are irrelevant to the upcoming movement plan.

In addition to the psychophysical studies outlined above, neurophysiological studies also support the notion that a number of upcoming locations may be selected at once - ERP evidence suggests that impending movement locations may be selected in parallel, showing that during the preparation of pointing sequences, the intended movement goals were selected before movement initiation, with the first and second movement goals being attended to about the same degree, again suggesting parallel processing (Baldauf & Deubel, 2009). As this study demonstrates, the neurophysiological pathways associated with pre-movement attention can give great insight into the spread of attention, and looking at this neurophysiological evidence can help to determine how attention may be linked to an impending movement. These neurophysiological correlates will be discussed in more detail in section 1.4.9.

So, it is evident that planning an eye or hand movement, whether alone, as a single movement, or within a sequence, carries with it some amount of attentional weighting. As this section has highlighted however, the way in which attention is deployed, and the spatiotemporal characteristics of this deployment may differ, depending on the type of movement being made. This has led researchers to question whether pre-saccade attention is the same as pre-reach attention, and how these attentional resources may, or may not, be shared between modalities.

1.4.6 ATTENTION, EYE AND HAND – SHARED OR DIFFERENT MECHANISMS?

The question of whether attention for perception and attention for action are the same is a pertinent one, and as discussed previously, has come under much scrutiny both experimentally and theoretically over the past twenty or so years. More recently however, researchers have been delving deeper into the nature of attention for action, and a new question of attentional dissociation has arisen: are the mechanisms which control attention for saccades, and attention for reaches, the same, or are they different? This problem is harder to tackle than the one of attention for action and perception, as eye and hand movements are so closely linked, and creating a paradigm to decouple them creates a number of confounds. There is diverging evidence on the subject, and there is as yet no definitive, unifying view.

1.4.7 EVIDENCE FOR SHARED RESOURCES

As outlined in section 1.1, vision and action are closely linked, and thus it would be a reasonable assumption that the attentional resources that drive the two are shared, and there is much evidence to support this notion. It has been found that target selection for saccades and reaches is tightly coupled, and when conducting a visual search task coupled with a reach, the final saccade is virtually always directed to the goal of a concurrent reaching movement when the saccade destination was unconstrained (Song & McPeek, 2009).

The issue of target selection adds more evidence for the hypothesis that vision and action share attentional mechanisms – Song & Bedard (2013) found that performance on an RSVP task was better at both reach and saccade goals than other locations, and this was the case even when these reach and saccade goals were dissociated. This suggests that attention selects both movement goals, and that the attentional mechanism responsible for this selection may be shared between the two effectors.

One study investigated the allocation of attention to both eye and hand movement targets, and found that during simultaneous eye and hand movements, when the eye and hand are directed to different locations, the amount of attention allocated to the reach goal is reduced (Khan et al., 2011). This is interesting, because the results suggest that attention is directed to the saccade goal, even when the reach target was different to this saccade goal, and even though the perceptual discrimination target was more likely to appear at the reach target. Behaviourally it would be logical to assume that attention would be allocated to the location where the perceptual discrimination task was more likely to appear, however this study showed rather that attention seemed to move with the saccade, irrespective of simultaneous reach or perceptual discrimination tasks. This suggests that reaches do not necessarily elicit a shift in attention on their own. This decrease in performance at the reach location when a saccade was being directed elsewhere suggests that the same mechanisms might underli.e. both saccade and reach, and the finding that attention always seemed to move with the saccade suggests that the initiation of a saccade is the driving force behind this attentional shift.

One of the major set-backs in trying to dissociate attention in target selection for saccades and reaches is that the way in which attention is measured is an inherently visual task – it is almost impossible then to try to measure the attention accompanying a reach without getting any interference from visual artefacts. Researchers have tried to overcome this problem by using the technique of saccadic adaptation – this creates a dissociation between target selection and motor processes, as the perceived location and representation of the target does not match the motor output in a saccade or reaching task (Collins et al., 2010). Indeed, when this technique was used and ERP responses were recorded at the adapted and non-adapted locations, results showed that both motor planning and target selection were relevant to attentional orienting. This suggests that mechanisms that control both the planning of a saccade, and the selection of targets may elicit an attentional shift, suggesting that target selection and motor planning may not always necessarily be coupled, and that attention is a resource that is used by both. This complex connection between target selection, action and attention is unresolved, and this issue will be discussed further in section 1.5.3 in relation to neurophysiological evidence, and in the next section in terms of psychophysical studies.

1.4.8 EVIDENCE FOR SEPARATE RESOURCES

While there is much evidence to support the notion that there are shared resources for perception and action, there is an equal amount of evidence to contradict this notion, suggesting that in fact the resources for perception and action are independent of one another.

Evidence from behavioural tasks have shown that in a finger tapping task, there were very weak/non-existent costs of preparing and executing a concurrent saccade while the finger movements were continuing. This provides support for separate resources as executing these concurrent tasks did not have an impact on overall performance for either task (Sharikadze, Cong, Staude, Deubel, & Wolf, 2009). However, it can be argued that finger tapping is a fairly automated process, so may not require any attentional supervision, as enacting an actual reach may do. As previously discussed, a study examining the shift of attention when there is either a reach or saccade being planned alone, or when both movements are being planned concurrently suggests that while saccades require an obligatory shift of attention, reaches do not require this shift of attention (Khan et al., 2011).

Examining the dynamics of movement latencies also provides a clue as to whether these resources are separate or shared: Jonikaitis et al. (2010) found that movement latencies were impacted when participants were undertaking a dual-task paradigm. However, they also found that participants could shift their attention to a saccade target while the concurrent reaching movement was being planned to an alternative location, which suggests that movement goal selection for the eye and hand is driven by different mechanisms.

Further evidence comes from patients with parietal lobe damage. Blangero et al. (2010) explored the attentional capacities of a patient with damage to the right posterior parietal lobe and unilaterial optic ataxia in his left visual field, without any visual field deficits, and found that covert attention shifts were impaired, but pre-saccadic perceptual facilitation was not impaired. This suggests that pre-saccadic perceptual facilitation and covert attention do not rely on the same processes, and specifically that pre-saccadic perceptual facilitation may result from a form of attention which is specific to the planning of a motor movement.

Khan et al. (2009) postulated that while the mechanisms for perception and action may be different, there is instead a functional coupling between saccade preparation and attention in the parietal cortex. This evidence again comes from the study of a parietal patient, although this patient displayed lesions in the occipto-parietal region and unilateral optic ataxia in the left visual field. The results of this study suggest that the shifting of attention and the preparation of a saccade may involve separate neural networks, and that an accurate saccade can be generated without a preceding shift of attention of the goal location. However, while these may have different underlying neural substrates, the parietal cortex is necessary for the coupling between saccade planning and presaccadic perceptual facilitation.

There is behavioural evidence for both attention and action being linked and being separate, and there is no consensus as to which is correct. Given the flexible nature of attention, depending on the task being carried out (as discussed in section 1.4.3), the differences could be due to the nature of the tasks – in experiments where the optimal behavioural strategy is to divide attention, it could be the case that attention is then dissociated. In those where the optimal strategy is to unify attention and movement planning, the two may be coupled. To get a deeper insight however into how attention and movement planning may be linked, we can look beyond the psychophysical evidence to the underlying neural mechanisms.

1.4.9 NEUROPHYSIOLOGICAL CORRELATES OF PRE-MOVEMENT ATTENTION

There are a number of complex and inter-linking neural correlates for the control of saccades, hand movements, and the accompanying attentional shift. While the interaction between attention and movement planning in these potential neural circuits will be discussed later in section 1.5.3, the basic underlying substrates will be outlined here.

Three of the major areas implicated in the control of movements and attention, and indeed the areas that may provide insight into their shared control, are the frontal eye fields (FEF), superior colliculus (SC) and lateral intraparietal area (LIP), each of which have been linked to the programming and execution of saccades, and have been further implicated in attentional processes (Moore, 2006). Indeed, studies have shown that for example, microstimulation of these saccadic planning areas also increased attentional sensitivity at the corresponding spatial location: this was found in the FEF (Moore & Fallah, 2004) and SC (Cavanaugh & Wurtz, 2004; Müller, Philiastides, & Newsome, 2005). Moore & Armstrong (2003) also demonstrated that microstimulation of the FEF produced enhanced responses in V4 neurons at retinotopically corresponding locations, while supressing the responses to surrounding locations. This suggests that the mechanisms involved in saccade triggering have a direct effect on the gain of the visual signals at the locations of upcoming saccades.

Many studies have found overlap in the neuronal areas that control saccades and attention. For example, during an attentional task, fMRI results showed that a common network of regions in the parietal, frontal and temporal cortex were activated, irrespective of whether the attention task was completed covertly, or with a concurrent saccade (1998). These regions included (but were not limited to) the FEF, SEF and IPS. Further fMRI studies have also shown an overlap in the fronto-parietal system during covert and overt attention tasks (de Haan, Morgan, & Rorden, 2008; Nobre, Gitelman, Dias, & Mesulam, 2000a).

The FEF is an area that has long been linked with the planning and execution of saccades; however recently, when exploring the function of this area on a neuronal level, it has become apparent that it may be important in the link between action and attention. Thompson, Biscoe & Sato (2005) found three classes of neurons in the FEF: visual, visuomotor and motor neurons. During a covert attention task, the visual and visuomotor neurons were enhanced, whereas the purely motor neurons were not. Similarly, both visual and visuomotor neurons in the SC were activated by a covert attention task, but motor neurons were not (Ignashchenkova, Dicke, Haarmeier, & Thier, 2003). This suggests that saccade planning and attentional shifts are closely linked on the neuronal level in the visuomotor and visual neurons, but also that they can be dissociated. In the case of covert attention, this explains how attention can be directed to a location in the visual field, while the eyes remain fixated. It also suggests that the link between attention and motor planning is still strong at the later stages of the saccade triggering pathway, and it is not just the initial target selection phase of planning a saccade which requires attentional facilitation (Moore, 2006).

This evidence that attention and movement planning may be tightly coupled on the neural level shows that attention is an integral part of making any movement, whether it is a saccade or reach. While we know that attention is linked to movements, an important question still remains, and that is whether the attention that accompanies eye movements and the attention that accompanies hand movements is driven by the same mechanisms, or separate mechanisms. This was mentioned briefly in section 1.4.1 in the context of the premotor theory of attention, but will be discussed in more detail henceforth.

1.4.10 NEURAL CIRCUITS - FURTHER EVIDENCE FROM NEUROPHYSIOLOGY

As outlined previously, there are a number of neurophysiological processes that have been implicated in the attentional process. Looking at these mechanisms may provide more insight into firstly what the mechanisms underlying the pre-motor attentional shift actually are, and secondly whether they are shared or not between the different motor effectors.

Apart from the separate neural regions associated with attention in general (as outlined in section 1.4.8), one of the most interesting aspects of the pre-movement attentional shift is the concept of a neurological circuit that controls eye movements, hand movements, target selection, and the allocation of attention. Such a loop seems a logical and parsimonious way to collect and transform the visual information needed for goal directed movements, and there is growing evidence that there may indeed be unified mechanisms for motor control and attention within this circuit. Attention and action seem to be very closely linked in both the planning and updating stages of a movement, and the PPC seems to be important in integrating visual information into motor plans at both the target selection phase, and the dynamic updating phase (Crawford, Henriques, & Medendorp, 2011). Figure 1.10 shows an overview of the cortical connections controlling eye and hand movements, and shows the areas that may control both eye and hand, and which may be responsible for the transformation of visual information into motor coordinates.

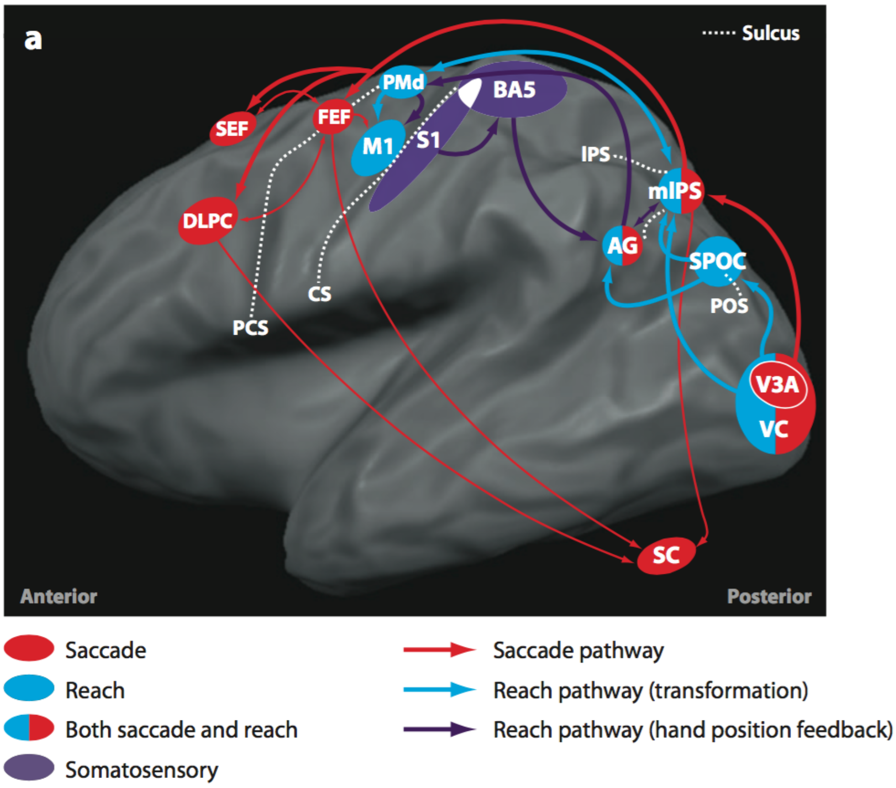

Figure 1.10 – an overview of visuomotor pathways in the brain, and the areas responsible for both separate and shared representations for both effectors (from Crawford et al., 2011).

The first stage in this possible circuit is the selection of targets for eye and hand movements. As previously discussed, there is psychophysical evidence that this may be a process that is common between eye and hand, and the neurophysiological evidence also supports this. One way this problem can be conceptualised is by looking at the frame of reference the arm motor system uses to program and plan a reach – if a reach is programmed in gaze-centric coordinates, it seems likely that the attentional control mechanisms may be shared. As discussed earlier in section 1.1, eye and hand movements are coupled, and visual information is vital for planning an accurate reach. Research has suggested that arm movements are planned in gaze-centric coordinates in the planning stages of the reach (Batista et al, 1999; Crawford, 2004), and that visual information is also important to update the motor plan to guide the hand throughout the reach. Indeed, fMRI evidence suggests that many cortical areas may encode space in a retinotopic reference frame (Gardner, Merriam, Movshon, & Heeger, 2008) rather than a spatiotopic reference frame. This gaze-centric encoding theory was demonstrated when participants planned a reach to a remembered location and fMRI measurements of the PPC showed that the coordinates of the reach location are encoded based on the intrinsic retinal coordinates rather than actual physical location of the reach or arm centred coordinates (Fernandez-Ruiz, Goltz, DeSouza, Vilis, & Crawford, 2007). Neurons in the PRR have also been found to code impending arm movements, with the response fields of these neurons being more tightly coupled with the position of the eyes than the hand or body (Batista, Buneo, Snyder, & Andersen, 1999; Snyder, 2000). Looking at how attention fits into this planning and feedback process in the brain may provide insight into which parts of the movement planning and control process are important and require the most attentional and visual control.

There is further evidence that reach plans may be encoded in eye coordinates at the neural level: neurons in area 5 of the PPC encode reach locations in reach coordinates as well as eye coordinates, suggesting that the PPC directly transforms between eye and reach coordinates (Buneo, Jarvis, Batista, & Andersen, 2002). This would seem to suggest that the PMC receives signals in this transformed, reach-centric frame, however Mushiake, Tanatsugu & Tanji (1997) found that activity in neurons in the PMv were modulated by gaze direction, suggesting that even at the level of the PMC, the motor plan may be encoded in gaze-centric coordinates. It must be noted however that this study also found that neurons in MI were not influenced by gaze, suggesting that by this later processing stage, the reach plan had been transformed into reach coordinates. This supports the idea that at the earlier stages of a movement plan, both reach and eye planning rely on a common, gaze-centric coordinate system. Snyder (2000) suggests that the PPC controls such processes as target selection, response decision, and transformation of initial effector signals into a unified coordinate system, before this signal is sent to the PMC to trigger a hand movement, or the FEF to trigger an eye movement. This suggests that the initial planning stages of saccade and reach are very much dependent on visual information, and thus, the perceptual changes elicited by attention would directly affect the planning of a visually guided reach.

Another stage of the eye-hand-attention link that may be useful in determining the neural links between perception, attention and action is how space is represented when the visual scene is updated across saccades and reaches. Single unit recording studies in monkeys suggest that when making hand movements, this updating occurs in gaze-centric coordinates in the PPC, rather than body or arm centred reference frames (Batista et al., 1999). Indeed, the PPC seems to play an important role as an updating and integration centre for saccades and reaches – studies have shown that the topographic representation, and dynamic updating of reach and saccades in the PPC is organised in gaze-centric coordinates (Medendorp, Goltz, Crawford, & Vilis, 2005; Medendorp, Goltz, Vilis, & Crawford, 2003). Additionally, neurons in the visual area V6A have been found to be modulated by the preparation and execution of reaching, even when there was no visual feedback (Fattori, Gamberini, Kutz, & Galletti, 2001). It was suggested that these neurons could calculate discrepancies between the movement plan and actual movement with the use of visual feedback, feeding into the dynamic online control of hand movements.

While there is an abundance of evidence suggesting that reach and saccade planning are closely linked via these neural networks, evidence also suggests that the parietal reach region (PRR), a region generally associated with the control of hand movements, plays an important role in the integration of separate eye and hand control pathways. This interesting dissociation between eye and hand control was demonstrated by Hwang et al. (2012) who found that inactivating the PRR produced impaired reaching ability, but not impaired saccades during a concurrent reach/saccade task (similar to the effects of optic ataxia), suggesting that PRR is primarily involved in the planning of reaches. There is however divergent evidence on whether the PRR may play a a more complex role in the coordination of eye and hand movements, as it was seen that PRR inactivation also caused a decoupling of eye and hand movements (Hwang, Hauschild, Wilke & Andersen, 2014), indicating that the PRR, situated early in the visuomotor pathway, may be an integral part of the circuit for both spatial and temporal eye-hand coordination at an early stage. Yttri et al. (2014) however argued against the involvement of the PRR in eye-hand coordination, as in this case inactivation of the PRR produced reaching deficits only, and did not affect the temporal coupling of saccades and reaches (interestingly, lesioning the PRR did not affect visual attention either). This suggests, converse to the previous study, that mechanisms for eye-hand coordination may occur later in the visuomotor pathways. This diverging evidence demonstrates that even at the neural level, the interconnectivity of the eye-hand coordination system is under debate, and the integration of the role of attention into this network merely adds another layer of complexity in trying to tease apart these neural and behavioural links.

This brief overview of possible neural links between eye and hand does show however that the planning and execution of hand movements is extremely reliant on visual information, and in fact the motor plan for reaches seems to be programmed in eye-centric coordinates up until the very last stage of processing in MI. Given the strong links between vision and attention, and the perceptual benefits elicited by attending to an area, it would seem that attention may have an important role to play in the visuo-motor control circuit. Additionally, given the shared processing resources, both at cortical and neural level, it is not implausible that the attentional mechanisms associated with eye and hand movements would also be shared.

1.5.4 PROBLEMS WITH CURRENT EVIDENCE

While the existing evidence strongly suggests that attention shifts before an eye or hand movement is made, the timeline of this shift, and the issue of whether the attentional shift for eye and hand are driven by the same or different mechanisms are still unclear, and the views divided. As previously mentioned, one major issue when trying to compare the current evidence is that the paradigms used to assess this connection are not consistent between studies, and there are a number of elements present within these paradigms that make them difficult to compare with each other. If the spatiotemporal profile of attention can change when different tasks are being enacted, then is important to look at some of the factors that may have influenced the observed discrepancies between studies.

Pre-cues

One of the experimental elements present in some of the previously discussed studies is the pre-cue (Deubel, 2008; Deubel & Schneider, 2003). This was discussed in section 1.3.2 in relation to measurements of covert attention, and the variable effects on these measures are equally as pertinent in the case of pre-movement attention. The argument for using a pre-cue is that it locks the location of attention to the cued location before the saccade is planned, thus measuring whether the locus of attention and the locus of the saccade can be dissociated via subsequent perceptual discrimination performance at that location. However, it is arguable that this pre-cued selection of the location would be using entirely different mechanisms than the attentional selection mechanisms activated by the planning of a saccade. If the location is pre-cued some 1000 ms before a saccade is being cued and thus planned, it is impossible to dissociate the facilitation caused by saccadic planning from the attention which had previously been directed to that location by the use of the pre-cue.

Another criticism of the literature in this area is the timing used in these studies, and the large gap between cue and stimulus. When there is a space of 500-1000 ms between cue and stimulus onset, it is arguable whether the performance on the perceptual task of the stimulus is due to motor planning at all. Many studies have shown that the time-scale of attentional facilitation due to saccade planning is in the order of 150 ms after saccade onset – by leaving a gap that is significantly greater than 150 ms the attentional shift caused by the saccade planning could be entirely lost and unmeasured in the SOA time. Indeed, an additional problem with long cue-stimulus gaps is that generally the accepted time-course of attentional facilitation measures the time it takes for the peak attentional facilitation to be observed at a location. This fails to account for the start of the attentional build-up, so the observed time-scale may be deceptively slow (Montagnini & Castet, 2007).

Cue length

In addition to the use of precues in some experiments, the length of time a cue is present differs vastly between experiments. Some experiments have a cue on for as long as 150 ms before a 'go' signal is presented (Deubel, 2008), whereas others have a cue for only 6.25 ms (Montagnini & Castet, 2007), or leave the cue on for the entirety of the experiment with a 50 ms SOA before the target appeared (Baldauf et al., 2006). Montagnini & Castet (2007) tested the effect of two different lengths of cue on subsequent attentional performance on a perceptual discrimination task, and found that attention starts to build up at the cued location after the cue was visible for only 6 ms, although greater attentional facilitation was seen when the time between cue onset and stimulus onset was 150 ms, which is consistent with other studies.

As with the criticisms regarding long pre-cues and long time lapses between cue presentation and stimulus presentation, having a cue presentation time that is too long will eclipse any attentional facilitation that is beginning to build up from the time of cue onset. As it was found that attention can start to build up at the cued location after the cue has been visible for only 6 ms (Castet et al., 2006), it could be the case that experiments which have cues on for significantly longer than this could be missing the beginning of the attentional shift. This could mean that the observed timing of the pre-saccadic shift could be more dependent on the timing of the cue than the planned movement – it could be the case that if the experiments used shorter cues, the pre-saccadic shift could be observed on an earlier timescale.

It may be the case that discrepancies in the timing and magnitude of the pre-motor attentional shift are due to the differing task demands between multitudes of different paradigms. Indeed, even within one study and utilising the same paradigm, differing effects of pre-motor attention were found when the task demands were altered – in this case planning a saccade to a target was found to either facilitate or inhibit attentional allocation at the target location depending on the probability of the saccade being cued to that location (Belopolsky & Theeuwes, 2009). If such a difference can be observed within a study, the differences between studies, and between paradigms where so many factors can be altered, are not necessarily an attribute of the profile or mechanisms of attention itself, but may reflect the reaction of the attentional and motor systems to the particular task demands. These differences form a strong motivation for the paradigm used in the three studies that form the experimental component of this thesis. In each of these studies, variables such as cue length, SOA length, reach/saccade target and stimulus appearance were all kept constant, with only the factors of interest, such as movement type and the spatial location of probe locations being modified between experiments. This then allows for a more meaningful comparison of variables of interest between studies.

1.6 ATTENTION, MOVEMENTS AND THE PRIORITY MAP – PUTTING IT ALL TOGETHER

The process of target selection, attentional facilitation, saccade planning, and reach planning is incredibly complicated, as is evident from the sheer number and diversity of studies in the area. While each piece of evidence tells a small part of the overall story of how we plan and execute eye and hand movements, it is important to try to integrate each stage into an overarching, unifying theory to explain how each of these areas connects, and how this ultimately results in our ability to seemingly effortlessly move around in the world. To do this, we must come right back to the beginning to the concept of salience and priority maps, which was raised in section 1.2.

This idea that the priority map may be distinguished from low-level motor processes is supported by Gersch et al. (2009), who found that when making sequences of saccades along a marked path it was possible to dissociate saccades and attention to some extent. Results showed that participants could perform a sequence of saccades without necessary attentional highlighting of the saccadic path, and that these upcoming saccade locations are not then included in any top down salience map of task relevant locations. This indicates that top down salience maps may be limited to representing locations that are only relevant for the immediate task demands, and any location other than the impending saccade may be represented by a separate map. This means that the attention which is allocated to the saccade location would be connected specifically to that saccade planning, and the attention which is allocated to upcoming locations for future saccades may be represented mainly by perceptual or visual mechanisms which are not linked to saccade planning. Functionally, this means that attention can select the saccadic target while at the same time extending perceptual awareness over a broader area to create a global salience map for general scene perception.

This has led to the suggestion that the planning of a sequence of movements leads to the formation of an attentional ‘landscape’ which tags all of the impending movement locations to a differing extent depending on the sequence of the upcoming movements (Baldauf & Deubel, 2010). This idea of an attentional landscape is not dissimilar to that of a priority map, and supports the notion that upcoming areas of behavioural importance in the visual field are selected in priority to non-behaviourally relevant areas, and the way in which this selection occurs is dependent on task demands.

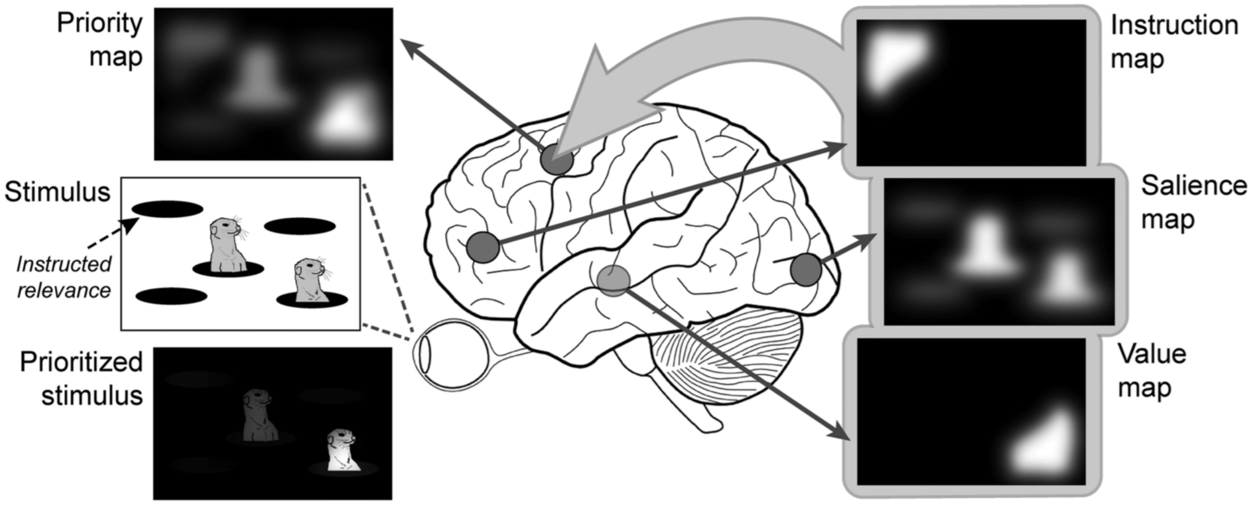

Figure 1.11 – basic schematic of how different maps may be organised in the brain (from Klink, Jentgens, & Lorteije, 2014). Stimuli are processed with the resulting salience information being represented by a value map, which is then converted to a salience map and instruction map, with the resulting instructions being sent to the eventual priority map.

Indeed, the previously discussed idea of a complex neural circuit that controls attention, eye and hand movements and target selection for these movements is consistent with the notion that there is some higher level priority map which aggregates the signals and feedback from each of these movement plans (and indeed, it could be argued that the notion of a priority map is merely a more parsimonious way of explaining the complex interactions between each of the links in the neural loop). Figure 1.11 gives a very basic representation of how each stage in formation of a priority map may be processed in the brain.

Additional neurological evidence also supports the idea that there is some sort of priority map guiding our motor movements, whether they be eye or hand movements. In a study which examined reaching and saccade performance during the temporary inactivation of the superior colliculus in monkeys, Song et al. (2011) found that this inactivation affected the choice of location for an impending reach, without affecting the lower-level motor execution of the reach. This study provided evidence that the intermediate layer of the superior colliculus has an influence on reach target selection – when the reaching goal was located in the affected part of the visual field, the monkeys made significantly more reaching errors to the distractor stimulus, but the accuracy of those reaches was unaffected. This suggests that the superior colliculus is part of a large-scale priority map that influences target selection for reaches as well as saccades, and suggests that while the low-level processes controlling motor movement remain unaffected, there is a higher-level process which controls target selection, which is independent, and can be independently impeded.

Hamker, Zirnsak, Calow, & Lappe (2008b) have suggested a model of spatial attention which in some ways bridges the divide between this problem of the 'map' that is used in target selection, and the ultimate behavioural and perceptual outcomes of the attentional shift and related phenomena such as receptive field shifts and remapping (Zirnsak & Moore, 2014). This model suggests that the planning of a saccade causes perisaccadic suppression, receptive field shifts and an increase in visual acuity at the saccade target, through the same neural mechanism. In basic terms, this mechanism may be a feedback signal that, through the planning of a saccade, encodes the saccade target and then causes the perceptual changes at this location. This model suggests that the feedback signal from visuo-motor maps in the FEF and SC is sent to corresponding cortical visuo-spatial maps around the time of saccade onset, which in turn increases the gain of the firing responses of the neurons responsible for that spatial location. This is analogous to the concept of a location in space being chosen for saccade planning, and this target localisation then affects the subsequent behavioural, attention, and saccade outcomes.

While the interaction between attention and motor planning is a complex one, and there are many different mechanisms implicated in this process, there may ultimately be some form of neural and behavioural guidance map that collates all of this disparate information, and informs decisions on where a movement needs to be made, and subsequently where attention should be allocated.

1.7 SUMMARY

The previous chapter has, in short, aimed to highlight the following basic concepts that eye and hand-movements are tightly linked, and that in turn attention and movements are also linked, though the exact nature of this coupling is unknown. There seems to be a complicated neural network controlling target selection and movement planning for eye, hand and attention, and this may all be integrated into an attentional priority map that determines where and when attention and movements are deployed. There are however problems with the current evidence, and specifically the paradigm differences amongst the outlined psychophysical studies make it hard to draw any firm comparisons or conclusions on the spatiotemporal nature of the pre-movement attention shift. The evidence and problems outlined will be referred to in the experimental work in the next chapters, as these experiments aim to disambiguate some of the discrepancies in the pre-movement attention literature.

1.7.1 AIMS OF THIS THESIS

The primary aim of the experiments in this thesis is to comprehensively map the spatiotemporal profile of attention relative to a saccade alone, a hand movement alone, and a saccade plus hand movement. As outlined in the introduction, the evidence surrounding the spatial and temporal properties of the pre-movement attention shift differs somewhat between studies. These experiments aim to use a consistent paradigm to compare how attention is deployed with different movements. Specifically, it aims to measure the temporal properties of a pre-movement attentional shift, and the spread of attention around a movement target. It also aims to investigate whether the direction of movement may have an effect on how attention is deployed. These data will allow comparison of the potential differences and/or similarities between the spatiotemporal profile of attention linked with saccades, and that linked with reaches.

2. PAPER 1 – THE SPATIOTEMPORAL CHARACTERISTICS OF THE ATTENTIONAL SHIFT RELATIVE TO A REACH

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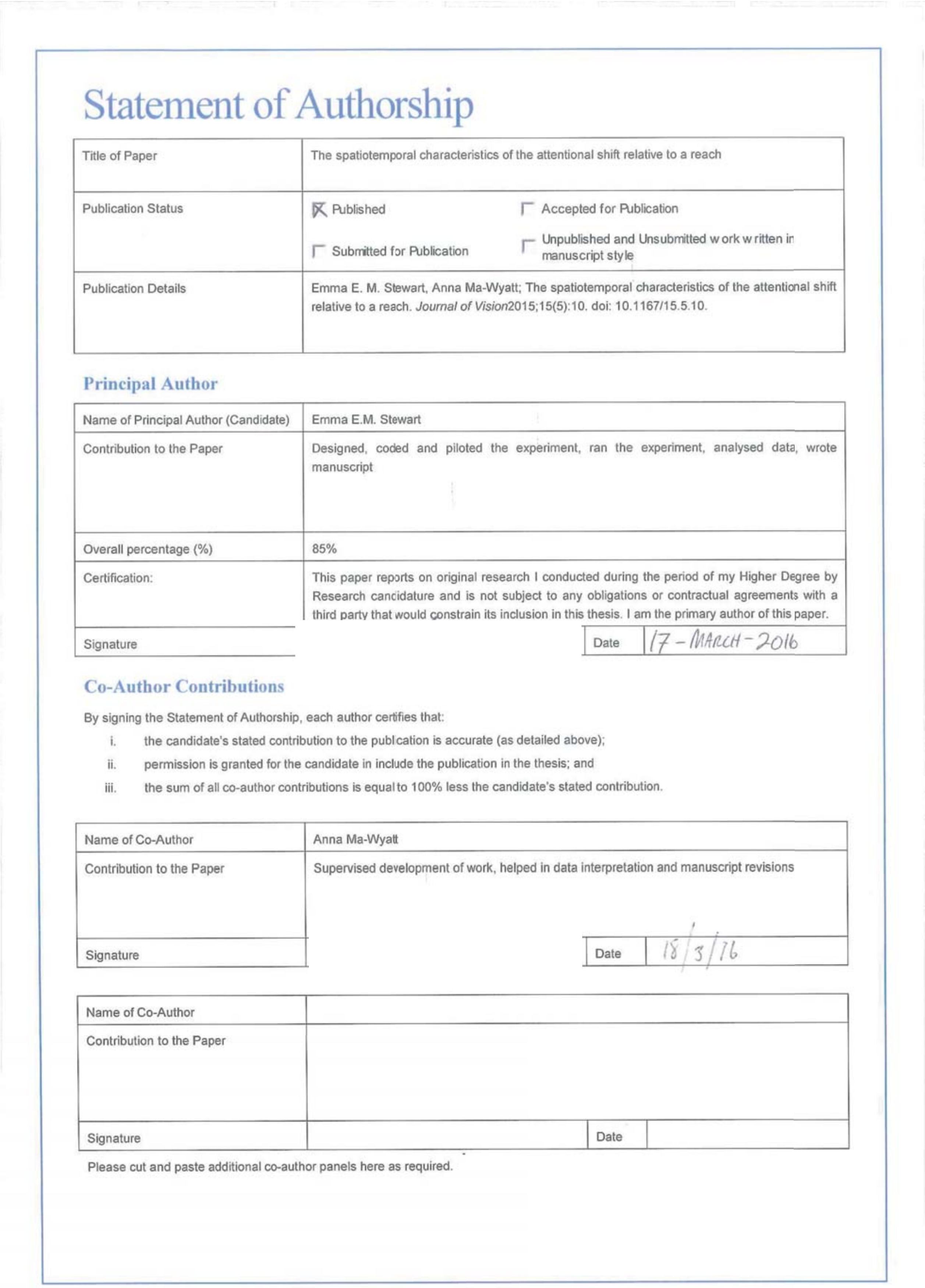
PUBLICATION NOTE:

The method section for the original published manuscript included a random delay between the button press to start a trial, and the onset of the cue. In fact, there was no random delay between the button press and the cue onset – it was a fixed interval. As this fixed interval was consistent across conditions, the conditions are still comparable and therefore the overall results should not have been affected. The corrections removed this random delay from the method section in the text and figures. Journal of Vision has agreed to publish an erratum to this effect. The manuscript included here is the corrected version, as it will appear on the Journal of Vision website.



Statement of Authorship

Title of Paper	The spatiotemporal characteristics of the attentional shift relative to a reach	
Publication Status	☒ Published ☐ Submitted for Publication	☐ Accepted for Publication ☐ Unpublished and Unsubmitted work written in manuscript style
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Principal Author

Name of Principal Author (Candidate)	Emma E.M. Stewart		
Contribution to the Paper	Designed, coded and piloted the experiment, ran the experiment, analysed data, wrote manuscript		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	17 - MARCH - 2016

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Anna Ma-Wyatt		
Contribution to the Paper	Supervised development of work, helped in data interpretation and manuscript revisions		
Signature		Date	18/3/16

Name of Co-Author			
Contribution to the Paper			
Signature		Date	

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2.1 ABSTRACT:

While the attentional shift preceding a saccadic eye movement has been well documented, the mechanisms surrounding the attentional shift preceding a reach are not well understood. It is unknown whether these mechanisms may be the same as those used in perceptual tasks, or those used in the planning of a saccade. We mapped the spatiotemporal properties of attention relative to a reach to determine the timecourse of attentional facilitation for hand movements alone. Participants had to reach to a target and during the reach a perceptual probe could appear at one of 6 locations around the target, and at 9 temporal offsets relative to the cue. Results showed a consistent pattern of facilitation in the planning stages of the reach, with attention increasing and then reaching a plateau during the completion of the movement before dropping off. These results demonstrate that planning a hand movement necessitates a shift in attention across the visual field around 150 ms before the onset of a reach. While these results are broadly consistent with the results of experiments mapping attentional shifts for saccades, the spatiotemporal profile of facilitation found shows that reaching without a concurrent eye movement also cause shifts in attention across the visual field. These results also suggest that the profile of the attentional shift preceding and during a hand movement is different at different locations across the visual field.

2.2 INTRODUCTION

In everyday life we are confronted with an overwhelming amount of visual information, some of which is behaviourally relevant, but most of which is not. Visual attention allows us to choose which areas are relevant, and can lead to a perceptual facilitation at those areas (Carrasco et al, 2004; Carrasco, 2006, Liu et al, 2009; Treue, 2004). Specifically, attention seems to play an important role in the planning and execution of saccades (Deubel & Schneider, 1996; Deubel, 2008; Kowler et al, 1995; Zhao et al, 2012), and studies have suggested that the same might be true of hand movements (Jonikaitis & Deubel, 2011; Song & Nakayama, 2006; Baldauf et al, 2006), with visual attention providing guidance for movements.

While the attentional shift surrounding hand movements has been explored relative to saccadic endpoint versus reach endpoint (Deubel & Schneider, 2003), or relative to the same or opposite pointing location (Rolfs et al, 2013), the specific spatial and temporal properties of this shift are still unknown, and in particular the precise perceptual benefit gained from a shift of attention preceding or during a reach is unclear. We measured the spatial and temporal spread of attention before and during a goal directed movement made without a concurrent eye movement.

2.2.1 ATTENTION AND MOVEMENT PLANNING

Much research has been conducted to determine how a shift in attention may relate to a movement, and the mechanisms underlying this allocation of spatial attention. Theories such as the premotor theory of attention argue that the mechanisms responsible for spatial attention and the programming of saccades are the same, that is, programming a saccade causes a shift in attention (Rizolatti et al., 1994). This link between attention and an impending movement has been primarily studied in relation to saccades. Some studies have suggested that there is a close link between attention and saccades (Deubel & Schneider, 1996; Deubel & Schneider, 2003). Contrary to these studies, there is some evidence to suggest that while attention plays an important part in saccadic programming, attention and saccades can be dissociated to some extent (Kowler, 1995).

Similarly, the evidence surrounding the link between attention, saccades and hand movements has not yet provided a definitive answer about whether the mechanisms underlying the attentional shift are the same for perception, saccade, and reach. Given the close link between saccades and reaches, it's important to note that measuring the spatiotemporal profile of attention during a reach may give a clue as to how attentional resources are shared between reaches and saccades. While this paper focuses on reaches alone, much research has been conducted to try to discern how attention may shift for these different, but closely linked, movements.

One of the ways in which researchers have attempted to dissociate the mechanisms underlying the shift for both saccades and reaches is by looking at the temporal profile of the attentional shift for these movements. If a difference in the timing of the attentional shift between these movements is found (e.g. Jonikaitis and Deubel, 2011), then it is taken as evidence for a different mechanism driving the attentional shift for each movement type. While many studies have examined the spatial properties of attention relative to a movement (Deubel, 2008; Deubel and Schneider, 2003), looking at the temporal properties may provide a clearer answer as to whether attention shifts on the same time-scale for eye and hand movements. If the time-course is similar, this would suggest a unified mechanism for these movements. If the time-course is different, it would suggest that the mechanisms driving the attentional shift may be separated.

2.2.2 THE IMPORTANCE OF VISION IN PLANNING A REACH

Visual information is very important in the planning of a precise and accurate hand movement (Sober and Sabes, 2005) both at the outset and during the completion of the reach (Ma-Wyatt and McKee, 2006; 2007). It is logical therefore to suggest that the visuomotor system would benefit from the increased perceptual sensitivity which attending to the reach location could provide.

This shift in attention relative to a reach has primarily been studied in relation to a concurrent saccade and reach, and it is not well understood how attention may shift when a reach is being completed in isolation. The link between attention and reaching has been studied in relation to the location of the attentional benefit accompanying both a saccade and a reach, and this research suggests that attention is tied to the location of the impending reach (Deubel and Schneider, 2003). Moreover, when multiple sequences of movements are being planned, attentional resources can be allocated to each of these upcoming reach locations in parallel (Baldauf et al, 2006). These studies show that the locus of attentional benefit is related to the locus of the planned reach. It is suggested therefore that attention is necessary for the planning of a hand movement, and it has been postulated that the trajectory of a reaching movement over the course of the reach could reflect the shifting locus of attentional focus, which also reflects the motor system’s internal target selection process (Song and Nakayama, 2006). This provides evidence for the idea that the locus of attention may also shift during the execution of a reach as the motor plan for the reach is updated throughout the movement.

Studies that have looked at sequences of hand movements (Baldauf et al, 2006) show that when movements are being planned there is a certain spatial “window” of attention that accompanies the movements. Baldauf et al. (2006) found that all impending reach locations showed an attentional benefit compared to non-target locations. It has also been observed that when preparing a reaching movement to a sequence of locations, attention spreads to all action-relevant goals in parallel, with the amount of the attentional enhancement reflecting the serial order of the impending movement goals (Baldauf & Deubel, 2010). Additionally, there is evidence to suggest that when preparing a bimanual reaching task, attentional facilitation is observed at both intended movement goals (Baldauf & Deubel, 2008), and that when planning a sequence of actions, the whole sequence is planned in advance of movement initiation (Hesse & Deubel, 2010). This parallel allocation of attention is also supported by ERP evidence, showing that multiple movement goals are attended to with the same level of attentional resource (Baldauf & Deubel, 2009).

This attentional selection of movement locations gives a broad idea of how large the attentional window might be, and how it might behave in relation to different movements. Indeed, it has been suggested that preparing a manual movement creates an ‘attentional landscape’ which takes into account all locations which are relevant for planned goal-directed movements (Baldauf & Deubel, 2010). If indeed attention is allocated only to the location of a reach, one would predict that locations close to the reaching target would show an attentional benefit whereas locations further away wouldn’t. If however the findings of a dissociation between saccade and attention along multiple paths hold true for reaches as well, one might expect a broader pattern of attentional facilitation across the visual field. The previous work in this area has not mapped in detail the manner in which attention may spread across the visual field relative to a reaching goal – while they have mapped attention in relation to a small number of sequential pointing locations, this does not indicate how attention spreads, and the temporal manner in which it may shift across the visual field relative to a reaching movement.

This does not however fully solve the problem of whether the mechanism that underlies attentional modulation for saccadic and perceptual tasks is the same as the mechanism used during the planning and execution of a hand movement. We are interested in the attentional mechanisms underlying both saccade and reach, even though this study aims to solely explore reaches. However, since saccades and hand movements are tightly linked, patterns of the time-course and spread of the attentional shift relative to a saccade may also hold true when looking at the attentional shift relative to a hand movement alone. In particular, if the mechanisms underlying both saccades and reaches are similar, we would expect a similar pattern of attentional facilitation for hand movements as that which has previously been seen for saccades. A number of studies have attempted to determine whether the mechanisms underlying saccade and reach preparation are shared, or whether they can be dissociated. While this paper does not directly compare these mechanisms, we believe that it is an important problem to note, and puts the results of this study into the context of a greater overall problem.

The evidence provides divergent results, with some studies suggesting a tight coupling between saccades and hand movements, and some suggesting that separate resources may be responsible. Evidence for dissociated resources can be seen in dual-task paradigms where a manual movement could be planned without an effect on a concurrent saccade task (Sharikadze et al, 2009; Jonikaitis et al, 2010). Brain lesion studies also provide compelling evidence for separate resources for different attentional tasks: in a study comparing covert attention and pre-saccadic attention, it was found that covert attention shifts were impaired but pre-saccadic perceptual facilitation was not impaired (Blangero et al, 2010). If this is the case then we would expect the spatiotemporal pattern of attention relative to a reach to be different to the profile that has been measured relative to saccades in these previous studies.

There is however evidence to the contrary, suggesting that attentional resources underlying reaches and saccades are tightly coupled. For example, in a visual search task the final saccade in each trial was always directed to the goal of a concurrent reaching movement, suggesting that the movements are coupled (Song & McPeek, 2009). Additionally, evidence for shared resources can be seen when the eye and hand must be directed to different goals – in this case the majority of the attentional resources are allocated to the saccadic task, leaving little attention to be directed to the goal of the hand movement (Khan et al, 2011).

This divergent evidence makes it hard to determine whether the attentional shift preceding a saccade is indeed comparable to the shift that occurs when a hand movement is being planned and executed. One method that can be implemented to dissociate the attentional mechanisms behind reaches and saccades is by examining the temporal profile of this attentional shift. This may prove useful in attempting to determine the mechanisms behind pre-saccadic and pre-reach attentional shifts, and give some insight into how these attentional resources may or may not be shared – this study provides a basis for future comparisons of saccades and reaches using this technique.

The temporal profile of attention relative to a reach has been studied to a far lesser extent than the time-course of the attentional shift preceding saccades alone. However, the benefit seems to be similarly demonstrated in the order of 100-150 ms before the reach onset (Jonikaitis & Deubel, 2011; Rolfs et al, 2013). Research by Jonikaitis and Deubel (2011) has also provided evidence that the time-course of attentional facilitation was different for saccades and hand movements - delaying an eye movement caused a delay in the attentional shift to the saccade location. However the deployment of attention to the reach location was unaffected. This dissociation in the timing of the attentional shift provides support for the notion that the attentional control mechanisms for eye and hand are temporally independent.

However, while this may provide an estimate of the temporal parameters surrounding this pre-reach attentional shift, there is no evidence suggesting exactly how and where this shift may occur, as the comparisons of attentional facilitation have primarily been tested by looking at perceptual performance at the reach location compared with a location on the opposite side of the visual field (e.g. Rolfs et al, 2013), which does not provide insight into the magnitude of the perceptual facilitation around the reach end-point. We would expect to see this attentional facilitation at the reach end-point specifically based on the previous literature which has shown that attention does enhance perceptual performance at the location of a planned reach (Deubel and Schneider, 2003).

This study aims to provide a comprehensive spatiotemporal map of the attentional facilitation preceding a reach. In this study we aim to map the attentional facilitation surrounding a hand movement without a concurrent saccade, which will provide a thorough overview of the spatiotemporal characteristics of the attentional shift relative to a reach alone. This quantification of the spread around the reach target, before the eyes move, is aimed to investigate covert attention at the reach target rather than the enhancement related to the increased resolution brought about by an eye movement. This is important as it will provide an understanding of how the planning and execution of a hand movement changes our visual representation of the world. While we are not testing the attentional shift that occurs with a concurrent eye and hand movement, this experiment will provide a solid basis for future mapping of the attentional shift with a concurrent eye and hand movement, which will then allow us to investigate the mechanisms which may be implicated in this shift.

By probing 6 locations around the reaching target on each side of the screen, over 9 time-points this study aims to resolve some of the ambiguity surrounding the pre-reach attentional shift, and aims to map this shift with both a finer temporal and spatial resolution than has been attempted by previous research in the area. By mapping this spatiotemporal shift it is hoped that the link between attention and the planning of a hand movement will become clear. Consistent with previous studies, it is expected that there will be a build-up of attention before the onset of the reach, and this will stabilise during the time-course of the reach. We also wish to quantify the difference between the peak attentional facilitation at different locations across the visual field during the reach, with the attentional facilitation at other time points during the reach. This will allow us to determine which time points during the reach attract the most amount of attentional resources. Additionally, this study includes a secondary paradigm which aims to compare the magnitude of attentional facilitation seen when a reach is being prepared with the magnitude of perceptual facilitation seen when a perceptual task is being completed with no concurrent movement.

2.3 METHODS

2.3.1 PARTICIPANTS

Six participants completed the study. Two were authors, four were naïve as to the purposes of the study. Four of the participants were experienced psychophysical observers (two of the naïve participants and the two authors). All had normal or corrected-to-normal vision. All participants comfortably used their right hand to point, with ages ranging from 22 to 41. Ethics approval was obtained from the School of Psychology, and all participants signed informed consent forms prior to participation. Participants completed approximately 15 hours of data collection in 1-hour blocks. All participants were free to withdraw without penalty at any time.

2.3.2 EQUIPMENT

Stimuli were presented on a 17-inch ELO touchscreen monitor, with a resolution of 1024x768 pixels and a screen refresh rate of 85 Hz. The monitor was calibrated prior to every session to ensure that contrast levels remained consistent across sessions, and to ensure that the monitor's non-linear gamma function was corrected to be linear. Eye movements were measured using a SR Research EyeLink 1000 eye tracker to record eye position during the task. Eye position was sampled at a rate of 1000 Hz with a spatial precision of 0.25°. The experiment was run using custom software written in Matlab using the psychophysics toolbox (Brainard, 1997; Pelli, 1997). The equipment was set up such that a mouse was located centred to the screen, and a keyboard was located to the left of the mouse to collect perceptual responses.

2.3.3 EXPERIMENTAL DESIGN

The experimental design was a novel paradigm that aimed to measure the perceptual facilitation on a perceptual task while a reach was being planned and executed. This methodology is based on studies such as Rolfs and Carrasco (2012, 2013) and Castet et al. (2006), which use a pre-determined threshold-level probe as a basis for determining the benefit in performance resulting from an attentional shift across the visual field.

The experiment was a fully repeated measures design. All participants first completed a contrast threshold detection task, followed by interleaved blocks of a reaching and a perceptual task. All participants completed between 30 and 45 blocks of data collection, depending on how many trials were excluded. Each block consisted of 216 trials.

The experiment comprised three separate tasks. The first task was a preliminary task which served to set individual contrast threshold levels for the perceptual probes that would appear in subsequent tasks. The second task was a reaching task measuring perceptual facilitation across the visual field while fixation was maintained and a reach was executed. The third task was a perceptual only condition that used the threshold-adjusted probes to determine the perceptual facilitation that occurs covertly, when no reach is being made.

2.3.4 CONTRAST THRESHOLD TASK

This preliminary task aimed to set the contrast value for the perceptual probe in the reaching and perceptual only conditions by measuring the contrast threshold for each observer for each possible probe location.

Individual contrast threshold measurements were taken for each participant at each of the 12 probe locations, with each location being tested separately. The participant maintained central fixation, and upon depressing a key the probe appeared at the location being tested. The probe was an oriented line (of the same length and orientation as the perceptual probes), which appeared for 20 ms. The participant reported the orientation of the line using the left or right arrows on the keyboard. Using a QUEST paradigm set to 82 % threshold level (Watson & Pelli, 1983), the luminance of the subsequent probe underwent an increment if the previous response was incorrect, and a decrement if the response was correct. The background luminance of the screen was 27.5cd/m^2. Forty trials were used to obtain the threshold measurement, and each location was tested three times, with the final threshold being the average of the three values. These values were then used such that each probe was presented at this threshold value for each participant.

2.3.5 POINTING TASK

At the start of each trial a grey screen appeared with a central fixation point, which was 0.25° in size and 21 % Michelson contrast from the background. Two touch targets located at 10° eccentricity from the centre also appeared. These targets were circles 0.75° in diameter, and 8 % contrast from the background. Each circle contained a cross of 9 % contrast, which formed the basis of the secondary discrimination task at the probe location (figure 1).

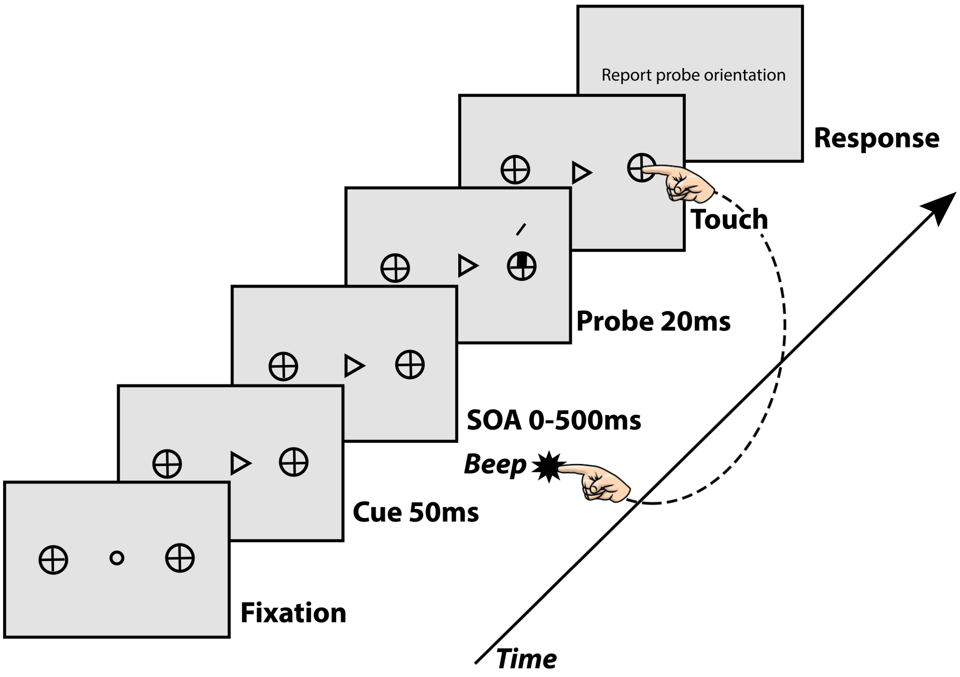

Figure 2.1 – Pointing task events. After a key press by the observer, a cue indicated the side of the screen to which the participant had to point. At a variable SOA after the cue, a perceptual probe (oriented line) appeared at one of six locations surrounding the reach target. A perceptual discrimination task also appeared at the touch location to ensure participants were directing their attention to that location.

As shown in Figure 2.1, the reaching trial started when the participant depressed a key on the mouse, which was affixed to the desk 40 cm from the screen, central to the screen and the participant's body. After a key press by the observer, a cue appeared at the center of the screen, signalling the side of the screen where the probe would appear (with 100 % validity), and the side to which the participant had to point.

The cue was a triangular arrow of 0.5° size and 17 % contrast, which pointed to either the left or right side. After the cue had been displayed for 50 ms, a beep sounded to signal that the participant could start their reach to the target on the cue side. This beep also signalled the start of the SOA, after which a perceptual probe would appear at one of 6 locations on the cued side, and a discrimination task at the touch target would occur.

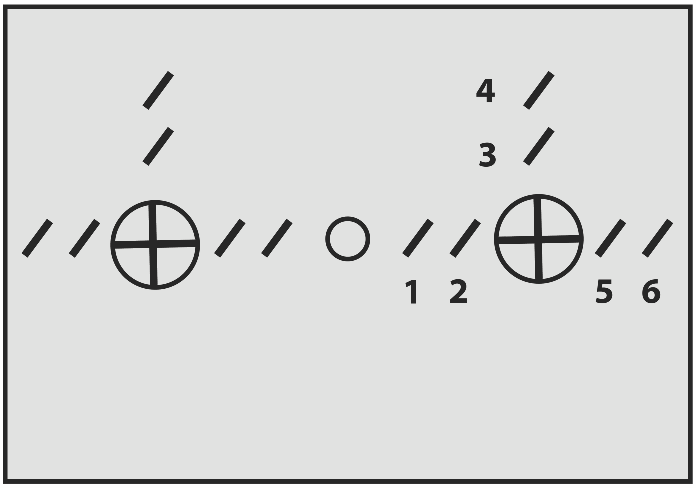

Figure 2.2 – Possible locations that the perceptual probe could appear. The probe could appear at any of the probe locations on the cued side of the screen.

Left and right cues occurred with equal probability and so perceptual probes appeared at any one of 12 locations around the screen with equal probability (see figure 2.2). These locations were 6, 8, 12, 14° from the fixation point along the central horizontal axis, and two locations 3 and 6° above the touch target at 10° from fixation point. These specific probe locations were chosen so that they would not be occluded by the hand during the end of the reach, and thus ensured that the reach did not affect performance on the perceptual discrimination task. The oriented lines were 0.5° in length, oriented at an angle of 45º left or right, and were at a contrast level determined by an individual threshold task for each participant. Either the top or bottom section of the cross inside the touch target would have an increase in contrast for 20 ms, which formed the basis of the secondary discrimination task.

The stimulus onset asynchrony (SOA) could be one of 9 different lengths – 0, 59, 118, 189, 248, 307, 354, 425, 496 ms, measured from 50 ms after cue onset. This range was chosen with the aim of capturing the attentional facilitation, which may accompany both the preparation and the completion of a reach. After the reach was completed, a post cue indicated whether the subject had to report the orientation of the perceptual probe (90 % of trials), or the discrimination task at the touch target (10 % of trials) using the arrow buttons on the keyboard (left/right for perceptual probe, up/down for target discrimination task). Auditory feedback was given for correct and incorrect answers. Feedback was also given if the participant reached too slowly (>600 ms) or if they started their reach too early (<100 ms), to try to constrain movements so that the probe appeared during the period of the planning and execution of the reach.

For each trial touch location, reach latency, reach time, reach accuracy and the perceptual response were recorded.

The secondary discrimination task was used to ensure that participants were not directing attention covertly to possible probes locations across the visual field. Although they were instructed to direct attention to the reach target, this secondary task aimed to ensure this was the case. The results of this secondary discrimination task were not analysed due to the occlusion of the target by the hand, making the results unreliable.

2.3.6 PERCEPTUAL TASK

This task was exactly the same as the pointing task, except that no reach was made. This task aimed to compare the performance when a reach was being made, compared with performance when no reach occurred. As with the pointing task, each trial started with a grey screen, central fixation point, and even though there was no pointing in this task, the pointing targets were maintained for accurate comparison of the tasks. To start a trial, participants pressed a key, and after a variable delay (calculated as in the pointing task) the central cue appeared, signalling the side on which the perceptual probe would appear (Figure 2.3). The discrimination task at the touch target appeared on 40 % of the trials as compared with 10 % of trials at the reaching task. This increase aimed to ensure that similar attentional priority was placed on the touch target as when a reach was being planned to that location.

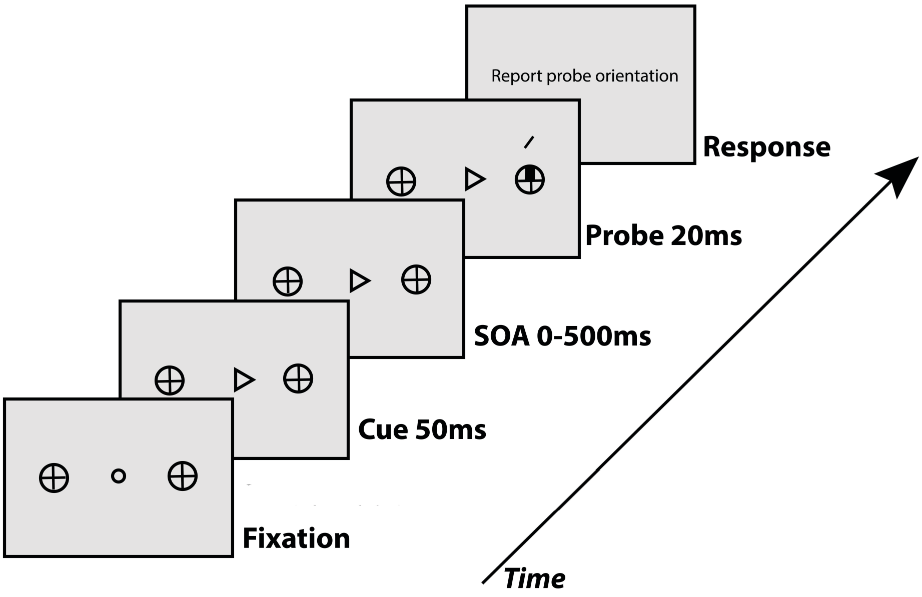

Figure 2.3 – Perceptual task events. As with the reaching task (figure 2.1) a cue indicated the side of the screen at which the perceptual probe (oriented line) would appear. This probe could appear at a variable SOA at any one of 6 locations. A perceptual discrimination task also appeared at the equivalent of the touch location in the reaching task, to ensure participants were directing their attention to that location.

As with the reaching task, after the cue had been displayed for 50 ms, both the perceptual task and the discrimination task at the targets would appear after a variable SOA from the same range as the pointing task. The responses and feedback were collected and presented as above. Eye movements were monitored at all times to ensure that the participants were maintaining fixations in both the pointing and perceptual tasks.

2.4 RESULTS

2.4.1 PRELIMINARY ANALYSES

Data Exclusions

Trials in which the participant failed to maintain central fixation were excluded. Based on the data recorded by the Eyelink, movements of >1 ° were excluded from further analysis. The remaining data were then filtered according to reach time and reach latency, such that ± 2 standard deviations from the mean of these measures were excluded. Individual reach dynamics are shown in Table 2.1. Reach latency was measured as the time from 'go' signal beep until the time the participant lifted their finger from the mouse button. Reach time was measured as the time from the lifting of the finger from the mouse to the time the screen was touched.

Table 2.1 – reach dynamics for each participant

	Reach time			*Reach latency*			*Excluded*
Participant	*Mean*	*SD*	*Median*	*Mean*	*SD*	*Median*	
S1	323 ms	7 ms	319 ms	255 ms	100 ms	247ms	2.65 %
S2	325 ms	110 ms	315 ms	176 ms	74 ms	175 ms	1.3 %
S3	375 ms	213 ms	357ms	178 ms	83 ms	173 ms	0.86 %
S4	404 ms	191 ms	390 ms	232 ms	127ms	219 ms	0.9 %
S5	391 ms	194 ms	398 ms	178 ms	151 ms	171 ms	0.46 %
S6	434 ms	310 ms	436 ms	264 ms	112 ms	261 ms	0.22 %
ALL	378 ms	203 ms	362 ms	210 ms	115 ms	200 ms	0.51 %

Data sorting

Data was sorted according to the time the perceptual probe appeared relative to the onset of the reach. This was done by sorting the data into 50 ms bins according to the time the perceptual probe appeared relative to the reach onset time, so for example if the perceptual probe appeared 50 ms before the onset of the reach, the results of that trial would be put in the -50 ms bin. Data were sorted into 12 bins that spanned the range -200 to 300 ms in 50 ms intervals. All data were analysed on a trial-by-trial basis to ensure that data were put into the appropriate bin for each trial. This was done in order to see how the onset and planning of a reaching movement affects the profile of attentional facilitation.

2.4.2 PERCEPTUAL PERFORMANCE – POINTING TASK

Data were weighted according to the number of trials per condition for each participant. Data were also collapsed across left and right sides such that only 6 locations were analysed (performance was analogous across left and right sides). Figure 2.4 shows mean performance across participants for each time bin and each location.

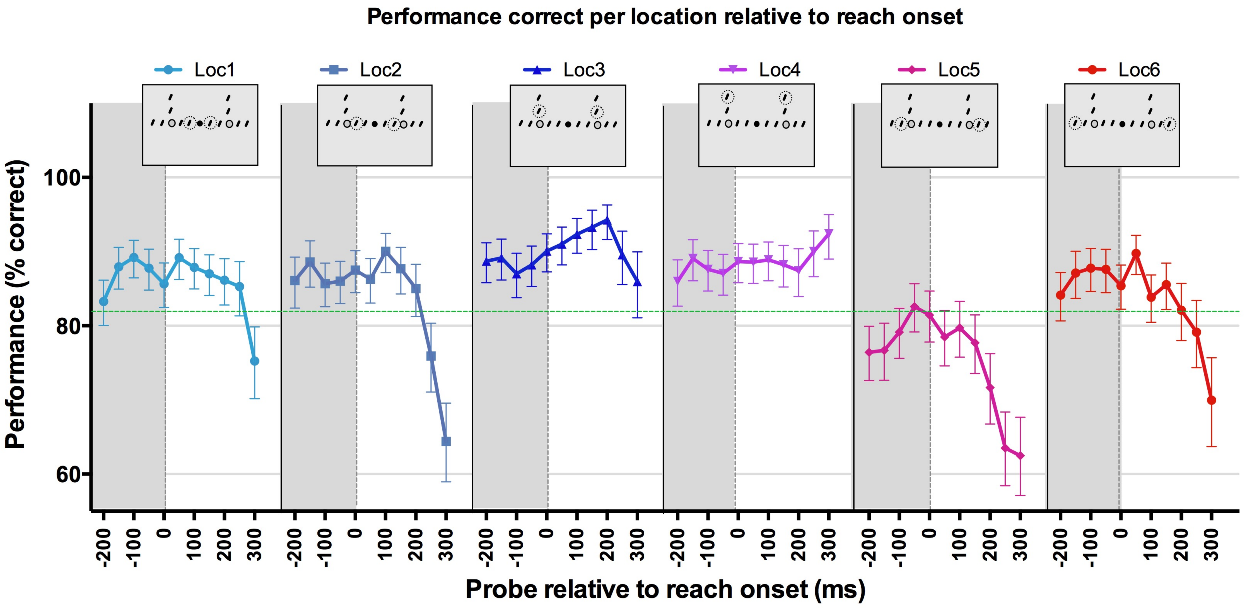

Figure 2.4 – Perceptual performance per bin per location. Grey areas indicate time bins before reach onset; white areas indicate time bins after reach onset. The dotted vertical line indicates reach onset time. Error bars are 95 % confidence intervals calculated using Jeffreys interval which uses a Bayesian approach to calculate confidence intervals in binomial data. The 82 % mark used to calculate baseline threshold values is indicated by the green horizontal line.

Percent correct varied as a function of time bin, for all locations. As can be seen from Figure 2.4, the pattern of variation was somewhat different across different locations. We used a linear mixed model to analyse significant effects in these data. The model used fixed effects of time bin and location, and a random effect of participant. There was a significant main effect for time bin (F(10,330) = 14.33, p = 0.00), location (F(5,330) = 54.60, p = 0.00). There was also a significant interaction between time bin and location (F(50,330) = 2.59, p = 0.00) on perceptual performance.

Attentional facilitation is the enhancement in the percent correct performance that is above the 82 % threshold level used to determine the baseline contrast threshold. The overall pattern of facilitation suggests that facilitation improves across the visual field before reach onset, and stabilises during the early part of the reach. The locations along the horizontal axis relative to the reach target show a marked drop off in performance later in the reach, while the locations above reach target remain stable. This suggests that the profile of attention along the horizontal and vertical axis relative to the reach target is different

2.4.3 MAXIMUM AND MINIMUM PERFORMANCE

From Figure 2.4, it is clear that attention builds up (that is, performance improves), and then generally drops off. This pattern is consistent with earlier findings that attention builds up over time at a location and that a peak in attentional facilitation can be identified relative to the onset of an eye movement or reach (e.g. Jonikaitis and Deubel, 2011; Rolfs and Carrasco, 2012). To quantify the magnitude of this attentional facilitation during the reach, we compared maximum and minimum performance at each location (see Figure 5). This difference gives a summary of the quantitative change in perceptual performance across the visual field, using the same data as shown in figure 2.4.

The maximum and minimum values for each participant were collated. Paired-samples t-tests were conducted to determine if the differences between the maximum and minimum performance at each location were significant. There were significant differences between the maximum and minimum values for location 1 (t(5)= 5.83, p= 0.002), location 2 (t(5) = 9.63, p = 0.000), location 3 (t(5) = 20.71, p = 0.000), location 4 (t(5) = 5.89, p = 0.002), location 5 (t(5) = 12.252, p = 0.000) and location 6 (t(5) = 6.65, p = 0.001). All locations except for location 4 showed that the maximum facilitation occurred earlier in the reach, with the minimum performance being observed late in the reach.

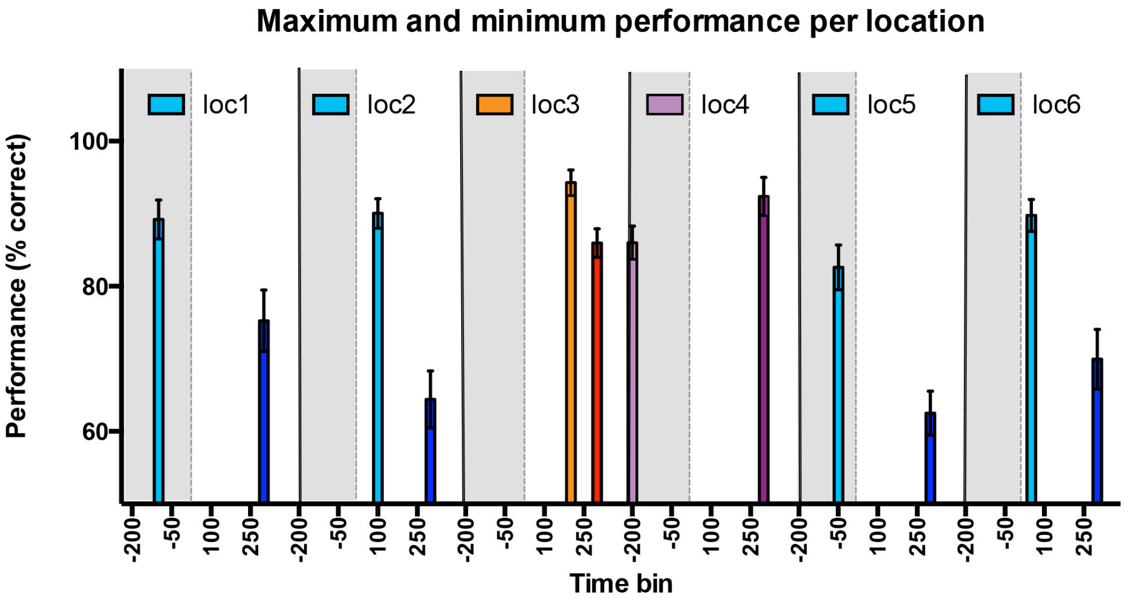

Figure 2.5 – Maximum and minimum performance per location, across all participants. Grey areas indicate time bins before reach onset; white areas indicate time bins after reach onset. The dotted vertical line indicates reach onset time. Error bars are standard error of the mean.

2.4.3 REACHING PERFORMANCE VS PERCEPTUAL PERFORMANCE

The difference between reach accuracy and performance on the perceptual probe task was compared to determine whether there was a trade-off of perceptual performance for reach performance, at different points during the reach. This was calculated by normalising the values for all data for both reach accuracy and perceptual performance for all participants, such that each measure was calculated as a ratio of the maximum value for that measure. These measures were compared for each time bin, to determine whether performance was weighted in favour of perceptual performance or reaching performance for each location within that time bin.

In Figure 2.6, each data point represents the averaged data across all participants for each location. Each point therefore represents approximately 1000 trials across participants, and approximately 150 data points per participant. The trade-off between reaching and perceptual performance in each time bin is shown in Figure

2.6. For each time bin, the locations where reaching performance was prioritised appear above the diagonal line, for those locations where perceptual performance was prioritised, the markers appear below the horizontal line. This figure provides an overview of how the priority changes from reaching performance to perceptual performance across time, and that this priority change is different across locations.

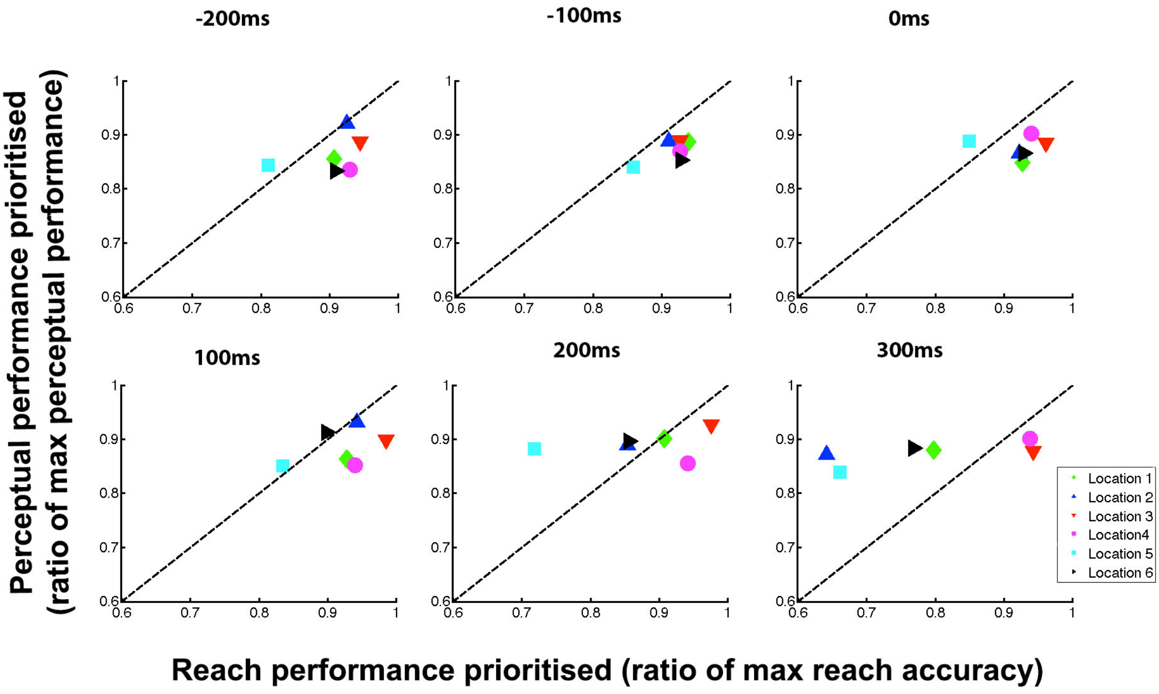

Figure 2.6 – Perceptual performance vs reaching performance. Points above the diagonal line indicate that perceptual performance is better than reaching performance for those conditions.

The trade-off between reaching and perceptual performance can be seen as the data points shift from reaching performance being better than perceptual performance, to perceptual performance being generally prioritised at a later stage during the reach. For time bins from -200 ms to +100 ms, the weighting is generally in favour of reaching performance, showing that during the preparation of the reach and the first stages of the reach, reaching performance was prioritised over perceptual performance. After this time, the trade-off between reaching and perception is more evenly distributed across locations, with the final time bin of +300 being in favour of perceptual performance for all locations apart from locations 3 and 4, which are above the reach target. This is intuitive as the reach would then be complete, so there is no need to favour reaching performance over perceptual performance across the visual field, however the probe locations which are the same eccentricity as the reaching target may still show a residual reaching benefit when compared with probe locations which are further away.

2.4.4 HEATMAP OF SPATIOTEMPORAL PROFILE OF PERFORMANCE

A heatmap of spatiotemporal performance was created to visualise the spread of attentional facilitation relative to the reach. Values for the heatmap were calculated by using perceptual performance across the different locations tested in the visual field during the reach task. Values for locations in time and space between these values were weighted and calculated using the distance between the desired point in the visual field and the experimental location. This distance, in addition to the required reliance on the nearest points and the grain size of the points to be estimated was used to estimate the values between the experimental locations.

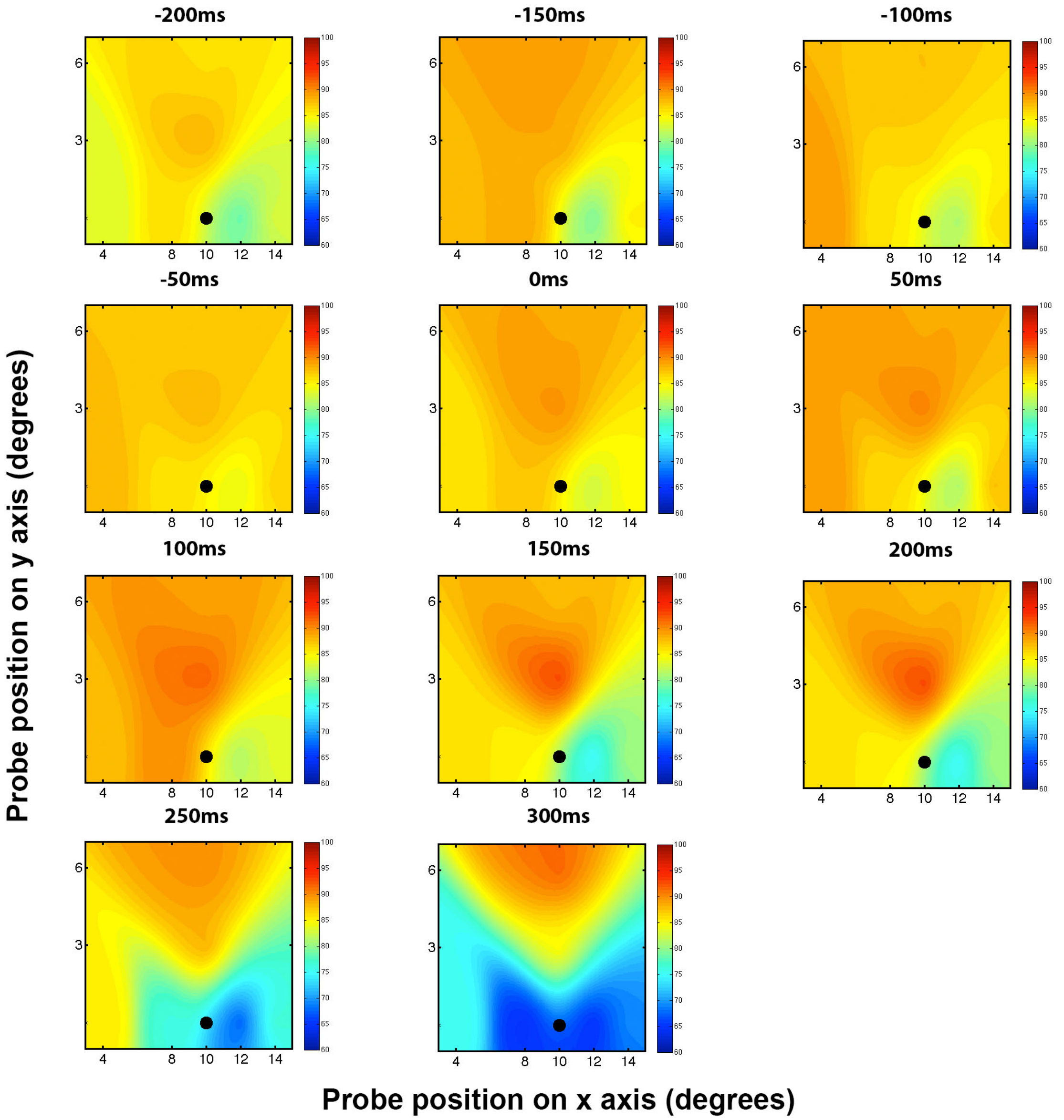

Figure 2.7 – Heatmap showing perceptual performance across all locations, per time bin. Reaching target location is indicated by a circle. Heatmap shows the visual field from 4° from fixation to 14° from fixation, as these were the range of locations tested. The 82 % baseline threshold level is indicated by the colour green. *note explain that colourbar is equivalent to the % correct

2.4.5 PERCEPTUAL PERFORMANCE WITHOUT POINTING

A secondary experiment was conducted (see figure 2.3) to determine the magnitude of the spatiotemporal facilitation when there is no reach being prepared. This experiment aimed to compare the facilitation that accompanies a reach with the facilitation observed in a purely perceptual paradigm.

We tested only four time-points, which were calculated using the average reach latency and reach time for each participant. As the reach latencies and reach times differed across participants, the timing of the perceptual probe differed slightly for each. There were 4 possible probe onset times for each participant, which were calculated using the mean reach onset time for the reaching task. This meant that there were two possible probe onset times before the mean reach latency, and two after. These points were then binned as being before or after the hypothetical reach onset time. Only 4 time bins were chosen as we wanted to test the overall magnitude of facilitation when no reach was being prepared, without comparing the fine-grain changes measured in the reaching task.

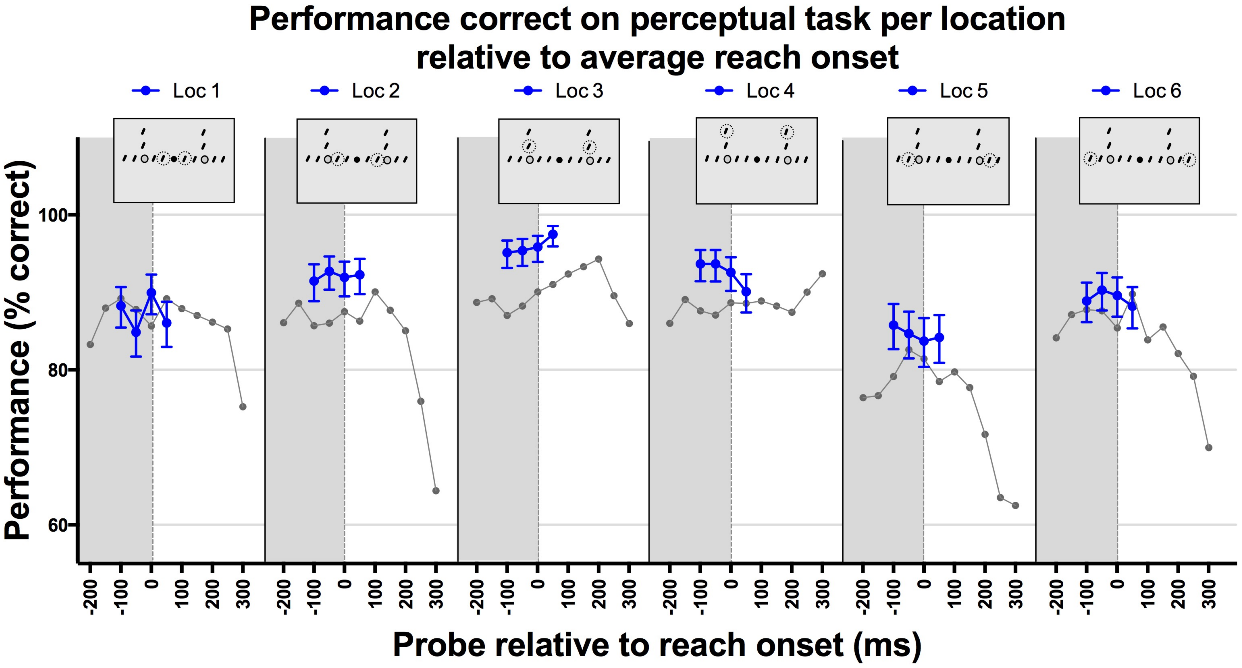

Figure 2.8 – Perceptual only performance is shown for all participants in blue. Error bars are 95 % confidence intervals calculated using Jeffreys interval as in Figure 2.4. Percentage correct data for the reach condition (per figure 2.4) is replotted in grey for comparison.

In figure 2.8 the timing of the perceptual probe relative to the average reach onset was estimated by averaging the data across participants, and using the average reach latency to calculate when the probe would have appeared relative to the reach, had there been a reach in that experiment. This means that even though there was no reach in this condition, using the average reach time for each participant, it can be estimated when the probe would have occurred relative to this averaged reach latency. It can be seen that at some locations the magnitude of facilitation is fairly similar (locations 2 and 6), whereas locations 1 and 5 see better performance in the reaching task, and locations 3 and 4 see better perceptual performance compared to early time bins in the reaching condition, and no difference at times after the onset of the reach.

2.5 DISCUSSION

2.5.1 ATTENTIONAL FACILITATION AT DIFFERENT LOCATIONS

We measured the spatiotemporal profile of attention during a rapid goal directed movement. We found that there was a shift in space and time, and this profile was different (though qualitatively similar) for each location, and markedly different for the horizontal and vertical axes tested. For locations between the central fixation and touch location (that is, along the horizontal axis), attentional facilitation was greatest approximately 50 ms before reach onset. For locations above the touch location (in the vertical axis), attentional facilitation was greatest between 100-300 ms after reach onset. The 6 spatial locations and 9 time points allowed a finer grained analysis of this shift in attention than has previously been measured. We also measured pointing performance and found the touchpoints to be quite consistent across probe times.

The build up before reach onset observed for targets along the same direction between the touch location and central fixation is consistent with previous results. Rolfs et al. (2012) reported an increase in performance from 150 ms before reach onset, and Jonikaitis and Deubel (2011) saw an increase in perceptual performance from about 150 ms before the reach, and then a stabilisation of performance during the reach itself. The broad pattern of attentional facilitation across the visual field supports the idea that the locus of attention can be spread to multiple locations (Baldauf & Deubel, 2010; Baldauf & Deubel, 2008), although this study involved only one movement instead of a series of movements. The nature of the attentional facilitation that we observed is in line with the idea of an attentional landscape, which highlights behaviourally relevant locations differentially (Baldauf & Deubel, 2010). This idea that it is not only the reach location which shows attentional facilitation is not only supported by studies showing multiple loci of attention during sequences of reaches, but by studies showing that in purely perceptual tasks attention can also be spread broadly beyond the immediate behaviourally relevant location (Koenig-Robert and Van Rullen, 2011).

Although this experiment examined the attentional shift relative to a reach whilst fixation was being maintained, the results can be compared to previous studies that have examined the attentional shift with both saccades and hand movements. Since saccades and reaching are linked, one can also compare the time-course of these two movements to try to discern if the attentional shift is due to a single mechanism that drives both the pre-saccadic shift and the pre-reach shift, or if the attentional resources for these movements are different. This shift has been studied to a greater extent in relation to saccades than relative to a reach, and one can compare these studies to see if the time-course is similar.

The time-course of the pre-saccadic attention shift has been studied in multiple experiments, with many different paradigms, however a discrepancy arises in the research surrounding the timing of the pre-saccadic attentional shift, with some studies claiming the shift accompanying a saccade can happen as early as 50-100 ms after a cue (Deubel, 2008), and others finding that this shift happens on a slower time-scale, of around 150-200 ms after cue (i.e. Castet et al, 2006; Montagnini & Castet, 2007; Jonikaitis & Deubel, 2011). Nakayama & Mackeben (1989) found the peak attentional facilitation in a covert attention task without any saccades to be about 200 ms after the cue, which would seem to be slower than the attention shift accompanying a saccade.

However, there are several key differences between our paradigm and that used by previous studies. Other studies have measured the attentional benefit relative to cue onset/offset (Deubel, 2008; Castet et al, 2006; Montagnini & Castet, 2007), and some relative to reach or saccade onset (Rolfs and Carrasco, 2012; Jonikaits & Deubel, 2011), and the paradigms differ in both stimuli and the timing of cue presentation, pre-cue presentation, and the time-points at which the attentional shift was actually recorded. It is therefore difficult to compare results directly.

One pattern that is observed at the locations horizontally in line with the reach target was the marked drop off in performance which occurred from 150-200 ms after reach onset. While there is no definitive answer as to why this occurred, a number of explanations may be plausible. The first is that the drop off may be due to the occlusion of the perceptual probes by the hand as it neared the end of the reach. The locations of the probes were chosen to avoid this problem, however there is a possibility that occlusion could have still occurred. Another explanation that could account for this pattern is inhibition of return, which could result in the inhibition of performance at those previously attended locations. This effect is seen to act on a similar timecourse to the inhibition shown here (Klein, 2000). However, a more likely explanation is that that the drop off is due to a general decay of attention that occurs after a certain time-point. Nakayama and Mackeben (1989) observed that attention seems to drop off from about 300 ms after the cue for 'transient' forms of attention, which is consistent with the pattern observed here. Similarly, Koenig-Robert and Van Rullen (2011) found that there were inhibitory areas across the visual field as well as facilitation. It seems logical in this case that the drop-off in attention would occur once the reach is nearing completion and the need for enhanced attentional resources is less. It is however difficult to make a direct comparison to previous studies investigating the time-course of attention relative to a reach, as they focus on the attentional build up prior to the reach as opposed to the pattern of attention for the entire reach, until the hand is very close to the target.

While performance at location 5 shows a change in percent correct over the time course of the reach that is similar to that observed for other horizontal locations, the overall percent correct appears shifted down. Performance at location 5 seems, by comparison, to be inhibited. This is a curious pattern and it could be due to a crowding effect from the neighbouring touch target and location 6 (Whitney & Levi, 2011). This seems unlikely however, as only one probe location is visible at a time, so the crowding effect would have to come from the touch target alone. Another possible explanation is that participants overshot their reach, thus obscuring the location 5 probe. As mentioned earlier however, the paradigm was designed specifically to avoid this. Further experiments investigating this pattern may provide a more parsimonious explanation of these aspects of the dataset.

2.5.2 THE TRADE-OFF BETWEEN PERCEPTUAL PERFORMANCE AND REACH PERFORMANCE

In the time bins before reach onset, performance seems weighted almost exclusively in favour of the perceptual task, for each of the probe locations, and it is only toward the end of the reach that the reaching performance seems prioritised. This result suggests there is a trade-off between reaching accuracy and performance on the perceptual task, which benefits performance on the perceptual probes in the planning stages of the reach. When the reach is well underway the priority shifts to reach accuracy being higher than the accuracy on the perceptual task – this is in line with the pattern shown in Figure 2.4, which shows a drop-off in perceptual performance in the later stages of the reach. When regarded in conjunction with the results in Figure 2.6, this drop-off could reflect the shift in priority from perceptual performance across the visual field to completing the reach accurately.

2.5.3 PERFORMANCE ON THE REACHING TASK VERSUS THE PERCEPTUAL ONLY TASK

Figure 2.8 shows the performance on the secondary task, which was a perceptual task with no reaching. This task sampled only four time points, which were calculated for each individual, based on the average reach latency for that participant. Thus, it is difficult to directly compare the time-points with the data in Figure 4 as the data are averaged across participants, and the timing of the probe appearance is slightly different for each participant. While not directly comparable, the performance on this secondary task seems to show a fairly similar pattern of attentional facilitation as the reaching task, in both the temporal profile, and the magnitude of facilitation seen at each individual location. This could indicate that the attentional mechanisms underlying perception and reaching may be similar. Alternatively, it could indicate that the paradigm was measuring attentional facilitation driven by perceptual mechanisms rather than the attentional facilitation driven by planning a hand movement. The nature of this paradigm however does not allow us to dissociate performance driven by perception, and performance driven by action. Comparing performance on the reaching and perceptual task with the perceptual only task is the only indicator of the potential dissociation of these different mechanisms.

2.5.4 MECHANISMS UNDERLYING THE ATTENTION SHIFT RELATIVE TO A MOVEMENT

The pre-motor theory of attention (Rizzolatti et al, 1994) postulates that different types of movements have their own, neurologically localised mechanisms controlling the orienting of attention to an impending movement location. There is evidence to suggest a dissociation between attention for perception and attention for action. Blangero et al. (2010) reported a dissociation between covert attention and pre-saccadic attention in patients with right posterior parietal damage. The idea that the parietal lobe is important for integrating attentional mechanisms was also suggested by Khan et al. (2008) who suggested that while there may be different mechanisms for perception and action, there could be a functional coupling of saccade preparation and attention in the parietal cortex. This suggests that while the mechanisms underlying attention for perception and attention for action might be different, the parietal cortex brings these mechanisms together.

Gregoriou et al. (2012) have also demonstrated that different patterns of activation are found in FEF when attending to a target or also planning a saccade to that target. It is possible that the attentional effects observed in the FEF may also be due to the connections from the FEF to other areas which are implicated in attention, such at the LIP and SC (Moore and Fallah, 2004). Indeed, it has been seen that microstimulation of the SC also increases perceptual performance at the relevant area of space, suggesting that the SC might also play a role in the orienting of attention (Muller et al, 2005).

Evidence suggests that there is a neural circuit that mediates the coordination of eye and hand movements (Crawford et al, 2004), and so it is possible that areas such as the FEF and SC which are implicated in saccade related attention may also be used to guide the attentional shift which results from the planning and execution of a hand movement.

Gherri and Eimer (2010) found that the preparation of a manual response could significantly modulate N1 components between 150 and 190 ms after stimulus onset. Baldauf and Deubel (2009) in an EEG study found that perceptual probes presented at the location of a reaching goal elicited a response from the N1 component, indicating the presence of attention at the reach target. While there may be a mandatory link between the locus of a movement and attention, it is still not clear whether this is due to shared or independent neural resources. The secondary condition revealed that there was a difference in performance between the conditions, and this difference varied across times and locations. The pattern of performance however was not markedly different from the pattern observed for the reaching condition, which may indicate that the mechanisms between perceptual and motor performance are shared.

While these studies provide evidence that mechanisms underlying saccades may be connected with the orienting of attention, it is still unclear how this may relate to the planning of other movements such as hand movements, and whether the attentional mechanisms for hand movements are the same as those which are involved in the pre-saccadic attention shift.

2.5.5 PRIORITY MAPS

What purpose might this attentional allocation play? It has been suggested that attentional shifts contribute to a priority map of relevant stimuli that is built up over time. This concept of a priority map proposes to integrate both top-down and bottom-up input to rank the behavioural relevance of locations across the visual field, and determines how visual attention should be directed – to the item with the highest attentional priority (Fecteau & Munoz, 2006; Bisley & Goldberg, 2010; Bisley et al, 2009). It may be the case that the attentional shift seen in this study has dual stages – firstly the priority map selects the behaviourally relevant location (in this case the reaching target), and this behavioural selectivity subsequently allows attention to be directed to the relevant location. Indeed, there is evidence to suggest that salience map models can account not only for the guidance of attention and eye movements, but also that of manual pointing movements (Zehetleitner et al, 2011).

This idea may also fit with previous experiments which have found that when there are multiple impending reach locations, these locations can be selected in parallel rather than serially (Baldauf & Deubel, 2006) – it may be the case that in this experiment, both the reach target and the perceptual probe locations could have been selected as being behaviourally relevant by the priority map, and attention could have been directed to these locations in parallel. An inherent problem with probing locations in this manner is that although the attentional facilitation caused by the planning of a reach may be measured across the visual field, it is hard to dissociate this from any attentional resources that may be allocated to the probe location as a result of the behavioural relevance of these locations.

2.5.6 ATTENTIONAL OSCILLATIONS AND THE ATTENTIONAL BLINK.

It has been shown that when attention is 'reset' using a visual or aural cue, there is a subsequent oscillation in attentional performance for the preceding second, with performance cycling at a rate of approximately 8 Hz (Landau & Fries, 2012). These patterns of oscillation performance are similar to the patterns shown in figure 2.4, but the period of the oscillations are much slower than 125 ms, observed in Landau & Fries (2012). We have sampled up to 400 ms after the cue, so we would expect about 3 cycles of oscillations during this period. However, we only see a period of increase followed by a decrease. Thus it is unlikely that our sensitivity modulation is due to attentional oscillations as described by Landau and Fries (2012).

In the attentional blink, attentional resources for subsequently presented stimuli are temporarily unavailable and therefore a downturn in performance is observed after the presentation of an attended stimulus (for review see Dux & Marois, 2009).

Similarly, it could be the case that the downturn observed for the horizontal locations is due to attentional resources being temporarily exhausted. This explanation does not however hold for the vertical locations which show little downturn in attention over time.

2.6 CONCLUSION

These results have demonstrated that there is an attentional shift which builds up before the onset of a reach, and that the temporal profile of this shift differs across the visual field. The results show a build-up of attention around 150 ms before the onset of a reach, which is in line with previous research. This study however also measures the profile of attention throughout the reach, and shows that once the movement is well under way, attention narrows around the touch target while the surrounding locations are suppressed. The profile of attention also seems to be different for locations along the horizontal and vertical axis, which is consistent with the idea that attention is restricted to the reach target later in the reach, when reach performance is prioritised.

Overall the results provide support for the notion that planning and executing a reach causes a shift in attention across the visual field, and specifically around the reaching target. These results also provide a solid basis for future comparisons of the mechanisms underlying both reaches and saccades.

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3. PREFACE TO PAPER 2

Paper one of this thesis (Chapter 2) provided a comprehensive insight into how attention shifts when a reach alone is being conducted, without a concurrent saccade. The results of this paper reveal a broad, sustained profile of attention across the visual field, with a subsequent dramatic drop in performance. In order to get a complete picture of how the pre-movement attentional shift may work, it is important to be able to compare this spatiotemporal profile with that accompanying a saccade alone, and a saccade-plus-reach. Previous studies have looked at the pre-saccadic profile of attention, for example (Castet et al., 2006; Deubel, 2008; Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013; Montagnini & Castet, 2007; Rolfs & Carrasco, 2012), however, as was discussed in Chapter 1, different spatial layouts and different types of perceptual discrimination tasks may have led to inconsistent results. This paper aims to use a similar paradigm to that in Chapter 2 in order to provide a more accurate comparison of the pre-saccadic and pre-reach attentional shift, and to do this at a number of time-points and locations surrounding the movement target. This will give an insight into how attention shifts between different types of movements, and how different movements may require attentional guidance at different points in the reach.

There are two key differences between Chapter 2 and Chapter 4. The first is the removal of the ‘go’ beep after cue onset. In Chapter 2, the onset of the reach was signalled by a beep 50 ms after the cue onset. This was to allow time for processing of the cue before a movement was initiated. A pilot study using this same paradigm in Chapter 4 however revealed that participants seemed to be starting their saccades before this ‘go’ beep, as the saccade latency distribution appeared to be cut off at the lower end. This didn’t affect reach latency distributions (as in Chapter 2), however Chapters 4 and 6 both measured saccade latencies. The paradigm was therefore adapted slightly so that the cue onset now signalled the start of both the reach and saccade, and the first SOA was measured at 13.3 ms after cue onset. The second difference is that in the experiments reported in Chapter 2, there was no random delay between the initial button press and the cue onset, whereas Chapters 3 and 4 both include this random delay. Despite this difference in the random delay, the reach latencies are comparable across studies.

4. PAPER 2 - DISSOCIATING THE PREMOTOR ATTENTIONAL SHIFT FOR SACCADES AND REACHES.

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Contribution to the Paper	Designed, coded and piloted the experiment, ran the experiment, analysed data, wrote manuscript		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	17-MARCH-2016

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Anna Ma-Wyatt		
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4.1 ABSTRACT

The preparation and execution of saccades and goal-directed movements elicits an accompanying shift in attention at the locus of the impending movement. Some key aspects of the spatiotemporal profile of this attentional shift between eye and hand movements are not however resolved. While there is evidence that attention is improved at the target location when making a reach, it is not clear how attention shifts over space and time as a saccade and a reach are made to the same target. We compared performance on a perceptual discrimination paradigm during a saccade-alone task and a saccade-plus-reach task to map the temporal profile of the premotor attentional shift at three locations around the movement target. The results suggest that attention shifts as a saccade is being initiated, and this shift occurs on a similar timescale when a reach is being made concurrent to a saccade. This provides insight into how the spatial and temporal profile of attention is comparable between saccades and reaches, and when these movements may require attentional guidance during movement planning and execution.

4.2 INTRODUCTION

The visual environment that we interact with is complex. We need attention to filter the relevant information from the irrelevant, and to select targets for upcoming movements. It has been well established that attention improves perceptual performance at the attended location (Carrasco, 2006; Carrasco, Ling, & Read, 2004; Liu, Abrams, & Carrasco, 2009; Treue, 2004). While it is apparent that attention shifts to an upcoming saccade location (Deubel & Schneider, 1996; 2003; Moore & Fallah, 2001), the role of attention in planning and executing hand movements is less clear.

Eye and hand movements are often coordinated, particularly when reaching rapidly to a visually defined target (Land & Hayhoe, 2001; Ma-Wyatt, Stritzke, & Trommershäuser, 2010; Neggers & Bekkering, 2001). This close coupling seems to make intuitive sense, given evidence that the same visual information is used to drive eye and hand movements both in the planning stages of the reach, and throughout the reach when visual information becomes crucial in updating the motor plan as the hand is in flight (Gegenfurtner & Franz, 2007; Ma-Wyatt et al., 2010; Ma-Wyatt & McKee, 2006; 2007; Stritzke & Trommershäuser, 2007). This is also the case in naturalistic tasks, where sequences of movements show that the eye precedes the hand, indicating visual information is important in the guidance of accurate sequences of hand movements (Land & Hayhoe, 2001). The benefit of this coordination seems to come not only from the new visual information acquired by foveating the target but also the proprioceptive information from the position of the eye (Prablanc, Echallier, Komilis, & Jeannerod, 1979; Ren, 2006). This close link between eye and hand movements suggests that the attentional guidance that accompanies eye movements may also be present when one is making a hand movement, and that this attentional guidance may play a role in the planning and execution of both saccades and any concurrent hand movements. However, while this research suggests that indeed eye and hand movements are linked with an attentional shift, the nature of the spatiotemporal shift in attention with eye and hand movements is not yet well understood.

Why is it important to understand the spatiotemporal profile of attentional shifts? In the real world, targets are not presented in isolation, and movements are made to targets embedded in complex visual arrays. Given that shifts of attention will occur over many locations, it is important to understand how attention is shifted from one location to another. Recent work suggests that this spatiotemporal profile of premotor attention around the target for a reach alone can involve both suppression and facilitation of performance (Stewart & Ma-Wyatt, 2015), similar to findings for covert attention (Koenig-Robert & Van Rullen, 2011). This study aims to compare the attentional shift prior to a saccade alone or a saccade accompanied by a reach, to examine both the spatial and temporal properties of this shift around the movement target. In each condition, the goal of the movement is identical for the eye and the hand. The temporal properties of the attentional shift were explored by changing the SOA of a perceptual probe during both eye and hand movements, and the spatial properties were explored by probing a location between cue and saccade/reach target, above the target, and beyond the target.

4.2.1 PRE-SACCADIC ATTENTIONAL SHIFTS

Before a saccade is executed, there is a shift of attention to the location of the upcoming saccade (Deubel, 2008; Deubel & Schneider, 1996; 2003; Jonikaitis & Deubel, 2011). Many studies have sought to determine how this shift in attention works, and have tested both the spatial extent of the attentional shift, and its time-course. However no study has yet provided a fine-grain spatiotemporal map of the pre-saccadic attentional shift. Indeed, the evidence remains unclear as to the exact timing of this attentional shift, with some studies claiming that attention can shift as early as 50-100 ms after a cue (Deubel, 2008; Rolfs & Carrasco, 2012), while others observe this shift happening on a longer timescale of approximately 150-200 ms after a cue (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Jonikaitis & Deubel, 2011; Montagnini & Castet, 2007). Castet et al. (2006) for example found that attention builds up at the saccadic location over a period of 150-200 ms after cue onset, and interestingly, this study found that it was not only the saccade location that showed an attentional facilitation, but neighbouring locations also showed a benefit in performance. This shows that the facilitation may not be tightly locked to the saccade target, but may provide a benefit in a broader spread around the target.

White et al. (2013) found that attention built up at the impending saccade location in the 50 ms before saccade onset. This attentional facilitation was higher at the saccade location than neighbouring non-saccade locations. Similarly, Rolfs & Carrasco (2012) found that attentional facilitation built up from 100 ms before saccade onset on an orientation discrimination task. Particularly, they found that participants perceived a stimulus to be of higher contrast at the location of the saccade target shortly before the saccade is executed.

These studies provide sound evidence that there is indeed an attentional shift at the target location before the initiation of a saccade, although the timing of this shift may vary depending on the particular paradigms employed. Indeed, it could be argued that some of the observed discrepancies in the timing of the pre-saccadic attention shift are due entirely to the task-demands, and specific timings of the task. For example, a pre-cue directs attention to a location before a cued saccade is made, and a subsequent perceptual discrimination can dissociate whether the locus of attention and the locus of the saccade are at that location (Deubel & Schneider, 2003). If the location is pre-cued some 1000 ms before a saccade is being cued and thus planned, it is impossible to dissociate the facilitation caused by saccadic planning from the attention which had previously been directed to that location by the use of the pre-cue. Additionally, when there is an SOA of 500-1000 ms, it is arguable whether the performance on the perceptual task of the stimulus is due to motor planning at all. Many studies have shown that the time-scale of attentional facilitation due to saccade planning is in the order of 150 ms before saccade onset (Castet et al., 2006; Jonikaitis & Deubel, 2011; Rolfs & Carrasco, 2012). By leaving a gap that is significantly greater than 150 ms, the attentional shift caused by the saccade planning could be entirely lost and unmeasured in the SOA time.

So, while there may be discrepancies in the exact timing of this shift, the evidence does agree that attention builds up at the location of an upcoming saccade during saccade preparation and execution. The locus of this attentional shift seems to be predominately at the location of the upcoming saccade, however this facilitation may spread to neighbouring locations. This is especially true when sequences of saccades are being made, and the locus of attention can be spread along the path of the upcoming saccade, either to multiple impending movement locations, or to the next movement location only (Gersch, Kowler, & Dosher, 2004; Gersch, Kowler, Schnitzer, & Dosher, 2009; Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012). This suggests that planning saccades can elicit a shift of attention that may be flexible depending on the task being performed (White et al., 2013). Preparing a hand movement has also been shown to elicit a similar attentional shift, and the time-course and spatial spread of this shift can be compared with that of pre-saccadic attention (Jonikaitis & Deubel, 2011).

4.2.2 ATTENTIONAL SHIFTS PRECEDING A HAND MOVEMENT

The attentional shift relative to a hand movement has been studied to a lesser extent, although it seems evident that, as with saccades, an attentional shift occurs before a hand movement is executed. For example, Rolfs, Lawrence & Carrasco (2013) found that discrimination performance was better at the reach target compared to a location on the opposite side of the screen, and Jonikaitis & Deubel (2011) found that attention shifted to the location of the reach before reach onset. Additionally, in a task where a reach alone was conducted while the eye was fixated, there was attentional facilitation around the reach endpoint, suggesting that reaching alone can trigger a shift in attention (Stewart & Ma-Wyatt, 2015).

It also seems to be the case that, as with saccades (Baldauf & Deubel, 2007; Gersch et al., 2004; 2009; Godijn & Theeuwes, 2003; Zhao et al., 2012), attention plays a role in the execution of sequences of hand movements, with attention being spread across all impending reach locations (Baldauf, Wolf, & Deubel, 2006). Indeed, it seems to be the case that attention can select multiple action-relevant goals in parallel, with attention being allocated according to the order in which the sequence is to be enacted (Baldauf & Deubel, 2010), and this entire sequence is planned before the first movement is initiated (Hesse & Deubel, 2010). Additionally, when planning a bimanual task, attentional facilitation is seen at both impending movement locations (Baldauf & Deubel, 2009). This evidence suggests that attention is important for the planning and enactment of hand movements, and also that it can be spread amongst multiple locations, depending on the particular demands of the task.

Previous studies have compared the spatiotemporal profile of saccades and reaches in an attempt to determine whether the underlying attentional mechanisms driving these shifts are similar for both movement types. For example, during simultaneous eye and hand movements to different locations, the amount of attention allocated to the reach goal is reduced in favour of the saccade location (Khan, Song, & McPeek, 2011). It was also found that target selection for saccades and reaches is tightly coupled (Song & McPeek, 2009), while the temporal coupling is less rigid, as attentional facilitation can be tied to both saccade and reach onset latency. This suggests that there may be an attentional coupling of eye and hand. While this is an interesting theoretical issue, we aim to compare the spatiotemporal profile of attention when a saccade and/or reach is being made, to see how attention may guide these movements. Past research has tried to dissociate the premotor attention for eye and hand by using paradigms where the eye and hand are directed to different locations, or attention is directed to a different location to the movement (for example Khan, Song, & McPeek, 2011). We aimed to use simpler task demands to directly compare the time-course of premotor attentional allocation for saccade alone versus saccade-plus-reach.

4.2.3 THE CURRENT STUDY

We used a perceptual discrimination task during a saccade and saccade-plus-reaching task to map the temporal and spatial properties of the attentional shift relative to both an eye and hand movement. This allows us to see how planning each of these movements may trigger a shift in attention, and allows us to see how attention may play a role in different planning and guidance stages of both saccade and reach. It also allows us to see how attention may spread around the target, and if this spread of attention differs between the movements. Three locations around the saccade/reaching target were probed to see how attention may spread around this target. The perceptual probe could appear at one of seven offsets relative to the movement, which allowed us to create a timeline of how attention acts over the course of the movement. By comparing the timeline of attention relative to either a saccade or reach, we aimed to dissociate the attentional facilitation that accompanies these movements.

4.3 METHOD

4.3.1 PARTICIPANTS

There were four participants: one was an author, and three were naïve as to the purposes of the study. Three were experienced psychophysical participants. All participants had normal or corrected-to-normal vision, and used their right hands to point – all participants were right hand dominant as classified by the Edinburgh handedness test. Ages ranged from 23 to 42. Ethics approval was obtained from the School of Psychology, and the work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Participants were free to withdraw at any time without penalty. Participants completed approximately 8 hours of data collection in 1-hour blocks.

4.3.2 EQUIPMENT

Stimuli were presented on a 17-inch ELO touchscreen monitor, with a resolution of 1024x768 pixels and a screen refresh rate of 75 Hz. The monitor was calibrated to ensure that contrast levels remained consistent across sessions, and to ensure that the monitor’s non-linear gamma function was corrected to be linear. Eye movements were measured using a SR Research EyeLink 1000 eye tracker to record eye position during the task. Eye position was sampled at a rate of 1000 Hz with a spatial precision of 0.25°. The experiment was run using custom software written in Matlab using routines from the psychophysics toolbox (Brainard, 1997; Pelli, 1997). A mouse was located central to the touchscreen, in front of the chin rest. Participants started a trial by depressing the mouse button. Touch responses were recorded when participants pointed to stimuli on the touchscreen monitor. A keyboard to the left was used to collect participant responses.

4.3.3 EXPERIMENTAL DESIGN

The experimental design is based on Stewart & Ma-Wyatt (2015), and aimed to measure the perceptual facilitation at different locations in the visual field during both a saccade-only task, and a saccade-plus-reach task.

The experiment comprised three separate tasks: the first was a contrast threshold task, which determined the stimuli presented to individual participants in the subsequent tasks. The second task was a saccade-only task, and participants had to make a saccade to the target while completing a perceptual discrimination. The third task was identical to the saccade task, with the addition of a reach to the reach/saccade target. The contrast threshold task was always completed first, and the subsequent saccade-only and saccade-plus-reach tasks were interleaved for all observers.

The experiment was a fully repeated measures design, with all participants completing the three tasks. Participants completed between 30-40 blocks of data, each of which contained 84 trials, for a total of 2520-3360 trials per participant. The number of blocks per participant was dependent on the number of trials excluded due to eye-tracking errors.

4.3.4 CONTRAST THRESHOLD TASK

Individual contrast threshold measurements were taken for each participant at each of the 6 probe locations (3 on the left and 3 on the right), with each location being tested separately. For each location the threshold was set individually so that the threshold accurately represented the threshold value for that location when a saccade was being made.

For each trial, the participant was required to fixate in the centre of the screen. The saccade target was visible on the side of the screen relevant to the probe location being tested. After depressing a key, a beep indicated that a saccade should be made to the saccade target. Given the variability in saccade latencies, we chose to present the probe at a set temporal offset from the initiation in saccade. Thus, 300 ms after the beep (saccade-go signal) a perceptual probe would appear at the location for which the threshold was being tested. The probe was an oriented line (of the same length and orientation as the perceptual probes in the actual experimental task), which appeared for 20 ms.

The participant reported the orientation of the line using the left or right arrows on the keyboard. Using a QUEST paradigm set to an 82 % threshold (Watson & Pelli, 1983), the luminance of the subsequent probe underwent a contrast increment if the previous response was incorrect, and a decrement if the response was correct. Trials in which the saccade endpoint was more than 1 degree from the saccade target were repeated, and the QUEST algorithm was not updated for that trial. The background luminance of the screen was 27.5cd/m^2. Forty trials were used to obtain the threshold measurement, and each location was tested three times, with the final threshold being the average of the three values. These values were then used such that each probe was presented at this threshold value for each participant.

4.3.5 SACCADE TASK

At the start of each trial, a grey fixation circle appeared in the middle of the screen which was 0.25° in size and 18 % Michelson contrast from the background. Two saccade targets appeared on the screen, one on either side of the fixation point, at 10° eccentricity. These targets were circles 0.75° in diameter, and 10 % contrast from the background.

As shown in Figure 1, the trial started when the participant depressed a key on the mouse, which was affixed to the desk 40 cm from the screen, central to the screen and the participant's body. After a delay (a randomly selected value from a range of 5 ms to 1000 ms, at 5 ms intervals calculated on a trial-by-trial basis using Matlab’s randperm function), a cue appeared at the centre of the screen, signalling the side of the screen that the probe would appear (with 100 % validity), and the side to which the participant had to make a saccade.

The cue was a triangular arrow of 0.5° size and 17 % contrast, which pointed to either the left or right side. The cue onset signalled the start of the SOA, after which a perceptual probe would appear at one of 3 locations on the cued side (consistent with Stewart & Ma-Wyatt, 2015; Castet et al., 2006;).

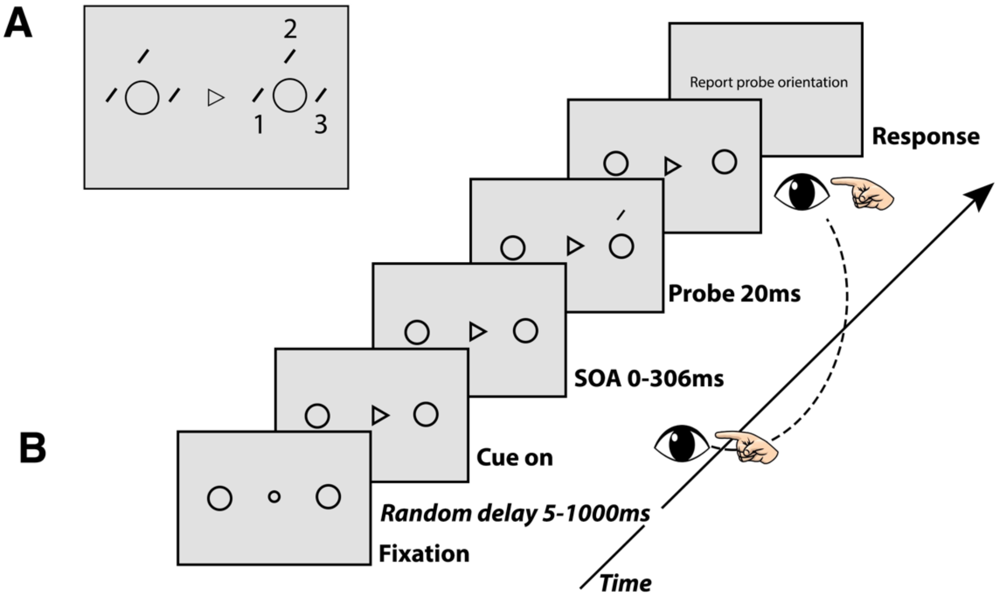

Figure 4.1 – Events in a saccade and saccade-plus-reach task trial. A) Probe locations. The probe (oriented line) could appear at one of three locations surrounding the reach/saccade target on either side of the screen. Location 1 is 8 degrees from the cue, location 2 is 3 degrees above the reach/saccade target and 10 degrees from cue, and location 3 is 12 degrees from cue. B) After a variable fixation period, a cue indicated the side of the screen to which the participant had to make a saccade, or in the reaching task, make a concurrent reach. At a variable SOA after cue onset, a perceptual probe (oriented line) appeared at one of 3 locations surrounding the reach target.

Left and right cues occurred with equal probability and so perceptual probes appeared at any one of 6 locations around the screen with equal probability (see Figure 4.1). The cues were always valid. The locations were 8 and 12° from the fixation point along the central horizontal axis, and one location 3° above the touch target at 10° from fixation point. These specific probe locations were chosen so that the data is directly comparable with Stewart and Ma-Wyatt (2015). The oriented lines were 0.5° in length, oriented at an angle of 45° left or right, and were at a contrast level determined by an individual threshold task for each participant.

The stimulus onset asynchrony (SOA) could be one of 7 different durations: 13, 53, 107, 147, 200, 253, 306 ms, measured from the cue onset. This range was chosen with the aim of capturing the attentional facilitation, which may accompany both the preparation and the completion of a saccade. After the saccade was completed, a post cue that the subject had to report the orientation of the perceptual probe using the arrow buttons on the keyboard (left/right). Auditory feedback was given for correct and incorrect answers.

For each trial, saccade endpoint saccade latency, saccade time, saccade accuracy and the perceptual response were recorded.

4.3.6 SACCADE-PLUS-REACH TASK

This task was exactly the same as the saccade-only task described above, except that in addition to a saccade, participants made a reach to the target on the cued side.

4.4 RESULTS

4.4.1 DATA EXCLUSIONS

Individual saccades were examined prior to analysis to ensure that trials in which saccades made to the wrong location, or in which the pupil was lost (e.g. due to blinking) were excluded. Saccades were classified using criteria of velocity of 35 deg/s and acceleration of 9500 deg/s. Saccade latency was measured as the time from the 'go' beep until the time the saccade was initiated.

For both saccade-only and saccade-plus-reach conditions, trials were excluded based on the following saccade-related criteria: trials in which the saccade latency was below 100 ms were excluded as it was unlikely that the programming of these saccades was influenced by the visual target (He & Kowler, 1989). Saccades initiated after 570 ms were excluded to avoid any trials where the probe would have appeared and disappeared before had even been planned or initiated (calculations based on the longest SOA value of 306 ms plus the average total saccade completion time). Trials where the probe appeared between 50 ms before saccade onset and 25 ms after saccade onset were excluded to eliminate any potential effects of saccadic suppression (Morrone, Ross, & Burr, 2005). Trials in which the eyes had landed at the movement target at the time of probe presentation were also excluded.

Additional exclusion criteria applied for the reaching task: trials in which the reach latency or reach time were ±2 standard deviations from the mean were excluded, and reaches which landed ±2 standard deviations from the mean were excluded.

Reach latency was measured as the time from cue onset until the time the participant lifted their finger from the mouse button. Reach time was measured as the time from the lifting of the finger from the mouse to the time the screen was touched.

Individual saccade and reach dynamics are shown in Table 1. Saccade latencies for individual participants are shown in figure 3 for both the saccade-only (4.2A) and reaching tasks (4.2B). Reach latencies (figure 4.2C) and eye-hand latencies (figure 4.2D) for individual participants are also shown in Figure 4.2. We tested the normality of the saccade latency and reach dynamics distributions using a lillietest, which revealed non-normality for all conditions, hence median values and interquartile ranges are reported.

Table 4.1 – movement dynamics for all participants. Median values are reported due to the non-normal distribution of latencies. Interquartile range of the 95 % confidence interval (IQR) is also reported.

	Participant	*Median reach latency*	*IQR reach latency*	*Median saccade latency*	*IQR saccade latency*	*Median eye-hand latency*	*IQR eye-hand latency*	*% excluded*
P1	Reach + sacc	234 ms	44 ms	172 ms	17ms	62 ms	43 ms	60 %
	Sacc only			176 ms	22 ms			29 %
P2	Reach + sacc	235 ms	49 ms	186 ms	21 ms	50 ms	46 ms	41 %
	Sacc only			190 ms	25 ms			29 %
P3	Reach + sacc	300 ms	56 ms	183 ms	30 ms	112 ms	56 ms	51 %
	Sacc only			197ms	30 ms			34 %
P4	Reach + sacc	343 ms	61 ms	214 ms	42 ms	122 ms	61 ms	50 %
	Sacc only			227ms	55 ms			27 %
ALL	Reach + sacc	270 ms	88 ms	187ms	31 ms	81 ms	70 ms	51 %
	Sacc only			194 ms	38 ms			30 %

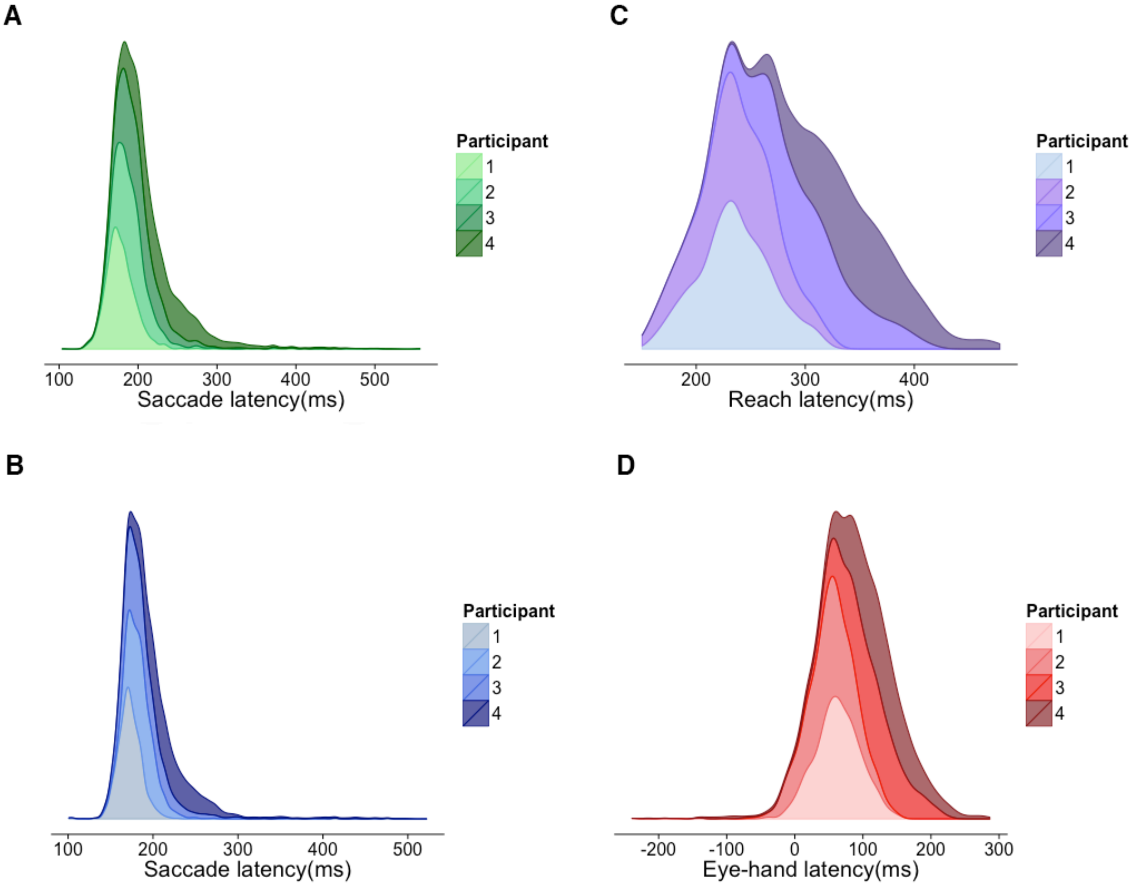

Figure 4.2 – Stacked density plots of saccade latencies for each participant (data has had exclusion criteria applied). Figure A represents saccade latencies for the saccade-only condition. Figure B represents saccade latencies for the saccade-plus-reach condition, Figure C represents reach latencies, and Figure D represents eye-hand latencies, both for the saccade-plus-reach condition.

4.4.2 PERCEPTUAL PERFORMANCE RELATIVE TO SOA

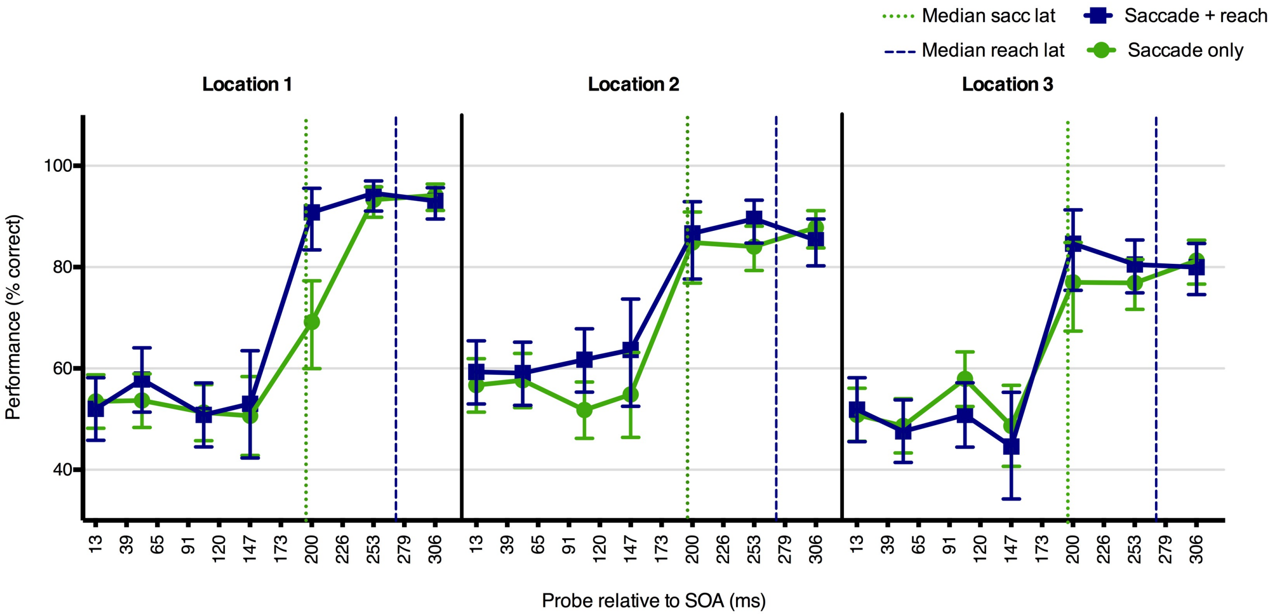

Figure 4.3 – perceptual performance relative to cue onset (SOA) for the saccade-only task (green) and the saccade-plus-reach task (blue). This data represents the weighted mean across all participants. The green dotted line represents the median saccade latency across participants, and the blue dotted line represents the median reach latency across participants. Error bars represent 95 % confidence intervals calculated using Jeffrey's interval, which provides a Bayesian calculation of confidence intervals in binomial data.

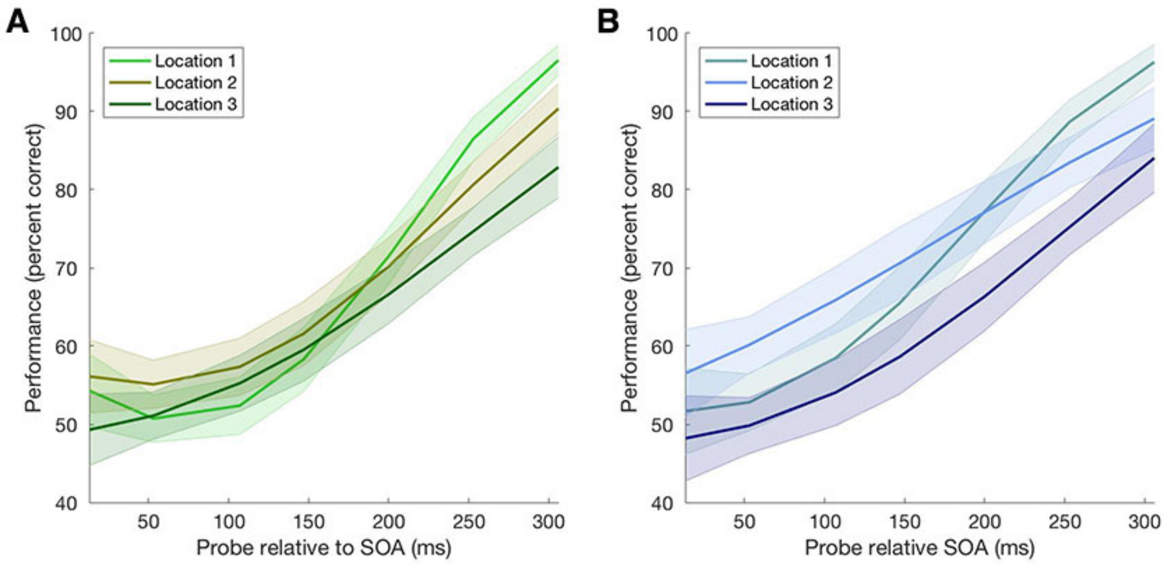

Figure 4.4 – Probit curves fitted to performance data for each location for the (A) saccade-only condition and the (B) saccade-plus-reach condition. Shaded areas represent the 95 % confidence intervals.

Performance on the perceptual probe discrimination task was plotted relative to SOA, for both the saccade-only condition and the saccade-and-reach condition (Figure 4.3). The profile of attentional facilitation is similar for both conditions; with attention increasing once the movement was initiated, with the higher level of attention being sustained throughout the course of the movement. Note that the high performance in later time-bins could not be due to the eye having landed on the target at those points, as trials in which the eye had landed at the time when the probe appeared were discarded. To compare performance within conditions, linear mixed models were conducted to determine the effect of location and SOA on performance for the aggregate performance of all participants. The models used fixed effects of SOA and location, and a random effect of participant, for each condition. For the saccade-only condition, there was a significant effect of SOA: F(1,77) = 82.36, p = <0.0001. For the saccade-plus-reach condition there was a significant effect of SOA: F(1,77) = 71.49, p <0.0001, and location: F(1,77) = 7.60, p <0.01. This effect of location in the reach plus saccade condition only suggests that planning a reach concurrent to a saccade may affect the spatial spread of attention differently to planning a saccade alone.

To compare the difference both within and between the two conditions, probit curves were fitted to the data for each participant, for each location and condition (similar to the comparison methods used by Jonikaitis & Deubel, 2011). Figure 4.4 shows the fitted curves for averaged data. The difference in performance at the 75 % mark was compared using a paired-samples t-test across individual participant data. There was no difference between conditions at location 1: t(3) = 1.24, p = 0.3; location 2: t(2) = 3.49, p=0.073; or location 3: t(2) = -0.02, p = 0.99.

In the saccade-only condition, there was a significant difference in performance between locations 1 and 2: t(2) = 5.15, p = 0.036; but there was no significant difference found between locations 1 and 3: t(2) = 2.74, p = 0.11; or locations 2 and 3: t(1) = -0.64, p = 0.63. In the saccade-plus-reach condition there was no significant difference found between locations 1 and 2: t(3) = 1.89, p = 0.15; locations 1 and 3: t(3) = 1.2, p = 0.31; or locations 2 and 3 : t(3) = -0.09, p = 0.93.

4.4.3 PERCEPTUAL PERFORMANCE RELATIVE TO MOVEMENT ONSET

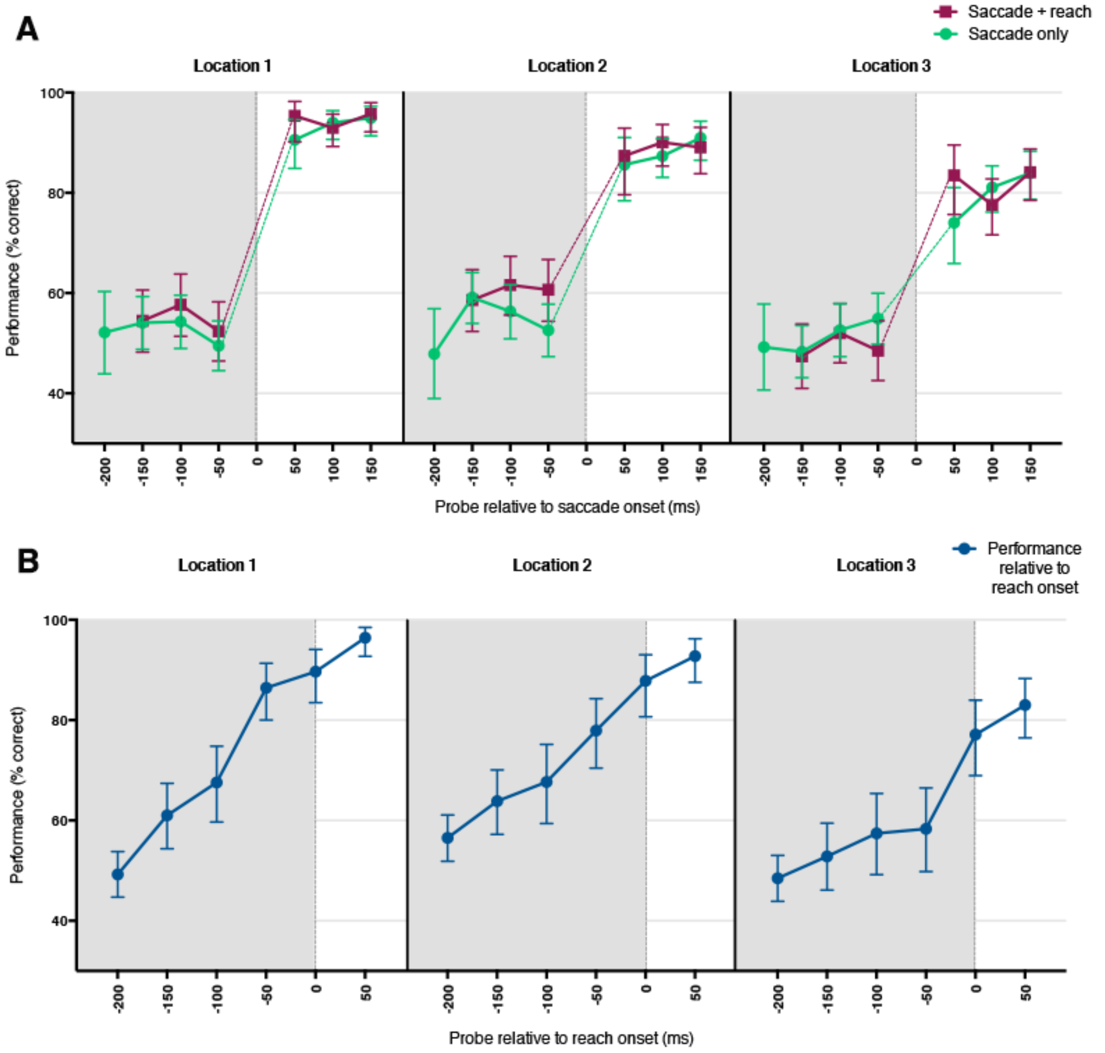

Figure 4.5 – A: Perceptual performance relative to saccade during the saccade-only task (green) and saccade-plus-reach task (maroon), which depicts performance relative to saccade onset. Due to saccadic suppression, the trials where the probe appeared around the time of saccade onset were excluded, thus a dotted line has been added to connect the data measured before and after saccade onset. B: performance relative to reach onset for the saccade and reach condition. Error bars are 95 % confidence intervals, calculated using Jeffrey's interval, as in figure 4.3.

To examine how attention shifts relative to a saccade, probe performance for both conditions was binned relative to either saccade onset (Figure 4.5A) or reach onset (Figure 4.5B). For each trial, the bin was determined by calculating when the probe appeared relative to the movement onset. For example, if the probe appeared 100 ms before the initiation of the movement, that trial would be put in the -100 ms bin. Data were sorted into 50 ms bins from 200 ms before movement initiation to 200 ms after initiation. There was no data in the bin that fell at 0 ms relative to saccade onset, as we removed any data which would be subject to saccadic suppression (Morrone, Ross & Burr, 2005).

There are an uneven number of data bins for the saccade-only and reaching conditions due to the difference in saccade dynamics between the conditions (Figure 4.2). This has not impacted the analyses conducted on the data as presented in Figure 4.3. When performance is considered relative to SOA there is an even amount of data present at each SOA, and therefore the reaching and saccade conditions can be directly compared using mixed models. In figure 4.5 it is only the earliest and latest time-bins that show a discrepancy, and these are generally beyond the range of time-bins considered important for the overall purposes of this study.

The profile of performance is similar for both the saccade-only and reaching task when binned relative to saccade onset (Figure 4.5A). Performance is low before the onset of the saccade, and increases markedly after the saccade is initiated. However, when performance is binned relative to reach onset (Figure 4.5B), the profile of the attentional increase shows a more consistent, almost linear increase before reach onset.

To quantify the change in attentional performance before and after the initiation of a saccade (as shown in Figure 4.5A), paired-samples t-tests were used. Due to the uneven number of points before and after the saccade in the saccade-only condition, a comparison was made using only the -150, -100 and -50 data points before the saccade. A significant difference in performance before and after saccade was found in the saccade-only condition for all locations: location 1: $t(11) = -20.98$, $p<0.001$; location 2: $t(11) = -8.09$, $p<0.001$; location 3: $t(11) = -3.8$, $p = 0.003$. For the reach plus saccade condition, a significant difference was found for all locations: location 1: $t(11) = -12.01$, $p<0.001$; location 2: $t(11) = -7.69$, $p <0.001$; location 3: $t(11) = -5.622$, $p<0.001$.

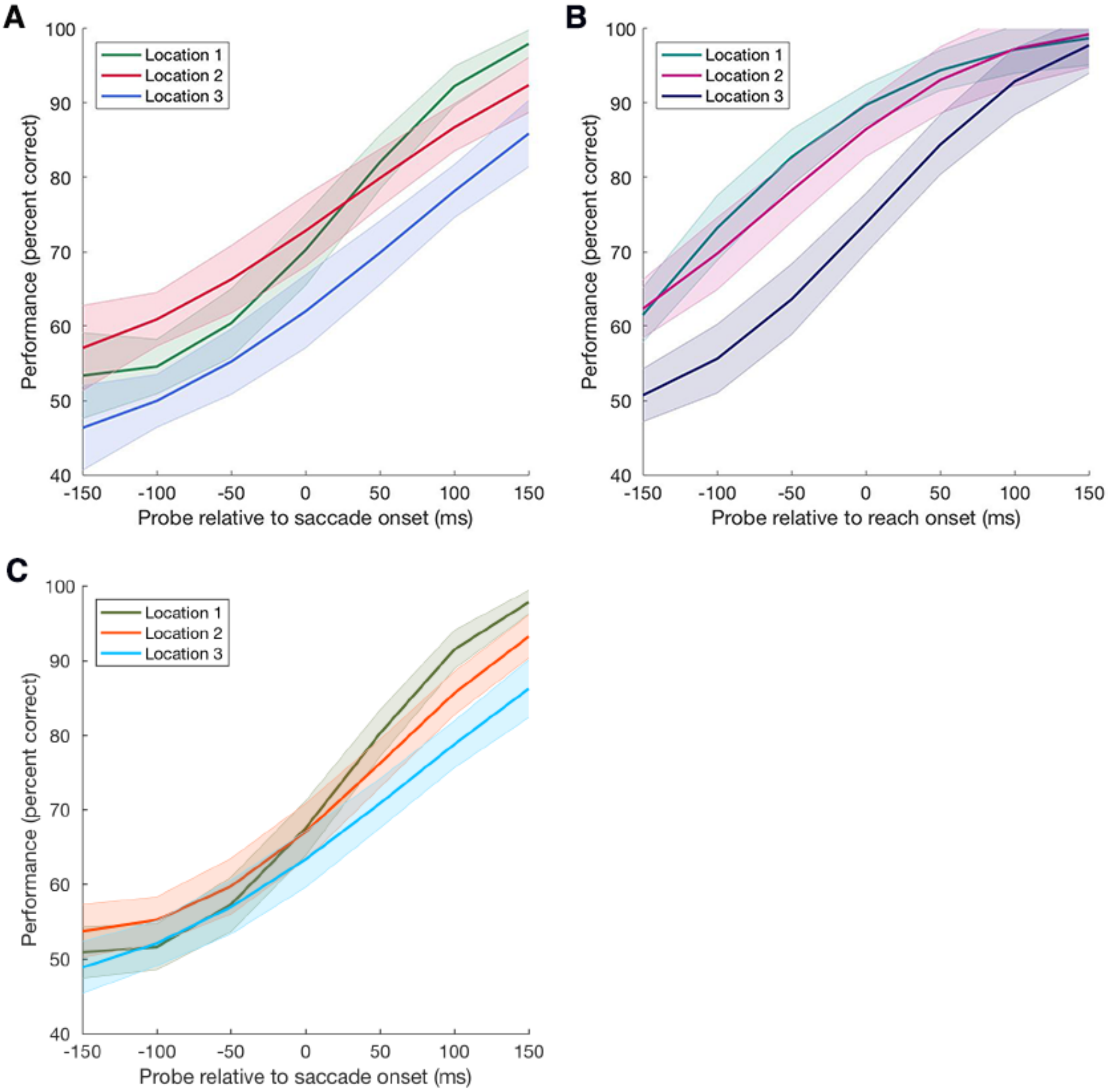

Figure 4.6 – Probit curves fitted to the average performance for each location. Saccade and reach performance is binned relative to saccade onset (A) or reach onset (B), and saccade-only performance is binned relative to saccade onset (C). Shaded areas represent the 95 % confidence intervals.

To compare the difference in performance for the reach plus saccade condition, when the data was binned relative to different movement onsets, probit curves were again fitted as in Figure 4.4 (Figure 4.6). Paired-samples t-tests revealed that there was a significant difference in when the 75 % performance point was reached when performance was binned relative to saccade or reach, at location 1: t(3) = 21.3, p=0.0002; location 2: t(3) = 4.38, p = 0.022; but not at location 3: t(3) = 2.82, p = 0.067.

This method was also used to compare performance between the conditions, when the data was binned relative to saccade onset (Figure 4.6C). Paired-samples t-tests revealed no significant difference in the 75 % performance point between the saccade-only and reach plus saccade conditions at any location: location 1, t(3) = 0.81, p = 0.48; location 2, t(3) = 1.82, p = 0.17; location 3, t(3) = 0.38, p=0.73.

4.4.4 HEATMAP OF PERCEPTUAL PERFORMANCE

Heatmaps of the spatiotemporal profile of attention for both the saccade-only and saccade-plus-reach conditions were created to compare the spread of attention across these conditions (Figure 4.7). Heatmap values were calculated using the three locations that were tested, and the values of the in-between locations were calculated based on the weighted values of the nearest tested locations, and the distance between these points. It must be noted that performance was not measured at the movement target, as the aim of the study was to measure attentional facilitation around a target, and as a design choice to minimise occlusion by the hand in the reaching condition. The heatmaps can thus provide an insight into the spatial spread of attention at the locations around the target, but may not be indicative of performance at the target itself. Previous studies have however found facilitation at the movement target (i.e. Deubel & Schneider, 1996; Deubel, 2008; Rolfs & Carrasco, 2012; Rolfs et al, 2013), so this was not the primary aspect of interest in this analysis.

The heatmap shows that performance peaks earlier in the reach-and-saccade condition compared to the saccade-only condition. Additionally, the heatmap indicates an asymmetry in performance across the locations in the reaching condition, suggesting that location 2 (above the target) receives a higher level, and more sustained attentional facilitation that locations 1 and 3.

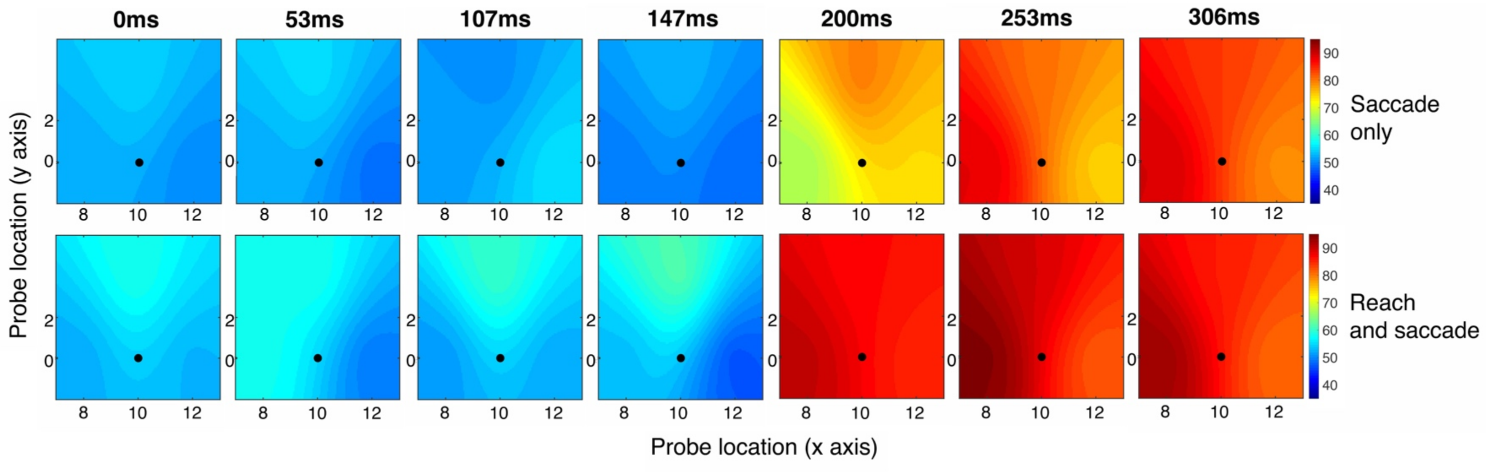

Figure 4.7 – Heatmap of performance change over time relative to SOA. The top row represents the data for the saccade-only condition. The bottom row represents data for the saccade-and-reach condition. Reach target is shown by the black circle. The colour-scale represents percentage correct. The position of the perceptual probes is indicated as degrees of eccentricity from the initial fixation point on either the X or Y axis.

4.5 DISCUSSION

4.5.1 THE TEMPORAL PROFILE OF ATTENTION FOR REACH AND SACCADE

We measured the profile of attention relative to a saccade alone and a saccade with a concurrent reach. When comparing the timeline of the attentional shift relative to the SOA, it can be seen that the profile of attention is similar between conditions (Figure 4.3), and when comparing the profile of attentional modulation relative to saccade onset, there is also no difference between conditions (Figure 4.6).

When plotted as a function of time relative to saccade onset, the pre-saccadic attentional shift is broadly consistent with the timeline recorded by previous studies, with an improvement in perceptual performance observed during the movement. However, the pre-saccadic shift observed in this experiment seems to be later than some previous literature would suggest, as the shift seems to occur around the same time as the saccade onset which is in contrast to studies suggesting it shifts as early as 50 ms (White et al, 2013) or 100 ms before saccade onset (Rolfs & Carrasco, 2012). Interestingly, when perceptual performance is plotted relative to SOA, the pattern of attention observed in this study shows only a very shallow build up of attention before the initiation of a saccade. This could be due to the spatial layout of the paradigm itself: in this study we measured attention around the movement target to determine the broader spatial profile of attention. The fact that there was no pre-saccadic attentional enhancement around the reach target is consistent with Deubel and Schneider's (1996) finding that attention is selective for the intended saccade target only. Additional evidence also suggests that attention is selective for a movement target, but not locations in between targets in the case of multiple movement paradigms (Baldauf & Deubel, 2008). It could be the case that in this study, the measured areas surrounding the movement target did not receive an attentional facilitation at the same time as the target itself, with the facilitation occurring/spreading from the movement target once the movement was initiated. This could suggest the need for a narrower window of attention to select a target for movement planning purposes, and a need for a broader attentional facilitation once the movement is underway, to accurately guide the movement to the target.

The shift of attention, when measured relative to a reach, follows a steady increase from 200 ms to 150 ms prior to reach onset, which is consistent with the timeline suggested by Jonikaitis & Deubel (2011) and Rolfs et al. (2013). There is a slight discrepancy in the timing of the attentional shift between studies, which may be due to the behavioural paradigms used, and the differences in the SOA lengths measured – it is conceivable that if the time-course measured is longer, then the shift in attention may reflect this more leisurely time-scale. If overall movement times are slower, there may be less time constraints on movements, and the general time-scale measured may be coarser and over a longer period of time. In fact there is evidence to suggest that covert attention can be temporally cued, and deployed at different times, depending on the timing of stimulus onset (Coull, Frith, Büchel, &

Nobre, 2000). It could be the case that premotor attention is similarly temporally cued by the particular movement latency or paradigm timing.

4.5.2 THE TEMPORAL PROFILE OF ATTENTION FOR REACH ALONE DIFFERS WHEN COMPARED WITH REACH PLUS SACCADE

Another interesting facet of the story is the profile of the attentional shift that occurs when a hand movement alone is made, without a concurrent saccade. In this case, attention is allocated to the locus of the reach target and surrounding locations, however the profile of this shift is quite different from the profile observed when a concurrent saccade is made (Stewart & Ma-Wyatt, 2015). Specifically, when a reach alone is being made, the temporal profile of attention shows a large drop in performance as the hand is reaching the target for locations that were horizontally in line with the reach target (analogous to locations 1 and 3 in this study), while performance remained stable for locations above reach target (analogous to location 2 in this study). It should be noted that although analogous locations were used, in the previous study there were more potential target locations, so the spatial layout of the paradigm differed slightly to this study, especially in relation to the amount of uncertainty surrounding where a potential probe would appear. Another observation that can be made by comparing the results of this study to those of Stewart & Ma-Wyatt (2015) is that the magnitude of the attentional shift is far greater when there is a saccade being made in addition to a hand movement. When the hand movement alone is being made, there is a 10-15 % facilitation on a perceptual task over the timecourse before movement onset (comparing the performance level before reach onset to after reach onset), whereas a concurrent saccade evokes a 30 % improvement. This may suggest that the primary driving force behind the attentional shift is the saccade rather than the hand. This is in line with previous research that suggests that the eye carries a greater attentional weighting than the hand (Khan et al., 2011). Given that these tasks involve a movement to a visually defined target, it is perhaps unsurprising that visually based attention may be dominant in this case, or that it may carry more weight in the guidance of this visually-guided hand movement.

This evidence suggests that the hand can evoke a shift of attention while the eyes are fixated elsewhere. However, when there is no concurrent saccade present the temporal profile of the attentional shift is different, suggesting that there must be some additive effect of the two movements being enacted. Indeed, it may be the case that the planning and execution of an accurate hand movement requires more attentional help than a mere saccade. This could then result in the faster deployment of attention, and the more sustained, higher level of attentional performance leading up to the reach onset when there is no eye movement available to provide any foveal information during the enactment of the reach (Stewart & Ma-Wyatt, 2015).

So, the fact that attention can be allocated in parallel, and can be allocated when a hand movement alone is being planned while the eyes fixate seems to suggest that attention is spatially pliable, and is able to adapt to the particular task demands of the experiment. The similar shape of the attentional profile for both eye and hand movements shown in this study may suggest that there is merely one attentional mechanism that has different subsets which are deployed at different intervals, when required by an upcoming movement.

4.5.3 THE SPATIAL PROFILE OF ATTENTION AT DIFFERENT LOCATIONS

The second aspect of attention that this study aimed to examine was the spatial properties of the attentional shift relative to saccade and reach. For both the saccade-only and saccade-plus-reach tasks, the pattern of facilitation is largely similar for all locations, suggesting that attention may spread around the impending target during the movement. Figure 7 shows a slight discrepancy in performance across locations over time, with location 2 (above the movement target) showing in particular a higher level of attention in the reaching condition than saccade condition across the time-course of the movement planning and execution. Although there was no statistical significance in the comparison of performance between the conditions at this location ($p = 0.073$), it is interesting to note that in our previous work (Stewart & Ma-Wyatt, 2015) when attention was measured relative to a reach, the analogous location also showed a higher and more sustained attentional profile than the locations analogous to locations 1 and 3.

This broad spread of attention is consistent with studies that have shown that indeed attention can be spread across multiple locations during sequences of hand movements (Baldauf et al., 2006; Baldauf & Deubel, 2010), or during sequences of saccades (Kowler, Anderson, Dosher, & Blaser, 1995). Additionally, during tasks requiring only a single movement, it has been seen that the locus of attentional facilitation is not always constrained to the specific saccade target (Castet et al., 2006). It seems to be the case that attention can be spread in a broad manner across the visual field, and this may be dependent on particular paradigms and task demands. Indeed, it could be the case that in this paradigm the screen layout was fairly simple, and thus attention could be spread in a broader fashion as there is no clutter to avoid.

Although there is diverging behavioural evidence for the arguments that the mechanisms underlying the allocation of premotor attention may be either shared or separate, when combined, this evidence is not inconsistent with the idea that there is one greater attentional resource, which is able to adapt to particular task demands. We know that attention can be deployed over a wide area if parallel locations need to be selected for a sequence of movements, can be deployed if only a hand movement is being made, without a saccade, and can be deployed on a different timescale, depending on the type of movement being made. Additionally, and despite all its other attributes, attention seems to be primarily linked to the planning and execution of a saccade. These results are consistent with recent evidence that even when there are competing target locations for the saccade and hand, attention tends to go with the hand (Khan et al., 2011).

4.5.4 EYE AND HAND – SHARED OR SEPARATE MECHANISMS?

Comparing the timing of the attentional shift for saccade versus saccade and reach has been used as a method to indicate that the mechanisms that drive the attentional shift may either be separate (Jonikaitis & Deubel, 2011), or alternatively, that there is a single attentional mechanism that is able to be shared differentially between the different modalities of movement (Khan et al., 2011). This study does not directly test this dissociation, but we discuss the transformation between attention and motor plans further in the following sections.

Previous work has argued that the attentional resources for eye and hand movements are shared, because when the locus of eye and hand movements are separated, performance decreases, with the majority of attention being directed to the saccade location (Khan et al., 2011). Additionally, during free visual search tasks, saccade and reach locations are nearly always coupled (Song & McPeek, 2009). It has been well established that eye and hand movements are typically coupled, especially when making a rapid goal-directed movement to a target (Land & Hayhoe, 2001; Ma-Wyatt et al., 2010; Neggers & Bekkering, 2001). This spatial coupling, along with the observed decrement in attentional facilitation when the locus of eye and hand movements are dissociated, seems like compelling evidence for a single, non-dissociable attentional resource. Indeed, given the strength of the relationship between eye and hand, it seems logical that the underlying attentional mechanisms that guide these movements may result from a shared resource in the planning stages of the movements.

However, studies examining how attention is allocated during sequences of movements are fairly consistent in their findings that attention can be spread across multiple locations, both during sequences of saccades (Gersch et al., 2009) and sequences of hand movements (Baldauf et al., 2006; Baldauf & Deubel, 2010). It has also been suggested that attention may form an ‘attentional landscape’ which selects all behaviourally relevant reach targets in parallel and provides guidance for the impending movement (Baldauf & Deubel, 2010; Land, 2006). Jonikaitis & Deubel

(2011) examined the temporal profile of the pre-saccadic and pre-reach attention shift to try to dissociate the mechanisms, and found that delaying the onset of one movement delayed the associated attentional shift to that movement location, but did not affect the other movement. This evidence that attention can in fact be spread across different locations, and can be temporally dissociated suggests that this attentional resource can have different spatial and temporal characteristics depending on the particular paradigm and task demands.

The results of this study strongly suggest that the spatiotemporal profile of attention is similar whether the task involves a saccade alone or a saccade with a reach. This seems to suggest that the mechanism may stem from a common attentional resource.

4.5.5 HOW MIGHT THESE MECHANISMS BE ORGANIZED?

Given the close link between eye and hand movements, it is not unreasonable to posit that the attentional mechanisms guiding both are linked at some stage, and the attentional resources pooled. It has been suggested that there is a complex neural circuit that controls eye movements and hand movements, and it is possible that the pre-motor allocation of attention for both eye and hand movements is controlled by a shared mechanism within this circuit. Indeed, models of eye-hand co-ordination propose that neural circuits for the visual representation of space are tightly linked to guiding movements. It is possible that the mechanisms that control saccades receive updates of the spatial coordinates of arm movements, and that updating occurs in eye-centric coordinates (Andersen, Snyder, Bradley, & Xing, 1997; Ren, 2006). Consistent with this idea, neurons in area V6A are responsible for visual encoding also encode reaching movements (Fattori, Gamberini, Kutz, & Galletti, 2001).

There is evidence that early in the reach planning stage, the reach is planned in gaze-centered co-ordinates that are then converted in the posterior parietal cortex (PPC) into the motor plan for the impending reach (Buneo, Jarvis, Batista, & Andersen, 2002; Crawford, 2004). Indeed, the PPC is well known to perform a number of sensorimotor transformations (Andersen et al., 1997). Additionally, in the parietal reach region (PRR), response fields of neurons coding upcoming arm movements were more tightly linked to the position of eyes than of hand (Batista, Buneo, Snyder, & Andersen, 1999; Snyder, 2000). It could be that the process of target selection, response decision, and transformation of signals into a common co-ordinate system occurs in the PPC, and this signal is then sent to the premotor cortex to trigger a hand movement, or the frontal eye fields (FEF) to trigger an eye movement (Snyder, 2000), and it has been suggested that this common signal is framed in gaze-centric co-ordinates, even when it has reached the premotor cortex (Mushiake, Tanatsugu, & Tanji, 1997; Snyder, 2000). Thus, the idea of a shared attentional mechanism for eye and hand movements is not inconsistent with the neurophysiological evidence, which suggests that this shared mechanism stems from the stage in the sensorimotor circuit when target selection is transformed into a common coordinate signal to trigger the respective movements.

The neural circuits that control this process are however extremely complex, with feedback and feed-forward loops between many regions such as the PPC, PRR, FEF, superior colliculus and premotor cortex (Snyder, 2000). It may be the case that when there are different task demands in selecting targets, and completing movements, the way in which attention is transformed and deployed in this complex system changes, which could explain the discrepant results from studies that have tried to dissociate attentional mechanisms driving eye and hand movements.

4.6 CONCLUSION

The aim of this study was to understand the spatiotemporal profile of attention when a saccade alone, or saccade with concurrent reach is made to the same visual target. This study has provided evidence that attention shifts in a broad manner to locations surrounding a movement target when a saccade is initiated, with attentional facilitation remaining high for the duration of the saccade. It has also shown that when a reach is being planned in addition to a saccade, attention shifts on a similar timescale to when a saccade alone is being produced, and the magnitude of the facilitation is the same. This pattern contrasts remarkably with the profile of attention relative when a reach alone is being conducted (Stewart & Ma-Wyatt, 2015). The similar profile of attention between the two tasks suggest that attention may be drawn from one common resource, and that when a concurrent saccade and reach is being made, the attention accompanying the saccade dominates the observed spatiotemporal profile.

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4.8 COMPARISON OF CHAPTER 2 AND CHAPTER 4

An interesting difference can be noted in the profile of attention between Chapter 2, where a reach alone was being made, and Chapter 4, where a concurrent saccade was being enacted. Figure 4.8 shows the data for the reach plus saccade condition in Chapter 4, plotted relative to reach onset, with the data for the analogous locations for the reach-only condition from Chapter 2, plotted relative to reach onset. It must be noted that there was a slight discrepancy in the paradigm, as Chapter 2 utilised a "go" beep, meaning that the earliest perceptual probe appeared 50 ms after cue onset, whereas Chapter 4 measured SOA from cue onset, with the earliest probe appearance at 13 ms. There is also a slight difference in the timing of the paradigms, as Chapter 2 did not have a random delay between the initiation of the trial and the cue onset, whereas Chapter 4 did. Additionally, the participants for each chapter were different.

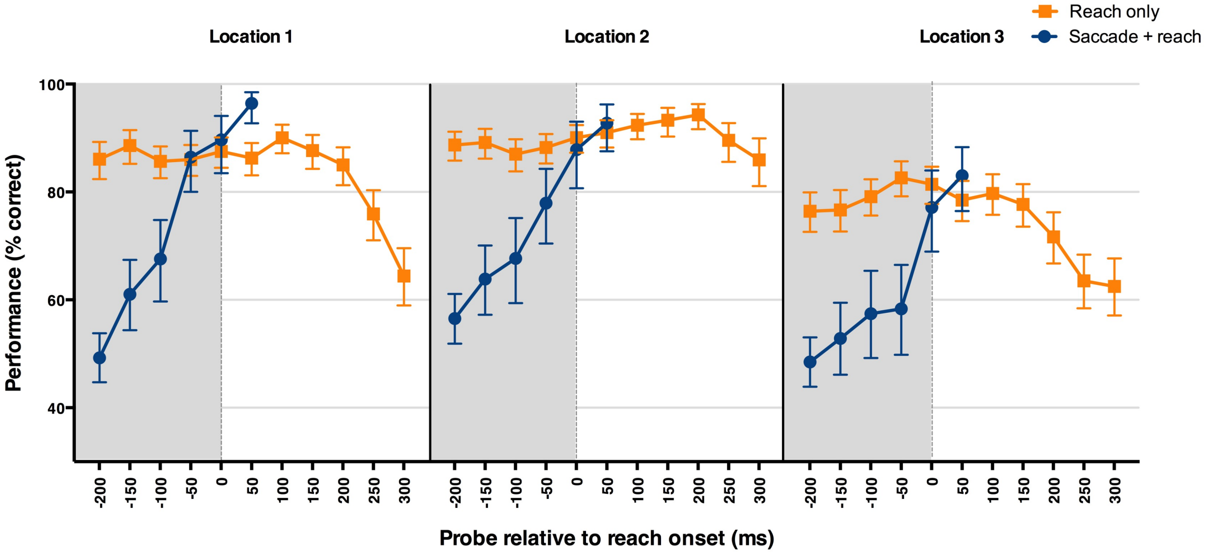

Figure 4.8 – Comparison of reach-only data from Chapter 2, and saccade-plus-reach data from Chapter 3, for each location, plotted relative to reach onset. Errors bars are Jeffrey's interval.

While the data is not directly comparable, due to slight differences in timing and the layout of the stimuli, this provides an insight into how the temporal profile of attention may change when a saccade is being planned and executed, compared to a reach alone. Although there seems to be a more pronounced temporal tuning in the saccade-plus-reach condition than the reach-only condition when the two sets of data are plotted together, it should be noted that there was still a significant difference in attentional performance across the timecourse of the the reach-only condition in Chapter 2. Interestingly, when a saccade and reach are being planned concurrently, the profile of attention shares the same characteristics as that of the saccade alone attentional profile. This suggests that when a saccade is being planned, the saccade planning may drive the attentional shift.

5. PREFACE TO PAPER 3

The previous papers have provided a comprehensive spatiotemporal map of how attention shifts when a reach alone, saccade alone, and saccade-plus-reach are being conducted. The profile of pre-reach attention in Chapter 2 revealed an interesting pattern, where the profile of attention at locations in line with, and orthogonal to the reach direction differed: locations orthogonal to reach direction had a higher overall performance, and a more sustained temporal profile of attention than those on the horizontal axis. The last paper in this thesis aims to tease apart any effects that movement direction may have on the spatiotemporal profile of attention. Previous work (Kaiser & Lappe, 2004) suggests that phenomena that occur during saccade preparation, such as perisaccadic mislocalisation may be subject to directional effects based on a stimulus location relative to movement direction, and given a proposed link between attention, movement planning and effects such as mislocalisation (Hamker et al, 2008), it may be the case that the location of a stimulus relative to the direction of a saccade or reach may affect how attention is deployed at that location. This study aims to investigate all effector combinations: reach-only, saccade-only, and reach and saccade to determine how these different types and directions of movement planning may affect the spatial spread of attention around the movement target.

6. PAPER 3 - THE PROFILE OF ATTENTION DIFFERS AT LOCATIONS ORTHOGONAL TO REACH DIRECTION

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Key words: reaching; action; attention; saccade; eye movement

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Principal Author

Name of Principal Author (Candidate)	Emma E.M. Stewart		
Contribution to the Paper	Designed, coded and piloted the experiment, ran the experiment, analysed data, wrote manuscript		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	17-MARCH-2016

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Anna Ma-Wyatt		
Contribution to the Paper	Supervised development of work, helped in data interpretation and manuscript revisions		
Signature		Date	15/3/16

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Contribution to the Paper			
Signature		Date	

Please cut and paste additional co-author panels here as required.

6.1 ABSTRACT

It has been well documented that attention shifts to the location of an upcoming movement, whether the movement is a saccade or a reach. The spatiotemporal profile of this premotor attention differs slightly between these different movements, and one study in particular suggested that the direction of a movement may influence the spatial spread of attention (Stewart & Ma-Wyatt, 2015). This previous work suggests that the profile of attention at a location may differ, depending on where that location is situated relative to the direction of movement. Some studies have also suggested that perisaccadic mislocalisation occurs differentially dependent on location of a probe relative to saccade direction (Kaiser & Lappe, 2004a): taken together these phenomena suggest that direction of movement relative to attended location may produce differing levels of attentional facilitation. The current study aimed to determine whether the profile of attention is different at locations orthogonal to a reach-only, reach plus saccade and saccade-only compared to locations in line with the direction of the movement direction. We found that the spatiotemporal profile of attention differs across different movement combinations, and that this profile is also different at orthogonal and parallel target locations relative to movement direction. These results suggest that attentional guidance may be more important at differing timepoints, depending on the type of movement being enacted.

6.2 INTRODUCTION

Attention is an important process that triggers a number of perceptual changes at the attended location, and which seems to be closely integrated into a myriad of visual and motor processes. Indeed, attention has been closely linked to both saccade and reach planning (Baldauf & Deubel, 2010; Deubel & Schneider, 1996; Jonikaitis & Deubel, 2011; Rolfs & Carrasco, 2012; Rolfs, Lawrence, & Carrasco, 2013; Stewart & Ma-Wyatt, 2015; White, Rolfs, & Carrasco, 2013), and has been implicated in the process of target selection and online movement guidance for both of these movement types (Song & Nakayama, 2006). It has been well documented that attention "shifts" to the location of an upcoming movement (Deubel, 2008; Deubel & Schneider, 1996), and the spatiotemporal profile of this shift provides insight into both the dynamic characteristics and functional benefits of the premotor attentional shift. This paper aims to determine how different movement effectors may affect how attention is spread around a movement target. Specifically, whether the location of an attentional probe relative to movement direction affects the spatiotemporal profile of attention at that location, and whether the movement, or combination of movements being enacted changes this profile.

6.2.1 ATTENTION AND THE PRE-MOVEMENT ATTENTIONAL SHIFT

Attending to an area elicits a range of perceptual benefits at the attended location, such as an increase in contrast sensitivity (Carrasco, 2011; Carrasco, Ling, & Read, 2004; Carrasco, Talgar, & Cameron, 2001), an increase in spatial resolution (Yeshurun & Carrasco, 1998), or enhanced perception of oriented lines (Blanco & Soto, 2002). This is true in covert attention tasks, and before movements such as saccades and reaches (Deubel & Schneider, 1996; Jonikaitis & Deubel, 2011; Rolfs et al., 2013; White et al., 2013), and many studies have seen an attentional facilitation at the location of an impending eye movement. Kowler et al. (1995) and Deubel and Schneider (1996) both found that perceptual performance on a letter discrimination task was better at the location of an upcoming saccade than at other locations, and similarly Zhao et al. (2012), Rolfs & Carrasco (2012), Deubel (2008), and Jonikaitis and Deubel (2011) all reported a perceptual benefit when a saccade was being planned to the location of the perceptual discrimination task. The temporal profile of this pre-saccadic attentional shift is interesting as it demonstrates that attention builds up in the period before the execution of the saccade, suggesting that attending to a location aids in the preparation and planning process of an eye movement. While there is a discrepancy in the exact timing of the pre-saccadic attentional shift, the majority of studies suggest that the largest increase in attention is observed around 150-200 ms after cue onset (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Jonikaitis & Deubel, 2011; Montagnini & Castet, 2007), or around 100 ms before saccade onset (Rolfs & Carrasco, 2012).

This pre-movement attentional shift has also been observed before the onset of goal-directed reaches, with attention increasing at the reach location at approximately 100 ms after cue onset (Rolfs et al., 2013) in one case, or 140 ms after cue onset in another (Jonikaitis & Deubel, 2011). This shift is on a similar timescale to that of the pre-saccadic attentional shift, although, similarly, there are discrepancies in the exact timing. A recent study by Stewart, Verghese & Ma-Wyatt (unpublished) directly compared these timescales and found that the attentional shift preceding a concurrent reach and saccade happens on a similar timescale to that which accompanies a saccade alone. Interestingly however, research suggests that when a reach alone is being enacted without an accompanying saccade, the profile of attention is substantially different. Stewart & Ma-Wyatt (2015) demonstrated that the pre-reach attentional shift for a reach alone happens far earlier, and the subsequent attentional benefit is far more transient, with a substantial drop in attentional performance as the reach nears endpoint.

The spatial properties of the pre-movement attentional shift also produce some interesting clues as to how attention is spread around the locus of an upcoming movement. The spatial spread and loci of attentional facilitation associated with premotor attention seem to be fairly pliable, depending on the particular task being completed. In terms of pre-movement attention shift, most studies have examined attentional performance at the planned movement location, compared to a movement irrelevant location (Deubel & Schneider, 1996; Kowler et al., 1995). While it seems clear that there is an attentional benefit at this location, the spread and shape of this attentional facilitation is unclear. Some studies suggest that there is a single, focused attentional locus (Song & Nakayama, 2006), while others argue for a broader, general attentional facilitation (Baldauf & Deubel, 2009; Gersch, Kowler, Schnitzer, & Dosher, 2009).

While most of the research has focused on the locus of facilitation caused by attending to the area, there is also emerging evidence that attending to an area may cause a corresponding inhibition in performance at neighbouring locations. A studying utilizing magnetoencephalographic recordings of cortical activity found that when attending to a stimulus, there was an enhancement at the focus of attention, surrounded by a narrow band of inhibition (Hopf, Boehler, & Luck, 2006). Performance then returned to a normal level at further eccentricities. This suggests that the mechanisms involved in attentional enhancement are combined with a simultaneous inhibition of performance at nearby locations. Other studies have also shown that attention may have ‘center-surround’ properties, and there is both physiological (Schall, Sato, Thompson, Vaughn, & Juan, 2004) and behavioural (Bahcall & Kowler, 1999; Caputo & Guerra, 1998; Kim & Verghese, 2012) evidence to support this idea. Indeed, psychophysical evidence suggests that an attended location may be surrounded by a area of suppression, with findings suggesting that attentional performance drops sharply at locations closest to the attended area, increases monotonically with eccentricity (Cutzu & Tsotsos, 2003). These spatial properties are important to keep in mind when investigating the relationship between the location of a target relative to a movement direction, which is an inherently spatially based problem.

6.2.2 ATTENTION AND MOVEMENT DIRECTION – A LINK TO PERISACCADIC MISLOCALISATION?

Interacting with the environment requires a multiplicity of eye movements to create a unified and dynamic view of the world, and to guide the hand movements we use to manipulate objects around us. In a complex environment there are a diverse number of directional hand movements we can make, and as a consequence there are numerous positions for a visual target to be located relative to the direction of any one of these movements. Each of these movements necessitates an accompanying shift in visual attention to aid in the guidance of movement planning and execution, hence it is important to understand whether the direction of a movement affects the premotor attentional shift to different locations relative to the movement direction. While the effect of movement direction on attention has not yet been directly tested, there is evidence to suggest that preparing an eye movement elicits perisaccadic mislocalisation at locations both in line with, and orthogonal to movement direction (Kaiser & Lappe, 2004b), and additionally research indicates that the spatiotemporal profile of attention relative to a reach may be different at locations in line with and orthogonal to reach direction (Stewart & Ma-Wyatt, 2015). It has been suggested that there may also be a relationship between mechanisms controlling processes such as target selection, receptive field shifts and perisaccadic remapping (Zirnsak & Moore, 2014), and that attention may act as a bridge between these closely linked phenomena (Hamker, Zirnsak, & Lappe, 2008a). If this is the case, then directional effects may also be seen in premotor attention, and it is important to determine how movement direction may affect the premotor attentional shift.

One aspect of saccadic eye movements that has been shown to have directional perceptual differences is perisaccadic mislocalisation. Studies have shown that when making a saccade to a target, the perceived location of the target is often mislocalised, and when a horizontal saccade is being made, the target is mislocalised along this horizontal axis, in the direction of the saccade (Lappe, Awater, & Krekelberg, 2000). There is however evidence to suggest that there may be differences in perisaccadic mislocalisation depending on whether a target is presented in line with or orthogonal to a saccade: Kaiser & Lappe (2004b) found perisaccadic mislocalisation occurred at locations orthogonal to saccade direction, with targets' locations again being perceived to be toward the saccade goal. This mislocalisation is also seen at locations beyond the saccade target, with those locations again being perceived as being further towards the target (Kaiser & Lappe, 2004b) – essentially, locations surrounding the saccade target are mislocalised as being 'compressed' toward the target.

Hamker et al. (2008b) suggest that the underlying mechanisms controlling perisaccadic compression, receptive field shifts, and pre-motor visual attention may be linked: it may be the case that a oculomotor feedback loop may transiently enhance the activity of the neural populations at the saccade target, while shifting the perceived location of surrounding locations towards this target. The increase of the mislocalisation/attentional facilitation as saccade onset draws nearer reflects the strengthening of this feedback signal in the time preceding the saccade initiation. If indeed these perceptual phenomena are linked, it would seem logical that the profile of attention at locations either in line with or orthogonal to the movement target would be differentially effected by the planned movement, consistent with the empirical evidence surrounding directional effects of perisaccadic mislocalisation (Hamker, Zirnsak, Calow, & Lappe, 2008b; Kaiser & Lappe, 2004b; VanRullen, 2004). This however only relates to cases where a saccade is being made to a target – to the best of our knowledge there is no evidence to suggest that there may (or may not) be an equivalent pattern of mislocalisation when a reach is being made without a concurrent saccade.

As far as we are aware, there has not yet been any work investigating the effects of saccade or reach direction on the spatial or temporal spread of attention, however some earlier findings (Stewart & Ma-Wyatt, 2015) suggest that the direction of a hand movement may affect the shape of the spread of attention around the reach target. This previous study suggests that locations orthogonal to the direction of the hand movement may see a more sustained temporal profile of attention, whereas the locations directly in line with reach direction see a decay in attention over the course of the reach. This profile was not however observed when saccade alone, or saccade-plus-reach tasks were conducted during an analogous study (Stewart, Verghese & Ma-Wyatt, unpublished). Taken together, these results suggest that the particular movement, or combination of movements, may affect how attention is spread around the target, and additionally that there may be some interaction between the type of movement and the location of the target relative to that movement, in determining where attention is allocated. Hence, the question of how movement direction may affect attentional facilitation in relation to these different combinations of movements remains unresolved.

6.2.3 THIS STUDY

A previous study (Stewart & Ma-Wyatt, 2015) suggested that the location of an attentional probe relative to movement direction may have an effect on the spatiotemporal profile of attention. In this experiment we aimed to determine whether the direction of a reach affects the way in which attention facilitates perceptual performance at the locations surrounding the reach target. Thus, the experiment aimed to measure the perceptual facilitation at locations in the visual field that were located with directly in line with, or orthogonal to a reach. As this study also aimed to investigate this attentional profile when different movements were being conducted, the experiment was comprised of a reach alone task, a reach plus saccade task, and a saccade alone task.

6.3 METHOD

6.3.1 EXPERIMENTAL DESIGN

Prior to the main experimental tasks, a contrast threshold task was conducted for each location, which determined individual observers' contrast thresholds for the stimuli at each target location in the subsequent experimental tasks. In the first of the main experimental tasks, observers had to reach to a cued location whilst maintaining central fixation. They also completed a perceptual discrimination task that occurred around the reach endpoint during the reach. The second main task was identical except participants had to saccade to the reach endpoint while they made a reach, and in the third task, participants had to make a saccade alone to the target.

The experiment was a fully repeated measures design, with all participants completing all three tasks. Participants completed approximately 20 blocks of data for each condition, each of which contained 80 trials. The number of blocks completed varied slightly between participants, as 3 blocks had to be excluded due to eye-tracking recording errors (e.g. blinks causing loss of pupil image). Participants collected between 19 and 21 blocks of data. Blocks for each condition were interleaved.

6.3.2 PARTICIPANTS

There were four participants. One was an author whilst three were naïve to the purposes of the experiment. Three were experienced psychophysical observers. All participants had normal or corrected-to-normal vision. Three participants were right hand dominant as classified by the Edinburgh handedness test, and used their right hand to point. One participant was classified as left handed, and used their left hand to point. As the task involved pointing to one side of the screen only, for the left-handed participant the screen was flipped so they were pointing to the left hand side of the screen with their left hand. Ages ranged from 23 to 29. Ethics approval was obtained from the School of Psychology. Participants were free to withdraw from the experiment at any time without penalty.

6.3.3 EQUIPMENT

Stimuli were presented on a 17-inch ELO touchscreen monitor, with a resolution of 1024x768 pixels, and a screen refresh rate of 75 Hz. The monitor was calibrated to ensure that the monitor’s non linear gamma function was corrected to be linear. Eye movements were measured using a SR Research EyeLink 1000 eye tracker to record eye position during the task. Eye position was sampled at a rate of 1000 Hz with a spatial precision of 0.25°, according the manufacturer's specifications. The experiment was run using custom software written in Matlab using routines from the psychophysics toolbox (Brainard, 1997; Pelli, 1997).

6.3.4 CONTRAST THRESHOLD TASK

Individual contrast threshold measurements were made for each observer at each of the four probe locations. This ensured that the probe at every location was presented at the observer's contrast threshold level for that specific location. Separate contrast thresholds were measured for the fixation and saccade tasks.

For the fixation condition, the participant maintained fixation in the centre of the screen. The target location equivalent to the reach target in the main task was visible. After depressing a key, the probe (and oriented line) appeared at the relevant location being tested. The observer had to indicate the orientation of this probe using the left or right arrow on the keyboard. A QUEST paradigm set to an 82 % threshold (Watson & Pelli, 1983) adjusted the luminance of the probe. The background luminance of the screen was 27.5cd/m^2. Forty trials were used to obtain the threshold measurement, and each location was tested three times, with the final threshold being the average of the three values. These values were then used such that each probe was presented at this threshold value for each participant.

Separate threshold measurements were taken for the tasks in which there was a concurrent saccade. To determine the thresholds for this task, a similar paradigm was used. As described above, the observer depressed a key, after which a beep occurred to signal the observer to saccade to the saccade target on the screen. The perceptual probe appeared 300 ms after the beep, in order to account for variable saccade latencies and to avoid any effects of saccadic suppression. Upon completion of the saccade the observer had to indicated the orientation of the line, and a QUEST paradigm was used, as described above.

6.3.5 REACH ALONE TASK

At the start of each trial, a grey fixation circle appeared in the middle of the screen that was 0.25° in size and 18 % Michelson contrast from the background. Two saccade targets appeared on the screen: one was to the right of the fixation point, at 10° eccentricity; the other was 10° above the fixation point. The targets were circles 0.75° in diameter, and 10 % contrast from the background. These locations were chosen such that probe locations could be placed both in line with the reach direction to the target and orthogonal to the direction of the reach.

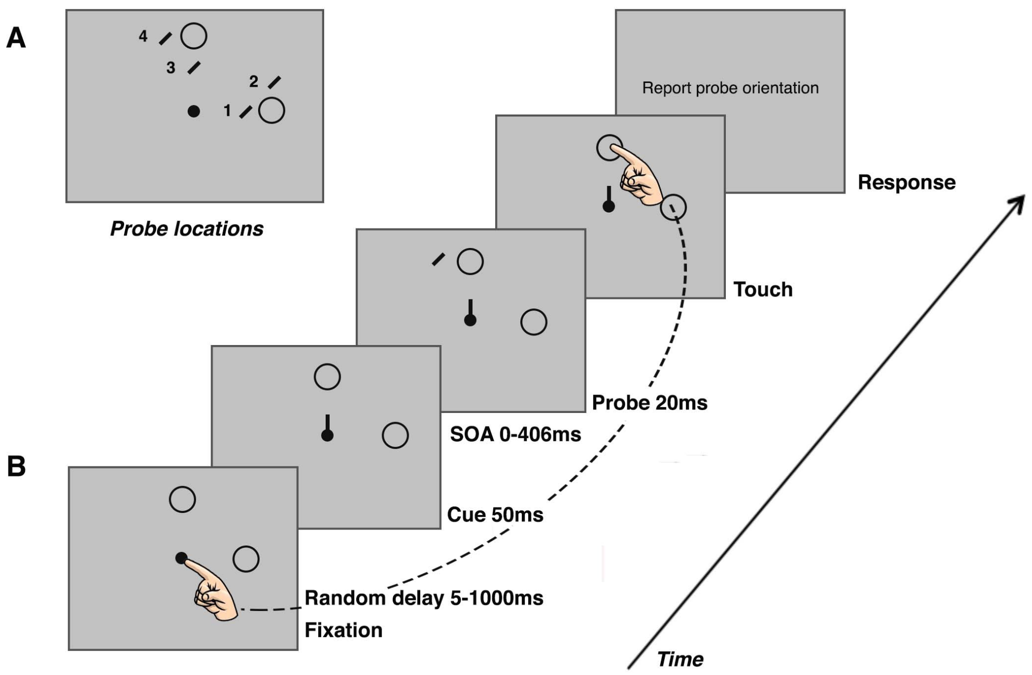

Figure 6.1 – A) The potential probe locations. Location 1 is 8° right from the fixation point. Location 2 is 10° right from the fixation point and 2° above the right touch target. Location 3 is 8° above the fixation point. Location 4 is 10° above fixation point and 2° to the left of the upper touch target. B) The timeline of events in a trial. Participants fixated a central fixation point, and touched this point to start a trial. After a variable delay, a cue indicated which target to reach to, and signalled the start of the movement. During the movement, at a variable SOA, the perceptual probe appeared. For reaching conditions, auditory negative feedback was given if the reach time was slower than 600 ms. After the movement was completed participants reported probe orientation.

As shown in Figure 6.1B, the reach trial started when the participant touched the central fixation point on the screen. After a random delay of 5 to 1000 ms (calculated at 5 ms intervals on a trial-by-trial basis using Matlab's randperm function), a cue appeared to signal whether a reach was to be made to the location at the right or at the top of the screen. This also indicated where the perceptual probe would appear, with 100 % validity.

The cue was a white line of 1.5° size and 17 % contrast, which pointed either rightwards or upwards. The cue onset also signalled the started of the SOA, after which the perceptual probe would appear at one of two locations next to the reach target. SOA lengths were 13, 107, 200, 306 or 400 ms. Participants were instructed to maintain central fixation at all times. Cues occurred with equal probability.

As shown in Figure 6.1A, the probe locations were located 2° from the fixation point, between the fixation and target, and 2° orthogonal to the reach target, at 90° to the direction of the reach.

6.3.6 REACH AND SACCADE TASK

The experimental paradigm was identical to the reach alone task as described above (see Figure 1), with the addition of a concurrent saccade to the target location.

6.3.7 SACCADE-ONLY TASK

The experimental paradigm was mostly similar to the reaching tasks, except a saccade alone was completed, with no concurrent reach. The only difference was that to start a trial participants depressed the enter key on the keyboard, and on the 'go' signal, made a saccade to the target.

6.4 RESULTS

6.4.1 DATA EXCLUSIONS

For the saccade-plus-reach condition, saccades were analysed and trials were excluded when the saccade was not to the target, where there was a blink, or where the eye-tracker dropped the eye trace. Additionally, trials in which the saccade latency was less than 100 ms were excluded to avoid anticipatory saccades (He & Kowler, 1989), and trials were also excluded where the probe appeared during a window from -50 to +25 ms around the initiation of the saccade, when saccadic suppression may have occurred (50 ms before the saccade was initiated until 25 ms into the saccade) (Morrone, Ross, & Burr, 2005). Additionally, any saccade where the probe would have appeared after the saccade had already been completed was removed so that the performance recorded was due to the saccade preparation and execution. Trials in which the eye had already landed at the movement target when the probe appeared were also excluded. Reaches were excluded where the reach latency, reach time, and reach accuracy were above +-2 standard deviations from the mean (percent exclusions per participant are shown in table 1). The proportion of trials excluded differs between conditions due to the differing exclusion criteria: for example, in the saccade-plus-reach condition, the exclusion rate is the highest as exclusions were made on the basis of both saccade and reach dynamics and accuracy.

6.4.2 MOVEMENT DYNAMICS

Movement dynamics for each observer and each movement condition are recorded in Table 6.1. Due to the non-normal nature of movement distributions, medians and interquartile ranges are reported. Movement dynamics for each participant are represented as stacked density plots in Figure 6.2. Saccades were classified as movements that exceeded velocity of 35deg/s and acceleration of 9500 deg/s. Saccade latency was measured as the time between the movement cue and the start of the saccade. Hand latency was measured as the time between the movement cue and the time the finger was lifted from the mouse button. Eye-hand latency was measured as the time between saccade onset and reach onset.

Table 6.1 – movement dynamics and exclusion rates for individual participants for each condition. Median values and interquartile ranges are reported due to the non-normal distribution of movement latencies.

	Participant	Median reach latency	IQR reach latency	Median saccade latency	IQR saccade latency	Median eye-hand latency	IQR eye-hand latency	% excluded
P1	Reach-only	278 ms	48 ms					15 %
	Saccade and reach	282 ms	46 ms	173 ms	17ms	108 ms	39 ms	40 %
	Saccade-only			169 ms	19 ms			28 %
P2	Reach-only	302 ms	56 ms					28 %
	Saccade and reach	320 ms	54 ms	200 ms	24 ms	119 ms	53 ms	44 %
	Saccade-only			199 ms	20 ms			27 %
P3	Reach-only	246 ms	66 ms					23 %
	Saccade and reach	253 ms	53 ms	165 ms	20 ms	86 ms	55 ms	50 %
	Saccade-only			173 ms	29 ms			38 %
P4	Reach-only	320 ms	54 ms					16 %
	Saccade and reach	302 ms	54 ms	165 ms	19 ms	136 ms	52 ms	46 %
	Saccade-only			173 ms	27ms			25 %
ALL	Reach-only	287ms	66 ms					21 %
	Saccade and reach	287ms	61 ms	174 ms	27ms	112 ms	52 ms	45 %
	Saccade-only			178 ms	30 ms			30 %

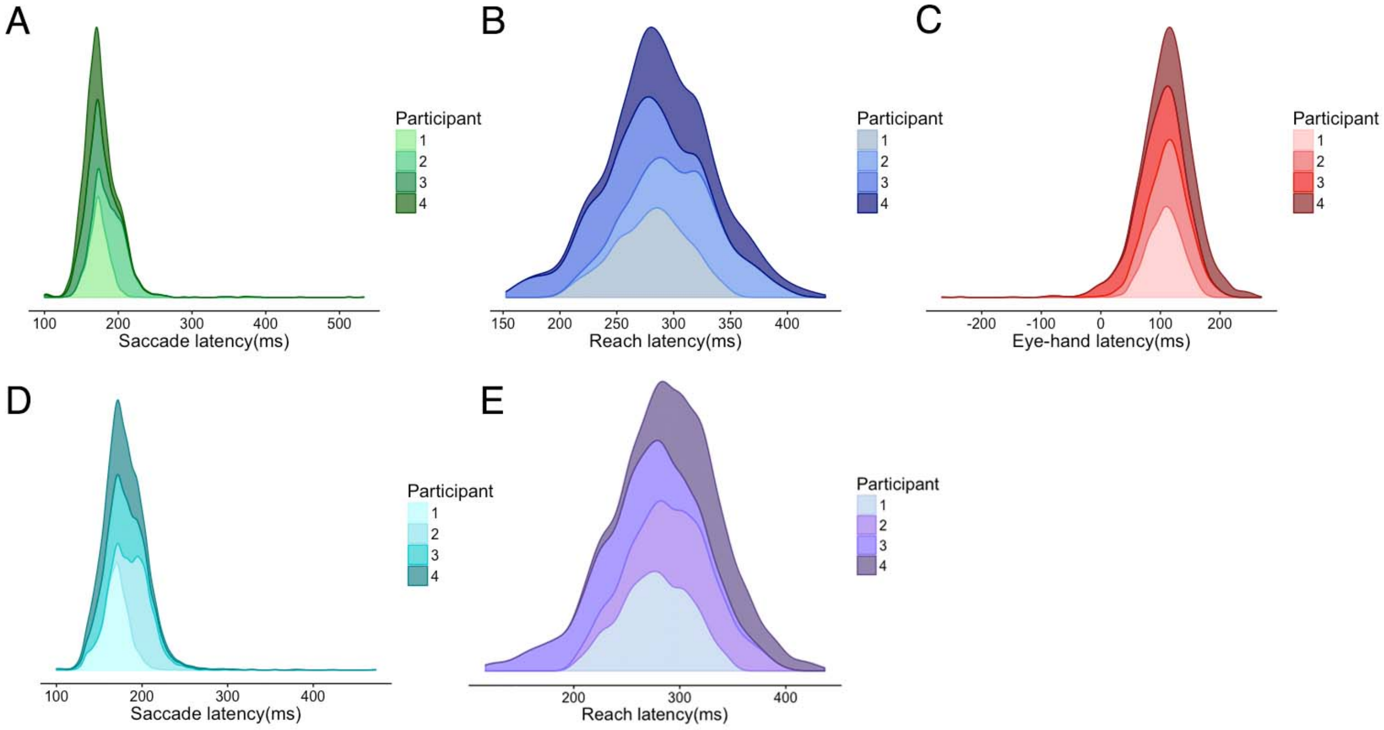

Figure 6.2 – Movement dynamics for each participant represented as stacked density plots. A) saccade latencies for the saccade-plus-reach condition. B) reach latencies for the saccade-plus-reach condition. C) eye-hand latencies for the saccade-plus-reach condition. D) saccade latencies for the saccade-only condition. E) reach latencies for the reach-only condition.

6.4.4 PERFORMANCE RELATIVE TO SOA

Performance at each location was measured at a time-point relative to the cue onset. Figure 6.3 shows this performance at each location. For the locations that were in line with the movement direction (1 and 3), it can be seen that in the reach-only condition, peak performance occurs at the shortest SOA, with performance degrading by about 30 % throughout the preparation and execution of the reach. Conversely, for the reach and saccade condition at these locations, performance remains fairly consistently low across all SOAs. For the locations orthogonal to the direction of movement (2 and 4), performance on the reach-only condition is similar to locations 1 and 3, except the drop in performance is approximately 10-15 %

difference. For the reach and saccade condition however, performance is lowest at the shortest SOA, and builds up by about 30 % with the peak after the 200 ms SOA.

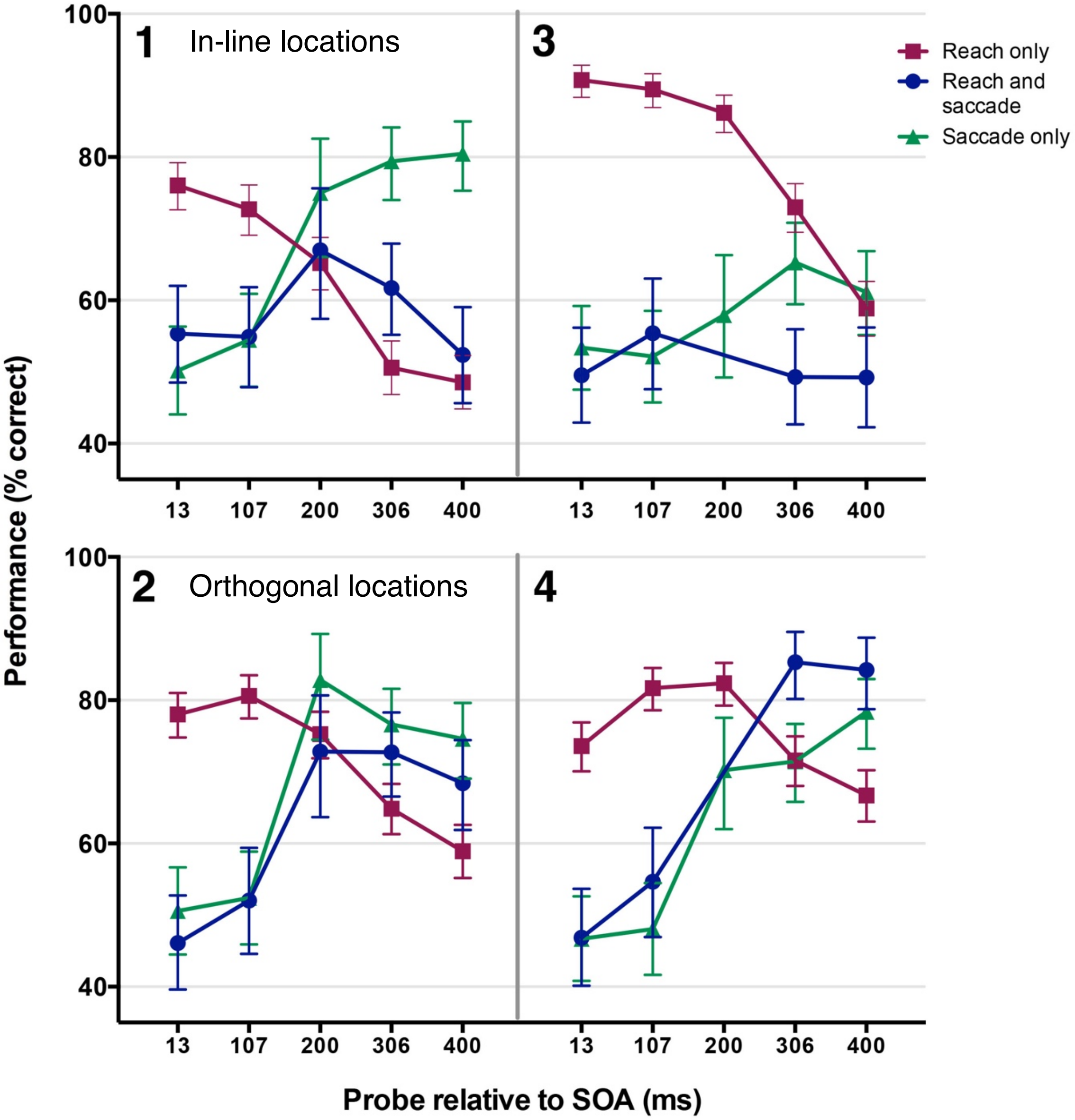

Figure 6.3 – Performance relative to SOA for each probe location for reach-only condition (square), reach and saccade condition (circle), and saccade-only (triangle). Data is the weighted mean across all participants. The top graphs (1 and 3) represent probe locations in line with reach/saccade direction. The bottom graphs (2 and 4) represent probe locations orthogonal to reach/saccade direction. Error bars are calculated using Jeffrey’s interval that provides a Bayesian calculation of confidence intervals in binomial data.

Linear mixed models were used to analyse the influence of SOA, location, and movement direction on performance (fixed effects: SOA, location, movement direction; random effect: participant). For the reach-only condition, there was a significant effect of the following on performance: SOA: F(1,69) = 151.24 p<0.0001; location: F(1,69) = 76.78, p <0.0001; movement direction: F(1,69) = 5.27, p=0.025; the interaction between SOA and location: F(1,69) = 7.8, p=0.0067; the interaction between SOA and movement direction: F(1,69) = 7.83, p=0.0067, the interaction between location and movement direction: F(1,69) = 21.59, p<0.0001; and the interaction between SOA, location and movement direction: F(1,69) = 6.18, p=0.0154. For the reach plus saccade condition, there was a significant effect of the following on performance: SOA: F(1,67) = 17.08, p=0.0001; movement direction: F(1,67) = 12.38, p=0.0008; the interaction between SOA and location: F(1,67) = 8.23, p=0.0055; the interaction between SOA and movement direction: F(1,67) = 11.50, p=0.0012; and the interaction between location and movement direction: F(1,67) = 8.0641, p=0.0060. For the saccade-only condition there was a significant effect of SOA only on performance F(1,69) = 40.81, p<0.0001.

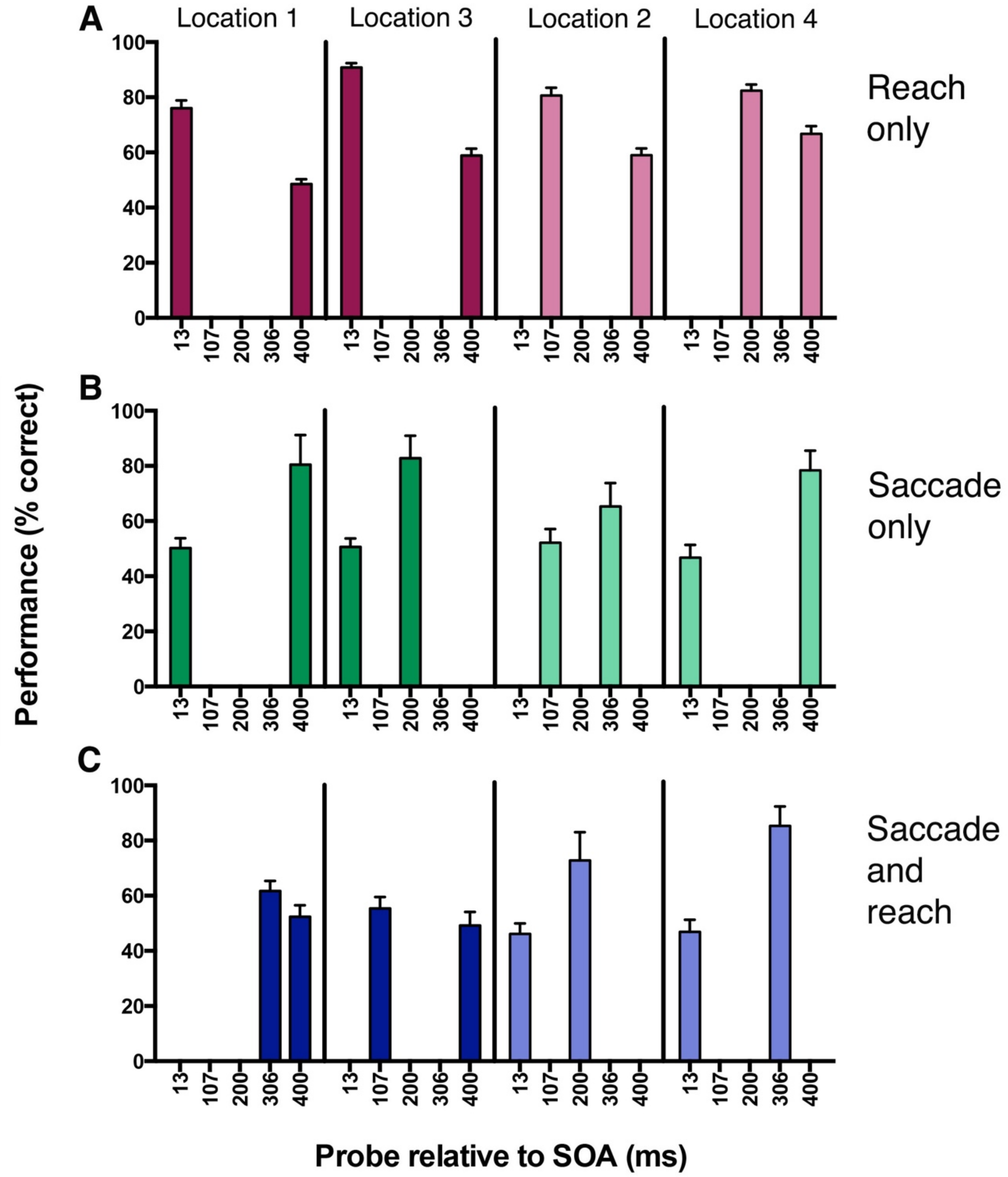

Figure 6.4 – Maximum and minimum performance for each movement condition and location. A) Reach-only; B) Saccade-only; C) Saccade and reach. Darker colours denote parallel probe locations, lighter colours represent orthogonal locations. Error bars are standard error of the mean.

Figure 6.4 shows the maximum and minimum performances at each location for each reach condition. This demonstrates where attention reached peak facilitation during the movement, and also demonstrates where in the movement attention was the lowest: this is comparable to the analysis of maximum and minimum performance in Stewart & Ma-Wyatt (2015). In the reach-only condition (Figure 6.4A), for the parallel locations, maximum performance is at the first SOA, and minimum performance is at the last SOA, while the orthogonal locations have the maximum at 107ms and 200 ms, and the minimum at the last SOA. This shows a general decrease in performance across the movement. In the saccade-only condition (Figure 6.4B) the minimum performance is at 13 ms for the parallel locations, with maximum performance at 400 ms and 200 ms. The orthogonal locations show minimum performance at 13 ms and 107ms, with maximum performance at 400 ms and 306 ms. This shows a general increase in performance across the saccade. In the saccade and reach condition (Figure 6.4C) maximum performance was at 306 ms and 107ms, and minimum performance at 400 ms for the parallel locations, and for the orthogonal locations, minimum performance was at 13 ms and maximum performance at 200 ms and 306 ms. This shows a general decrease in performance for the parallel locations, and general increase for the orthogonal locations. For the reach-only, paired-samples t-tests revealed a significant difference between maximum and minimum performance for: location 1, t(3) = 5.47, p =0.012; location 2, t(3) = 9.23, p=0.0027, location 3, t(3) = 12.43, p=0.0011, and location 4, t(3) = 18.32, p=0.0004. For the saccade-only condition there was a significant difference for location 1, t(3) = 3.87, p=0.031, location 3, t(3) = 3.67, p=0.038, and location 4, t(3) = 6.50, p=0.007. For the saccade and reach condition there was a significant difference for location 1, t(3) = 3.65, p=0.036, location 3, t(3) = 4.73, p=0.018 and location 4, t(3) = 3.65, p=0.035.

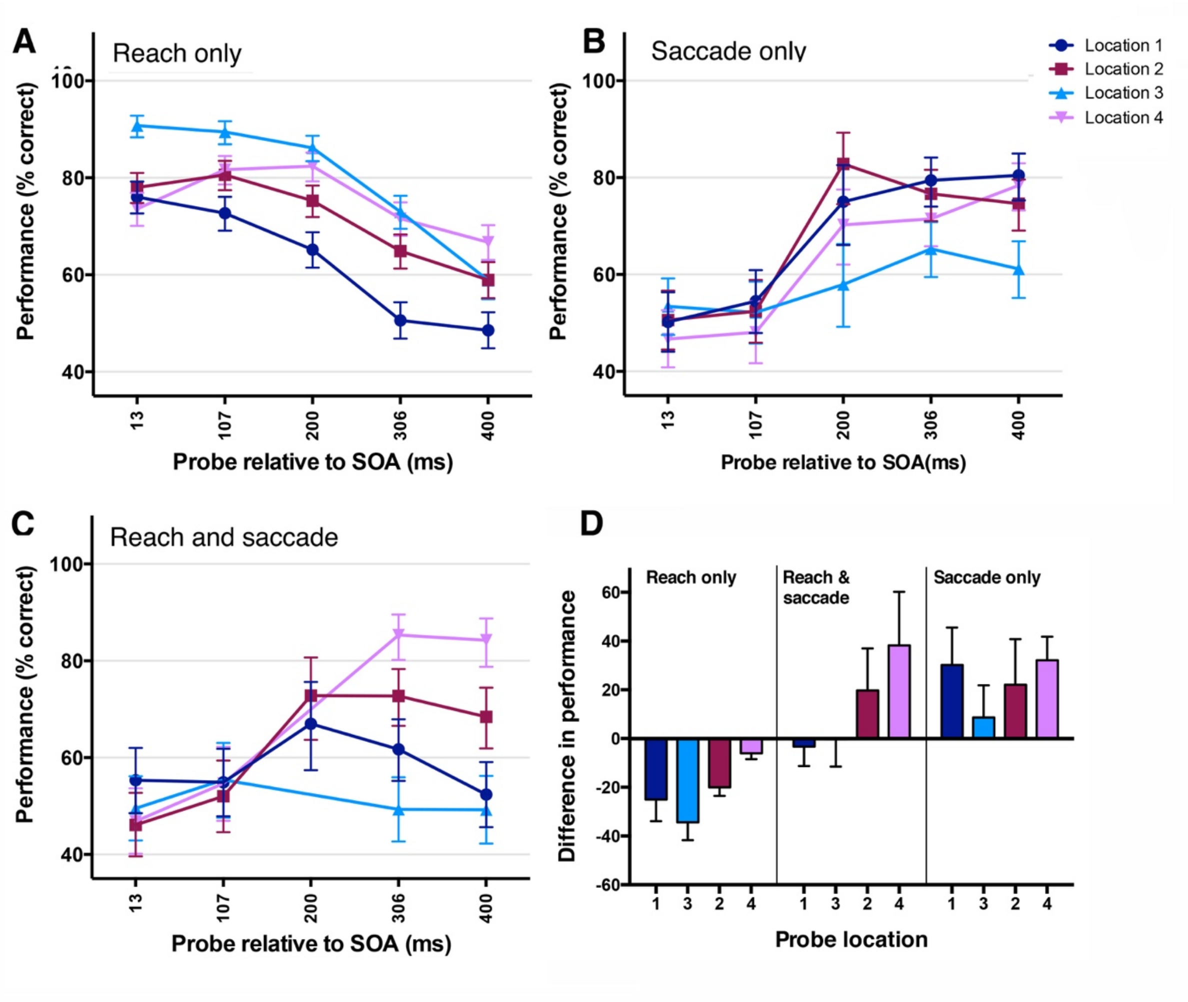

Figure 6.5 – Performance relative to SOA, grouped by experimental condition. A) Performance relative to SOA in the reach-only condition. B) Performance relative to SOA in the saccade-only condition. C) Performance relative to SOA in the reach and saccade condition. Error bars for Figures A, B and C are Jeffrey's intervals. D) Difference in performance between the shortest SOA and longest SOA for each condition. Blue bars represent parallel probe locations, maroon bars represent orthogonal probe locations. Error bars are 95 % confidence intervals across participant means.

Figure 6.5 shows the performance relative to SOA for each individual condition in order to further quantify the way in which attention generally increases or degrades throughout the reach. This shows that for each condition, reaching performance is generally better during different parts of the movement preparation. For example, peak performance for the reach-only condition generally occurs at an earlier SOA (Figure 6.5A), whereas peak performance in the reach and saccade condition occurs at different points, depending on probe location (Figure 6.5C). This difference in performance across the time-course was quantified by comparing the difference between the first SOA and the last SOA across participants for each movement condition (Figure 6.5D). This allows a visualization and comparison of the overall trend in the increase/decrease in attention across different movements.

A linear mixed model revealed that there was a significant difference in performance across the time-course of the movements between movement conditions: $F(1,37) = 69.11$, $p<0.0001$; target locations: $F(1,37) = 5.62$, $p=0.023$, and also between movement directions: $F(1,37) = 12.29$, $p=0.0012$. It can be seen that for the reach and saccade condition in particular, the movement direction affects whether there is an overall increase or decrease in performance throughout the movement: for parallel locations (1 and 3), performance decreases throughout the reach, and for orthogonal locations (2 and 4), performance increases throughout the reach. This shows that different types of movement require peak attentional guidance at different points during the movement, and in particularly in the case of the reach and saccade condition, the direction of movement additionally affects this.

6.4.5 PERFORMANCE RELATIVE TO MOVEMENT ONSET

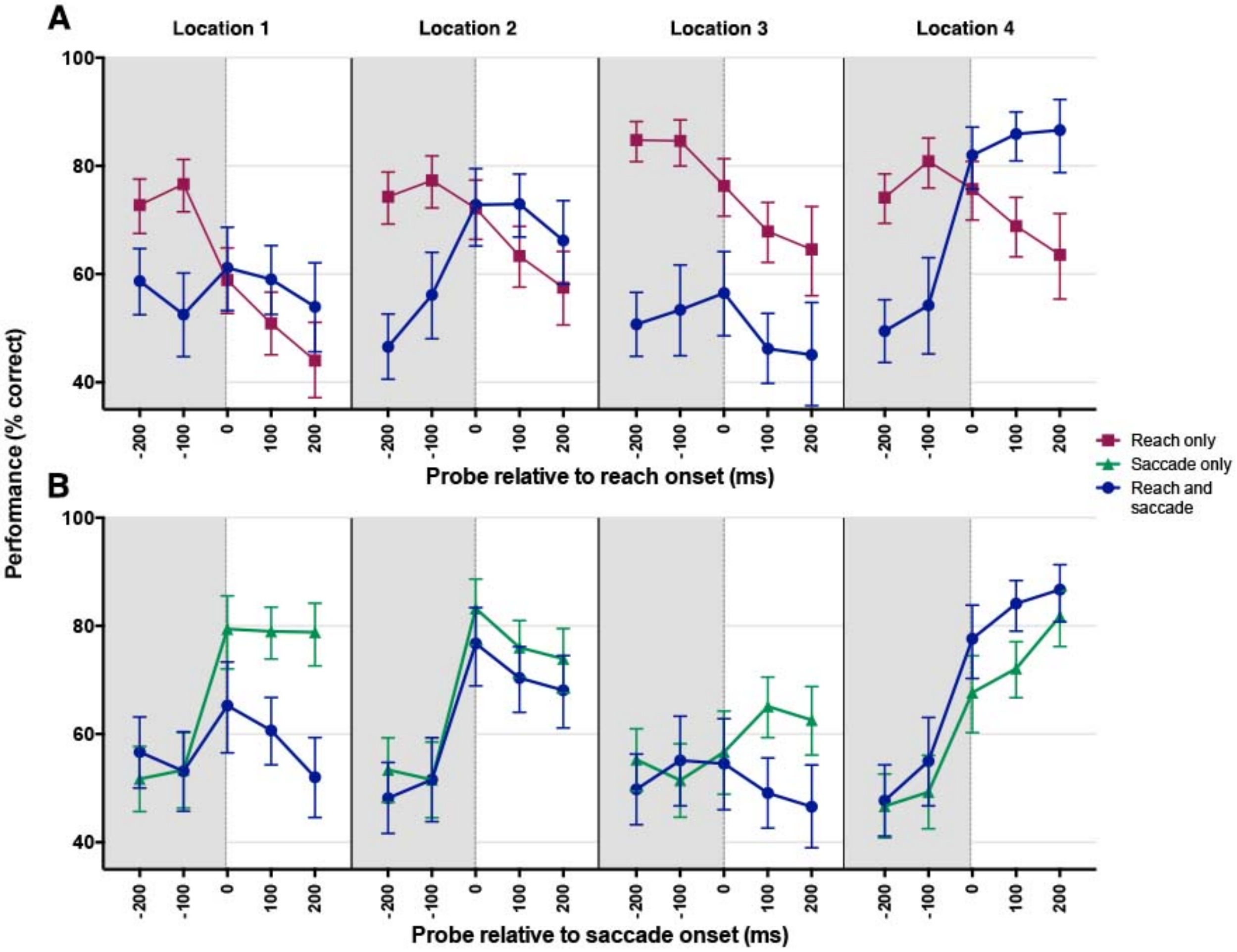

Figure 6.6 – performance relative to movement onset for the reach-only, saccade-only and saccade-plus-reach conditions. A) performance relative to reach onset for reach-only (red, squares) and reach plus saccade (blue, circles). B) performance relative to saccade onset for saccade-only and reach plus saccade condition. Error bars are Jeffrey's intervals.

To compare the performance between the reach-only, saccade-only and reach plus saccade conditions, attentional performance was binned relative to movement onset, to see whether the different movement effectors may play a role in the allocation of attention. Figure 6.6 shows the performance in the two reaching conditions binned relative to either reach onset (A) or saccade onset (B). Note that due to the large bin sizes used (100 ms), there is still data at the 0 ms time bin, despite exclusions for saccadic suppression (given the saccadic suppression exclusions were 50 ms before saccade onset to 25 ms after saccade onset, and the 0 ms bin should include data from -50 ms to +50 ms, data actually included at the 0 ms bin would be from 25-50 ms after reach onset). Paired-samples t-tests were used to quantify the difference in performance before and after movement onset. Data was pooled for each location across the time bins before the movement onset, and the time bins after movement onset. For the reach plus saccade condition, when binned relative to saccade onset, there was a significant difference for the orthogonal positons: location 2, t(7) = -2.87, p = 0.024; location 4, t(7) = -4.6, p = 0.0025, but no significant different for the parallel locations: location 1, t(7) = -1.81, p=0.11; location 3, t(7) = 0.73, p = 0.49. For the reach plus saccade condition, when binned relative to reach onset, there was a significant difference at the orthogonal locations: location 2, t(7) = -2.6, p = 0.033; location 4, t(7) = -3.22, p = 0.014, however again there was no significant difference at the parallel locations: location 1 t(7) = -0.65, p = 0.54; location 3 t(7) = 0.99, p = 0.35. For the reach-only condition, when binned relative to reach, there was a significant different before and after movement onset for all locations: location 1, t(7) = 5.69, p = 0.0007; location 2, t(7) = 4.008, p = 0.0051; location 3, t(7) = 3.50, p = 0.01; location 4, t(7) = 3.92, p = 0.006. For the saccade-only condition, there was a significant difference at location 1, t(7) = -4.35, p = 0.003; location 2, t(7) = -3.76, p = 0.007 and location 4, t(7) = -8.81, p = 0.00004, but not at location 3, t(7) = -1.55, p=0.16.

6.4.6 HEATMAP OF PERCEPTUAL PERFORMANCE

To compare the spatiotemporal profile of attention for locations in line with or orthogonal to movement target, heatmaps were created for each movement condition (Figure 6.7). Heatmap values were created by averaging the performance across participants at each of the parallel locations (1 and 3), and the orthogonal locations (2 and 4). Values of the in-between locations on the heatmap were calculated based on the weighted values of the nearest tested locations and the distance between each of these points. It is worth noting that the heatmap averages across the location of the movement target. We did not test this target location, as this effect is well documented (i.e. Deubel, 2008; Deubel & Schneider, 1996; Jonikaitis & Deubel, 2011). Therefore the heatmap is indicative of performance around the target location, but not at the target location itself.

Figure 6.7 clearly shows the difference in the decrease in attentional facilitation across the time-course of the movement (reach-only), and the increase in attentional facilitation for the saccade-only and saccade-plus-reach conditions. It also demonstrates the difference in performance at locations in line with and orthogonal to the movement direction for each of the movement conditions.

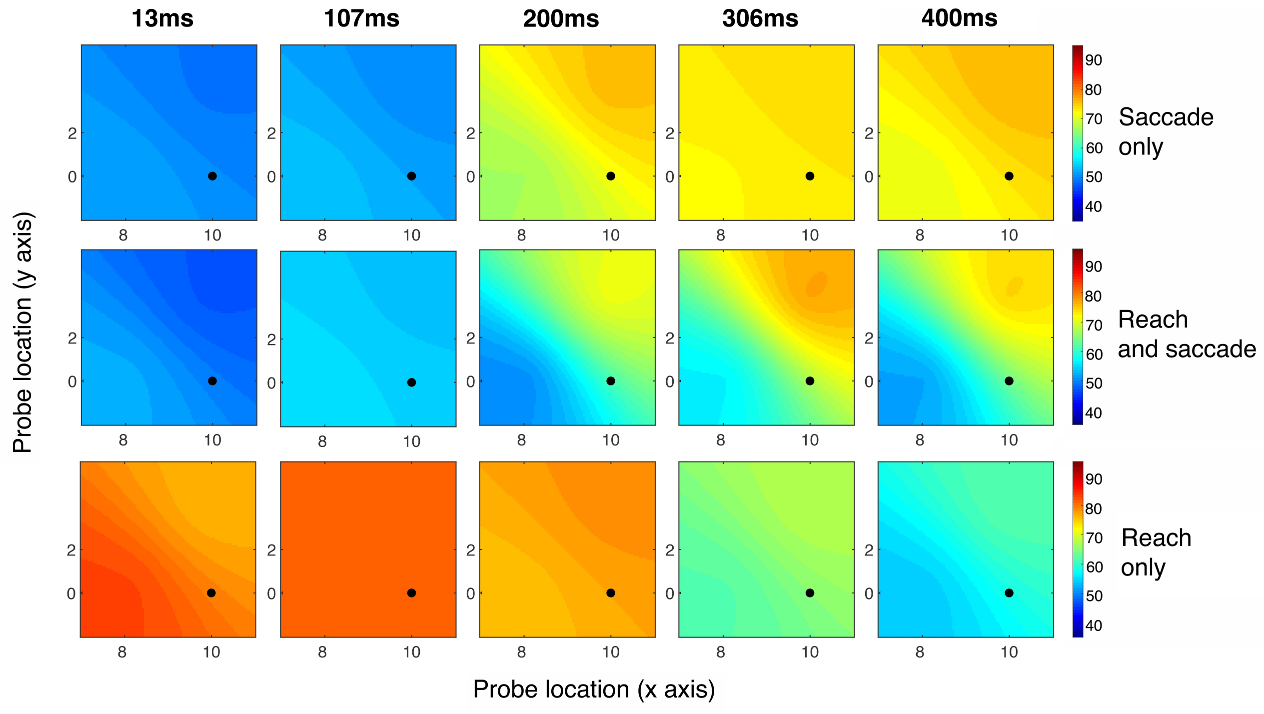

Figure 6.7 – heatmap of performance for each time bin (relative to SOA), for each location. The top row represents data for the saccade-only condition, the middle row represents data for the reach and saccade condition, and the bottom row represents data for the reach-only condition. The movement target is depicted by the black circle. The colour scale represents percentage correct. The location on the x and y axes represents the eccentricity in degrees from the central fixation point.

6.5 DISCUSSION

The two overarching aims of this experiment were to investigate firstly whether the movement effector affects the timecourse of attention, and secondly whether the direction of these movements has an effect on the spatiotemporal characteristics of attention. The overall pattern of results showed that there was a major difference in the timecourse of attention depending on whether an eye movement, hand movement, or both were being enacted, and additionally that there was a difference in locations in line with or orthogonal to the reach, and this too differed between the different movement conditions. It should be noted that the overall aim of the experiment was to map the spatiotemporal profile of attention around the movement target, as facilitation has been found in a number of previous studies at the target location itself (i.e. Deubel & Schneider, 1996; Deubel, 2008; Jonikaitis & Deubel, 2011). The aim of this study was to compare performance across movement combinations at locations surrounding the movement target.

6.5.1 TIMECOURSE OF ATTENTION IS DEPENDENT ON MOVEMENT EFFECTOR

A comparison of the pre-movement attention shift between effectors shows that there is a marked difference between saccade-only, saccade-plus-reach, and reach-only conditions in terms of where the peak attentional facilitation is throughout the movement (Figure 6.6). These differences were quantified in terms of where the peak maxima and minima occurred throughout the movement, and how this affects the overall increase or decrease in attentional facilitation throughout each movement (Figures 6.4 and 6.5). It can be seen that in conditions where a saccade is being made, attention peaks toward the end of the movement, whereas when a reach alone is being conducted, attention decreases across the timecourse of the movement. These differing temporal profiles may be indicative of which stage in the movement planning and execution process requires the most attentional guidance.

When a reach alone was being enacted, attention peaked toward the start of the movement, degrading during the reach, with lowest attentional performance occurring at the longest SOA (as seen in Figure 6.4). When a saccade alone was being completed, the converse trend was observed, with attention generally increasing over the timecourse of the movement (Figure 6.6). These patterns seen in the saccade and reach alone conditions are consistent with our previous work with analogous temporal and spatial paradigms, with the reach alone paradigm showing a general degradation across the timecourse of the reach (Stewart & Ma-Wyatt, 2015), and the saccade alone paradigm showing a general increase (Stewart, Verghese & Ma-Wyatt, unpublished: Figure 4). The saccade condition is also generally consistent with prior research showing this pre-saccadic attentional shift happens around 200-300 ms after the cue (Castet et al., 2006; Deubel, 2008; Rolfs & Carrasco, 2012). The condition that incorporated both saccade and reach showed a less consistent timecourse across locations however, and it differs from the pattern that one would expect given analogous paradigms in past work (Stewart, Verghese & Ma-Wyatt, unpublished). As Figure 6.4 shows, for the locations orthogonal to the direction of the movements (locations 2 and 4) the peak facilitation is at the end of the movement, with lower levels at the start, resulting in an overall trend of an increase in attention across the movement. This is in line with our previous work, and coheres to the general temporal pattern of pre-motor attention observed in past research (Jonikaitis & Deubel, 2011; Rolfs et al., 2013; White et al., 2013). The locations that are parallel with the target (locations 1 and 3) however are less consistent with prior empirical evidence, as the performance is relatively flat, and there is little difference between maximum and minimum points at these locations: indeed, these locations are also somewhat depressed compared to the other conditions. Possible reasons for this suppressed performance will be discussed further in the following sections.

Taken together, these results provide solid evidence that different movement effectors trigger a peak attentional facilitation at different points during a movement, and that the type of movement being made determines whether attention builds up or degrades across the course of that movement. These differences in attentional peaks may reflect the how attention is utilized during different types of movement planning. For example, for a reach alone, it seems that peak attentional guidance is needed at the outset of the movement planning phase, and one the hand is nearing the target, attention is not so important. This reflects the importance of vision in the planning stage of an accurate hand movement (Ma-Wyatt & McKee, 2006; 2007). When a movement alone is being planned, there is no saccadic guidance to provide information from the fovea, hence the role of attention in providing higher acuity visual information in its place may be imperative for planning an accurate hand movement.

6.5.2 LOCATION RELATIVE TO MOVEMENT DIRECTION AFFECTS ATTENTIONAL PERFORMANCE

The other major question that was investigated in this study was how the direction of movement might affect the spatiotemporal profile of attention. Our results suggest that there is a difference in performance between locations in line with and orthogonal to movement direction, but this depends on the type of movement being enacted. These differences suggest that attention might be differentially, and asymmetrically spread around a movement target depending on the type of movement being made.

For the reach-only condition, the locations which were horizontally in line with the direction of movement show a pattern of initial attentional facilitation, before a decrease in performance over the course of both the planning and execution of the reach (locations 1 and 3, Figure 3). The locations orthogonal to the movement direction (locations 2 and 4, Figure 3) are also broadly consistent with this previous study, as the temporal profile at these locations shows far less of a decrease in attentional performance over the course of the reach. The temporal pattern of performance is consistent between the relative locations of the probes, suggesting that the relative position of a stimulus compared to the direction of a reach does have an effect on the subsequent attentional performance at that location.

When performance is compared across conditions and locations when binned relative to movement onset, it can be seen that for the reach and saccade condition, there is a marked difference in performance at the parallel and orthogonal locations (Figure 6.6A). Comparing this performance to the saccade-only condition when binned relative to saccade onset (Figure 6.6B), it can be seen that performance at the orthogonal locations follows the same general trend between these conditions, while performance at the parallel conditions follows a different pattern between conditions. This suggests that the planning and execution of a reach may differentially affect the profile of attention at parallel and orthogonal locations when that reach is accompanied by a saccade. It also seems to suggest that when a saccade is being made concurrent to a reach, the saccade drives the observed attentional effect, as the profile of attention is markedly different when no saccade is being conducted.

Prior research has shown no evidence to suggest that this effect may also be seen during the planning of a reach, however these results are consistent with research showing that related movement planning phenomena may show a directional effect in perceptual measures. Perisaccadic mislocalisation has, for example, been shown to have differential effects at locations horizontally in line with and orthogonal to a saccade (Kaiser & Lappe, 2004b), and while this study does not directly test the relationship between aspects of pre-movement perception such as mislocalisation, attention and motor control (Hamker, Zirnsak, Calow, & Lappe, 2008c), it may provide a clue as to how pre-movement attention may fit into this complex system. Hamker et al. (2008c) suggested that patterns of mislocalisation and receptive field changes during saccades may also be observed during covert attention (with the argument that covert attention is a planned, but not executed, saccade), and that pre-motor attention would even more strongly be implicated in this process of receptive field shifts and compression. If that is the case, then findings that attention acts differently at parallel and orthogonal locations relative to a movement may reflect some shared mechanism between these systems, and reflects findings that perisaccadic mislocalisation acts differently at parallel and orthogonal locations relative to a saccade (Kaiser & Lappe, 2004b). This general neural circuit underlying premotor attention shifts may also provide an insight into the premotor planning mechanisms underlying saccade and reach. For example, there is evidence that during the planning and control of reaches, movement guidance and the visual representation of space are closely linked in the early stages of movement planning (for example Andersen, Snyder, Bradley, & Xing, 1997; Ren, 2006). The differentiation of the profile of attention between saccade and reach alone seen in this study may be indicative of differences in the underlying mechanisms between saccade and reach planning during these early stages of perceptual visual information integration and movement planning: the shift of premotor attention when a saccade is being conducted seems to be a distinct signature of underlying saccade-related mechanisms, which is markedly different from that of a reach alone.

This raises the question though of whether the observed directional effects on attention may just be an artefact of covert attention, as during the reach-only conditions participants had to maintain fixation at the centre of the screen. The argument could therefore be made that participants are essentially just directing covert attention to the peripheral targets as they complete the reach, and the observed attentional facilitation is merely an artefact of this attentional process rather than an attentional shift elicited by the reach itself. It has been suggested that covert attention is a mechanism triggered by a saccade that is planned but not executed (Hamker, 2004; Rizzolatti, Riggio, & Sheliga, 1994), and thus the patterns of mislocalisation seen during actual saccades may also be seen in covert attention (Hamker, Zirnsak, Calow, & Lappe, 2008c). By this logic, the observed attentional facilitation, and the difference between orthogonal and parallel locations could merely be reflective of general pre-saccadic perceptual mechanisms, which are also implicated in the horizontal and orthogonal mislocalisation of locations during saccades.

However, given the research suggesting that hand movements do indeed elicit a distinct attentional shift (Jonikaitis & Deubel, 2011; Rolfs et al., 2013; Stewart & Ma-Wyatt, 2015), and that the temporal profile of covert attention differs from the profile observed here (Ling & Carrasco, 2006; Mackeben & Nakayama, 1993; Muller

& Rabbitt, 1989), explaining this pattern as a covert attention shift seems unsatisfying. Rather we would suggest that perhaps planning and executing a reach triggers an attentional shift, and the spatial properties of this shift differ depending on the location of the target relative to the movement direction, and whether or not there is an accompanying eye movement. The possibility that a perceptual change, elicited by the visuomotor feedback loop during reach planning necessitates a similar effect as that seen in perisaccadic mislocalisation, is interesting, however is as yet untested (see Hesse & Deubel, 2010).

The ways in which the direction of a movement may affect attention is also an important problem to consider in the broader context of completing a reach in a more complex or naturalistic task, where movements may be enacted in a multitude of different directions. This multi-dimensional attentional problem has been conceptualized in terms of a general priority map that selects targets in a scene and then directs attention to that location (Fecteau & Munoz, 2006) and that indeed attention may form an active “attentional landscape” to select upcoming movement locations (Baldauf & Deubel, 2010). It is not unreasonable to suggest that in the course of creating such a multi-dimensional map, the direction of an upcoming movement may be taken into account by attentional selection mechanisms, and attention may be spread in a non-uniform manner to locations in line with or orthogonal to a particular movement target. These ideas about attentional priority maps, target selection, attention, and perisaccadic mislocalisation may seem disparate, however they ultimately aim to explain how enacting a movement changes perception at the movement target, and how this may affect attentional allocation and the role it plays in the execution of complex motor movements.

6.5.4 SUPPRESSED PERFORMANCE – AN ARGUMENT FOR ATTENTIONAL INHIBITION

The saccade-only condition is fairly consistent across both parallel and orthogonal locations, with the exception of location 3, which shows a consistent depression. For the saccade and reach condition, orthogonal locations show a similar pattern to the saccade-only condition, but the parallel locations both show a depression in performance. There is no one factor in this experiment which parsimoniously explains why attentional performance should be uniformly worse at these locations when both a saccade and reach are being made, compared to one movement type alone, nor at location 3 when a saccade alone is being made. There are a number of possible explanations for this pattern, and these will be outlined. Overall, methodological issues that may explain this depressed performance can be dismissed, and it seems more likely that attention is being inhibited at those locations. The saccade and reach condition will be discussed first.

The most obvious explanation would be to assume that the hand movement blocked the probe during the course of the reach, hence suppressing performance. This is unlikely, given the high performance in the reach-only condition - if hand interference was the issue, performance in both reach conditions should be suppressed. Additionally, given the timing of reach latency and reach time, this would be unlikely: the average reach latency was 287ms and the average reach time was 222 ms, meaning the total average reach from cue to touch was 509 ms. Given that the last SOA was at 400 ms, it is unlikely that the hand would have been occluding the probe by that timepoint, and it is extremely unlikely that the hand would have been occluding the probe at any earlier timepoints.

Another possible explanation is that individual differences in movement latencies may have eclipsed any attentional effect when the data was collapsed across participants. We investigated this by conducting correlations between reach latency, saccade latency, eye-hand latency, and attentional performance across all participants, at each location and SOA. Results showed that none of these factors were associated with higher or lower performance at these locations (or indeed any locations).

One other explanation for this pattern is that there is an interference effect between the attentional allocation for the two motor effectors. This could on the surface seem to explain the inconsistencies with the results of the attentional performance seen at analogous locations in past studies, where there was no observed depression (Stewart, Verghese & Ma-Wyatt, unpublished). This prior study involved hand movements that were made from the top of a desk to the eye-level monitor, whereas the current study involved hand movements from the centre of the screen to the target location. It could be that this directional change affected the way in which attention was directed.

An alternate explanation is that the direction of the saccade had an effect on the perceptual representation of the probes as horizontal and vertical saccades are controlled by different mechanisms, however this does not seem likely to have caused any effect, as previous studies suggest that perceptual changes such as perisaccadic mislocalisation are no different between horizontal and vertical saccades (Honda, 1989; 1991).

The most parsimonious explanation for this observed depression is that it reflects the dual facilitation/inhibition nature of attention, and this explanation can be used to explain the observed depression in the saccade-only condition too. There are numerous studies suggesting that attention may actively inhibit stimuli at non-attended areas, or areas surrounding the attended zone: in visual search tasks, items neighbouring the attended area were found to be suppressed (Bahcall & Kowler, 1999; Caputo & Guerra, 1998), and attention has also displayed centre-surround facilitation/inhibition properties in both psychophysical studies (Cutzu & Tsotsos, 2003) and neurophysiological studies (Hopf et al., 2006; Kim & Verghese, 2012; Schall et al., 2004). Additionally, in sequential movement studies, non-relevant upcoming movement locations were found to be suppressed compared to locations where future movements were to be directed (Baldauf & Deubel, 2009; Baldauf, Wolf, & Deubel, 2006; Doré-Mazars, Pouget, & Beauvillain, 2004). Indeed, it seems that attentional facilitation is not necessarily uniformly distributed across the visual field – Koenig-Robert & VanRullen (2011) saw that while mapping covert attention across the visual field, there were many areas of facilitation, but equally there was a large distribution of inhibited areas patch-worked throughout these facilitated areas.

In terms of the current study, it could be that when planning the reach and saccade to the target, locations 1 and 3 become inhibited due to its proximity to the target. It is unclear why this may happen only at these locations, during this one condition, but it could be due to the behavioural irrelevance of the location in comparison to the more important movement target: when conducting a movement toward the target in a direction in line with the target, it may be that the probe at 8 degrees was suppressed in order to enhance facilitation at the 10 degree target.

6.5.5 CONCLUSION

This study has shown that the spatiotemporal profile of attention is different across different movement combinations. It additionally demonstrates that the position of a location relative to movement direction can affect the temporal profile of attention at that location, and this changes between eye and hand movements. The results suggest that peak attentional guidance is required at different points in the planning and execution of a movement depending on the type of movement being enacted. These findings indicate that while enacting a movement elicits an attentional shift to an upcoming movement location, the spread of this attentional window is not symmetrical, and making different types of movements in different directions changes when and where attention is allocated.

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7. DISCUSSION

7.1 OVERVIEW

The experimental work in this thesis comprised three studies: the first examined the spatiotemporal profile of attention during a hand movement alone, the second examined the spatiotemporal profile of attention during a saccade and saccade plus concurrent reach, and the third study aimed to determine whether the profile of attention was different at locations in line with or orthogonal to movement direction. The main results of this thesis can be easily categorised into three main findings: the spatiotemporal profile of attention differs when a saccade is being conducted with or without a reach, to when a reach alone is being conducted; the location of a target relative to the direction of movement affects the way in which attention is allocated; and this attentional allocation varies depending on the type of movement being enacted.

7.2 TEMPORAL PROFILE OF ATTENTION DIFFERS WITH AND WITHOUT SACCADE

One of the major aims of this thesis was to explore how the spatiotemporal profile of attention differs when saccades and reaches are being made either concurrently or on their own to the same target. In general, it was seen that the profile of attention was similar when a saccade was being made with or without a reach, and this differed markedly from when a reach alone was being conducted. There are a number of possible explanations for why this pre-movement attention seems to be saccade-driven.

7.2.1 WHY MIGHT ATTENTION DEGRADE DURING A REACH WHEN THERE IS NO ACCOMPANYING SACCADE?

Both studies one and three showed a similar trend of attention decaying throughout the duration of a reach when no concurrent saccade was being made. This pattern is in direct contrast to previous studies examining the profile of attention during reach and saccade planning (Jonikaitis et al., 2013; Rolfs et al., 2013; Rolfs & Carrasco, 2012; White et al., 2013), and to the results of saccade-plus-reach tasks in the analogous paradigms of experiments 2 and 3. This pattern suggests that attention is allocated differently when an eye movement is being planned, in comparison to when a reach alone is being planned.

There are two main factors to be considered here: the initial stages of reach planning when there is no preceding saccade, and the online control of the reach as it is being enacted. The pattern of results shows that attentional facilitation is quite high at the target location before reach onset, suggesting that enhanced visual information at the target location is crucial to the planning stages of the reach. It could be the case that during the reach, the online control process does not require this attentional resource to be allocated to the target, hence the observed drop in attention. Indeed, studies have suggested that attentional models such as VAM (Schneider, 1995 see section 1.4.1) may apply to the planning stages of a reach, but may not be applicable to the online control of the reach actually being enacted. Evidence shows that dual-task interference costs have been recorded in the planning stages of the reach, but not during the reach itself (G. Liu, Chua, & Enns, 2007a), suggesting pre-reach attention is most important in the reach planning stage. Additionally, research investigating the online control of reaches has shown that the visual information needed to plan an accurate reach is most important in the initial stages of a reach (Ma-Wyatt & McKee, 2007), hence the pattern showing greater attentional performance at the start of the reach could be the result of this need for higher acuity visual information in these early stages of the reach. Once the reach is under way, the need for attentional guidance and higher acuity visual information is less, hence the decay throughout the time-course of the reach. As evidenced by the results in Chapter 2, the general spatial extent of the pre-reach attentional shift is fairly broad, and this general facilitation was seen even at the most eccentric locations from the reach target. This broad facilitation is in line with sequential movement studies that showed that when a reach was being conducted, the spread of attention across the visual field was broader than in tasks where sequences of saccades alone were being made (Baldauf et al., 2006; Gersch et al., 2004; 2009; Hesse & Deubel, 2010). This suggests that pre-movement attentional mechanisms may be somewhat flexible, depending on the task being carried out, and that tasks that require sequential planning, or multiple target selection might elicit a broader shift of attention to accommodate these demands. These results are in line with the suggestion that planning hand movements may require a broader attentional allocation than just planning saccades. Even though paradigms differ markedly between these sequential movement studies, there is still a consistent observable patterns than when a reach is involved, attention is allocated in a broader manner (Baldauf et al., 2006; Hesse & Deubel, 2010; Baldauf & Deubel, 2009) than in paradigms where saccades alone were being made (Gersch et al., 2004; 2009). This could be due to the greater motor requirements of making a hand compared to an eye movement, and it may also relate to the greater risk of making an inaccurate hand movement compared to a saccade: if a saccade does not reach a target with accuracy, a secondary corrective saccade can easily be made. If a hand misses a reach target it could result in harm to the hand, or other people, and in simple evolutionary terms, it can be argued that guiding a hand accurately to a target may require, and necessitate, a higher level of attentional control.

From a functional point of view though, most hand movements humans make in daily life are accompanied by saccades, as this visual information allows for more accurate hand movements. It is more uncommon for hand movements to be made without this saccadic guidance, so it is possible that attention is allocated differently in situations where no eye movement is being made. The pertinent question then, is why the profile of attention differs so much when a saccade is or isn't being made, and why the profile of a combined saccade and reach reflects that of a saccade alone, rather than a reach alone.

7.2.2 SACCADES DRIVE THE ATTENTIONAL PROFILE DURING CONCURRENT SACCADE AND REACHING TASKS

Comparing the pattern of attention when there is either a saccade alone or a saccade-plus-reach being planned (in both experiments 2 and 3), it can be seen that the general temporal profile is fairly similar across these conditions, and it is in marked contrast to the profile of reach alone, as discussed in the previous section. The first, and obvious option that must be addressed (as is discussed in paper 3), is that when a reach is being made without a concurrent saccade, the profile of attention could just reflect a covert attentional shift, and indeed Chapter 2 shows that the profile of attention for reach alone and an analogous covert attention task is not too dissimilar. This could suggest that the reach itself does not carry any attentional weighting, so the attentional shift seen for concurrent movement tasks is entirely due to the influence of saccade planning. This explanation however seems unlikely, as Chapter 4 shows a number of differences in the timecourse of attention between different movement effectors, suggesting different attentional requirements for different movement combinations.

The most parsimonious explanation would be to suggest that when conducting concurrent movements to the same target, planning a saccade may carry more attentional weighting than reach planning. Evidence supports this notion that saccades may be more highly attentionally weighted: Khan et al. (2011) found that attentional allocation always shifted with the eye, even when task demands favoured a different reach movement target. On a superficial level, the fact that attention may “go with the eye” may not be that surprising – as previously mentioned, hand movements are generally accompanied by saccades, and this preliminary eye movement is able to capture higher acuity visual information needed to plan and guide a subsequent hand movement. It seems logical then that pre-movement attentional guidance would occur before this first saccade, and the temporal profile of attention when a saccade is being made would thus reflect the pre-saccadic attentional shift.

In terms of the actual planning process of these movements, this phenomena can potentially be related back to the suggestion that hand and attention all form a complex neural circuit in areas such as the PPC (Crawford et al., 2011). As discussed in detail in section 1.4.10, there is evidence that motor plans may be formed in gaze-centric coordinates (Batista et al., 1999; Medendorp et al., 2003; Snyder, 2000) – this early and ongoing guidance system for both eye and hand is calculated relative to the eye, so it is logical that pre-movement attention would also be primarily linked to saccade planning, and the profile of attention would reflect this. There is evidence to suggest that reach and saccade planning are closely linked via neural networks in the PPC, with evidence showing shared mechanisms for both target selection and updating (Crawford et al., 2011), however it is unclear whether this coupling occurs early or late in the visuomotor pathway, as there is diverging evidence on whether this coupling occurs in the PRR, an early processing region classically associated with visuomotor planning (Yttri et al., 2014).

Further research on the temporal evolution of visuomotor control has also suggested that this coupling of eye and hand movements only occurs at a later stage (. Franklin, Reichenbach, Franklin, & Diedrichsen, 2016). The similarities in the profile of attention when a saccade is being planned with or without a reach may reflect this early coupling in the planning stages of the movements. Additional evidence however also suggests that saccades and reaches can be dissociated by inactivation of the LIP, a region classically associated with attention (Yttri et al, 2013). This suggests that attentional resources for directing saccades might be separate from those directing reaches, and attention for the different movements may be mediated in different regions (for example the PRR for reaches). If this hypothesis is correct, the differences in the neural origins of pre-movement attention could reflect the differences in the timeline of attention when a saccade is being planned with a reach compared to a reach alone, and could also suggest that the pre-movement attentional resources for these movements may be dissociable at the planning stages of the movements.

An interesting further study relating to the issue of temporal differences between movements would be to use ERP to more accurately decode the pre-movement attentional shift for different types of movements, to determine if this similarity in timing between saccade and reach, and the difference in timing compared to a reach alone, can be seen in early, pre-movement neural signals. A technique such as multi-variate pattern analysis (MVPA) can be used as a means of determining how mental representations unfold over time, and specifically, it is able to decode the point in time at which a certain piece of information is explicitly coded in brain activity (King & Dehaene, 2014). In this case, MVPA could be used to decode the point in time before at which the different movement effectors elicit a pre-movement attentional response. Comparing the time-course and magnitude of this response could provide an insight into whether these early neural signatures of pre-movement attention reflect the psychophysical similarities/differences between reaches and saccades, and thus would provide further insight into the potential coupling of attentional resources for movement planning.

7.3 ATTENTIONAL PROFILE CHANGES RELATIVE TO MOVEMENT DIRECTION

The effect of reach direction on the spatiotemporal profile of attention is a question that has not yet been explored before now. The results of experiment 1 suggested that the profile of attention during a reach alone may be different at locations orthogonal to the reach direction to the locations in line with the reach direction – specifically, in Chapter 2, attention did not degrade to such a large extent at the orthogonal locations as it did in the parallel locations. This interesting result motivated the experimental paradigm in Chapter 4, to determine whether the location of a target relative to the direction of movement has any effect on how attention is allocated to that location.

Chapter 4 again showed an interesting distinction in attentional performance between locations in line with, or orthogonal to the movement direction, and this depended on the type of movement, or movement combination, being enacted. This suggests an asymmetric distribution of attention, depending on the direction of a movement. As discussed in Chapter 6, there are a number of reasons why these results may have occurred, and one important issue to note is that the directionality effect being tested in this experiment was dependent on the location of a perceptual probe relative to the direction of the movement, and not on the actual physical direction of the movement itself. With this in mind, confounding factors that may be an issue can (and must) be dismissed. It is unlikely that the difference in the temporal profile of attention when the probe was in line with as opposed to orthogonal to the direction of the saccade/reach was caused by the fact that saccades were made both horizontally and vertically in Chapter 4. Although the planning of vertical and horizontal saccades involves slightly different mechanisms, studies have shown that the perceptual outcome is the same, irrespective of saccade direction. Honda (1991) showed that the time-course of perceptual mislocalisaton and the magnitude of the error observed was no different between horizontal saccades (as measured in Honda, 1989), and vertical saccades (Honda, 1991). This demonstrates that the perceptual change was direction independent, and if indeed the perceptual attributes of motor planning are linked with the target selection process and attentional allocation (as argued in this thesis), the implications can be extrapolated to suggest that making a saccade in a different direction should not cause any difference in the perceptual patterns observed in these attention tasks, and rather it is the relative position of a probe to the movement that produces this asymmetric attentional effect.

This finding is completely novel, hence there is no direct behavioural evidence to draw on for comparison, however studies into perisaccadic mislocalisation have found differences in the direction and magnitude of the mislocalisation, depending on whether a target is in line with or orthogonal to a saccade (Kaiser & Lappe, 2004). This similarity between these phenomena is interesting as it is an accord with suggestions that pre-movement mechanism such as mislocalisation, attention, and motor control may all be linked (Hamker, Zirnsak, & Lappe, 2008a). However, the links between the present results and these other effects remain conjecture for the present, but may provide an interesting psychophysical measure for investigating the relationship and interdependence between these mechanisms.

7.4 ATTENTIONAL INHIBITION

This work has provided insight into the way in which attention is allocated across different types of movements, however there are a number of questions that remain unanswered. The first of these is how the dual process of attentional facilitation and inhibition works. In each of the studies, a particular location, or locations demonstrated inhibited attentional performance compared to the surrounding locations. For example, in Chapter 2, location 5 showed this inhibition and for paper 2 the analogous location 3 showed this inhibition. These locations were beyond the reach/saccade target, so it was argued that this location could have been marked as behaviourally irrelevant, hence less attention was directed to that location (see section 2.5.1). However, Chapter 4 demonstrated a different pattern of inhibition, but only across certain movement modalities: inhibited performance was seen at the locations horizontally in line with the direction of reach when a reach and saccade was being made, but not when a reach-only was being made, and only at one location when it was a saccade-only being made (see Figure 6.3). These studies together strongly suggest that preparing a movement may cause attentional inhibition as well as facilitation, however it is not clear why some locations are inhibited while others aren't, and particularly in the case of Chapter 4, why inhibition was only observed with certain movements. One explanation for this disparity in results is that Chapters 3 and 4 utilised slightly different paradigms – while the timings and stimuli remained consistent, the experimental question in Chapter 4 required a reach to be made from the centre of the screen rather than the desk (as in Chapter 3). It is possible that this slight directional change may have affected how attention was spread around the target, which demonstrates that planning not only different types of movement, such as saccade and reach, but also planning different types of one movement could require different patterns of attentional guidance. If this is the case, it merely highlights the notion that attention is flexible, and is extremely dependent on the requirements of a particular task.

It would be interesting to conduct further experiments to understand why certain locations are inhibited, and why this changes across different movement types and combinations – this would provide insight into how the mechanisms underlying pre-movement attention may work, and how saccade and reach may use these pre-movement attentional resources. Additionally, it would be interesting to see whether neurophysiological correlates of attention, such as ERP responses, show the same patterns of attentional inhibition during certain movements. As discussed in section 1.3.3, EEG has been used to study patterns of attentional facilitation, and has also shown attentional inhibition in certain circumstances (Kim & Verghese, 2012). Previous EEG work (Baldauf & Deubel, 2009) has demonstrated that when preparing a sequence of movements, locations between impending movement targets show an inhibited ERP response, compared to the actual target locations. Using this methodology should therefore allow an accurate measure of potential attentional inhibition at various points across the visual field, when different movements are being made. This would allow for a neurophysiological correlate of the behavioural results outlined in this thesis. For example, the N1 component has been used as a reliable measure of attention (Vogel & Luck, 2000; Luck 2000), so the amplitude of this component could be used as a comparison of attention across conditions. One would therefore expect to see a weaker ERP response when a perceptual probe appears at an inhibited location than at a location which shows no pattern of inhibition, and if, as Chapter 4 suggests, this changes with motor effector, the magnitude of this response at each location should also change depending on whether a saccade or reach is being prepared.

7.5 PRE-MOVEMENT ATTENTION – CAUSE OR EFFECT?

While the aims of this thesis were not to disambiguate the theoretical tangles surrounding the pre-movement attention shift, it is still important to place the results within the broader theoretical framework that was discussed in section 1.4.1. The results of these studies show that planning and executing a movement does induce a shift of attention to the movement target, and this is in agreeance with both the pre-motor theory of attention, and VAM. What is less clear is whether this shift was necessarily caused by the movement planning (pre-motor theory), or whether it is merely a separate resource that has been utilised for the purposes of movement guidance (VAM). To reiterate, it was not the aim of these experiments to directly test either of these assumptions, but the results can be discussed in this context. An interesting starting place is to examine the pattern of results seen in Chapter 2, where a covert attention task, analogous to the reaching task, was conducted to compare the timeline of attention with and without a movement. The profile of covert attention seen in this condition was not remarkably different from that of the reaching task (although this was variable between probe locations, see Figure 2.8), and, as discussed in section 2.5.3, this could suggest a shared attentional mechanism for reaching and covert attention. If this is the case, it would support the pre-motor theory's suppositions that attention for action and attention for perception are inextricably linked, and could suggest that the covert attentional facilitation observed is merely a planned but uninitiated movement that has caused a preparatory attentional shift. Additionally, these results could arguably support a VAM view of the world, with the similarity in performance being attributed to the reach planning systems utilising the covert attention mechanisms for the purposes of reach guidance, hence the profile of pre-reach attention being reflective of the covert attentional task. Of course another option may be that, as discussed in section 7.3.3, as the reach task in this study was conducted without a concurrent eye movement, the observed profile could have been due to covert attention alone, or the profile of attention driven by reach planning alone is just coincidentally similar to that of covert attention. The most likely explanation however is that there is some overlap between covert and movement planning attentional systems, however it is unclear whether the reach is the cause of this attentional facilitation, or if the reach-planning systems are merely hitching a ride on the covert attentional train.

7.6 ATTENTIONAL SELECTION AND THE PRIORITY MAP

The results of this thesis can be extended to a broader discussion of how people integrate visual information into the formation of a motor plan, and how this has an affect on where in the general environment attention will be allocated. As mentioned in section 1.6, it has been suggested that in order to determine where attention is allocated, and where an eye or hand movement is inevitably directed, a behavioural and neural priority map is formed. The spatiotemporal profile of attention may be informative in determining how a priority map is formed, how information is integrated into this priority map, and how the planning of different movements may affect how a location is selected for attentional priority. The changing spatiotemporal profile of attention during the planning and execution of movements could represent the changing priority of locations as they become relevant for the movement planning and control process. Looking at where attention is allocated when a movement is being planned is also reflective of which parts of a scene are behaviourally and attentionally relevant for movement planning.

One methodology that could be used to explore the issues of attentional priority in movement planning would be to investigate the temporal aspects of attention during sequences of movements. As discussed throughout this thesis, the spatial spread of attention during sequential tasks has been quite comprehensively studied (Baldauf et al., 2006; Baldauf & Deubel, 2009; Gersch et al., 2004; 2009; Hesse & Deubel, 2010), however, more fine-scale temporal aspects of this shift are still unclear. Spatial mapping of impending targets in a sequence indicates that a parallel selection strategy may be used, but it would be interesting to map when exactly attention shifts to each upcoming location during movement preparation. For example, if movements have to be prepared to a number of upcoming locations, the temporal profile of attention during this movement preparation can be measured at each location. This would give an insight into the time-point at which attention shifts to each location: if locations are selected in temporal parallel it suggests equal priority is being given to each upcoming movement. However, if there is a temporal order to the attentional selection, for example if the temporal profile indicates that attention shifts to targets earlier in the sequence than later ones, it would suggest that priority is given to earlier targets in a sequence than later ones. Looking at this spatiotemporal shift in an active task requiring multiple movements would provide a more accurate representation of how attentional priority may be allocated to locations during movement planning.

The results of the experiments in this thesis also indicate that the spatiotemporal profile of pre-movement attention is flexible, and very much depends on the type of movement being enacted. It also seems that changing the task demands of the attentional task may change the way in which attention is allocated. For example, Handy, Kingstone and Mangun (1995) found that the spread of attentional facilitation was smaller when the perceptual targets were less salient. This suggests that as task demands become more difficult, the spread of attention is narrower, and shows that factors such as salience, which are inherently incorporated into the idea of the formation of a priority map, may have a direct effect on the spatial profile of attention.

An interesting question which would follow from this thesis, and which extends on the idea of movement planning forming an attentional priority map, is the way in which attention might be allocated during a more dynamic reaching task. The studies in this thesis all used a static movement target, hence the profile of attention reflects the planning and control processes for a single movement. While the role of attention in sequential movements has been studied (Baldauf, 2011; Baldauf & Deubel, 2009), it is unclear how attention may act if the location of the target itself was less certain. Research has shown that online control is important in making an accurate reach, and when the target is visible throughout the duration of the reach, accuracy is much better than if vision is occluded at various points during the reach (Ma-Wyatt & McKee, 2007). The results in both studies 1 and 3 of this thesis show that during reaching movements alone, vision degrades over the time-course of the reach, and this may reflect the fact that the target is visible throughout the entirety of the reach, so the visual information used to make the initial motor plan for the movement will not change. If however these visual conditions changed and the reach target disappeared halfway through the reach, it may be the case that more attentional guidance is needed to accurately guide the hand to its endpoint. It is possible that the profile of attention would remain more stable then, rather than diminishing, as has been shown to be the case when reaching to a stable, visible target.

8. OVERALL CONCLUSION

Chapter 1 explored issues and evidence surrounding pre-movement attention by exploring both psychophysical and neurophysiological evidence, to outline both the behavioural outcomes of attention, and the neural mechanisms that may underpin this phenomenon. Chapter 2 mapped the spatiotemporal profile of attention relative to a reach alone. These results showed that conducting a reach necessitates a shift of attention that is broader and more sustained than the attentional shift that has been seen to accompany saccades or combined saccade and hand movements, which is a pattern of pre-movement attention that has not been previously shown in the literature. As discussed earlier, this pattern has implications for determining how reaches may be planned, and how attention may play a role earlier in the movement planning process when reaches are being conducted alone than when saccades are being conducted. Chapter 3 extended the experimental conditions in experiment one, and investigated the spatiotemporal profile of attention relative to a saccade, and a saccade-plus-reach. These results showed that when a reach and saccade were being planned, attention on a similar timescale to when a saccade alone was being conducted. These results again have interesting implications for suggesting how attentional guidance may be driven by the saccade when concurrent movements are being made. Chapter 4 explored how the location of an attentional target relative to the direction of movement may have an effect on how attention is allocated at that location. The results of this experiment provided completely novel evidence that the attentional shift may not be symmetrical, and the spread of attention at a probed target location is dependent on the location of the target relative to movement direction, and also the specific type of movement being enacted. This study also provided evidence that different types of movements require attentional guidance at different points during the movement planning and execution process.

Taken together, these experiments provide a comprehensive overview of how pre-movement attention shifts when different movements are being made, and explores the temporal and spatial aspects of this shift. These results provide insight into not only the way in which attention may play a role in movement planning, but looking at the timeline of attention during different movements allows for further insight into how eye and hand planning mechanisms may be coupled, and where this coupling takes place in the scheme of visuomotor planning. Ultimately however, these results demonstrate two things: that the timing of the pre-movement attentional shift differs depending on the type of movement being enacted, and that different movements require attentional guidance at different points during the reach. There are still questions to be resolved surrounding the mechanisms underpinning attention, eye and hand movements, and where the coupling of movements and attention takes place, and these results have added a piece of the puzzle comprising these complex interactions. While we aim to resolve these problems however, attention keeps moving on its never-ending journey through the brain, through time, and through space.

9. REFERENCES

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