

A JOURNEY THROUGH TIME AND
SPACE: THE SPATIOTEMPORAL
PROFILE OF ATTENTION RELATIVE
TO SACCADE AND REACH

Emma Elizabeth Marshall Stewart

School of Psychology

University of Adelaide

2016



THE UNIVERSITY
of ADELAIDE

Thesis submitted for the degree of Doctor of Philosophy

TABLE OF CONTENTS

Table of Contents	3
Abstract	9
Declaration by author.....	11
Acknowledgements	13
List of figures.....	15
List of tables	17
Abbreviations (in order of appearance)	19
Summary of thesis.....	21
Introduction	25
1.1 Interacting with the environment: visually guided action	29
1.1.1 Vision is important for action	29
1.2 The problem of finding things in the environment – from salience to priority maps	32
1.2.1 Salience.....	32
1.2.2 Computing Salience	33
1.2.3 How does salience affect behaviour?	35
1.2.4 Top down vs Bottom up.....	35
1.2.5 The priority map	37
1.3 Visual Attention	42
1.3.1 Attention elicits perceptual benefits	42
1.3.2 Attention shifts – the profile of covert attention	47
1.3.3 The Spatial Properties of Attention – Facilitation and Inhibition	51
1.4 Attention and action	55
1.4.1 Current theories of pre-movement attention	55
1.4.2 Pre-movement attention shift	58
1.4.3 Temporal dynamics - saccades	61
1.4.4 Temporal dynamics - reaches	65
1.4.5 Attention during sequences of movements	67

1.4.6 Attention, Eye and Hand – Shared or Different Mechanisms?	70
1.4.7 Evidence for shared resources.....	70
1.4.8 Evidence for separate resources	72
1.4.9 Neurophysiological correlates of pre-movement attention	74
1.4.10 Neural circuits - further evidence from neurophysiology.....	76
1.5.4 Problems with current evidence.....	80
1.6 Attention, movements and the priority map – putting it all together	83
1.7 Summary	87
1.7.1 Aims of this thesis.....	87
2. Paper 1 – The spatiotemporal characteristics of the attentional shift relative to a reach	89
2.1 Abstract:.....	93
2.2 Introduction.....	95
2.2.1 Attention and movement planning	95
2.2.2 The importance of vision in planning a reach.....	96
2.3 Methods	102
2.3.1 Participants.....	102
2.3.2 Equipment	102
2.3.3 Experimental design	102
2.3.4 Contrast threshold task	103
2.3.5 Pointing task	104
2.3.6 Perceptual task	107
2.4 Results	109
2.4.1 Preliminary analyses	109
2.4.2 Perceptual performance – pointing task	110
2.4.3 Maximum and minimum performance	112
2.4.3 Reaching performance vs perceptual performance	113
2.4.4 Heatmap of spatiotemporal profile of performance	115
2.4.5 Perceptual performance without pointing	117
2.5 Discussion	119
2.5.1 Attentional facilitation at different locations	119
2.5.2 The trade-off between perceptual performance and reach performance.....	122
2.5.3 Performance on the reaching task versus the perceptual only task.....	122

2.5.4 Mechanisms underlying the attention shift relative to a movement	123
2.5.5 Priority maps.....	124
2.5.6 Attentional oscillations and the attentional blink.	125
2.6 Conclusion	126
2.6.1 Acknowledgements	126
2.7 References	127
3. Preface to paper 2	133
4. Paper 2 - Dissociating the premotor attentional shift for saccades and reaches.	
.....	135
4.1 Abstract	137
4.2 Introduction.....	139
4.2.1 Pre-saccadic attentional shifts.....	140
4.2.2 Attentional shifts preceding a hand movement	142
4.2.3 The current study	144
4.3 Method.....	144
4.3.1 Participants	144
4.3.2 Equipment	144
4.3.3 Experimental design	145
4.3.4 Contrast threshold task	146
4.3.5 Saccade task	146
4.3.6 Saccade-plus-reach task	149
4.4 Results	149
4.4.1 Data exclusions	149
4.4.2 Perceptual performance relative to SOA.....	153
4.4.3 Perceptual performance relative to movement onset	156
4.4.4 Heatmap of perceptual performance	160
4.5 Discussion	161
4.5.1 The temporal profile of attention for reach and saccade.....	161
4.5.2 The temporal profile of attention for reach alone differs when compared with reach plus saccade.....	163
4.5.3 The spatial profile of attention at different locations	164
4.5.4 Eye and hand – shared or separate mechanisms?	166

4.5.5 How might these mechanisms be organized?	167
4.6 Conclusion	168
4.6.1 Acknowledgements	169
4.7 References	170
4.8 Comparison of Chapter 2 and Chapter 4.....	177
5. Preface to paper 3	179
6. Paper 3 - The profile of attention differs at locations orthogonal to reach direction.....	181
6.1 Abstract.....	183
6.2 Introduction.....	185
6.2.1 Attention and the pre-movement attentional shift.....	185
6.2.2 Attention and movement direction – a link to perisaccadic mislocalisation?	188
6.2.3 This study.....	190
6.3 Method.....	190
6.3.1 Experimental design	190
6.3.2 Participants	191
6.3.3 Equipment	191
6.3.4 Contrast threshold task	192
6.3.5 Reach alone task.....	193
6.3.6 Reach and saccade task	195
6.3.7 Saccade-only task	195
6.4 Results	196
6.4.1 Data exclusions	196
6.4.2 Movement dynamics	196
6.4.4 Performance relative to SOA	199
6.4.5 Performance relative to movement onset	206
6.4.6 Heatmap of perceptual performance.....	207
6.5 Discussion	210
6.5.1 Timecourse of attention is dependent on movement effector	210
6.5.2 Location relative to movement direction affects attentional performance.....	212
6.5.4 Suppressed performance – an argument for attentional inhibition.....	215
6.5.5 Conclusion	218

6.6 References	219
7. Discussion	227
7.1 Overview	227
7.2 Temporal Profile of attention differs with and without saccade	227
7.2.1 Why might attention degrade during a reach when there is no accompanying saccade?	227
7.2.2 Saccades drive the attentional profile during concurrent saccade and reaching tasks.....	230
7.3 Attentional profile changes relative to movement direction	232
7.4 Attentional inhibition	234
7.5 Pre-movement attention – cause or effect?	236
7.6 Attentional selection and the priority map.....	237
8. Overall conclusion	241
9. References.....	243

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.

DECLARATION BY AUTHOR

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968.

The author acknowledges that copyright of published works contained within this thesis resides with the copyright holder(s) of those works.

I also give permission for the digital version of my thesis to be made available on the web, via the University's digital research repository, the Library Search and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

Emma E.M. Stewart

ACKNOWLEDGEMENTS

First and foremost, I would like to acknowledge and thank my supervisor, Associate Professor Anna Ma-Wyatt, for all of her guidance, support, and birthday cakes over the course of my PhD. I'd also like to thank Associate Professor Nick Burns for providing support and assistance, and Dr Preeti Verghese for many valuable discussions.

I'd like to thank my fellow PhD friends and labmates, both past and present: Jess, Dinis, Adam, Heidi, Lauren, Drew, Wai Keen, Steve, Simon, Steph and Adella. I'd also like to thank my other friends for their continuing support, and a huge thankyou to those amongst them who also gave their time to participate in my experiments for no reward other than my everlasting gratitude and many cups of tea. And a special thankyou to Gordon for being so patient and supportive, and for always knowing when any PhD problem could be solved with a glass of wine and some cheese.

Finally, I'd like to thank my parents for all of their patience and support throughout not only my PhD but my past 12 years at university which have culminated at this point. Last, and least only in stature, I'd like to acknowledge my cat, Jid, for steadfastly sitting beside me through many late nights of writing and coding.

LIST OF FIGURES

Figure 1.1 - The salience map as conceived by Itti & Koch (2001).	34
Figure 1.2 – Model of how an attentional guidance map may be calculated. From Navalpakkam & Itti (2002).....	39
Figure 1.3 – The ‘schema system’ uses task information and action scripts to determine where the eyes and hands should be next directed (Land, 2009)....	41
Figure 1.4 – Two possible mechanisms of how attention may alter stimulus appearance (from Carrasco, 2011).....	43
Figure 1.5 – Receptive field map of macaque MT neuron (from Anton-Erxleben et al., 2009)	46
Figure 1.6 – The spatiotemporal properties of the covert attentional shift, from (Koenig-Robert & VanRullen, 2011)	50
Figure 1.7 – Timeline of pre-saccadic attention from Deubel (2008).....	63
Figure 1.8 – Pre-saccadic attentional shift as measured by White et al. (2013).	64
Figure 1.9 – The timeline of pre-movement attention from Jonikaitis & Deubel (2011).....	66
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).....	77
Figure 1.11 – Basic schematic of how different maps may be organised in the brain (from Klink, Jentgens, & Lorteije, 2014).	85
Figure 2.1 – Pointing task events.	104
Figure 2.2 – Possible locations that the perceptual probe could appear.....	105
Figure 2.3 – Perceptual task events.	108
Figure 2.4 – Perceptual performance per bin per location.	111
Figure 2.5 – Maximum and minimum performance per location, across all participants.	113
Figure 2.6 – Perceptual performance vs reaching performance.....	114
Figure 2.7 – Heatmap showing perceptual performance across all locations, per time bin.....	116

Figure 2.8 – Perceptual only performance for all participants.....	118
Figure 4.1 – Events in a saccade and saccade-plus-reach task trial.	148
Figure 4.2 – Stacked density plots of saccade latencies for each participant.	152
Figure 4.3 – Perceptual performance relative to cue onset (SOA) for the saccade-only task and the saccade-plus-reach task.....	153
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.	154
Figure 4.5 – A) Perceptual performance relative to saccade and B) performance relative to reach onset..	156
Figure 4.6 – Probit curves fitted to the average performance for each location.....	159
Figure 4.7 – Heatmap of performance change over time relative to SOA.	161
Figure 4.8 – Comparison of reach-only data from Chapter 2, and saccade-plus-reach data from Chapter 3	177
Figure 6.1 – A) The potential probe locations. B) The timeline of events in a trial ..	194
Figure 6.2 – Movement dynamics for each participant represented as stacked density plots.....	199
Figure 6.3 – Performance relative to SOA for each probe location	200
Figure 6.4 – Maximum and minimum performance for each movement condition and location.....	202
Figure 6.5 – Performance relative to SOA, grouped by experimental condition	204
Figure 6.6 – Performance relative to movement onset for the reach-only, saccade-only and saccade-plus-reach conditions.	206
Figure 6.7 – heatmap of performance for each time bin (relative to SOA), for each location.....	209

LIST OF TABLES

Table 2.1 – Reach dynamics for each participant.....	109
Table 4.1 – Movement dynamics for all participants.....	151
Table 6.1 – Movement dynamics and exclusion rates for individual participants for each condition.....	198

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.