The cost of parallel processing in the human visual system

Reuben Rideaux

A thesis submitted for the degree of Doctorate of Philosophy (PhD)
The Australian National University

January 2016

Research School of Psychology
College of Medicine, Biology and Environment
The Australian National University
Canberra ACT, Australia

© Copyright by Reuben Rideaux 2016
All Rights Reserved
Declaration

This thesis is submitted to The Australian National University in fulfilment of the Doctorate of Philosophy (PhD) degree. The work presented in this thesis is, to the best of my knowledge, original except as acknowledged in the text. I hereby declare that I have not submitted this material, either in full or in part, for another degree at this or any other institution. This thesis includes two original papers that have been published in peer review journals and two that are under review for publication. The ideas, development and writing of these papers and the thesis were the principal responsibility of myself, the candidate. The inclusion of co-authors reflects the input of my supervisors, Dr Mark Edwards, Dr Stephanie Goodhew, Dr Jason Bell, and Dr Deborah Apthorp who provided advice on the design, statistical analysis and assisted with proofreading. In the case of publishable papers my contribution involved the following:

<table>
<thead>
<tr>
<th>Thesis Chapter</th>
<th>Publication Title</th>
<th>Publication Status</th>
<th>Nature and extent of candidate’s contribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>Information extraction during simultaneous motion processing</td>
<td>Published <em>Vision Research</em>, DOI: 10.1016/j.visres.2013.11.007</td>
<td>Conceptual development, design, participant recruitment, administration, data analyses and principal author</td>
</tr>
<tr>
<td>5</td>
<td>Evidence for parallel consolidation of motion direction and orientation into visual short-term memory</td>
<td>Published <em>Journal of Vision</em>, DOI: 10.1167/15.2.17</td>
<td>Conceptual development, design, participant recruitment, administration, data analyses and principal author</td>
</tr>
<tr>
<td>6</td>
<td>The cost of parallel consolidation of orientation and motion direction into visual short-term memory</td>
<td>Published <em>Journal of Vision</em>, DOI: 10.1167/16.6.1</td>
<td>Conceptual development, design, participant recruitment, administration, data analyses and principal author</td>
</tr>
<tr>
<td>7</td>
<td>A biased competition account of parallel consolidation into visual short-term memory</td>
<td>In preparation</td>
<td>Conceptual development, design, participant recruitment, administration, data analyses and principal author</td>
</tr>
</tbody>
</table>

____________________  ____________________ ____________________
Reuben Rideaux  Mark Edwards  Date
Acknowledgements

I would like to acknowledge and thank my supervisor and friend Dr Mark Edwards for all his help and support over the previous three years. He played an instrumental role in sparking my interest in vision science, and when times were tough he was always there to remind me of the things I love about research. Some of the best memories I have as postgraduate were our discussions in his office where together we would wrestle with complex problems and design experiments to test our ideas.

I would also like to thank all of my secondary supervisors; Stephanie Goodhew, Deborah Apthorp, and Jason Bell, for all their additional support, feedback, guidance, and friendship, over the last three years. Thank you Steph for helping me with all things cognitive and thank you Deb for your MATLAB support. Thank you Jason for always putting things into perspective.

Thank you to all those friends who endured hours and hours of testing around threshold, a truly generous gesture I won’t forget.

Thank you to my family for their love and support.

Finally, thank you to Claire for her love and support. It’s been wonderful having a partner who understands my research and is always available with emotional support and encouragement when needed.
Abstract

Our environment is visually rich, containing a multitude of objects that can be defined by many different features, e.g. shape, colour, and motion. To navigate and interact with the environment, we must process this information efficiently. The human visual system can process information either serially or in parallel. While there is a clear timesaving benefit of parallel processing, its cost is less well understood. Consequently, the aim of this thesis is to address three key theoretical questions underlying the cost of parallel processing.

The first aim was to determine how the capacity of parallel processing varies as a function of the detail of information extraction. Previous research has demonstrated that brief presentations of five and six motion signals can be differentiated; this suggests that up to five signals can be simultaneously processed. However, it is unclear how much information is being extracted, i.e. whether observers are extracting direction information from all five signals. To examine this we presented observers with multiple moving objects and evaluated their parallel processing capacity as a function of the information required to perform the task. We found that the resolution of parallel motion processing varies as a function of the information that is extracted; specifically, as information extraction becomes more detailed, the capacity to process multiple signals is reduced.

The second aim was to investigate whether there is a cost to the fidelity of information that is processed in parallel. Previous research suggests that there may not be a cost associated with parallel consolidation of information from sensory to visual short-term memory (VSTM). Here we examined this by first determining that motion direction, and possibly orientation, can be consolidated in parallel, then explicitly evaluating the cost to the fidelity of information consolidated in parallel, compared to serially. We found that there is a twofold cost associated with parallel consolidation: a reduction in resolution of encoded items due to spreading of spatial attention, and an increase in the likelihood of consolidation failure due to interference between items.

The third aim was to examine whether the cost associated with parallel processing can ultimately explain its capacity. We extended our previous findings regarding the cost associated with parallel consolidation to examine whether the capacity of parallel consolidation results from biased competition, the same mechanism proposed to account for spatial attention and VSTM storage, as evidenced from the interference between items presented simultaneously. This was achieved by demonstrating that parallel consolidation performance is influenced by factors predicted by a biased competition model. Furthermore, we found evidence suggesting that the capacity may be as high as three, with increasingly poorer resolution and higher consolidation failure-rates.

Together, these results demonstrate that a) parallel processing is limited by the complexity of information to be processed, b) there is a twofold cost of processing information in parallel, and c) that increasing the amount of information processed in parallel also increases this cost to the fidelity of the information and ultimately leads to the capacity of this process.
Contents

Declaration ........................................................................................................................................ 2

Acknowledgements .................................................................................................................. 4

Abstract ........................................................................................................................................ 6

Contents ......................................................................................................................................... 8

List of Figures .............................................................................................................................. 12

List of Tables .............................................................................................................................. 13

Chapter 1. Overview and aims ................................................................................................. 14
  1.2. Overview of the thesis ...................................................................................................... 17
  1.3. A note regarding the thesis format ................................................................................. 18

Chapter 2. Parallel motion processing .................................................................................... 20
  2.1. Transparent motion ...................................................................................................... 21
  2.2. Form-specific motion .................................................................................................. 23
  2.3. Levels of information extraction ................................................................................ 26

Chapter 3. Visual short-term memory ..................................................................................... 29
  3.1. Visual short-term memory processes .......................................................................... 30
  3.3. Models of parallel consolidation capacity .................................................................. 36
Chapter 4. Information extraction during simultaneous motion processing

4.1. Context statement

4.2. Introduction

4.3. Experiment 1: Number of signals
   4.3.1. Method
   4.3.2. Observers
   4.3.3. Apparatus
   4.3.4. Stimuli and procedure
   4.3.5. Results and discussion

4.4. Experiment 2: Directions present
   4.4.1. Method
   4.4.2. Observers
   4.4.3. Stimuli and procedure
   4.4.4. Results and discussion

4.5. Experiment 3: Post-cue target location with iconic store inhibition
   4.5.1. Method
   4.5.2. Observers
   4.5.3. Stimuli
   4.5.4. Results and discussion

4.6. General discussion

Chapter 5. Evidence for parallel consolidation motion direction and orientation into visual short-term memory

5.1. Context statement

5.2. Introduction

5.3. Experiment 1: Parallel consolidation of motion directions
   5.3.1. Method
   5.3.2. Observers
   5.3.3. Apparatus
   5.3.4. Stimuli
   5.3.5. Procedure
   5.3.6. Results and discussion

5.4. Experiment 2: Effects of spatial attention and feature interval separation
   5.4.1. Method
   5.4.2. Observers
   5.4.3. Stimuli and procedure
   5.4.4. Results and discussion

5.5. Experiment 3: Parallel consolidation of orientation
   5.5.1. Method
   5.5.2. Observers
5.5.3. *Stimulus and procedure* ................................................................. 89
5.5.4. *Results and discussion* ................................................................. 89
5.6. *General discussion* .............................................................................. 91

Chapter 6. The cost of parallel consolidation of orientation and motion
direction into visual working memory .............................................. 94
6.1. *Context statement* ............................................................................ 94
6.2. *Introduction* ...................................................................................... 94
6.3. Experiment 1: The cost of parallel consolidation .................................... 98
   6.3.1. *Method* ..................................................................................... 98
   6.3.2. *Observers* ................................................................................ 98
   6.3.3. *Apparatus* ................................................................................ 99
   6.3.4. *Stimuli* ................................................................................... 99
   6.3.5. *Procedure* ................................................................................ 101
   6.3.6. *Data analysis* .......................................................... 102
   6.3.7. *Results* .................................................................................... 102
   6.3.8. *Descriptive statistics* ............................................................. 103
   6.3.9. *Model fit* ................................................................................. 104
   6.3.10. *Discussion* ............................................................................. 106
6.4. Experiment 2: Parallel consolidation of orientation and motion direction .... 108
   6.4.1. *Method* .................................................................................... 109
   6.4.2. *Observers* .............................................................................. 109
   6.4.3. *Stimuli and procedure* ............................................................ 109
   6.4.5. *Results* ................................................................................... 110
   6.4.6. *Threshold exposure duration* .................................................... 110
   6.4.7. *Descriptive statistics* ............................................................... 110
   6.4.8. *Model fit* .............................................................................. 111
6.5. *General discussion* ........................................................................... 117

Chapter 7. A bilateral hemifield advantage for parallel consolidation
into visual working memory .......................................................... 120
7.1. *Context statement* ............................................................................ 120
7.2. *Introduction* ...................................................................................... 120
7.3. Experiment 1: A bilateral hemifield advantage for parallel consolidation ...... 125
   7.3.1. *Method* .................................................................................... 125
   7.3.2. *Observers* .............................................................................. 125
   7.3.3. *Apparatus* .............................................................................. 126
   7.3.4. *Stimuli* ................................................................................... 126
   7.3.5. *Procedure* .............................................................................. 128
   7.3.6. *Data analysis* .......................................................... 129
   7.3.7. *Results* ................................................................................... 129
List of Figures

2.1. Examples of the global-motion stimulus.................................................................22
2.2. A diagram the brain depicting the dorsal (green) and ventral (purple) visual processing
streams. .........................................................................................................................24
3.1. An example of a mixed distribution of offsets, i.e. differences between target and response
orientation/direction........................................................................................................35
3.2. Schematic of the consolidation bandwidth limit model...............................................39
4.1. An example of the stimuli used in Experiment 1..........................................................47
4.2. Results for Experiment 1. ..........................................................................................48
4.3. An example stimuli used in Experiment 2.................................................................52
4.4. Results for Experiment 2. .........................................................................................53
4.5. An example of stimuli used in Experiment 3.............................................................60
4.6. Results for the control experiment. ...........................................................................65
5.1. An example of the stimuli used in Experiment 1..........................................................77
5.2. Mean performance across observers in Experiment 1 for each presentation type
(simultaneous & sequential) as a function of the number of items presented. .................80
5.3. Mean performance across observers within the 3 item sequential condition (match trials) of
Experiment 1 as a function of target item presentation order..........................................81
5.4. Examples of the stimuli used in the spatial uncertainty condition of Experiment 2........85
5.5. Mean performance across observers in Experiment 2 for each presentation type
(simultaneous & sequential) as a function of the condition (reduced range & spatial uncertainty).
.........................................................................................................................................86
5.6. An example of an orientation stimulus (left) and mask (right) used in Experiment 3........89
5.7. Mean performance across observers in Experiment 3 for each presentation type
(simultaneous & sequential) as a function of the condition (spatial un/certainty). ...............90
6.1. Examples of the presentation sequence used in Experiment 1.....................................101
6.2. Experiment 1 raw offset data. ....................................................................................104
6.3. Experiment 1 model parameter analysis. ...................................................................106
7.1. An example of the stimuli used in Experiment 1.........................................................128
7.2. Experiment 1 raw offset data. ....................................................................................130
7.3. Experiment 1 model parameter analysis. ...................................................................131
7.4. An example of the stimuli used in Experiment 2.........................................................134
8.1. An example of the relationship between the resolution of items and interference........148
List of Tables

4.1. Observer performance in Experiment 3..................................................60
Chapter 1. Overview and aims

At any given time, there are multiple objects within the visual field, defined by many different types of information, such as colour, orientation, and motion direction. To effectively navigate through and interact with the environment, our visual system must process this information efficiently. One way this is achieved is by processing information in parallel, as opposed to serially. However, while the timesaving benefit of parallel processing is clear, the cost of this process is less well understood.

Often, when investigating parallel processing within a given system, the first aspect that is examined is the capacity, i.e. the maximum number of items that can be processed in parallel. One area in which the capacity of parallel processing has been investigated is motion processing. Based on results from an $n$ vs. $n + 1$ motion signals discrimination task, a limit of three global-motion signals (Greenwood & Edwards, 2006) or five spatially localized common-fate motion signals (Edwards & Rideaux, 2013) has been proposed. However, given the nature of the tasks, it is not clear what information is extracted during this parallel processing; only that observers can discriminate between this number of signals and pure noise. Understanding how these parallel processing limitations relate to information extraction would imbue them with greater meaning and also provide insight into the cost of this process.
Deeper investigation of parallel processing limitations and costs requires consideration of different mechanisms. For example, to perform an \( n \) vs. \( n + 1 \) discrimination task, storage of relatively coarse information is required, such as that the first presentation contained more or fewer signals than the second. However, as the complexity of information required to perform the task increases, e.g. from indicating the number of signals present to indicating the direction of each signal, so too does the amount and complexity of information which must be stored. Thus, while previous research on parallel motion processing considered only the capacity which can be represented in the initial sensory stage of processing, further investigation of the capacity as a function of information complexity must consider the second stage of visual memory, visual short-term memory (VSTM).

VSTM is the first potentially durable representation in which visual information can be stored. Once consolidated/encoded into VSTM, information can be maintained, manipulated, or replaced. Information is initially stored in sensory memory, which is characterized as high capacity memory whose contents decay within a few hundred milliseconds (Sperling, 1960, 1963). Following this, a small proportion of the information stored in sensory memory is transferred to VSTM (Cowan, 2001, 2010), where it either eventually decays or is consolidated into long-term memory. While the capacity of VSTM storage exceeds the capacity found for parallel processing of motion directions, it is not clear whether information that is simultaneously processed in sensory memory is then consolidated into VSTM in parallel.

Initially, research suggested that consolidation of information into VSTM was restricted to serial processing, i.e. only one item could be consolidated at a time (Huang, Treisman, & Pashler, 2007). However, recently, several studies have found evidence indicating that parallel consolidation of colour is possible (Mance, Becker, & Liu, 2012), but that orientation is restricted to serial consolidation. Thus, despite findings from
previous motion studies, given the current state of play in the VSTM literature, it is uncertain whether parallel consolidation of motion direction is possible. Determining whether motion direction can be consolidated in parallel will further elucidate the characteristics of features that govern the capacity to process them in parallel and further our understanding of this core cognitive mechanism.

To this end, the aim of this thesis is to address three fundamental issues in parallel processing. Firstly, how the capacity of parallel motion processing varies as a function of the complexity of the to-be-extracted information. Previous research has indicated a limit of three for some signals and five for others (Edwards & Rideaux, 2013; Greenwood & Edwards, 2006); however, it is unclear what information is being extracted in order to perform the task. Thus, we conducted experiments to determine the resolution of parallel motion processing as a function of information complexity.

Second, we asked whether there is a cost to the fidelity of information that is processed in parallel. Previous research indicates that not all features can be consolidated in parallel (Becker, Miller, & Liu, 2013), and those that can are done so at no cost to the fidelity of the information (Miller, Becker, & Liu, 2014). Thus, we first ran experiments to determine whether motion direction (and orientation) could be consolidated in parallel, then to evaluate the cost of parallel consolidation in terms of loss of resolution and increased frequency of consolidation failure.

Finally, we asked whether the cost associated with parallel processing could ultimately explain its capacity. Previous research suggests that the limit is either two or three (Mance, Becker, & Liu, 2012) and no convincing explanations have been proposed to account for the capacity. Thus, we ran experiments to explicitly determine the size of the capacity, as well as the mechanisms that determine this limit.
1.2. Overview of the thesis

An examination of parallel motion processing first requires an understanding of the stimuli used to investigate this phenomenon, as outlined in Chapter 2. Similarly, an examination of parallel consolidation into VSTM requires an understanding of VSTM, including current models of operation and limitations, as outlined in Chapter 3. Included in these chapters, at the appropriate stages, are the precise experimental aims of this thesis. Experiments addressing the resolution or capacity of parallel motion processing as a function of the complexity of information that is extracted are detailed in Chapter 4.

Having determined that the resolution of parallel processing is reduced as a function of information complexity, we conducted experiments to investigate parallel processing at the next stage of storage, i.e. VSTM. Thus, experiments examining the ability to consolidate motion direction (and orientation) information into VSTM in parallel are described in Chapter 5. Having found evidence that these features can be consolidated in parallel in Chapter 5, with the results suggesting a cost associated with this, Chapter 6 explicitly investigates whether there is a cost associated with parallel consolidation of direction and/or orientation information, i.e. reduced resolution of encoded items and/or increased likelihood of consolidation failure. The results in Chapter 6 show that motion direction (and possibly orientation) can be consolidated in parallel, and that there is a twofold cost associated with parallel consolidation, both reduced resolution of encoded items and increased likelihood of consolidation failure. Furthermore, they indicate a potential mechanism behind the capacity of this process; thus, Chapter 7 investigates the viability of this mechanism as an explanation for the limitation of parallel consolidation in addition to explicitly determining its capacity. A summary of the experiments and final discussion of related issues is then presented in Chapter 8.
1.3. A note regarding the thesis format

Because this thesis is prepared ‘by publication’, each of the empirical chapters represent a paper that is either published or has been submitted for review. The text within these chapters is identical to these papers, though alterations have been made to the numbering system of the experiments, sections, and figures within each chapter to allow consistent reference across the thesis as a whole. A context statement has also been included at the beginning of each chapter to place the experimental work within the greater theoretical aims of the thesis. As the published versions of these chapters are referred to within some chapters, I include their full references below.

Chapter 4, outlining the relationship between the resolution of parallel motion processing and the complexity of to-be-extracted information, is referred to within other chapters as Rideaux and Edwards (2014) and has been published as:


Chapter 5, which details the capacity to consolidate multiple direction and orientation items into VSTM in parallel, is referred to within other chapters as Rideaux, Apthorp, and Edwards (2015) and has been published as:

Chapter 6, containing experiments designed to investigate the cost associated with parallel consolidation of information into VSTM, is referred to within other chapters as Rideaux and Edwards (2016) and has been published as:


Finally, Chapter 7, which describes experiments examining the capacity of parallel consolidation, has also been submitted for publication and is referred to within other chapters as Rideaux and Edwards (*in preparation*). It will appear in print as:

Chapter 2. Parallel motion processing

When two or more moving objects are contained within the visual field, the visual system must engage in multiple motion processing. While much research has been conducted on single motion processing (Burr & Thompson, 2011; Nishida, 2011), occurrences outside the lab where multiple motion processing is employed are frequent, e.g. a busy traffic intersection or while walking along a path alongside a running stream; however, relatively few studies have investigated its underlying mechanisms. Multiple motion processing occurs in at least two stages: an initial parallel stage (parallel motion processing), followed by a serial stage (Edwards & Greenwood, 2005; Mulligan, 1992). Using the above example of a busy traffic intersection, during the initial stage of multiple motion processing a number of the cars can be processed in parallel. Following this, attention would be shifted among the remaining moving cars as they were processed serially.

Determining the degree to which parallel motion processing occurs can prove challenging, as the difference between parallel and rapid serial processing is difficult to evaluate. This is reflected in the debate surrounding multiple object tracking. Studies show that observers can track multiple (~4) objects through space (Pylyshyn & Storm, 1988), and interpretations of this vary between theories offering a parallel processing
account, e.g. the FINST model (Pylyshyn, 1989), and those offering a serial account (d'Avossa, Shulman, Snyder, & Corbetta, 2006; Oksama & Hyönä, 2008). However, one clear example of where parallel processing occurs is during the perception of transparent motion. Transparent motion is defined as multiple velocity fields in the same part of the visual field, and results from partial occlusions of moving objects or overlapping semitransparent surfaces (Qian, Anderson & Adelson, 1994), e.g. a school of fish swimming upstream through moving water. The capacity to perceive both the motion of the fish in one direction and the motion of the water in another direction, in the same spatial region at the same time, is considered an example of parallel motion processing. Unsurprisingly, transparent motion came to be the first stimulus used in the investigation of parallel motion processing (Mulligan, 1992).

2.1. Transparent motion

Transparent motion can be simulated experimentally using several types of stimuli. However, the majority of studies investigating this phenomenon have employed a modified global-motion stimulus (Newsome & Pare, 1988). The original global-motion stimulus consisted of a population of intermingled dots within the same aperture that either belonged to the signal component, moving in a uniform direction, or to the noise component, moving in random directions (see Fig. 2.1A & 2.1B). To investigate transparent motion processing, this stimulus was modified such that multiple signal components defined with either different directions or speeds were present within the same aperture (see Fig 2.1C). With this stimulus, two dot groups defined by distinct velocities give rise to the percept of multiple overlapping surfaces. An important advantage of this stimulus is the ability to manipulate the intensity of each component signal. Here, signal intensity is defined as the proportion of dots moving in one of the
signal directions relative to the proportion of dots moving in other directions, either as noise (i.e. randomly moving dots) or in other signal directions (Snowden & Braddick, 1989; Edwards & Nishida, 1999).

Figure 2.1. Examples of the global-motion stimulus. Unidirectional motion at (A) 100% and (B) 50% signal intensity. In (A) the aperture consists wholly of signal dots moving in a uniform direction whereas in (B) 50% of the dots move in the signal direction while the remaining dots move in random directions. Bidirectional transparent motion is shown in (C) where 50% of the dots move in one signal component direction and the remaining dots move in another component direction.

Using this stimulus, Edwards and Greenwood (2005) demonstrated that no more than two transparent motion signals, defined only by direction, could be simultaneously processed. The authors proposed that this limit is due to elevated signal intensity thresholds. That is, whereas the threshold for detecting unidirectional motion is ~10-15% (Edwards, Badcock, & Smith, 1998), transparent motion requires over 40% signal intensity for each component. This was later confirmed, when they demonstrated that the limit of two could be extended to three by additionally defining the signals by differences in speed and depth (Greenwood & Edwards, 2006a, 2006b). By additionally defining the signals by these characteristics, they engaged speed and disparity tuned global-motion channels with independent pooling (Edwards, Badcock, & Smith, 1998; Hibbard & Bradshaw, 1999; van Boxtel & Erkelens, 2006), i.e. signal dots pooled in one channel did not act as noise for signal dots pooled in another. This allowed them to effectively double the available signal intensity. Furthermore, Greenwood and Edwards (2009) also extended the limit to three by presenting signals within spatially contiguous regions, as
opposed to in one overlapping region, demonstrating that the global-motion system is capable of spatial segmentation.

By additionally defining signals by speed and direction, or presenting them in spatially contiguous regions, the initial issue of elevated signal threshold was able to be overcome. However, given the consistent finding across these studies of a limit of three even when signal intensity was elevated, a higher order limit was proposed.

2.2. Form-specific motion

The visual system can be broadly categorized into two main processing streams: the ventral and dorsal streams (see Figure 2.2). The ventral stream processes information relating to object identity, whereas the dorsal stream processes information such as location, orientation and direction, i.e. the “what & where” streams (Mishkin & Ungerleider, 1993; Ungerleider & Haxby, 1994). The global-motion stimuli used in previous parallel motion processing studies is processed by the standard motion system, and is characteristic of dorsal stream processing. Information, e.g. moving dots, is pooled together within common channels regardless of luminance-polarity or colour (Edwards & Badcock, 1994, 1996; Murray, Sekuler, & Bennett, 2003; Snowden & Edmunds, 1999). In contrast, luminance-polarity and colour information that is processed within the ventral stream, e.g. static form information, is typically pooled independently (Badcock, Clifford, & Khuu, 2005; Wenderoth, 1996; Wilson, Switkes, & De Valois, 2004). These differential pooling characteristics reflect the mechanisms that they facilitate. That is, while optic flow information, i.e. motion resulting from self-movement, is generated by
all objects in the visual field, so that segmenting objects out would be maladaptive, segmentation is crucial during object identification to determine features such as shape.

Figure 2.2. A diagram the brain depicting the dorsal (green) and ventral (purple) visual processing streams. Adapted from illustration "Ventral-dorsal streams" by Selket. Licensed under CC BY-SA 3.0 via Wikimedia Commons - https://commons.wikimedia.org/wiki/File:Ventral-dorsal_streams.svg#/media/File:Ventral-dorsal_streams.svg.

The division between the dorsal and ventral streams become apparent after early visual processing areas V1 and V2. “Where” information, e.g. motion direction & velocity, is projected along occipitoparietal cortical pathway areas V1, V2, V3, middle temporal areas (V5/MT), and medial superior temporal area (MST), whereas “what” information, e.g. colour and shape, is projected along occipitotemporal cortical pathway areas V1, V2, V4, and inferior temporal areas TEO and TE (Maunsell & Newsome, 1987). While “what” and “where” information is primarily processed within dorsal and ventral streams, respectively, there is considerable interaction between these pathways. Examples of interaction between motion (dorsal) and form (ventral) processing include motion streaks (Geisler, 1999), biological motion (Johansson, 1973), and the Gestalt principle of common-fate grouping (Wertheimer, 1923).
In a demonstration of the motion-form interaction which occurs during common-fate grouping, Edwards (2009) showed that when four moving signal dots are locally arranged into particular patterns, e.g. a square, similar selective pooling, such as that observed in the processing of static form information, is observed, i.e. luminance-polarity signals are pooled independently. This was interpreted as signalling the existence of a form-specific motion system, which processes the motion of discrete objects that are segmented from the background. Importantly, this putative system appears to be more sensitive to motion than the standard motion system, as evidenced by lower signal intensity detection thresholds.

Returning to the discussion of parallel motion processing, although a capacity of three was consistently found in previous studies, a common characteristic among these was the use of transparent motion stimuli, processed by the standard global-motion system. However, it is extremely rare to encounter three or more of these kinds of motion signals outside the laboratory, thus it is perhaps unsurprising to find such a limit using transparent motion. In contrast, occurrences of three or more spatially localized motion signals in the environment, likely processed by the form-specific motion system, are relatively common, e.g. cars and pedestrians at busy traffic intersection. Furthermore, while a limit of three was also found for spatially segmented global-motion signals (Greenwood & Edwards, 2009), this may have been due to insufficient signal intensity. That is, it is unclear how efficiently global-motion signals were segmented, and thus their effective signal intensities (which may have been below the required signal intensity to process four signals in parallel).

To investigate this possibility we presented observers with multiple motion signals comprised of four dots locally arranged into square patterns, in order to drive the aforementioned form-specific motion system and overcome potential signal intensity issues (Edwards & Rideaux, 2013). Using these stimuli, we extended the capacity of
parallel motion processing to five. Furthermore, we demonstrated that this capacity, similar to that initially found for transparent motion, is intrinsically linked to the signal intensity of the components. That is, by increasing or decreasing the signal intensity we were able to increase the capacity to six or decrease it to four, respectively.

Throughout all the previously mentioned studies investigating parallel motion processing, the same experimental paradigm was used to infer the capacity of this mechanism. Observers were presented with two temporally separated intervals, one containing $n$ motion signals and the other containing $n + 1$. The observers’ task is to indicate the interval containing more (or fewer) motion signals. The capacity is then inferred from the value $n$ of the highest comparison they are able to accurately discriminate. That is, if observers are capable of differentiating between up to three vs. four signals, this is taken to mean that they can simultaneously process three signals, and the interval containing four was perceived as noise. While this is informative, and provides insight into the capacity of parallel processing, it is not clear what information is actually extracted in order to perform the task at this level.

2.3. Levels of information extraction

To perform a temporal two alternative forced-choice (2AFC) $n$ vs. $n + 1$ task, observers are required to indicate which interval contained more/fewer stimuli. In previous parallel motion processing studies, the stimuli employed are motion signals, usually defined by direction (Edwards & Greenwood, 2005; Greenwood & Edwards, 2006). For motion signals which drive the standard global-motion system, i.e. transparent motion and spatially segmented global-motion, the limit found using this paradigm is three, and for motion signals which drive the form-specific motion system, the limit appears to be considerably higher, i.e. up to six (Edwards & Rideaux, 2013). Currently,
these limitations only indicate the point at which accurate discriminations can be made between this number of signals and more signals. That is, they demonstrate only that observers are capable of extracting sufficient information from the presentations to perform a discrimination task.

Multiple types of information can be extracted from any given stimulus. This ranges from the luminance and polarity of a plain white field, to the practically immeasurable multitude of information that can be extracted from a complex natural scene. Similarly, different types of information can be extracted from the stimuli used to determine the capacity of parallel motion processing. For example, information can be extracted regarding a) the direction of every motion signal, b) the presence/absence of a particular motion direction, or b) the number of distinct motion signals present. Importantly, the $n \ vs. \ n + 1$ discrimination task used to determine the capacity of parallel motion processing in previous studies can be performed with minimal information extraction. That is, to perform this task, observers are only required to indicate which interval contains more/fewer signals, and thus are not even required to extract the actual number of signals present, let alone the direction of each motion signal.

While determining the capacity of parallel motion processing using the $n \ vs. \ n + 1$ paradigm has provided considerable insight into how the visual system processes motion, and the factors that constrain the capacity of this mechanism, e.g. signal intensity, is remains unclear what information is being extracted at this level of parallel processing. This is an important question, as it adds further meaning to the value of the capacity, and additional insight into this process and its limitations. Thus, the first aim of this thesis was to determine the content of information extracted during parallel motion processing, and whether a relationship exists between the complexity of the to-be-extracted information and the limit of parallel processing. We conducted a number of psychophysical experiments towards this end; these are discussed in Chapter 4.
By changing the task and requiring observers to extract increasingly complex information, other (higher level) processes must now be considered, both in their capacity to process information simultaneously and the mechanisms which limit them. One such process is the consolidation of information into VSTM. That is, while many signals may be initially processed simultaneously, for the information to be extracted and stored for more than a couple of hundred milliseconds it must be consolidated into a durable representation. As previously mentioned, the $n \text{ vs. } n + 1$ paradigm used to determine the parallel motion processing limit could be performed with only having consolidated a single “unit” of information, i.e. the number of signals present. In contrast, to extract and store the directions of the signals requires multiple units of information to be consolidated into VSTM. Thus, Chapter 3 discusses VSTM, with an emphasis on the process of consolidation of information into VSTM.
Chapter 3. Visual short-term memory

Ever since the pioneering study by Phillips (1974), demonstrating the existence of VSTM using patterns, representation of visual information has been a central issue in cognitive research. Phillips (1974) presented observers with patterns made from square matrices with randomly filled in cells for 1 sec, followed by a blank interval and then either the same, or a new pattern. He found that observers’ recall accuracy was high when the delay between matched patterns was less than 100 ms; but when the delay was longer, or the pattern was moved or masked, accuracy varied as a function of pattern complexity. While sensory/iconic memory had been discovered previously by Sperling (1960, 1963), explaining observers’ ability to recall patterns separated by a delay of less than 100 ms regardless of complexity, Phillips (1974) had demonstrated the existence of a second distinct visual memory store that is capable of considerably longer information retention.

VSTM is thought to be a core cognitive mechanism that underpins a range of behaviours, from perception to problem solving to motor control. Considerable research has been and continues to be undertaken to understand the various aspects of VSTM. The question which has received by far the most attention relates to its storage capacity, i.e. how much visual information can we retain from one moment to the next? However, this thesis is concerned with capacity of another important aspect of this mechanism:
PARALLEL PROCESSING IN THE HUMAN VISUAL SYSTEM

consolidation, i.e. the encoding of visual short-term representations. Specifically, whether parallel consolidation of direction information is possible, whether there is a cost associated with it, the limit of this mechanism, and what determines this capacity. This Chapter will begin with a description of relevant VSTM processes, followed by an outline of the current state of play within the literature concerning parallel vs. serial consolidation, and end with a discussion of models currently proposed to explain the capacity of parallel consolidation.

3.1. Visual short-term memory processes

Visual short-term representations are the first durable state that visual information can be stored as within the cortex. Once consolidated/encoded into VSTM, information can be maintained, manipulated, or replaced with new information, which is why it is also often referred to as visual working memory. However, while these terms are often used synonymously, it is important to note that they are distinct (Diamond, 2013): visual working memory refers to the buffer that allows manipulation of stored information, while VSTM refers only to the storage of information. Sensory memory is characterized as high capacity memory whose contents decay within a few hundred milliseconds (Sperling, 1960, 1963); however, note recent evidence indicating limitations of its capacity for motion direction (Ogmen, et al., 2013). This is a result of the transient persistence of photoreceptors and neurons which are activated by visual stimuli, and as such is retinotopically stored (Coltheart, 1980). Sensory memory can be categorized into two stages of encoding: sensory and perceptual encoding. Sensory encoding is massively parallel (Zeki, 1993) and provides information about basic features, i.e. colour and orientation, to later systems through a series of high capacity channels (Cavanagh, 1988; Treisman & Gelade, 1980; Zeki, 1993). Perceptual encoding is the recognition of patterns
within this information (Jolicoeur & Cavanagh, 1992; Pinker, 1984) and the subsequent activation of identity information, e.g. letter identities (Duncan, 1980, 1983). In contrast, long-term memories are the result of activity-dependent changes in synaptic efficiency, i.e. the synapse linking two cells is strengthened if the cells are active at the same time (Bliss & Collingridge, 1993; Hebb, 1949; Konorski, 1948). While long-term memory is also characterized by its high capacity, its contents can potentially be retained for a lifetime. Compared to these memory stores, VSTM has a relatively small capacity (~4) (Cowan, 2001, 2010). VSTM is thought to result from the maintained activation of specific neurons via a neurotransmitter feedback loop between the prefrontal cortex and posterior visual areas (Phaf & Wolters, 1997; Ungerleider, Courtney, & Haxby, 1998; Wilson, O'Scalaihehe, & Goldman-Rakic, 1993). Thus, sensory, short-term and long-term memory can be classified as electrical, chemical, and physical, respectively. VSTM processes can be broadly categorized into consolidation, storage, manipulation, and maintenance; however there is considerable overlap between these functions.

While a great deal is known about the storage capacity of VSTM (Ma, Husain, & Bays 2014), the impact of memory load on resolution (Alvarez & Cavanagh, 2004; Awh, Barton, & Vogel, 2007; Vogel, Woodman, & Luck, 2001), and how multiple competing items are selected for storage (Schmidt, Vogel, Woodman, & Luck, 2002; Woodman & Vogel, 2008), relatively little is known about how VSTM representations are encoded, i.e. consolidation. In one of the first studies to investigate VSTM consolidation, Jolicoeur & Dell'Acqua, (1998) demonstrated that the process required time, with more time required for more items, and employed central functions implicated in dual-task slowing. Vogel, Woodman, and Luck (2006) extended these findings by examining the precise duration required to consolidate items. Observers performed a change detection task, similar to that used by Phillips (1974), with arrays of coloured squares. Importantly, the researchers presented pattern arrays to backward mask the coloured squares in the first
interval, preventing any further information extraction from sensory memory, and varied the delay between the colour and mask presentation. They found that observers were more accurate when longer delays were used, and proposed a consolidation rate of approximately 50ms per item. However, the authors conceded that the results could not distinguish between a serial consolidation account or a parallel account where parallel consolidation required a longer duration.

### 3.2. Serial vs. parallel consolidation

Distinguishing between serial and parallel processing in the visual system is a challenging (but important) undertaking (Townsend, 1990). For example, assuming that a system processes information serially or in an unlimited parallel manner, i.e. there is no cost or capacity of processing elements simultaneously, this can be difficult if one considers that elements processed serially may be being processed at such a rate that it is practically indistinguishable from parallel processing. However, the distinction becomes even less clear when one considers the possibility of limited parallel processing, i.e. there is a cost and capacity of processing multiple elements simultaneously, because now parallel processing can be so limited as to be practically indistinguishable from serial processing (Townsend & Ashby, 1978). Nevertheless, there have been and continue to be many attempts to make this distinction, and while much has been learned regarding the limitations of various experimental paradigms (Townsend, 1990), conclusions drawn from this evidence are rarely irrefutable; for a comprehensive discussion of the issue see Townsend and Ashby (1983). Bearing this in mind, while the following discussion of serial and parallel consolidation into VSTM will at times use language which suggests certainty regarding this distinction, there is always some degree of uncertainty.
In an attempt to determine whether multiple items can be consolidated in parallel, Huang, Treisman and Pashler (2007) employed a matching task where observers were presented with multiple coloured squares, then asked to report whether a probed colour was present in the preceding presentation. During the initial presentation, coloured items were either presented sequentially or simultaneously for a brief fixed exposure duration, i.e. in the sequential condition each item was presented for 50ms whereas in the simultaneous condition all items were presented at once for 50ms. While they found recall of the targets spatial locations was the same in both conditions, for colour, recall was better in the sequential condition, even when only two items were presented; they interpreted these results as evidence that consolidation of colour is limited to serial processing, i.e. only one item can be encoded into VSTM at a time.

Mance, Becker and Liu (2012), concerned that previous studies had unfairly compared target recall performance between sequential and simultaneous presentation of items, further examined the possibility of parallel consolidation by removing certain presentation contingencies, i.e. particular pairs of items being presented in the same locations, which they believed may have selectively disadvantaged performance in the simultaneous condition. Their results supported this; that is, a difference between simultaneous and sequential conditions was only observed in conditions where the presentation contingencies were used; once removed, performance became equivalent between presentation conditions. Although some evidence had been found previously suggesting that certain “high capacity individuals” may have the ability to consolidate colour items in parallel (West, Pun, Pratt, & Ferber, 2010), these results were the first compelling evidence that parallel consolidation into VSTM is possible.

Having demonstrated that parallel consolidation is possible, and developed an elegantly simple experimental paradigm to examine the process, Becker, Miller, and Liu (2013) proceeded to investigate whether the ability to consolidate information in parallel
is limited to colour or whether it can be achieved with other features, i.e. orientation, as well. Over a series of experiments, they consistently found poorer performance on the matching task when observers were presented with orientation items simultaneously, and interpreted these results as indicating that orientation is “severely” limited to serial consolidation. Liu and Becker (2013) extended this investigation using a technique which allowed them to examine the types of errors observers were making when presented with two items simultaneously, compared to sequentially. In previous studies, the matching task provided researchers with a binary measure of performance, i.e. correct or incorrect. Here, observers were presented with multiple orientation items, either sequentially or simultaneously, and asked to respond with the orientation of one of the items, which was cued after the initial presentation.

In contrast to the binary response output of the matching task, this paradigm produced a distribution of offsets, i.e. the difference in orientation between the cued item and the observer’s response on each trial. This distribution is composed of two types of error, which result from two types of trials. The first is where the observer successfully consolidates the cued item, resulting in a Guassian distribution with a mean and standard deviation. The standard deviation of this distribution is an inverse measure of the resolution/precision at which the items are encoded. The second type of trial is where the observer fails to consolidate the cued item and must guess, resulting in a rectangular (or flat) distribution of offsets. An example of a mixed distribution is depicted in Figure 3.1.
Figure 3.1. An example of a mixed distribution of offsets, i.e. differences between target and response orientation/direction. The dash blue represents the distribution of offsets from trials where the observer has successfully consolidated target item into VSTM. The dashed red line represented the distribution of offsets from trials where the observer has failed to consolidate the target item and must guess. The solid black line represents the combined distribution obtained from these two types of trials.

Liu and Becker (2013) used model fitting to evaluate precision and guess rate parameters, which were then compared between presentation conditions. The researchers had previously conceded that poorer performance observed on the earlier matching paradigm, when orientation items were presented simultaneously, may have been the result of lower resoultion encoding of items consolidated in parallel. That is, there may have been a cost to resolution associated with consolidating orientation in parallel, resulting in an increased likelihood of mistakenly mismatched items during the response stage of the task. Liu and Becker (2013) did not find any evidence for this, instead their results indicated that while there was no difference in resolution between sequential and simultaneous conditions, the guess rate was significantly higher in the simultaneous condition. The researchers interpreted these results as reflecting observers having used a serial consolidation strategy in the simultaneous condition, i.e. only being able to consolidate a single item, consistent with their previous claim that orientation was strictly limited to serial consolidation.
Returning to the question of whether parallel consolidation is possible for all features (excluding spatial position), or unique to colour, the results of Liu & Becker (2013) indicate that it may be uniquely limited to the consolidation of colour. At the least, it appears as though parallel consolidation can be achieved with some features and not with others. Previous parallel motion processing and multiple object tracking studies suggest that multiple motion directions can be processed; however, the degree to which information is processed in parallel and how much information is retained has not yet been explicitly investigated. For example, while the presentation durations used in parallel motion processing studies were brief (~150ms), given the estimated duration required to consolidate a single item (~50ms), a serial consolidation strategy may have been employed by observers. Similarly, while proponents of parallel processing accounts of multiple object tracking may claim that parallel consolidation is occurring, the display durations of many seconds used in these presentations makes conclusive interpretation of this challenging. Thus, the second aim of this thesis was to determine whether direction information could be consolidated into VSTM in parallel and if so, whether there is a cost associated with this. Experiments described in Chapter 5 are concerned with issue.

3.3. Models of parallel consolidation capacity

The most studied aspect of VSTM has been, and continues to be, its storage capacity. For a considerable length of time it was largely agreed among researchers that three or four items could be retained within VSTM (Cowan, 2001; Vogel, Woodman, & Luck, 2001). However, the convenient notion that there are a number of discrete “slots” within VSTM that can be used to store items has since been contended, and consensus appears to be moving towards other models to explain the capacity, such as limited resource (Bays & Husain, 2008) and biased competition models (Franconeri, Alvarez, &
Cavanagh, 2013; Shapiro & Miller, 2011). Importantly, just as the study of the storage capacity of VSTM progressed to examination of models explaining how this capacity is imposed, models have also been proposed to account for the capacity of parallel consolidation. Furthermore, given that the capacity of parallel consolidation appears to be different (smaller) than that for storage, different mechanisms likely impose limitations on these processes. This is consistent with behavioural studies demonstrating a dissociation between VSTM consolidation and maintenance (Woodman & Vogel, 2005), and neuroimaging evidence linking these operations to differential activation of cortical substrates (Curtis & D’Esposito, 2003; Passingham & Sakai, 2004; Wager & Smith, 2003).

Upon finding evidence indicating that orientation information cannot be consolidated in parallel, Becker et al. (2012) proposed that this may be due to the size of the perceptual space of orientation, compared to colour. Perceptual space can be conceptualized as the physical range of a feature, e.g. 0-180° for orientation, divided by the smallest difference along this dimension that can be detected, i.e. the just noticeable difference (JND). This space is a reflection of the tuning bandwidths of cells sensitive to the feature, i.e. narrower bandwidths result in smaller JNDs, and thus the bigger the perceptual space. The perceptual space of orientation, which varies by a single dimension, is relatively small compared to colour, which can be varied along three dimensions (hue, saturation, & luminance), and has smaller JNDs (Witzel & Gegenfurtner, 2013). Becker et al. (2012) suggested that this may explain the apparent inability to consolidate orientation in parallel; namely, that greater interference between overlapping representations within a small perceptual space could prevent efficient consolidation. They extended this by suggesting a potential neural mechanism whereby the synchronized firing of neural assemblies important for encoding the features of an object in VSTM (Luck & Vogel, 1998; Raffone & Wolters, 2001) are prevented from being
established simultaneously for orientation due to the interference between overlapping representations.

In a follow-up study, Miller, Becker, & Liu (2014) sought to further examine this account by comparing performance between sequential and simultaneous presentation of a mixture of orientation and colour items on a matching task. The authors reasoned that if the apparent inability to consolidate orientation in parallel was due to interference between items represented in a small perceptual space, observers should be capable of consolidating two different feature items (colour and orientation) in parallel, as they would likely be discretely represented and share no overlap. However, the results did not support this; performance in the simultaneous condition was significantly worse than the sequential condition, which the authors interpreted as reflecting use of a serial consolidation strategy in both conditions. To account for these findings, Miller et al., (2014) proposed a novel information bandwidth model to explain why the ability to consolidate in parallel appeared to be limited to colour.

The information bandwidth model claims that the bandwidth required to cortically represent different features varies, and that the capacity to pass through a putative consolidation bottleneck in parallel is determined by the size of these bandwidths. That is, they claim that while the bandwidth of colour is small, allowing at least two items to move through this bottleneck in parallel, the bandwidth of orientation is relatively large, preventing more than one item through at a time. The example provided by Miller et al., (2014) to justify the claim that the information bandwidth of colour is smaller than orientation is that colour can be extracted from a single pixel, whereas to extract orientation, information must be pooled over a number of pixels. A schematic of the consolidation bandwidth limit model is depicted in Figure 3.2.
This account is troubling for two reasons. First, while the statement regarding the area in the visual field required to extract these features is true, that is, a smaller area is required to extract colour, the suggestion that this maps directly onto the size of the cortical representation of these features is unfounded. If this were the case, one would expect that the spatial frequency of an oriented grating would determine whether it could be consolidated in parallel, as this dictates the spatial area over which information must be pooled for extraction. Second, the suggestion that poorer performance on a matching task using two different features, i.e. orientation and colour, when presented simultaneously, rules out the possibility that interference could account for the capacity, is potentially misleading. The biased competition account of attention proposed by

![Figure 3.2. Schematic of the consolidation bandwidth limit model. The consolidation bandwidth is depicted here as the space between perceptual encoding and working memory, with the height of this rectangle symbolising its limited capacity. The figure shows two hypothetical scenarios, where either two colours (left) or orientations (right) are presented simultaneously. Both are encoded in parallel at the perceptual stage, however the size of the features’ information bandwidth (depicted here as the height of the feature rectangles) dictates whether they can pass through the consolidation bandwidth in parallel, i.e. colour can but orientation cannot. Reproduced with permission from Figure 9 of Miller, Becker, & Liu (2014).](image-url)
Desimone and Duncan (1995), which is gathering popularity as an account for the capacity of VSTM storage, suggests that items that are highly heterogeneous, e.g. different features, actually result in greater competition/interference when presented simultaneously. Furthermore, it is presumptuous to make direct comparisons between parallel consolidation of the same feature, i.e. two colours, and a mixture of features, i.e. colour and orientation, as the latter is likely influenced by different factors than the former.

Given these issues with the information bandwidth model, and the limited number of studies to base explanations upon, further investigation of the mechanism which restricts parallel consolidation is clearly required. Indeed, Miller et al., (2014) concede that additional research is required to explain the differences between consolidation of orientation and colour. Thus, the third aim of this thesis was to investigate the capacity of parallel consolidation: both with regard to the precise number of items which can be consolidated, and with regard to what determines this limit. Experiments detailed in Chapter 7 are concerned with this.
Chapter 4. Information extraction during simultaneous motion processing

4.1. Context statement

As described in Chapter 2, previous studies indicate the capacity of parallel motion processing is around five (Edwards & Rideaux, 2013). However, due to the paradigm used to determine this limit, it is unclear how much information is being extracted at this level and thus precisely what this capacity reflects. The first experiments of this thesis were designed to examine how the complexity of information that is extracted during parallel (motion) processing impacts the capacity of this process. Note that this chapter appears in print as:

4.2. Introduction

Extensive research has been conducted on the perception of motion, most of which has concentrated on the processing of single motion signals (Nishida, 2011). However, outside the lab, multiple motion signals within the visual field are common, e.g. the cars and pedestrians at a busy traffic intersection. While it is clear that we are capable of processing these signals, the precise mechanism and capacity of this ability remains relatively unknown.

There are at least two stages in which multiple motion signals can be processed by the visual system: an initial stage in which signals are processed in parallel (simultaneous motion processing) followed by a sequential stage (Edwards & Greenwood, 2005; Mulligan, 1992). Using the above example of a busy traffic intersection, during the initial stage of multiple motion processing a number of people and/or cars could be processed simultaneously. Following this, attention could be shifted among any remaining moving objects to process them sequentially.

It is difficult to determine the degree to which simultaneous processing occurs while navigating through a busy traffic intersection, as the difference between processing distinct moving targets such as people or vehicles in series or in parallel can be hard to estimate. This is reflected in the current debate over the mechanism of multiple object tracking. While some theories suggest simultaneous processing occurs, e.g. the FINST model (Pylyshyn, 1989)\(^1\), others offer a sequential account (d'Avossa, Shulman, Snyder, & Corbetta, 2006; Oksama & Hyönä, 2008). However, one clear example of where simultaneous motion processing occurs is during the perception of transparent motion. Transparent motion is defined as more than one velocity field in the same part of the

---

\(^1\) See also Howe, Cohen, Pinto, & Horowitz (2010) and Howe & Ferguson (2015) for evidence in favour of a parallel account.
visual space and is due to either partial occlusions of moving objects or overlapping semitransparent surfaces (Qian, Anderson & Adelson, 1994), e.g. a school of fish swimming upstream through moving water. The ability to perceive both the movement of the fish in one direction and that of the water in the other is an example of simultaneous motion processing. Thus, it is not surprising that the first studies investigating simultaneous motion processing employed transparent motion stimuli to explore this phenomenon (Mulligan, 1992).

Using a modified global-motion stimulus (Newsome & Pare, 1988), Edwards & Greenwood (2005) demonstrated that the maximum number of transparent motion signals defined only by differences in direction which could be simultaneously processed was two. They proposed that this limit of two was due to the elevated signal intensity threshold, defined as the proportion of motion signals within a given area moving at one velocity, relative to all others (Snowden & Braddick, 1989; Edwards & Nishida, 1999). Whereas the threshold for detecting unidirectional motion is around 10-15%, transparent motion requires over 40% for each signal. They later confirmed this, showing that the initial limit of two could be extended to three by additionally defining the signals by differences in speed and depth (Greenwood & Edwards 2006a, 2006b). In doing so they engaged speed and disparity tuned global-motion pathways with independent pooling (Edwards, Badcock, & Smith, 1998; Hibbard & Bradshaw, 1999; van Boxtel & Erkelens, 2006), allowing them to effectively double the available signal intensity.

A common characteristic among the aforementioned studies was the use of spatially spread-out/transparent motion stimuli. However, outside the lab, occurrences of encountering three or more of these kinds of motion signals simultaneously are extremely rare. In contrast, occurrences of three or more spatially localized motion signals within the visual field are relatively common, e.g. a busy traffic intersection. Thus, while a limit of three may exist for processing transparent motion signals, this may not extend to
motion signals which are spatially localized. Indeed, we recently investigated this hypothesis by asking observers to differentiate between two temporal presentations of \( n \) and \( n + 1 \) spatially localized motion signals (Edwards & Rideaux, 2013). We found that observers were able to differentiate between presentations containing five and six motion signals, suggesting a capacity to simultaneously process five signals. Additionally, by either increasing or decreasing the signal intensity we were able to increase the capacity to six and reduce it to four respectively, demonstrating the important role that signal intensity continues to play in determining the limit of this process, even when the signals are localized. Although the results from the discrimination task suggest a simultaneous motion processing capacity of at least six, it remains unclear as to what information is actually extracted at this level.

Progressing from low to high detail information extraction, here we investigate observers’ ability to identify: (a) the number of signals present; (b) the actual directions present; and (c) the direction of a specific element. By measuring the capacity to extract these different types of information from multiple motion signals, we aim to determine whether the resolution of processing during the simultaneous stage varies as a function of information detail.

The findings from this study will also have considerable impact on the current debate between simultaneous and rapid sequential processing models in the field of multiple object tracking. Research shows that about four spatially localized objects can be accurately tracked (Pylyshyn & Storm, 1988). By determining what information can be simultaneously processed and from how many signals, we can demonstrate the in/feasibility of a putative simultaneous tracking model.

\(^2\) Note that this depends on the speed of objects and in some circumstances can be higher than four (Alvarez & Franconeri, 2007).
4.3. Experiment 1: Number of signals

We recently demonstrated that observers were capable of discriminating between presentations containing five and six motion signals (Edwards & Rideaux, 2013). While this indicates a capacity to simultaneously process at least five motion signals, it remains uncertain whether observers were aware of the actual number of signals present as opposed to simply being able to determine that one interval contained more signals than the other. The aim of this experiment was to determine the maximum number of signal directions observers are capable of identifying during the simultaneous stage.

4.3.1. Method

4.3.2. Observers

Three observers were used, one of the authors (RR) and two others who were naïve with respect to the aims of the study. All had normal or corrected to normal acuity.

4.3.3. Apparatus

Stimuli were presented on a Phillips Brilliance 202P4 cathoderay-tube monitor which was driven by a Cambridge Research Systems VSG 2/5 graphics card in a host Pentium computer. The monitor had a spatial resolution of 1024 x 768 pixels and a frame rate of 100Hz.

4.3.4. Stimuli and procedure

A modified version of the stimulus used in our previous study was employed (Edwards & Rideaux, 2013). A single interval five-alternate forced-choice procedure was
used. Each presentation contained between three (12 dots) and seven (28 dots) signal groups. The signal groups were defined by four dots arranged into a square pattern. These were formed by randomly selecting the location of the first dot while ensuring that it could move over the three motion frames without moving beyond the spatial extent of the viewing aperture. The remaining three dots were offset horizontally and vertically by $0.34^\circ$ to form a square pattern. The total number of dots was kept constant at 60 by the addition of noise groups. Thus, in the three signal condition there were 12 (48 dots) noise groups and in the seven signal condition there were eight (32 dots) noise groups. All dots started off in the same four dot square pattern. The squares composed of signal dots kept their shape as they moved, as each dot making up that square moved in the same direction on each motion frame transition, while squares composed of noise dots fell apart as each dot moved in a different randomly selected direction across the motion sequence. Each motion sequence consisted of three image frames, with each frame being presented for 60ms. The observer’s task was to indicate how many signal groups were contained within each presentation (from 3 – 7). A typical motion sequence with a signal level of five is shown in Figure 4.1. The directions that each signal group moved in were randomly chosen from eight directions: the four cardinal and four diagonal directions. While no two signal groups could move in the same direction, the direction of the noise dots, fixed across each motion sequence, was unconstrained. That is, each noise dot could move in any direction over the full $360^\circ$. Observers ran 10 blocks of trials, with breaks as needed, each consisting of 50 presentations. The signal number conditions were randomly interleaved throughout each trial.
To prevent observers using just the static image in the last motion frame in each sequence to perform the task, a mask frame was presented at the end of each motion sequence. The mask consisted of 300 randomly positioned dots and was presented for 240 ms. In our previous study we found this mask to be effective (Edwards & Rideaux, 2013). The background had a mean luminance of 62 cd/m$^2$, and the dots had a positive Weber contrast of 20% and were 0.25° in diameter. The dots were displaced by 0.32° on each frame transition resulting in a speed of 5.3°/s and were presented in circular aperture with a diameter of 20°. The observer sat 50 cm from the monitor, with their head supported on a chin rest.

Figure 4.1. An example of the stimuli used in Experiment 1. The images in the three-frame motion sequence are shown in (a) to (c) with a signal level of five. An example of the mask is shown in (d).
4.3.5. Results and discussion

The results of the three observers are shown in Figure 4.2. Performance, percentage of trials the observers got correct, is plotted against the number of signals present. Given a 5AFC was used, threshold performance was set at halfway between chance (20%) and 100%, i.e. 60%\(^3\). The pattern of results was similar for all observers. Only presentations containing up to four signals were performed at or above 60% (i.e. the 60% level fell within or below the 95% confidence intervals around the observer’s performance level) meaning that observers could accurately identify the presence of up to four motion signals.

\[\text{Figure 4.2. Results for Experiment 1. The performance (percentage of responses that were correct) is plotted against the signal level. The dotted line indicates the above-chance performance threshold while the dashed line represents chance-level. Error bars indicate 95\% confidence intervals.} \]

\(^3\)Note that this threshold may have been overestimated, as not all of the responses were necessarily as likely to be selected. That is, if seven signals were presented, observers were probably more likely to respond with five or six than two.
Additionally, two of the observers performed significantly above chance at a signal level of five. However, this can likely be attributed to a response bias within the higher signal level conditions (5, 6, & 7), indicated by performance at a signal level of seven which has a similar magnitude of displacement from chance in the opposite direction, i.e. below chance.

These results are largely consistent with our previous findings, demonstrating multiple motion processing of more than three signals (Edwards & Rideaux, 2013). However, whereas in our previous study, which employed an n vs. n + 1 paradigm, we found a limit of five when we employed the same signal to noise levels as used here, the results from the current experiment suggest observers were only capable of identifying the number of signals present up to four. The difference suggests that the resolution of motion during simultaneous processing varies as a function of the type of information being extracted. When the task requires observers to discriminate between two presentations containing n vs. n+1 numbers of motion signals, they can perform this accurately up to five vs. six signals. However when an observer is required to respond with the actual number of signals contained within a single presentation, they can only accurately perform this task with up to four signals present.

While the current experiment demonstrates that accurate numerosity judgements can be made with up to four signals, the next experiment determines to what extent motion information such as direction is extracted from these signals during simultaneous processing.

4.4. Experiment 2: Directions present
Experiment 1 demonstrated that observers are capable of identifying the presence of up to four distinct motion signals from brief presentations. This shows that during simultaneous processing, information regarding the number of signals present within an area can be extracted. However, whether information regarding the direction of motion is also extracted from these signals remains to be seen. The aim of Experiment 2 was to determine whether motion direction information is extracted during the simultaneous stage of multiple motion processing and if so, at what resolution this can be performed.

4.4.1. Method

4.4.2. Observers

Three observers were used, one of the authors (RR) and two others who were naïve with respect to the aims of the study. All had normal or corrected to normal spatial acuity.

4.4.3. Stimuli and procedure

The stimulus was the same as in Experiment 1 except that the noise dots and mask were removed and end frame altered. The end frame, the image presented after the motion sequence, was altered such that it now consisted of an arrow in the location of the fixation cross. The procedure was similar to that used in Experiment 1, except the observer’s task now was to indicate whether the direction given by the arrow, out of eight possible directions, was present or absent within the preceding presentation. There was an equal chance of the target direction being present or absent. In the previous experiment the task required observers to identify the number of motion signals present. Noise dots were used to prevent observers from discerning the total number signal dots present without first
recognising them as the target elements, i.e. signal groups, through identifying their common motion. As the task in the current experiment required observers to identify the direction of the signal groups, discerning the total number of dots present would no longer act as a useful cue in performing the task. Thus, the noise dots were removed. However, by removing the noise dots the signal intensity across all signal levels was increased relative to the previous experiment and varied as a function of the number of signals present, i.e. the fewer signals the higher the signal intensity. As the static afterimage of the final frame could not be used as a cue to perform the task, the mask was also removed. Additionally, the signal level range was moved to two to six. An example of the motion sequence and end frame are shown in Figure 4.3.
4.4.4. Results and discussion

The results of the three observers are shown in Figure 4.4. The same performance criterion as used in Experiment 1 was employed, i.e. midway between chance and 100%. Given that a 2AFC was used, threshold performance was set at 75%. The pattern of results was similar for all observers. Only presentations containing up to three signals were performed at or above 75% (i.e. the 75% level fell within or below the 95% confidence intervals around the observer’s performance level) meaning that observers could extract direction information from up to three signals.

Figure 4.3. An example stimuli used in Experiment 2. The images of the three frame motion sequence are shown in (a) to (c) with a signal level of four. An example of the post-cue target direction end frame is shown in (d).
At higher signal levels (4, 5 and 6) performance gradually declined but remained significantly above chance and at or above 75% for one of the observers (RR), the most experienced observer, at a signal levels four and five. Previous studies using transparent motion show that when the number of motion signals present exceeds the capacity of simultaneous motion processing, observers report perceiving noise and performance drops to chance (Edwards and Greenwood, 2005; Greenwood and Edwards, 2006a, 2006b). Here, the gradual decline in performance as a function of the number of signals present suggests that although the capacity of simultaneous processing was exceeded, observers extracted sufficient direction information to perform at above chance-levels. These results are consistent with a two stage multiple motion processing mechanism.
where during the initial simultaneous stage information from a subset of signals is extracted leaving the remaining to be processed sequentially, i.e. as the number of signals increased the chance of the target direction being among the processed subset was reduced.

If observers were extracting information from a subset of signals when the number of elements exceeded the capacity to simultaneously process then modifying the chance and threshold levels at each signal level to reflect this interpretation may be more informative. For instance, with around 90% performance accuracy in the two signal level condition it is clear that observers are capable of processing at least two signals simultaneously. Thus, in the three signal level condition, if observers are processing only two signals, when the direction cue matched either of the two signals processed (on 33.3% of the trials, given the target was absent on half the trials), they would have a 90% chance of detecting this, i.e. 29.97% correct total responses. On the remaining 66.7% of trials the target direction would either be absent or present and matched to the unprocessed third signal; in which case observers would be expected to perform at chance-levels, i.e. 33.3% of correct total responses. The sum of these two scores (63.3%) can now be applied as an adjusted chance level for the three signal level condition, with a corresponding adjusted threshold level of 81.7%. As performance in the three signal level condition exceeds this adjusted threshold, it is clear that observers were capable of simultaneously processing three signals. By applying the same principles to the remaining signal level conditions (4, 5 & 6), assuming that a subset of three signals is processed in each presentation, adjusted chance and threshold levels which may more accurately reflect the mechanism of simultaneous processing can be set. The addition of these adjusted chance/threshold levels, shown in Figure 4.4, indicates that observers were capable of processing three signals, even when the number of signals present exceeded this.
Experiment 2 builds on the previous experiment by showing that during simultaneous motion processing observers are capable of extracting motion direction information from multiple signals. Furthermore, just as the limit found for numerosity identification of multiple signals (4) was lower than that of discrimination (5), the capacity found in the current experiment investigating motion direction extraction (3) is reduced further still. The reduced capacity is not due to a reduction in signal intensity as the total number of dots in the current experiment was less than that used in the previous. Thus, this finding provides additional credence to the notion that the resolution of simultaneous motion processing is also dependent upon the level of information extraction in question.

While Experiment 2 further demonstrates the degree of information extraction which occurs during simultaneous motion processing, i.e. the presence of a particular motion direction, it remains uncertain whether this information can then be bound to its corresponding signal. For example, following the multiple direction extraction seen in the current experiment, can the direction of a specific element be identified? Experiment 3 investigates direction binding.

4.5. Experiment 3: Post-cue target location with iconic store inhibition

Experiment 3 aimed to determine whether during simultaneous motion processing, direction information which is extracted is bound to its corresponding signal.

4.5.1. Method
4.5.2. Observers

Three observers, including one of the authors (RR), were used. All had normal or corrected to normal vision.

4.5.3. Stimuli and procedure

The stimulus was the same as that used in Experiment 2, except a dynamic mask was introduced and the end frame altered. During pilot testing it was discovered that the task could be performed with relatively high accuracy even when the number of signals present far exceeded that which could be processed in the preceding experiments, i.e. 20. These results are characteristic of those found in partial report tasks, where a stimulus is briefly presented, followed by a cue indicating target items (Sperling, 1960). The observer’s task during partial report tasks is to respond with information about the target items, i.e. orientation, colour, etc. Even though the number of elements present exceeds that which a person can perceive in such brief presentations, i.e. the span of apprehension (Catell, 1885), if the proceeding cue is presented soon enough following this observers perform the task with high accuracy. This is due to iconic memory. Many types of information are stored in iconic memory; including orientation and spatial frequency (Magnussen, Idas & Myhre, 1998), colour (Nilsson & Nelson, 1981), and motion direction (Demkiw & Michaels, 1976; Shooner, Tripathy, Bedell & Ogmen, 2010; Triesman, Russell & Green, 1975). Recovery of information from iconic memory demonstrates a relatively rich but transient capacity for storage and retrieval of briefly presented images (Sakitt, 1975, 1976). However, during partial report tasks a target subset of elements is selected, usually indicated by a cue following the presentation. Although
all of the elements are stored in iconic memory\(^4\), only information from the target subset is processed, i.e. encoded into working memory (Averbach & Coriell, 1961). The current experiment aimed to investigate the capacity of observers to extract information from multiple signals then indicate the direction of a single target element from within that group. The ability to use iconic memory to perform the task would allow observers to forgo processing multiple signals during the presentation; instead retroactively extracting the direction of the target signal once it has been cued. Thus, performance based on extraction of information from this store would not represent simultaneous motion processing as information is only extracted from one signal. In order to investigate the capacity to bind direction information which is extracted during simultaneous motion processing, the use of iconic memory must be prevented.

A static visual stimulus presented for duration of 130ms or more persists in the iconic store for between 100ms to 250ms after its offset (Efron, 1970; Sperling, 1960). It has been suggested that the iconic representation of motion information may decay more slowly than static information and is therefore accessible for a longer duration (Demkiw & Michaels, 1976). Treisman, Russell & Green (1975) found a significant reduction in partial report performance of motion between presentations where observers were cued at the stimulus offset and 1000ms after the offset, however as no intermediate delays were tested the precise duration of persistence cannot be inferred. In contrast, Shooner, Tripathy, Bedell & Ogmen (2010) examined partial report performance at a range of delays between stimulus offset and 3000ms and found a steep decline in performance between offset and 500ms and similar performance at delays of 500, 1000, and 3000ms. Thus, a 500ms delay between the motion sequence offset and post-cue would be sufficient to prevent observers from using the location of the post-cue to extract the direction of the

\(^4\) Although see Ogmen et al, (2013) for evidence indicating a limited capacity of the number of motion items stored in iconic memory.
target signal from iconic memory. However, studies using static stimuli have shown that in the absence of a post-cue or mask, observers will process as much information as possible from the iconic store sequentially before it decays, referred to as “nonselective readout” (Averbach & Coriell, 1961). While this has only been examined using static images, it is possible that observers can also use nonselective readout to extract motion information. Thus, in order to prevent iconic memory being used either in conjunction with the post-cue or the potential to process signals sequentially, it must be interrupted at the offset of the stimulus using a mask.

Interruption of iconic memory occurs when the test stimulus is followed by a noise mask within the next 75ms, depending on the conditions (Spencer, 1969; Spencer & Shuntich, 1970; Sperling, 1963). To achieve this, a dynamic mask was developed during pilot testing. Although there is considerable research on iconic memory and masks which are effective in inhibiting its use (for a comprehensive review see Breitmeyer & Ogmen, 2000 and/or Scheerer, 1973), there is little on iconic memory of motion and none regarding its masking. As a result, many masks had to be trialled during pilot testing before an effective one was found, i.e. the dynamic mask. The dynamic mask was created by drawing four static masks, as used in Experiment 1, and presenting each for 30ms. This gave the impression of dots in random motion and looks similar to the black and white static observed on a television. As the aim of the current experiment was to determine the number of signal directions which can be simultaneously extracted during the brief presentation, the function of the dynamic mask was to interrupt iconic memory, not to disrupt the storage of information extracted during the presentation.

To demonstrate the effectiveness of the mask and that performance in this condition was a reflection of information extraction which occurred during simultaneous

5 Although see Ogmen et al., (2013) and Huynh et al., (2015).
processing, one third of the presentations were followed by a 120ms dynamic mask before the end frame was displayed, one third had a 500ms delay during which only the fixation cross remained present and the remaining third had no delay. Performance in these conditions was expected to reflect simultaneous processing of the stimulus, a combination of simultaneous processing and sequential processing of signals stored in iconic memory and the use of the cue in conjunction with iconic memory, respectively. To observe the effect of signal level in the above three conditions, two signal level conditions, one with four signals present and one with eight, were randomly interleaved within each block. The end frame consisted of the final frame of the motion sequence with all but the target signal and fixation cross removed. Using arrow keys on the number pad of a keyboard, the observer’s task was to indicate the direction of the post-cued target signal from eight possible responses: the four cardinal and four diagonal directions. Observers ran 10 trials, each of which consisted of 120 presentations. An example of the dynamic mask sequence and end frame are shown in Figure 4.5.
4.5.4. Results and discussion

The results of the three observers are shown in Table 1. The procedure employed an 8AFC design so chance performance was set at 12.5%. The pattern of results was
similar for all observers. In all conditions observers performed significantly above chance. Given the interpretation taken from the previous experiment, that when presented with a number of signals exceeding the simultaneous processing limit the visual system will select a subset of these to process, expressing performance as the number of signals processed in each signal level condition is substantially more informative than what can be interpreted from a simple assessment of whether performance is above chance. However, in order to accurately translate performance into signals processed, accurate performance due to chance must first be removed. The higher performance is, the fewer correct responses are due to chance; between chance performance, where all are due to chance, and 100% performance, where none are due to chance. To determine the proportion of correct responses which are due to chance we must assume that incorrect responses represent responses which failed to be correct through chance. Given that chance was 12.5%, the proportion of incorrect responses represents the 87.5% of responses which failed to be correct through chance. Thus, the remainder of this 87.5% of responses are those that are correct due to chance. For example, if an observer’s performance was 60%, the remaining 40% of (incorrect) responses represents 87.5% of responses which were guessed and failed to be correct due to chance. The proportion of the 60% correct responses which were correct due to chance can be determined by calculating the remainder of the of guessed responses, i.e. 40/87.5*12.5 = 5.7%. Once chance performance is removed, the adjusted performance can be used to accurately express the number of signals processed. The adjusted performance for each condition is shown in Table 4.1.
Table 4.1. Observer performance in Experiment 3.

<table>
<thead>
<tr>
<th>Observer</th>
<th>Condition</th>
<th>Signal level</th>
<th>Mean % correct</th>
<th>Adjusted mean</th>
<th>SD</th>
<th>Signals processed</th>
</tr>
</thead>
<tbody>
<tr>
<td>RR</td>
<td>No Delay</td>
<td>4</td>
<td>92</td>
<td>91</td>
<td>4.0</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>77</td>
<td>74</td>
<td>7.7</td>
<td>5.9</td>
</tr>
<tr>
<td></td>
<td>Delay</td>
<td>4</td>
<td>68</td>
<td>64</td>
<td>11.4</td>
<td>2.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>46</td>
<td>38</td>
<td>11.0</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td>Mask</td>
<td>4</td>
<td>75</td>
<td>71</td>
<td>9.3</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>42</td>
<td>33</td>
<td>12.1</td>
<td>2.7</td>
</tr>
<tr>
<td>PM</td>
<td>No Delay</td>
<td>4</td>
<td>71</td>
<td>66</td>
<td>11.7</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>54</td>
<td>47</td>
<td>9.3</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td>Delay</td>
<td>4</td>
<td>44</td>
<td>36</td>
<td>12.0</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>27</td>
<td>17</td>
<td>14.9</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>Mask</td>
<td>4</td>
<td>50</td>
<td>43</td>
<td>15.6</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>30</td>
<td>20</td>
<td>9.9</td>
<td>1.7</td>
</tr>
<tr>
<td>CR</td>
<td>No Delay</td>
<td>4</td>
<td>92</td>
<td>91</td>
<td>6.1</td>
<td>3.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>75</td>
<td>72</td>
<td>9.9</td>
<td>5.8</td>
</tr>
<tr>
<td></td>
<td>Delay</td>
<td>4</td>
<td>75</td>
<td>71</td>
<td>9.3</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>43</td>
<td>35</td>
<td>14.3</td>
<td>2.8</td>
</tr>
<tr>
<td></td>
<td>Mask</td>
<td>4</td>
<td>69</td>
<td>64</td>
<td>15.4</td>
<td>2.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>40</td>
<td>32</td>
<td>15.5</td>
<td>2.6</td>
</tr>
</tbody>
</table>

When performance is expressed as the number of signals processed from each presentation, by multiplying the number of signals presented by performance, the results show significantly better performance when more signals are presented in the no delay condition, (RR) \( t(18) = 11.42, p < .001 \), (PM) \( t(18) = 5.61, p < .005 \), & (CR) \( t(18) = 10.62, p < .001 \). In contrast, while performance was slightly better when fewer signals were presented in the delay and mask conditions, no significant differences were found.

Expressing performance as the number of signals processed is appropriate when the strategy of the visual system is to select a subset from those presented and accuracy reflects the probability of the target element being contained within this subset, i.e. if the visual system can process three signals simultaneously and is presented with four then with an increasing number of trials performance will approach 75%. However, if the

---

* Correction. The degrees of freedom for the \( t \) values should be 2.
strategy of the visual system is to use iconic memory to retroactively extract information from the target element, expressing performance as the number of signals processed is misleading as the number of signals which need to be processed to obtain high accuracy using this strategy is only one, i.e. the target. This is clearly the case in the no delay condition where performance expressed as the number of signals processed would suggest a higher capacity of signal processing when the signal level was increased. Given the strategy in the no delay condition employed iconic memory and thus accurate performance could be achieved from extracting information from only one signal, the results from this condition cannot be used to infer the capacity of simultaneous processing. In contrast, consistent performance between signal levels in the delay and mask conditions indicates that observers were capable of simultaneously extracting direction information, bound to a location, from a subset of up to three signals.

A defining characteristic of iconic memory is the relatively small effect which the number of items present has upon performance in a partial report task because only the target subset is processed (Sperling, 1960). However, given there were significant differences in performance between signal levels in the no delay condition for all observers, (RR) $t(18) = 6.21, p < .05$, (PM) $t(18) = 3.15, p < .05$, & (CR) $t(18) = 6.08, p < .05$, this indicates that increasing the number of signals presented had a negative effect on observers ability to extract motion information of a signal from iconic memory. This suggests that motion information stored in iconic memory may be less robust than static information.

Interestingly, performance represented as the number of signals processed was similar in the delay and mask conditions, suggesting two points. First, the additional duration in which it was proposed that signals stored in iconic memory may be

---

7 However, see Ogmen et al. (2013) for evidence suggesting this may not be true for motion information.
8 Correction. The degrees of freedom for the t values should be 1.
sequentially processed in the delay condition did not significantly improve performance, (RR) $t(19) = -.4, p > .05$, (PM) $t(19) = .762, p > .05$, & (CR) $t(19) = 1.87, p > .05$. As research investigating nonselective readout has not yet been conducted using motion stimuli, this process may only apply to other characteristics of elements, e.g. orientation and colour. Secondly, the difference in signal intensity between the two signal levels did not have a significant effect on the number of signals which could be processed. Studies of simultaneous motion processing using transparent motion stimuli have shown that the signal intensity required to process two signals is around three times greater than that needed to process one (Edwards & Greenwood, 2005). Similarly, we previously found that by reducing the intensity of spatially localized signals from around 7% to 5%, the number of signals observers were capable of discriminating between fell from five to four (Edwards & Rideaux, 2013). In the current experiment the signal intensity was halved, from 25% to 12.5%, between signal level conditions, yet the same number of signals appeared to be processed. While this is a relatively large reduction in signal intensity, as the signal intensity in the eight signal level condition (12.5%) still exceeds those tested in Edwards & Rideaux (2013) discrimination experiment, this may suggest that this is still sufficiently high not have an impact on the number of signals which can be processed. This further demonstrates that the mechanism of processing spatially localized signals is far more robust to noise than that used to process spatially spread-out signals (transparent motion).

Due to the nature of the task, i.e. motion signals moving in discrete directions, the ability to examine the degree of error regarding direction judgements was limited. This in turn restricts the capacity to compare the results of the current study with those of previous studies which have investigated this, such as Shooner, Tripathy, Bedell & Ogmen (2010). While this is an important aspect of multiple motion processing, mapping
out directional judgement errors was peripheral to the aim of the present study, i.e. to
determine the capacity of simultaneous motion information extraction.

During the current experiment it became apparent that iconic memory of motion
may have been used to perform the task in Experiment 2. Thus, a control experiment was
run using a signal level of four to compare performance with and without the dynamic
mask. The three observers from the previous experiment were used. The results are shown
in Figure 4.6. Given that no significant differences between performance in the ‘no delay’
and ‘dynamic mask’ conditions were found, this indicates that iconic memory was not
used to perform the task. The inability to use iconic memory to perform the task is likely
due to the type of post-cue employed.

![Figure 4.6](image)

**Figure 4.6.** Results for the control experiment. The performance (percentage of responses that were correct) is given for each condition; a) no delay vs. dynamic mask. The dotted line indicates the above-chance performance threshold while the dashed line represents chance-level. Error bars indicate 95% confidence intervals.

### 4.6. General discussion
The main findings from the present study were that during the simultaneous stage of multiple motion processing, it is possible to extract the number of elements present, the actual directions of the signals, and the direction of a specific element. Furthermore, the resolution of simultaneous processing varies as a function of the information which is extracted. For instance, in our previous study we demonstrated that observers were capable of differentiating between presentations of up to five vs. six signals (Edwards & Rideaux, 2013), whereas here we show they were only capable of identifying the number of signals present up to four (Experiment 1). The resolution is further reduced to between two and three when observers are required to extract motion directions and identify the direction of a specific element (Experiments 2 & 3).

There are a number of implications from these results. The first is that while the simultaneous processing limit of three found by Greenwood & Edwards (2006) can be exceeded, the degree of information extraction suffers to the extent that motion direction information is lost. For instance, while the observer is aware of the presence of four distinct motion signals, they are only capable of extracting the direction of three during the simultaneous stage. Note that caution must be taken when comparing the limit found by Greenwood & Edwards (2006) to those in the current study. The task in their study required observers to discriminate between n vs. n+1 transparent global-motion signals. It remains unknown whether or not the same limit they found for a discrimination task (3) would apply to the extraction of global-motion signal directions or if this would have a lower capacity, as demonstrated in the current study using localized motion signals. Further research is required to investigate the differences and similarities between the simultaneous processing of these two types of motion signals.

The second implication of the current study relates to the capacity to extract motion information from multiple signals even when the capacity is exceeded. As
previously mentioned, studies in which transparent motion stimuli were used to measure the capacity of simultaneous motion processing found that when the capacity was exceeded, observers were unable to extract coherent motion and reported seeing noise (Edwards & Greenwood, 2005; Greenwood & Edwards, 2006a, 2006b). Thus, when presented with three transparent signals observers were able to extract the presence of all three, but when an additional signal was added they were unable to extract any. In contrast, when viewing a number of spatially distinct motion signals exceeding this same limit, observers were still capable of extracting direction information from a subset of these. This indicates that the visual system is capable of selecting a subset of motion signals, from a sample exceeding its capacity to simultaneously process, and extracting information from these before proceeding to sequentially process the remaining. While the mechanism of this process remains unknown, as this could not be achieved using transparent motion stimuli this suggests it operates on a spatially dependant basis, i.e. the area of motion extraction within the visual field is reduced to one which only contains up to the limit of signals which can be processed. However, it is likely that while in the current study this mechanism occurred passively, if the properties of the elements such as polarity were varied, i.e. half light/half dark, it is possible that an observer could actively process a subset using this characteristic as a cue (Edwards, 2009). We are currently investigating this possibility.

Finally, both of the abovementioned findings have important implications for multiple object tracking. Findings from multiple object tracking literature indicate that the maximum number of elements which can be tracked is around four, beyond which performance decreases (Allen, McGeorge, Pearson, & Milne, 2006; Pylyshyn & Storm, 1988). While the limit for this process has generally been established, the mechanism has not. While some theories suggest simultaneous processing occurs, e.g. the FINST model (Pylyshyn, 1989), others offer a sequential model (d'Avossa, Shulman, Snyder, &
Corbetta, 2006; Oksama & Hyönä, 2008). In the present study we demonstrate that observers are capable of simultaneously extracting motion information from up to three signals, providing support to a simultaneous processing model of multiple object tracking. It is important to note, however, that due to the structure of the signals used, i.e. four dots moving in the same direction, the task required the additional process of grouping. While this may explain the difference in between the capacity found in the present study (3) and those in multiple object tracking tasks (4) it also dictates that caution must be taken in comparing the two. However, stimuli used in multiple object tracking tasks incorporate both target and distractor signals. The distractor signals in these tasks are analogous to the remaining signals outside the subset selected for simultaneous processing during the task in the present study. Thus, while some differences exist between these tasks, i.e. grouping, the relevance of our findings to multiple object tracking is given extra credence by the demonstration that observers can simultaneously process a subset of signals in the presence of a larger sample.
Chapter 5. Evidence for parallel consolidation motion direction and orientation into visual short-term memory

5.1. Context statement

As described in Chapter 3, previous research suggests that not all features can be consolidated from sensory to VSTM in parallel (Liu & Becker, 2013). However, to date, this has only been investigated using colour and orientation, thus, the experiments in the current chapter further explore parallel processing by determining whether motion direction can be consolidated in parallel, then re-examining parallel consolidation of orientation. Note that this chapter appears in print as:

5.2. Introduction

A great deal is known about the capacity of VSTM, i.e. the number of items that can be stored; for a review, see Ma, Husain and Bays (2014). However, relatively little is known about how information is consolidated from sensory memory into VSTM, i.e. the formation of VSTM representations. Sensory memory is characterized as high capacity memory whose contents decay within a few hundred milliseconds (Sperling, 1960, 1963), whereas VSTM has a considerably lower capacity which is more sustainable (Cowan, 2001). A number of studies have examined the time course of this consolidation, and determined that the transfer of information from sensory to VSTM takes around 50ms per simple item (Jolicoeur & Dell'Acqua, 1998; Vogel, Woodman, & Luck, 2006). Importantly, these studies do not attempt to discriminate between serial and parallel models of consolidation, noting that both could account for the data. While items could be processed serially, each taking 50ms, multiple items might be processed in parallel, together requiring a longer total duration. Given the importance of the mechanism that transfers information from sensory memory to VSTM, understanding the nature of this process, i.e. whether information can be consolidated in parallel, is essential to a complete understanding of memory processes.

Recently, a number of studies have addressed this question. Huang, Treisman and Pashler (2007) used a task where observers were shown simple items (coloured squares), either serially or simultaneously and then asked to respond whether a probed colour was present. As matching performance was worse in the simultaneous condition even when only two items were presented, the authors concluded that consolidation occurs serially. However, Mance, Becker and Liu (2012) argue that a number of presentation contingences in these experiments, i.e. certain pairs of items consistently being presented in the same locations, led Huang, et al. (2007) to underestimate participants’ capacity to
consolidate items in parallel. Their results supported this, indicating that these presentation contingencies had selectively handicapped performance in the simultaneous condition. In conditions where the contingencies were removed, observers were capable of performing the simultaneous task with the same accuracy as the serial task with two, and possibly three, items. To account for these results, the researchers proposed that parallel consolidation is possible but may be limited to two items.

Becker, Miller and Liu (2013) extended this work by using a similar paradigm to investigate whether orientation information can be consolidated in parallel. Over a series of experiments they consistently found better performance when two items were presented serially compared to simultaneously, leading them to conclude that orientation information, unlike colour information, cannot be processed in parallel. The notion that such marked differences exist between categories in the capacity to process simple information is unexpected. Initially the researchers proposed the difference between the perceptual spaces of the two types of information, i.e. colour and orientation, may account for the findings. That is, while colour has a rich space, varying in hue, saturation and luminance, orientation has a relatively poor space, only varying along a single dimension. They argued that this difference may have led to greater interference between feature intervals used to define items within the orientation dimension than those used within colour as a result of the proximity of these items in their corresponding perceptual spaces.

In a follow-up study, Miller, Becker and Liu (2014) demonstrated that a combination of colour and orientation information could not be consolidated in parallel, which the authors interpreted as suggesting that the inability to consolidate orientation information in parallel may not be due to interference within a small perceptual space. However, the unknown impact of using features from within different dimensions makes it difficult to compare these results with previous studies involving only a single feature type. Some evidence for a shared mechanism was found for the consolidation of colour
and orientation, and to account for the difference in the capacity of this mechanism to consolidate these two features, the authors proposed that while only a small information bandwidth is required to encode colour, the information bandwidth required to encode orientation is too large for the system to consolidate in parallel.

Thus, currently the answer to the question posed previously regarding the debate between parallel and serial consolidation is not a simple yes or no, but appears to be contingent upon the type of information being consolidated, e.g. colour or orientation. Given the importance of this question, if the nature of the consolidation process does vary between serial and parallel as a function of the type of information being processed, it is of interest to determine how other types of basic information are consolidated. Determining this is not only useful in isolation, but will ultimately lead to a deeper understanding of the nature of information processing in memory consolidation.

One type of information that would be a good candidate for parallel consolidation is motion direction. Previous studies have investigated simultaneous processing with global-motion signals defined by direction, presented in the same spatial region (transparent motion) or in different spatial regions (Edwards & Greenwood, 2005; Greenwood & Edwards, 2006; Qian, Andersen, & Adelson, 1994). Over a number of studies, the researchers consistently found that observers were capable of making $n$ vs. $n + 1$ motion signal discriminations with up to $n = 3$ signals. The researchers interpreted these findings as indicating a higher order limit restricting the simultaneous processing of motion to three directions. More recently, this research has been extended by the demonstration that during brief presentations of multiple spatially localized motion signals, observers are capable of extracting direction information from up to three items (Edwards & Rideaux, 2013; Rideaux & Edwards, 2014).

Importantly however, none of these motion studies explicitly differentiated between rapid serial and parallel accounts of consolidation; due to the length of
presentation durations in these studies, it is impossible to discriminate between these accounts. Given the similarity between orientation and motion direction information (Clifford, 2002), it is likely that the factors preventing parallel consolidation of orientation information proposed by Becker et al. (2013) may also apply to direction. For instance, while the range of possible directions is twice the size of possible orientations, i.e. 360° as opposed to 180°, the perceptual space appears to be equivalent. Adaptation studies show that the tuning bandwidths for motion direction are twice that for orientation (Albright, 1984; Britten & Newsome, 1998; McAdams & Maunsell, 1999), and the threshold orientation required for discrimination of motion direction is about twice the size of that needed for orientation (De Bruyn & Orban, 1988; Webster, De Valois, & Switkes, 1990). Thus, if interference resulting from proximal intervals within a small perceptual space does account for the inability to consolidate in parallel, we would expect to find the same results using motion direction, even though it has a larger physical range. Additionally, it is conceivable that the size of the information bandwidth required to encode direction, like orientation, is larger than needed for colour, as information must be pooled over space and time. Thus, if the ability to consolidate in parallel is related to the size of the information bandwidth required to process a given feature, it is likely that parallel consolidation of motion direction will not be possible.

In summary, in the light of recent findings indicating that the capacity to consolidate information into VSTM varies as a function of the type of information encoded, we set out to determine whether motion direction information is capable of being consolidated in parallel. To the best of our knowledge this will not only be the first test of whether motion direction can be consolidated in parallel, but the first test of this kind with a dynamic feature, i.e. motion.
5.3. Experiment 1: Parallel consolidation of motion directions

Using a similar paradigm to that employed by Mance et al. (2012), here we directly investigate whether motion direction information can be consolidated into VSTM in parallel or if, like orientation information, it is limited to rapid serial processing. Specifically, the aim of the experiment was to determine the shortest stimulus duration necessary to consolidate a single item and then examine whether observers were capable of consolidating two items presented simultaneously for this duration. To balance other factors associated with processing and storing multiple items between the methods of consolidation, performance consolidating \( n \) number of items in parallel was compared to performance processing \( n \) number of items serially, with sufficient time between serial presentations for optimal performance. If direction information can be consolidated in parallel, we would expect observers to perform equally well when items are presented simultaneously as when they are presented sequentially.

5.3.1. Method

5.3.2. Observers

Ten observers participated in the study: one of the authors (RR) and nine others who were naïve with respect to the aims of the study. All had normal or corrected to normal acuity and gave informed written consent to participate in the study.

5.3.3. Apparatus

Experiments were run under the MATLAB (version R2013a) programming environment, using software from the PsychToolbox (Brainard, 1997; Pelli, 1997).
Stimuli were presented on a Phillips Brilliance 202P4 CRT monitor that was driven by an Intel Iris graphics card in a host MacBook Pro computer. The monitor had a spatial resolution of 1024 x 768 pixels and a frame rate of 120Hz.

5.3.4. Stimuli

The stimulus presentation sequence consisted of a motion sequence, a fixation period and a probe sequence, respectively. The motion sequence contained one or more motion stimuli presented either simultaneously or sequentially. The motion stimuli were square apertures (8° × 8° visual angle) positioned evenly around an imaginary circle (8° radius) centred on fixation. Each stimulus contained 100 Gaussian blobs (0.3° radius), which moved in a consistent direction within each square, wrapping around when they reached the edges, to form the percept of a coherent motion within each aperture. For each trial the direction of the motion stimuli was randomly selected from the four possible oblique directions without replacement, i.e. 45°, 135°, 225° and 315°, avoiding presentation contingencies, e.g. only presenting certain items in some locations, which have been shown can selectively hinder parallel consolidation (Mance, et al., 2012). Oblique, as opposed to cardinal, directions were employed to encourage observers to use visual rather than verbal short-term memory, i.e. it should be more difficult to verbally encode diagonal directions than up/down/left/right. During the motion sequence the motion stimuli were presented for a predetermined duration, the determination of which is later described, and then replaced by a 200ms dynamic mask. The mask consisted of an aperture equal to the size and shape of the motion stimuli containing 300 blobs which were rapidly randomly positioned and repositioned for its duration, giving a similar impression to the static observed on a television without reception. The mask was
employed to interrupt sensory persistence of the motion signal, and has previously been shown to be effective (Rideaux & Edwards, 2014).

When motion stimuli were presented sequentially, each stimulus was separated by a 500ms fixation period, where only the fixation cross was present. To reduce temporal uncertainty, a tone was played 200ms before each motion stimulus was presented. Following the motion sequence/s there was another fixation period; in the sequential condition this was 500ms and in the simultaneous condition this was the combined duration of the fixation periods in the corresponding sequential condition. That is, when two motion stimuli were presented in the simultaneous condition, the fixation period was 1000ms; when three were presented, it was 1500ms. This was done in order to balance the duration that information needed to be maintained in VSTM between the simultaneous and sequential conditions; otherwise this may have selectively handicapped performance in the sequential condition (Mance, et al., 2012). In the sequential condition, the interval between each item presentation and the probe varied depending on the order of presentation, whereas in the simultaneous condition the duration of this interval was equal to the longest interval in the corresponding sequential condition for all items. Thus, information in the simultaneous condition was required to be maintained for longer on average and similar performance between these conditions cannot be interpreted as reduced performance in the sequential condition resulting from longer retention periods.

Finally, the probe sequence, consisting of a motion stimulus similar to that used in the motion sequence, centred on fixation, was presented for 500ms followed by a fixation period. The probe stimulus moved in either one of the directions presented in the preceding motion sequence (match) or one of the remaining directions (mismatch). Examples of the presentation sequences are shown in Figure 5.1.
The background was grey (mean luminance, 12 cd/m$^2$) and the blobs were white (mean luminance, 63 cd/m$^2$). The blobs were displaced 0.082° each frame, resulting in a speed of 9.8°/s. The observer sat 50 cm from the monitor, with their head supported on a chin rest.

5.3.5. Procedure

Observers were instructed to maintain fixation on the fixation cross throughout the experiment. Their task was to indicate whether the probed direction was present or absent in the preceding presentation using the ‘z’ and ‘1’ keys. The minimum duration mentioned earlier was determined by taking the mean of five 3 down/1 up staircases to find the 79% threshold duration for which observers were capable of serially
consolidating two items using the stimulus described above. This duration was determined for each observer and used to test this observer in all subsequent presentations, to account for individual variation in consolidation efficiency. The frame rate was 120Hz, i.e. 8ms per frame, and at least two frames are required to produce motion, thus the minimum possible duration was 16ms. To balance experience with the stimuli, observers also ran five staircases using simultaneous presentation during threshold determination; however this data was not used.

Following determination of the minimum duration for consolidation, 240 trials were run using both simultaneous and sequential presentation of two and three motion signals. Thus, the experiment was a $2 \times 2$ design (simultaneous/sequential presentation $\times$ 2/3 items) with a total of 960 trials. Trials were run in blocks of 48, with the condition held constant within blocks and randomly interleaved between blocks. Blocks were counterbalanced so on half the trials the probe matched one of the test directions, and each test location had an equal probability of being the target. Finally, for match trials within the sequential condition blocks targets selected as a function of presentation order was also counterbalanced.

5.3.6. Results and discussion

The average threshold duration was 82ms (range, 37 – 154ms; SD, 44ms). This is somewhat longer than the corresponding mean thresholds found for colour (60ms) (Mance, et al., 2012) and orientation (55ms) (Becker, et al., 2013); however, this is unsurprising, given that colour information can be extracted from a single static image whereas motion direction requires at least two frames before information extraction is possible. Furthermore, a number of studies indicate that colour is processed more rapidly
than motion direction (Arnold & Clifford, 2002; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002).

In the subsequent trials examining proportion of correct responses, the same pattern of results was found for all observers. Average performance is plotted in Figure 5.2. A repeated measures analysis of variance (ANOVA) was used to compare performance across the four conditions. Significant main effects for both presentation type (simultaneous/sequential) and item number (2/3) were found, $F(1, 9) = 11.65, p < .001$ and $F(1, 9) = 120.96, p < .001$ respectively. A significant interaction effect was also found, $F(1, 9) = 19.29, p < .01$. Paired t-tests revealed that while mean performance between simultaneous/sequential conditions was the same when two items were presented, $t(9) = 0.60, p > .05$, performance was significantly higher in the sequential condition when three items were presented, $t(9) = 3.96, p < .001$. Note that the average performance in the two item conditions is higher than the threshold used to determine the exposure duration, 79%. This is likely due to the increased temporal certainty in the main experiment compared to the threshold determination experiment, i.e. the exposure duration during the threshold determination experiment varied constantly from trial to trial. In addition, there may have been a practice effect, as observers were more familiar with the stimuli/task during the main experiment.
Interestingly, performance was higher when only two items (as opposed to 3) were presented in the sequential condition, $t(9) = 6.54, p < .001$. To examine whether this was due to information decay resulting from increasing the number of directions which were required to be held in VSTM, performance as a function of the order in which the target item was presented (for match trials) within the sequential three item condition was analysed (mean performance is shown in Figure 5.3). A significant main effect of target presentation order was found, $F(2, 9) = 5.12, p < .05$, demonstrating that observers performed worse at the task when the target was presented earlier in the sequence. This indicates that the reduction in performance between two and three items presented sequentially was, at least partially, due to the information decay of older items. This is surprising given that storing three motion directions is within the capacity of VSTM (Blake, Cepeda, & Hiris, 1997) and no difference in performance was found between
targets presented first and second in the corresponding two item condition $t(9) = 1.55, p > .05$.

The results show that parallel consolidation of motion direction information from sensory to VSTM is possible and suggest that this process is limited to two items. Indeed, if observers were only capable of consolidating two items during the three item/simultaneous presentation condition, with the exception of trials where one of the consolidated items was probed (0.33), all other trials would be performed at chance because it would be unknown whether the probed item was the missed item or not. Thus, the expected performance level would be equal to the product of mean performance in the two item condition and the proportion of trials where the consolidated items were probed ($0.91 \times 0.33 = 0.30$), plus the product of chance performance and the remaining proportion of trials ($0.5 \times 0.66 = 0.33$), i.e. 63%. Given that performance in the three item/simultaneous condition is not significantly different from this value, $t(9) = 1.76, p > .05$, the results support this interpretation.

Experiment 1 demonstrated that two motion directions can be consolidated in parallel from sensory to VSTM. Given that evidence suggests that the perceptual space available to direction is equivalent to orientation, this finding is inconsistent with the

![Figure 5.3. Mean performance across observers within the 3 item sequential condition (match trials) of Experiment 1 as a function of target item presentation order. Error bars indicate ±1 SEM.](image)
claim that the incapacity to consolidate orientation information in parallel is due to its relatively smaller (than colour) perceptual space. However, given that the physical range of directions is twice that of orientation, caution must be taken when comparing the perceptual spaces of these features. This finding appears to be inconsistent with the claim that the size of the information bandwidth required to encode orientation is responsible for the inability to consolidate this feature in parallel (Miller, et al., 2014), as the information bandwidth required to encode motion is likely the same as if not larger than orientation, e.g. to extract motion direction information must be pooled over both space and time.

However, in addition to using motion direction (as opposed to orientation) to examine parallel consolidation, another potentially important difference relating to the presentation of items may have been responsible for the distinct results found here. That is, spatial attention, which allows localized enhancement of perceptual processing (Lee, Itti, Koch, & Braun, 1999), was facilitated through the use of consistent item locations. In contrast, Becker, et al. (2013) presented orientation items randomly in four possible locations. If consolidating information in parallel results in reduced resolution of encoded information, when information encoded serially is already encoded at high resolution, facilitation of spatial attention may be more beneficial for parallel than serial consolidation. Liu and Becker (2013) found no evidence for this interpretation, their results indicating that when presented with two orientation items simultaneously, observers consolidated one item at high resolution and failed to consolidate the other. However, the task used in their experiment required observers to respond with the precise orientation of a single probed item, which may have resulted in observers using a single consolidation strategy rather than consolidating two items at low resolution. In contrast, the resolution required to complete the task in the current experiment is considerably
lower, possibly encouraging the employment parallel consolidation, at the cost of resolution.

Given the relative proximity of feature intervals used to define targets by orientation and direction compared to colour, the susceptibility to interference of information encoded at reduced resolution is greater for these types of information. Thus, while it may not be necessary to consolidate colour in parallel, facilitation of spatial attention may be required to achieve this with motion direction and orientation information. Experiment 2 investigates whether these explanations account for the ability to consolidate direction information in parallel.

5.4. Experiment 2: Effects of spatial attention and feature interval separation

Becker, et al. (2013) found that observers were not capable of consolidating orientation information in parallel, which contrasted with their previous finding indicating that this was possible using colour information (Mance, et al., 2012). To account for this discrepancy the authors proposed that the size of the perceptual space afforded to orientation, considerably smaller than that of colour, may have resulted in interference between the two items, preventing parallel consolidation. The results of Experiment 1 would appear to be inconsistent with this account, given that evidence indicates the perceptual space of motion and orientation are equivalent (Clifford, 2002). However, although adaptation/discrimination studies suggest that the perceptual spaces of these features are equivalent, it is possible that motion direction has a larger perceptual space, afforded to it by its wider physical range, which allows direction to be consolidated in parallel where orientation cannot. Alternatively, spatial attention may have been facilitated in Experiment 1 by presenting items in consistent locations, i.e. observers
could anticipate the location of items being presented and direct their attention to those locations, and this may be necessary to achieve parallel consolidation of direction information. Here we explore these two possibilities by a) reducing the range of motion directions used in the task and b) increasing the spatial ambiguity of targets, using the same design as Becker, et al. (2013), i.e. presenting the targets pseudo-randomly in four possible locations. If either of these factors plays a significant role in parallel consolidation, this should result in differential performance compared to that found in Experiment 1.

5.4.1. Method

5.4.2. Observers

Ten observers participated in the study: one of the authors (RR) and nine others who were naive with respect to the aims of the study. All had normal or corrected to normal acuity and gave informed written consent to participate in the study.

5.4.3. Stimuli and procedure

The stimuli and procedure were largely the same as that used in Experiment 1. Given that we found observers were only capable of parallel consolidation with two items in Experiment 1, here we only compared performance between sequential and simultaneous presentation using two items.

To examine whether parallel consolidation is possible when the physical range of directions used is reduced to that available to orientation (180°), a condition was run where the directions used were changed from the four diagonals to 0°, 45°, 90°, and 135°, where 0° was represented by leftward motion. To investigate whether spatial certainty is
necessary to achieve parallel consolidation, another condition was run where the targets were randomly presented in two of four possible locations on each trial, as opposed to the same locations on every trial. The four possible target locations were on the corners of an imaginary square (12° × 12°), centred on fixation. Thus, the experiment was a 2 × 2 design (simultaneous/sequential presentation × reduced range/spatial uncertainty). The same stimuli and procedure used in Experiment 1 was employed to determine observers’ minimum threshold duration. Examples of the presentation sequences used in the spatial uncertainty conditions are shown in Figure 5.4.

![Figure 5.4](image)

**Figure 5.4.** Examples of the stimuli used in the spatial uncertainty condition of Experiment 2. A) An example of the presentation sequence in the simultaneous condition (match trial). B) An example of the presentation sequence in the sequential condition (mismatch trial). The black arrows in the motion sequence and probe frames have been added to illustrate the motion direction of the blobs.

### 5.4.4. Results and discussion

The average threshold duration was 64ms (range 32 – 192ms, SD = 56ms). In the main experiment, a similar pattern of results was found for all observers; mean
PARALLEL PROCESSING IN THE HUMAN VISUAL SYSTEM

performance across all observers is shown in Figure 5.5. While performance for items presented sequentially was significantly better in the reduced range condition, $t(9) = 4.16$, $p < .01$, no difference was found between sequential or simultaneous presentation in the spatial uncertainty condition, $t(9) = 0.31$, $p > .05$.

![Figure 5.5](image)

Figure 5.5. Mean performance across observers in Experiment 2 for each presentation type (simultaneous & sequential) as a function of the condition (reduced range & spatial uncertainty). Error bars indicate ±1 SEM.

These results could be interpreted as indicating that reducing the range of directions presented resulted in an inability to consolidate items in parallel, while increasing the spatial uncertainty of item presentation did not. However, by applying the same logic used in Experiment 1 to predict performance based on the number of items consolidated, it is clear that even in the condition where performance was the lowest (reduced range/simultaneous) the mean was still significantly higher than the most conservative estimate of performance assuming a single item was consolidated at 100% accuracy, i.e. 62.5%, $t(9) = 3.87$, $p < .01$. Thus, a more likely interpretation of the results is that in both the simultaneous conditions parallel consolidation was possible.

The results show that by reducing the range of feature intervals used to define items, parallel consolidation was significantly more adversely affected than serial consolidation. This suggests that the perceptual space of direction may not be equivalent to that of orientation, despite proportional discrimination thresholds and tuning
bandwidths, and that this may explain the difference in performance between serial and parallel consolidation for orientation information found by Becker, et al. (2013). The finding that a combination of orientation and colour information cannot be consolidated in parallel appears to be inconsistent with this interpretation (Miller, et al., 2014); however, the increased complexity of consolidating different types of information may introduce additional restrictions unrelated to perceptual space size. For example, in visual search, while search for a single feature is a parallel process, search for a conjunction of features is restricted to serial processing (Treisman, 1982). In contrast, increasing spatial uncertainty had an equivalent effect on serial and parallel consolidation. This effect is illustrated by the significantly lower performance in the spatial uncertainty condition than in the two item condition of Experiment 1, both of which can be collapsed across presentation type conditions due to their similarity, \( t(19) = 3.45, p < .01 \).

Experiment 2 demonstrated the importance of adequate feature interval separation for parallel consolidation and equivalent effect of spatial attention on both serial and parallel consolidation. Experiment 3 investigates whether parallel consolidation of orientation information can be achieved when spatial attention is facilitated.

### 5.5. Experiment 3: Parallel consolidation of orientation

Two factors influence the degree of decision uncertainty when comparing representations held in VSTM to a probed item: the separation between feature intervals used to define items and the resolution of the representations held in VSTM. If separation is relatively small and the resolution of representations is low, the probability of mistaking one item held in VSTM as a neighbouring item is increased. Physiological and

---

9 However, see Wolfe, Cave and Franzel (1989) for a discussion of example that represent exceptions to this notion.
psychophysical studies show that spatial attention locally enhances information processing by increasing the signal gain of a stimulus (Luck, Chelazzi, Hillyard, & Desimone, 1997; McAdams & Maunsell, 1999), resulting in higher resolution encoding. Thus, if poorer recall performance when orientation information is presented simultaneously, rather than sequentially, is due to a combination of inadequate feature interval separation and low resolution encoding, facilitation of spatial attention may overcome this by narrowing the signals’ bandwidths and increasing the resolution of the encoded items. However, if it is due to the size of the region from which information must be pooled in order to encode a meaningful signal, i.e. information bandwidth, increasing the resolution of this information by facilitating spatial attention should not overcome this.

5.5.1. Method

5.5.2. Observers

Ten observers participated in the study: one of the authors (RR) and nine others who were naïve with respect to the aims of the study. All had normal or corrected to normal acuity and gave informed written consent to participate in the study.

5.5.3. Stimuli and procedure

The stimuli and procedure were similar to that used in the previous experiment, except now instead of moving dots, the items presented to observers were sinusoidal gratings (contrast, 0.7; spatial frequency, 1 cycles/deg) within a circular aperture (4° radius). The edge of the aperture was smooth, leaving no sharp contrast between target and background. The gratings had four possible orientations: 0°, 45°, 90°, and 135°, where 0° was horizontal. The mask was a circular aperture (4° radius) containing pixel
noise of random luminance levels with a uniform distribution (0 – 63 cd/m²). An example of an orientation stimulus and mask are shown in Figure 5.6.

![Figure 5.6. An example of an orientation stimulus (left) and mask (right) used in Experiment 3.](image)

To investigate whether facilitation of spatial attention would improve performance during parallel consolidation of orientation information, two conditions were employed: a condition where items were presented in one of four possible locations and another where items were always presented in the same two locations. The presentation locations used in the spatial uncertainty condition here were the same as those in Experiment 2, whereas only the upper left and right locations were used in the spatial certainty condition. Across all conditions, only two items were presented. Thus, the experiment was a $2 \times 2$ design (simultaneous/sequential presentation $\times$ spatial un/certainty). The stimuli described above and the procedure used in Experiments 1 and 2 was employed to determine observers’ minimum threshold duration.

5.5.4. Results and discussion

The average threshold duration was 32ms (range, 16 – 112ms; SD, 18ms). In the main experiment a similar pattern of results was found for all observers; mean performance across all observers is shown in Figure 5.7. A repeated measures ANOVA
revealed main effects of both spatial (un/certainty) and presentation (sequential/simultaneous) conditions, $F(1, 9) = 5.78, p < .05$ and $F(1, 9) = 5.56, p < .05$ respectively, and a significant interaction effect, $F(1, 9) = 13.84, p < .01$. While performance was better in the spatial certainty condition for items presented simultaneously, $t(9) = 3.14, p < .05$, no difference was found between the conditions when items were presented sequentially, $t(9) = 0.16, p > .05$. However, this is likely due to a ceiling effect in the sequential conditions. Performance for items presented sequentially was significantly better in the spatial uncertainty conditions, $t(9) = 2.75, p < .05$, while no difference was found between sequential or simultaneous presentation in the spatial certainty condition, $t(9) = 1.54, p > .05$.

Figure 5.7. Mean performance across observers in Experiment 3 for each presentation type (simultaneous & sequential) as a function of the condition (spatial un/certainty). Error bars indicate ±1 SEM.

One interpretation of these results is that parallel consolidation was possible in the spatial certainty condition but not in the spatial uncertainty condition, and thus facilitation of spatial attention overcame the inability to consolidate orientation information in parallel. However, for the same justification provided in Experiment 2, it is more likely that even in the spatial uncertainty condition parallel consolidation was achieved, i.e. performance is significantly higher than the predicted accuracy for
consolidation of a single item, $t(9) = 4.68, p < .01$. Thus, a more fitting interpretation of the results is that orientation information that is consolidated in parallel is encoded/stored at a lower resolution than when consolidated serially, but that facilitation of spatial attention can mitigate the effect of this by enhancing the resolution of items at the encoding stage. Note that while Mance, et al. (2012) found no evidence for an advantage of simultaneously presenting items in the same or different hemifields using colour, it is possible that spatial attention was, at least partially, facilitated here by presenting items in different hemifields (Alvarez & Cavanagh, 2004; Delvenne & Holt, 2012), as opposed to by reducing spatial ambiguity.

5.6. General discussion

Our main findings indicate that both motion direction and orientation information can be consolidated from sensory to VSTM in parallel. Experiment 1 demonstrated that multiple directions can be consolidated in parallel and indicated that this process is limited to two items. Experiment 2 showed that adequate separation between feature intervals used to define items, and thus the size of the perceptual space, is more important for parallel than serial consolidation. Finally, Experiment 3 demonstrated that orientation information can be consolidated in parallel and that facilitation of spatial attention can be used to improve performance of parallel consolidation.

It appears that the capacity for parallel consolidation does not vary as a function of type of information. That is, while previous research has shown that colour can be consolidated in parallel, and suggested that orientation cannot, here we provide powerful evidence indicating that both motion direction and orientation can be also consolidated in parallel.
Rather than a model that excludes certain features from parallel consolidation due to their informational bandwidth (Miller, et al., 2014), our results indicate the heightened importance of feature interval separation during parallel consolidation, compared to serial consolidation. The finding that facilitating spatial attention mitigated the effects of inadequate feature interval separation suggests that items consolidated in parallel are encoded at a lower resolution than those consolidated serially. That is, by spreading cognitive resources to consolidate two items in parallel, the items become encoded at a lower resolution than if all resources were used to process a single item; consistent with our previous study that found the capacity of motion processing varies as a function of the detail of information extracted (Rideaux & Edwards, 2014). Items encoded at a lower resolution have an increased susceptibility to being mistaken for neighbouring items along a feature dimension, especially when the separation between intervals used to define items along that dimension is small. This results in greater uncertainty during the comparison stage of the task and subsequently reduces performance. However, by facilitating spatial attention, which locally enhances processing, the resolution of encoded items is increased, mitigating this effect.

If reduced resolution encoding is a limiting factor on the capacity/effectiveness of parallel consolidation, this may explain why colour appears to be consolidated more effectively than orientation. That is, recent evidence suggests that colour may be consolidated in a qualitatively different way than orientation, such that its representations are not subject to resolution degradation (Ye, Zhang, Liu, Li & Liu, 2014). Future research could explicitly address this question by measuring parallel consolidation performance with a reduced range of colours, e.g. red/yellow/orange.

This interpretation conflicts with Liu and Becker (2013), who directly examined this possibility and found evidence for a strictly serial, high resolution consolidation mechanism for orientation. However, in addition to spatial ambiguity of item
presentation, in their study a high resolution representation was required to perform the task, i.e. indicating the orientation of an item drawn from a set of items separated by $14^\circ$ increments, here the task could be performed with a low resolution representation. Thus, these distinct task demands may have led observers to employ different strategies; high resolution serial processing to perform the task in the Liu and Becker (2013) study and low resolution parallel consolidation here. Clearly, further research is required to determine the impact of task demands on the employment of parallel consolidation.

Importantly, we believe that a significant difference between recall performance when orientation information is presented sequentially and simultaneously is not necessarily accounted for by an inability to consolidate this information in parallel. Rather, the evidence indicates that parallel consolidation of orientation information is possible, but that the resolution of items suffers.
Chapter 6. The cost of parallel consolidation of orientation and motion direction into visual working memory

6.1. Context statement

Results from the experiments described in Chapter 5 indicate that there is a cost associated with consolidating information into VSTM in parallel, compared to serially. The experiments reported in the current chapter extend these findings by explicitly examining the cost of parallel consolidation. Note that this chapter appears in print as:


6.2. Introduction

While our environment is visually rich, only a small proportion of the information that enters the retina is stored as a durable representation. Information is initially stored
in sensory (iconic) memory, which is characterized as high capacity memory whose contents decay within a few hundred milliseconds (Sperling, 1960, 1963). Following this, a small proportion the information stored in sensory memory is transferred to visual working memory (VWM), aka visual short-term memory (Cowan, 2001, 2010). While determining the precise capacity of VWM, and the nature of this capacity, has been the focus of a vast number of studies (for a review, see Ma, Husain, and Bays, 2014), another important aspect of VWM that has been drawing progressively more attention is the process of consolidation, i.e. the formation of VWM representations.

Initially, research suggested that consolidation of information into VWM was restricted to serial processing, i.e. only one item could be consolidated at a time (Huang, Treisman, & Pashler, 2007). However, recently several studies have found evidence indicating that parallel consolidation of colour is possible, albeit restricted to two or three items (Mance, Becker, & Liu, 2012). While initially it was suggested that the capacity to consolidate information in parallel may be limited to colour (Becker, Miller, & Liu, 2013; Liu & Becker, 2013), we recently found compelling evidence that it is also possible with motion direction, and some evidence to suggest it may even be possible with orientation, at different levels of accuracy (Rideaux, Apthorp, & Edwards, 2015). One potential explanation we flagged for this difference in accuracy is that the precision of items consolidated in parallel (compared to serially) is reduced.

In our previous study, a matching task was employed in which observers were presented with a number of items and then required to indicate whether a subsequently presented item was among them (present) or not (absent) (Rideaux, et al., 2015). We found that performance was the same for two motion direction items presented sequentially or simultaneously. However, when the range of items used was reduced from 360° to 180°, while serial consolidation performance remained the same, parallel consolidation suffered. We then examined performance on the task using orientation and
found it was similar to that in the second reduced range motion direction condition; worse in the simultaneous condition, yet better than predicted by purely serial consolidation.

To account for these findings, we proposed that items consolidated in parallel may be encoded at a lower precision than those consolidated serially, and that the difference in performance between sequential vs. simultaneous conditions reflects an interaction between this reduction in precision and the similarity of items within a relatively small perceptual space. That is, as the precision of encoded representations relative to the separation of items along a feature dimension is reduced, the probability of them being mistaken for neighbouring items (during the decision stage of the task) is increased. In line with this, Umemoto, Drew, Ester, and Awh, (2010) found evidence that the precision of multiple (4) orientation items was reduced when presented simultaneously (relative to sequentially). However, the authors were not explicitly controlling for serial consolidation and given the exposure duration (300ms) and lack of backward masking in their experiment, observers likely employed a serial strategy even in the simultaneous condition. The notion of a cost associated with processing multiple items is not unusual; in the motion processing literature the cost associated with processing two (or more) motion direction signals simultaneously (relative to one signal) is well established (Edwards & Greenwood, 2005; Edwards & Rideaux, 2013; Qian, Andersen, & Adelson, 1994; Rideaux & Edwards, 2014).

However, another potential source of error which may account for the poorer performance observed in the simultaneous condition on the matching task may have been an increase in consolidation failure. A number of studies have demonstrated that when items are presented simultaneously, as opposed to sequentially, competition between items can result in consolidation failure (Ihssen, Linden, & Shapiro, 2010a; 2010b; Scalf
& Beck, 2010). Indeed, such findings have prompted the claim that this competition is directly responsible for the capacity of VWM, i.e. the biased competition model of VWM (Shapiro & Miller, 2011), and are supported by neuroimaging studies which show a reduced BOLD signal when items are presented simultaneously compared to sequentially (Beck & Kastner, 2007; Kastner & Ungerleider, 2001).

Originally proposed by Desimone and Duncan (1995) to explain the capacity of visual selective attention, the general principle of the biased competition model is that items within the visual field compete for representation within the limited capacity of regions (aka content maps) in the visual cortex. These regions can be conceptualized as two-dimensional areas of the cortex with coherent spatial organization where the preferred stimuli of neurons change smoothly from one location to the next, e.g. area MT where neurons vary in motion direction selectivity (Albright, Desimone, & Gross, 1984). According to this account, a number of factors moderate the degree of competition between items including the size of the receptive fields in visual areas, the number of items, item similarity, and item spatial proximity (Franconeri, et al., 2013; Kastner & Ungerleider, 2001). In contrast to unlimited parallel models that claim no loss of accuracy or increased consolidation failure, e.g. the consolidation bandwidth model (Miller, Becker, & Liu, 2014), this model would predict that the likelihood of consolidation failure may increase when items are presented simultaneously.

In summary, there are two potential sources of error that may account for poorer performance on a matching task when items are presented simultaneously, compared to sequentially: the precision of encoded items may be reduced and/or the likelihood of consolidation failure may be increased. The most compelling evidence for parallel consolidation is a reduction in the precision of encoded items. In contrast, strict serial consolidation would predict no change in precision and an inability to encode more than
one item on each trial, i.e. a 50% consolidation failure rate. However, a mixture of these resulting from parallel consolidation can also be explained, under a biased competition framework. Here we explicitly examine the sources of error, in terms of precision and consolidation failure, associated with attempting to consolidate motion direction and orientation in parallel. Although we found partial evidence to indicate that orientation can be consolidated in parallel, this conflicts with previous findings (Liu & Becker, 2013); thus, this test will also serve to clarify whether there is a flexible time-accuracy trade-off associated with parallel consolidation, i.e. reduced precision, or if one or both of these features are strictly limited to serial processing, i.e. increased (50%) consolidation failure.

### 6.3. Experiment 1: The cost of parallel consolidation

We previously found evidence suggesting that that both orientation and motion direction information can be consolidated into VSTM in parallel (Rideaux, et al., 2015). Furthermore, the results suggested that items consolidated in parallel are encoded at a lower resolution than those consolidated serially, which may account for the differential performance of parallel consolidation observed for different types of information. Here we explicitly examine the source of error associated with attempting to consolidate these features in parallel to determine whether there is a cost to the resolution of items encoded in parallel, or if they are limited to serial processing.

### 6.3.1. Method

### 6.3.2. Observers
Twenty-four observers participated in the study (mean age, 22). All had normal or corrected to normal acuity and gave informed written consent to participate in the study. All observers were compensated $20 for participation.

6.3.3. Apparatus

Experiments were run under the MATLAB (version R2013a) programming environment, using software from the PsychToolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on a Phillips Brilliance 202P4 CRT monitor that was driven by an Intel Iris graphics card in a host MacBook Pro computer. The monitor had a spatial resolution of 1024 x 768 pixels and a frame rate of 120Hz.

6.3.4. Stimuli

The stimuli and procedure were similar to those employed by (Liu & Becker, 2013). A 2 x 2 experimental design was used: presentation (sequential/simultaneous) x feature (orientation/motion direction). The general presentation sequence consisted of a stimulus interval/s followed by a cue, and then a response interval. In each stimulus interval two items were either presented sequentially or simultaneously (40ms) followed by a mask (200ms) to prevent further processing from iconic memory. This exposure duration was chosen as it is approximately the average duration required to consolidate a single item, or two items in parallel (Mance, et al., 2012; Rideaux, et al., 2015). Items presented sequentially were separated by a 500ms inter-stimulus interval (ISI) where only the fixation cross was present. Items/masks were presented 8° (visual angle) to the left and right of fixation, with the left item always presented first in the sequential condition.
In the orientation condition the stimuli were Gabors (contrast, 0.7; spatial frequency, 1 cycles/°; random phase) within a Gaussian envelope (4° radius) and the mask was pixel noise of random luminance levels with a uniform distribution (0 – 63 cd/m²) within a circular aperture (4.2° radius). In the motion direction condition stimuli consisted of 100 Gaussian blobs (0.3° radius), to allow sub pixel resolution movement, within a circular aperture (4° radius), which wrapped around when they reached the edge of the aperture. The blobs were displaced 0.082° each frame, resulting in a speed of 9.8°/s. The mask in this condition consisted of 300 Gaussian blobs within a circular aperture (4.2° radius), positioned randomly on each frame, creating a percept of dynamic noise. The orientation/direction of each pair of items were determined pseudo-randomly from between 0-179° and 0-359°, respectively, with the constraint that they must be separated by at least 15°.

The stimulus interval/s and cue were separated by a 500ms ISI. The cue consisted of a white circle (500ms) presented in the location of one of the items. The location was determined pseudo-randomly such that the cue appeared in each location an equal number of times. Finally, the cue was followed by a response interval consisting of either a Gabor, identical to those used in the stimulus interval, (orientation condition) or an arrow (length 6°) extending from fixation (direction condition). During the response interval, the cursor became visible and the orientation/direction of the Gabor/arrow could be manipulated by moving the mouse. Examples of the presentation sequence are illustrated in Figure 6.1.
Figure 6.1. Examples of the presentation sequence used in Experiment 1. An example of a) simultaneous presentation of orientation items and b) sequential presentation of motion direction items.

The background was grey (mean luminance, 12 cd/m²) and the blobs in the motion condition were white (mean luminance, 63 cd/m²). The observer sat 50 cm from the monitor, with their head supported on a chin rest.

6.3.5. Procedure

The observer’s task was to match the orientation/direction of the Gabor/arrow in the response interval to that of the cued item in the preceding stimulus interval. No duration limit was used to restrict responses, once the observer had moved the Gabor/arrow with the mouse to the orientation/direction they believed matched that of the cued item, they would left-click to indicate their response and initiate the next trial. Observers were instructed to maintain fixation throughout the presentation sequence and to remember both items in order to perform the task accurately.
Observers were randomly split into two groups; half were run in the orientation condition and the other half in the direction condition. Initially, observers spent approximately 10min performing the task without recording data, in order to familiarize them with the stimuli/task. Following this, each observer ran six blocks of each presentation condition, i.e. sequential/simultaneous, randomly interleaved within a mega block. Each block consisted of 50 trials, totalling 1200 trials and an approximate testing duration of one hour per observer.

6.3.6. Data analysis

For each trial, the offset (error) was calculated by subtracting the orientation/direction recorded from the observer’s response from that of the cued item. Initially, the raw mean and variance of the offset was analysed for each participant. However, there are two sources of variability within the offsets, resulting from two types of trials. One where the observer successfully consolidates the cued item into VSTM, resulting in a normal distribution of offsets with a mean (μ) and standard deviation (σ). The other where they fail to consolidate the item and must guess (g), resulting in a rectangular or even distribution. Thus, in order to examine whether there is a (resolution) cost associated with parallel consolidation, a mixture model must be fit to the offset data to isolate these sources of variation. A model was fit to individual offset data within each feature condition using a standard maximum-likelihood method. Data analysis was performed using the MemToolbox (Suchow, Brady, Fougnie, & Alvarez, 2013).

6.3.7. Results
6.3.8. Descriptive statistics

The raw offset data for orientation and motion direction was analysed separately for bias (mean) and variability (variance) using a one-way repeated measures analysis of variance (ANOVA). One observer (in the orientation condition) reported being unable to perform the task even in the sequential condition; their data reflected this (flat distribution of offsets) and was omitted from analysis. The mean of the offset data was equivalent between presentation conditions for both orientation and direction, \( F(1,10) = .1 \) & \( F(1,11) = .3 \), respectively, and one-sample t-tests revealed that none of the means differed significantly from zero (all \( p > .17 \))(Fig. 6.2a). In contrast, variance differed considerably between conditions (Fig. 6.2b), however because it was not normally distributed, this was transformed by taking the logarithm prior to analysis. The log variance differed significantly between conditions for both features, \( F(1,10) = 13.3 \ p < .01 \) (orientation) & \( F(1,11) = 9.0 \ p < .05 \) (direction)(Fig. 6.2c). These results show that the offset between target and response orientation/direction was more variable when items were presented simultaneously than sequentially. This pattern of results was highly consistent across individual participants (Figs. 6.2e & 6.2d).
Figure 6.2. Experiment 1 raw offset data. The (a) grand-average offset between target and response orientation/direction, (b) average variance in offset, and (c) average log variance in offset. Data from sequential and simultaneous conditions are represented by light and dark grey bars, respectively, in (a), (b) and (c), error bars in (a) and (c) represent ±1 SEM. Scatterplots (d) and (e) show individual observer variance in the simultaneous condition as a function of variance in the sequential condition; circles and squares represent observers in the orientation and motion direction conditions, respectively. Points above the dotted line indicate higher variance in the simultaneous condition relative to the sequential condition.

6.3.9. Model fit

A mixed model was fit to individual observer’s data and statistical analysis was performed on model parameters to evaluate how the guess rate (g) and standard deviation (σ) of responses varied between sequential and simultaneous presentation of items. The
Bayesian information criterion (BIC) was used to compare the fit of three types of mixed models: standard mixture model, variable precision model, and swap model. While a standard mixture model assumes precision remains constant, a variable precision model assumes precision is normally distributed and calculates its mean and standard deviation (Fougnie, Suchow, & Alvarez, 2012). In addition to partitioning sources of variance into guess rate and precision, like the former two models, a swap model isolates a third potential source of variation: responses made based on the orientation/direction of the non-target item (Bays, Catalao, & Husain, 2009). A standard mixture model was used as it was found to fit individual observer data better than the variable precision and swap models (standard mixture model BIC scores were lowest for over 90% of data sets [supplementary material]). In the VWM storage literature, studies conducting more systematic model comparisons have tended to reject the mixture model in favour of other models, e.g. swap and variable precision (Fougnie, et al., 2012; Van den Berg, Awh, & Ma, 2014; Sims, 2015). Here, the rejection of these models in favour of the mixture model may reflect differences in the nature of the cognitive process being investigated: VWM consolidation, as opposed to storage.

Model fit was evaluated using Kolmogorov-Smirnov (K-S) tests, revealing that the standard mixture model fit the data well (all ps > .3). This model decomposes data into a mixture of parameters that are characterized by either a uniform or von Mises distribution of errors (Zhang & Luck, 2008). Note that although we found a mixture model fit the data best, we cannot rule out that a proportion of the responses categorized as guesses were actually a result of spatial binding errors (swapping), simply that this proportion was not sufficiently large enough to tip the balance in favour of the swap model during model comparison. Both the guess rate (g) and standard deviation (σ) parameters significantly increased from sequential to simultaneous presentation for
orientation, \( t(10) = 3.4 p < .01 \) & \( t(10) = 2.3 p < .05 \), and direction, , \( t(11) = 2.7 p < .05 \) & \( t(11) = 3.6 p < .01 \), respectively (Fig. 6.3). Note that the standard deviation (\( \sigma \)) parameter is an inverse measure of precision, i.e. higher values indicate poorer precision.

![Figure 6.3](image1)

**Figure 6.3.** Experiment 1 model parameter analysis. The average (a) guess rate (\( g \)) and (b) standard deviation (\( \sigma \)) model parameters of observers in sequential/simultaneous conditions for orientation and motion direction. All error bars indicate ±1 SEM.

Given the average retention interval, i.e. the duration between each item exposure and the response interval, was less in the simultaneous (1200 ms) than the sequential condition (1550 ms), these results must be due to processes impacted at the consolidation stage, not during storage. This is further evidenced by the similarity across all parameters between models fit to the trials where the cued item was in the first compared to the second interval, in the sequential condition, for both features (all ps > .05).

6.3.10. Discussion

The increased rate of guessing found in the simultaneous conditions across both features suggests that observers may not have been capable of parallel consolidation of these features. However, the guess rate in these conditions is smaller than that predicted by a strictly serial consolidation strategy (i.e. 50%). Two possible explanations could account for this result. Either observers are capable of performing parallel consolidation of these features, but incur an increased likelihood of consolidation failure as a result, or
observers are not able to consolidate items in parallel but the exposure duration employed allowed them to serially consolidate a second item on a number of trials. The exposure duration used in Experiment 1 (40ms) was less than that used in a previous study in which the authors claimed the duration was sufficiently short to prevent serial consolidation of more than one item (150ms)(Liu & Becker, 2013). Thus, is seems surprising that observers would have been capable of serially consolidating items in the simultaneous conditions here. However, given that the average guess rate in the sequential conditions is around 5%, it is possible that the difference in guess rate between the sequential and simultaneous conditions may have been underestimated due to a ceiling effect in the sequential conditions.

The reduced precision found in the simultaneous conditions is compelling evidence that observers were employing parallel consolidation, and as a result, items were encoded at a lower resolution. It is likely that this is due to spreading of cognitive resources employed during consolidation. However, another potential mechanism for this resolution loss concerns the spatial attention that can be employed to enhance processing of the items during encoding. That is, given that the order and location of item presentation was consistent through the experiment, observers may have been making covert attentional shifts to the locations of the items in the sequential condition. In contrast, in the simultaneous condition attention would be spread across the two locations, resulting in less effective facilitation of spatial attention (Castiello & Umiltà, 1992; Eriksen & Yeh, 1985). This would explain why in previous studies, where the location of presented items was randomized, no difference in precision was found (Liu & Becker, 2013; Miller, Becker, & Liu, 2014).

The current results provide partial evidence that both orientation and motion direction can be consolidated in parallel; that is, the difference in guess rate is less than
would be predicted by a serial consolidation strategy and, more importantly, modulation of precision between sequential and simultaneous conditions was found, indicating loss of resolution resulting from parallel consolidation. However, the difference in guess rate between sequential and simultaneous conditions may have been underestimated due to an overly long exposure duration, and the modulation of precision may have been due to facilitation of covert attentional shifts in the sequential conditions. Experiment 2 was run to investigate these possibilities.

6.4. Experiment 2: Parallel consolidation of orientation and motion direction

Although the modulation in precision found between presentation conditions in Experiment 1 suggests that observers were performing parallel consolidation of orientation and motion direction, this may have been a result of covert attentional shifts in the sequential condition. To examine this possibility we will compare precision between fixed and random sequential presentation. If the difference in precision is due to covert attention, we should observe better precision in the fixed sequential condition, compared to the random sequential condition. However, if it is due to parallel consolidation, we would expect that precision in the simultaneous condition will be less than in both sequential conditions.

Furthermore, the magnitude of the difference in guess rate between the sequential and simultaneous conditions in Experiment 1 may have been underestimated. That is, there may have been a ceiling effect in the sequential condition due to an overly long exposure duration, which may also have resulted in observers employing serial consolidation in the simultaneous condition. Here we investigate this possibility by tailoring the exposure duration of the stimuli to each individual, in order to bring
performance in the sequential condition to threshold and ensure serial consolidation cannot be used in the simultaneous condition.

6.4.1. Method

6.4.2. Observers

Twenty-four observers participated in the study (mean age, 22). All had normal or corrected to normal acuity and gave informed written consent to participate in the study. All observers were compensated $20 for participation.

6.4.3. Stimuli and procedure

The stimuli and procedure were the same as that used in Experiment 1, with a few notable exceptions. To examine whether the difference in precision found between sequential and simultaneous conditions in Experiment 1 resulted from spreading (or splitting) of attention in the simultaneous condition, here we ran two sequential presentation conditions: one with fixed presentation order (replicating Experiment 1) and one with randomized presentation order.

In order to calibrate the exposure duration of the stimuli such that performance would be closer to threshold in the sequential condition, and thus examine the possibility that the difference in guess rate between sequential and simultaneous conditions in Experiment 1 was underestimated, a threshold exposure duration was determined for each observer before running the main experiment. The threshold exposure duration stimuli and procedure were the same as those used in the sequential condition of the main experiment, except that now an adaptive staircase procedure was employed using software from the Palamedes Toolbox (Prins & Kingdom, 2009), varying the exposure duration of the items. The staircase uses a “psi-marginal” adaptive method, based on
Kontsevich and Tyler’s (1999) psi-method, which allows any of the four parameters of the psychometric function to be treated as a parameter of primary interest, a “nuisance” parameter, or a fixed parameter (Prins, 2013). Responses were considered correct if they were within 30° of the target orientation/direction (i.e. ~± 2 SD of the precision found in Experiment 1). This resulted in a chance level of .33 and .16 for orientation and direction, respectively; thus, the threshold performance levels used were .66 and .58, respectively.

Here, as in Experiment 1, observers were randomly split into two groups; half were run in the orientation condition and the other half in the direction condition. Initially, observers’ exposure duration threshold was determined using the previously reported staircase procedure. Following this, each observer ran six blocks of each presentation condition (i.e. fixed/random sequential & simultaneous) randomly interleaved within a mega block. Each block consisted of 50 trials, totalling 900 trials and an approximate testing duration of one hour per observer.

6.4.5. Results

6.4.6. Threshold exposure duration

The average threshold duration was 43.3ms (range, 16 - 88ms; SD, 20.6ms) for orientation and 89.3ms (range, 40-160ms; SD, 40.1ms) for direction. This is similar to the exposure duration for these features found in previous studies (Becker et al., 2012; Rideaux, et al., 2015).

6.4.7. Descriptive statistics
The raw offset data for orientation and motion direction was analysed separately for bias and variance using a one-way repeated measures ANOVA. Because it was not normally distributed, variance was transformed by taking the logarithm prior to analysis.

No main effects of mean or log variance were found for orientation between the three presentation conditions, \( F(2,11) = .4 \ p = .69 \) & \( F(2,11) = 2.9 \ p = .08 \), respectively (Figs 6.4a & 6.4b). While no main effect of mean was found for direction, \( F(2,11) = .4 \ p = .66 \), a significant main effect of log variance was found, \( F(2,11) = 28.3 \ p < .001 \), (Figs 6.4c & 6.4d). Thus, while the preliminary results for direction mirror those found in Experiment 1, those for orientation suggest that the offset between target and response was similarly variable between sequential and simultaneous presentation conditions, and between fixed and random sequential presentation conditions.

**Figure 6.4.** Experiment 2 raw offset data. The grand-average offset between target and response and average log variance in offset for orientation (a & b) and direction (c & d), respectively. All error bars represent ±1 SEM.

**6.4.8. Model fit**

To evaluate the differences in guess rate and standard deviation between
presentation conditions, a standard mixture model was fit to individual’s offset data and a one-way repeated measures ANOVA was run on each parameter. Consistent with Experiment 1, a mixture model was used as it was found to fit individual observer data better than the variable precision and swap models (standard mixture model BIC scores were lowest for over 95% of data sets [supplementary material]), and overall the models fit the data well (95% of ps > .05, assessed using K-S tests).

For orientation, no main effect of standard deviation was found, $F(2,11) = 1.3 \ p = .28$, and although precision is poorest in the sequential random and simultaneous conditions, none of the differences between conditions were significance (all ps > 0.15, assessed using paired t-tests) (Fig 6.5a). In contrast, a main effect of standard deviation was found for motion direction, $F(2,11) = 17.6 \ p < .001$, with paired t-tests revealing significant differences between fixed/random sequential and simultaneous conditions, $t(11) = 5.2 \ p < .001$ and $t(11) = 4.7 \ p = .001$, respectively, but no difference between sequential conditions, $t(11) = .1 \ p = .92$, (Fig 6.5c). Thus, these results show that the modulation in precision found in Experiment 1 (at least for motion direction) was not a result of covert attentional shifts, but likely due to spreading of other cognitive resources engaged during consolidation.

Significant main effects of guess rate were found for both orientation, $F(2,11) = 4.2 \ p = .02$, and motion direction, $F(2,11) = 12.3 \ p < .001$, (Fig 6.5b & 6.5d). Paired t-test revealed a similar pattern of results for both features - no significant differences between fixed and random sequential conditions (all ps > 0.15), and differences between sequential and simultaneous conditions were all significant (all ps < 0.05) with the exception of that between random sequential and simultaneous conditions for orientation, $t(11) = 2.1 \ p = .06$. 
Comparative analysis of parameters derived from models fit to the trials where the cued item was in the first or second interval (in the sequential condition) yielded similar results to those found in Experiment 1. That is, no difference between parameters (all ps > .05), with the exception of the standard deviation of orientation in the random sequential condition which increased significantly when the cued item was presented in the second interval, $t(11) = 2.6, p = .02$. In this condition, the spatial location of the first item could not be anticipated, but the location of the second item could, as there were only two possible locations and items were not presented in the same location within a trial. This finding suggests that the capacity to anticipate the location where the orientation item was to be presented worsened the precision at which it was encoded. Alternatively, this finding could suggest that having an existing item stored in VWM reduces the precision of subsequently stored items; however, as this was not replicated in
the fixed condition or the previous experiment, this seems less likely.

6.4.9. Discussion

In Experiment 1, although the average guess rate in the simultaneous condition was significantly below the most conservative estimate predicted by a serial consolidation strategy (50%), it was also significantly higher than the guess rate in the sequential condition. Furthermore, this differential may have been underestimated due to a ceiling effect in the sequential condition, in which the average guess rate was around 5%. That is, while performance indicated observers were capable of parallel consolidation in the simultaneous condition, performance in the sequential condition suggested that the exposure duration may have been sufficient to consolidate more than one item serially. In the current experiment, given that the average guess rate in the sequential conditions is around 15-20%, performance in these conditions cannot reflect a ceiling effect.

For motion direction, the modulation of precision was replicated in Experiment 2. Furthermore, the similarity between precision in the fixed and random sequential conditions demonstrates that this difference is not due to covert attentional shifts. Thus, this is convincing evidence that motion direction can be consolidated in parallel and that as a result, items are encoded at a reduced precision.

In contrast, for orientation, as the result of tailoring the exposure duration to individual observers, precision was not modulated here, as in Experiment 1. Given that no difference in precision was found here between fixed and random sequential presentation, it is unlikely that modulation of precision in Experiment 1 was a result of covert attentional shifts. Rather, it is possible that in Experiment 1, the fixed duration employed allowed (some) observers to serially consolidate two items in the simultaneous presentation consolidation; however, items were consolidated in a shorter duration,
resulting in lower precision encoding. This, in addition to the increased guess rate in the simultaneous condition could indicate that observers are limited to serial consolidation of orientation, consistent with previous research (Liu & Becker, 2013). However, this strategy would predict a guess rate of at least 50%, which is considerably more than what we observed (~25%), showing that on a number of trials observers were capable of consolidating both items in the simultaneous condition.

One possibility is that certain combinations of orientations, e.g. horizontal and vertical, can be consolidated as one item due to their activating higher-level structures, e.g. a cross. Indeed, a number of studies have found evidence supporting summary statistics or hierarchical representations in VWM (Brady & Alvarez, 2010; Brady & Tenenbaum, 2013; Orhan & Jacobs, 2013; Orhan, Sims, Jacobs, & Knill, 2014). To evaluate this possibility, we included the midpoint of orientation/direction items within each trial as a possible swap model ‘distractor’ and compared the fit of this new “averaging model” with the standard mixture model. No evidence was found that the averaging model could explain the data better than the standard mixture model (mixture model BIC scores were lowest for over 99% of data sets in Experiments 1 and 2 [supplementary material]), thus it seems unlikely that these results can be accounted for by hierarchical representations/summary statistics.

Alternatively, the results may indicate that orientation, like motion direction and colour, can be consolidated in parallel, but suffers an increased likelihood of consolidation failure as a result of simultaneous presentation. Indeed, it is interesting that for both features there was a significantly higher likelihood of consolidation failure when items were presented simultaneously. However, as previously mentioned, there is convincing evidence to suggest that the guess rate would be higher in the simultaneous condition (Ihssen et al., 2010a; 2010b; Scalf & Beck, 2010). That is, studies show that
presenting items simultaneously results in increased likelihood of consolidation failure due to competitive interference between representations. This interference is known to be influenced by the similarity of items (Shapiro & Miller, 2011).

In order to examine whether this could account for the difference in guess rate between sequential and simultaneous conditions, we plotted the known guess responses across all observers in Experiment 1 as a function of the angular difference between items on corresponding trials. Responses were considered guesses if they fell more than two standard deviations (derived from the model) away from the target orientation/direction. The results of this analysis are presented in Figure 6.6. There appears to be no relationship between item similarity and likelihood of consolidation failure in the sequential conditions, indicated by a flat distribution. In contrast, it appears that there is a relationship between these factors in the simultaneous conditions such that items of greater similarity are more likely to result in interference between 20-70°, with this relationship reversing with separation greater than 70° (plateauing after 115° for direction). The evidence of interference within the simultaneous condition, but not the sequential condition, is consistent with biased competition models of VWM/attention and would explain the difference in guess rate between these conditions within a framework of parallel consolidation.

Figure 6.6. Frequency of guess responses as a function of the angular separation between presented items in the (a) orientation and (b) motion direction conditions of Experiment 1.
Differentiating between serial and parallel models is often challenging; however, modulation of precision is compelling evidence for the latter. While we found no difference in precision between conditions for orientation, the results for motion direction clearly indicate that observers were capable of parallel consolidation and, as a result, items were encoded at a reduced precision.

### 6.5. General discussion

The main findings were that motion direction can be consolidated in parallel and that there is a twofold cost: reduced precision encoding and an increase in consolidation failure. The evidence found for orientation was less conclusive and could plausibly be explained by either a serial or a parallel account. The reduction in precision observed for motion direction is likely due to spreading of cognitive processes associated with parallel consolidation. For instance, the implicit goals of observers may have differed between conditions (Sims, 2015), i.e. devaluing precision in the simultaneous condition in order to achieve parallel consolidation. As evidenced by the post hoc analysis of guess responses and item similarity, the increase in consolidation fail-rate may be due to interference between items presented simultaneously, as opposed to sequentially.

In our previous study, we suggested that a reduction in the precision of items consolidated in parallel may account for the difference in performance observed between sequential and simultaneous conditions. The results of the current study confirm this interpretation for motion direction. The previous results were also suggestive that both orientation and motion direction can be consolidated in parallel, with stronger evidence for direction than orientation. While here we have found compelling evidence for parallel consolidation of motion, once again the results for orientation are less conclusive.
Previous research indicated that while colour can be consolidated in parallel (at no cost), orientation is limited to serial consolidation (Liu & Becker, 2012). An all-or-none ‘unlimited parallel’ model of consolidation was proposed to account for these results, where it was claimed that the information bandwidth of colour was small enough that two items could pass through simultaneously, while the bandwidth of orientation was too large to accomplish this (Miller, et al., 2014). As this model does not predict any cost of parallel consolidation, it cannot explain the current findings; that is, the reduction in precision observed when motion direction items are consolidated in parallel. The information bandwidth model is resonant of current discrete models of VWM storage, characterized by precision invariant storage in a discrete number of ‘slots’. However, the current findings are more parsimoniously explained by consolidation that draws upon a continuous resource, which can be allocated among a number of items, with a relationship between resource allocation and consolidation precision.

A possible explanation for the apparent discrepancy between the cost of parallel consolidation for colour and motion direction is that colour is processed more categorically than motion direction and thus less susceptible to precision decay. There is some evidence for this from event-related potential (ERP) studies where the pattern of results observed when the contralateral delay activity (CDA), a physiological indicator of both the number and precision of items stored in VWM, is measured while storing either orientation or colour in VWM. While the pattern of results for orientation reflect a continuous resource model of VWM storage (Gao, Yin, Xu, Shui, & Shen, 2011; Machizawa, Goh, & Driver, 2011), results using colour reflect a discrete model (Ikkai, McCollough, & Vogel, 2010; Luria, Sessa, Gotler, Jolicoeur, & Dell’Acqua, 2010; Ye, Zhang, Liu, Li, & Liu, 2014). However, it is difficult to make direct comparisons, as this technique has not yet been used to investigate VWM storage of motion direction. Furthermore, it is important to note that numerous behavioural studies investigating
VWM storage of colour, orientation, and motion stimuli have reported a pattern of results consistent with a resource model (Bays & Husain, 2008; Bays, et al., 2009; van den Berg, Shin, Chou, George, & Ma, 2012; Zokaei, Gorgoraptis, Bahrami, Bays & Husain, 2011).

We also found that, up to around 70°, similar items were more susceptible to consolidation failure; this is consistent with our previous study where we found that reducing the separation between motion direction items (from 90 to 45°) resulted in a differential between sequential and simultaneous conditions. This may also explain why here we found increased consolidation failure for orientation and motion direction, which have relatively small perceptual spaces (Clifford, 2002; Foster & Ward, 1991; Webster, De Valois, & Switkes, 1990), and why no difference was found for colour (Miller et al., 2014), which has a relatively large perceptual space (Nagy & Sanchez, 1990; Witzel & Gegenfurtner, 2013). Indeed, the minimum separation between colours presented by Miller et al. (2014) was relatively large, i.e. 45° on the colour wheel; perhaps reducing this would result in the same increase in consolidation failure observed here.

In summary, the current findings are consistent with our previous study indicating that motion direction can be consolidated into VWM in parallel (Rideaux, et al., 2015). However, we extend this by demonstrating that, unlike colour, there is a twofold cost associated with parallel consolidation of motion direction: the precision at which items are encoded is reduced and the likelihood of consolidation failure is increased. Evidence is also found suggesting that parallel consolidation of orientation may be possible, but is not conclusive. These findings emphasize that parallel consolidation is not unique to colour, and suggest that part of the cost of parallel consolidation may be mediated by the size of the perceptual space of these features.
Chapter 7. A bilateral hemifield advantage for parallel consolidation into visual working memory

7.1. Context statement

As outlined in Chapter 3, the *information bandwidth* model has been proposed to account for the capacity of parallel consolidation; however, this model fails to account for findings from Chapters 5 and 6. Furthermore, the precise capacity of this process has not yet been convincingly determined. The experiments reported in this chapter were designed to establish the capacity of parallel consolidation and investigate the plausibility of an alternative account of the mechanism underlying this limit, i.e. biased competition.

Note that this chapter appears in print as:

Rideaux, R., & Edwards, M. (*in preparation*). A bilateral hemifield advantage for parallel consolidation into visual working memory.

7.2. Introduction
Visual working memory (VWM) representations are the first (potentially) durable form which visual information can assume. A fraction of the information that is initially stored in sensory memory, characterized as a high capacity memory whose contents decay within a few hundred milliseconds (Sperling, 1960, 1963), is consolidated and can be maintained and manipulated in VWM. While considerable research has focused on the storage capacity and the selection of items (Cowan, 2001, 2010), increasing focus has been directed at the nature of consolidation, i.e. the formation of VWM representations.

Initially it was thought that consolidation of [colour] items into VWM was strictly limited to serial processing, i.e. only one item could be consolidated at a time (Huang, Treisman, & Pashler, 2007; Jolicoeur & Dell'Acqua, 1998). However, by demonstrating that two (or three) items can be consolidated in the same time required to consolidate a single item, several recent studies have indicated that parallel consolidation is possible with a number of features including colour (Mance, Becker, & Liu, 2012), orientation, and motion direction (Rideaux, Apthorp, & Edwards, 2015; Rideaux & Edwards, 2016). Note that while the evidence for parallel consolidation of colour and motion direction is clear, the support for orientation remains inconsistent (Liu & Becker, 2013). Although there is considerable evidence that parallel consolidation is possible, both the maximum number of items that can be consolidated, and the underlying mechanisms that impose this capacity, are unknown.

In response to evidence suggesting that orientation cannot be consolidated in parallel while colour can, apparently at no cost to the fidelity of the representations, Miller, Becker, and Liu (2013) proposed the consolidation bandwidth model to explain the capacity of parallel consolidation into VWM. This model states that the capacity to consolidate items in parallel is dependent on the size of an item’s information bandwidth relative to a putative consolidation bottleneck. That is, while the bandwidth of colour is small enough to allow two items to pass through the bottleneck in parallel, orientation is
too large and must be processed serially. Based on the evidence at the time, the consolidation bandwidth model adequately accounted for the capacity to consolidate some features in parallel, but not others. However, in addition to not linking either of the relevant factors to neural architecture, i.e. the bandwidth of items and the consolidation bottleneck, the model fails to account for our recent findings regarding motion direction and orientation (Rideaux & Edwards, 2016). That is, we recently demonstrated that there is a twofold cost associated with parallel consolidation: both the resolution at which items are encoded is reduced and the likelihood of failing to consolidate one (or both) item/s is increased. This cannot be explained by the information bandwidth model, which is resonant of discrete “slot” models of VWM storage and claims that if items can be consolidated in parallel then this is achieved at no additional cost, relative to serial consolidation.

In contrast, a model that does account for the cost observed for parallel consolidation, and whose underlying neural mechanisms are explicitly defined, is that of biased competition. Originally proposed by Desimone and Duncan (1995) to explain the capacity of visual selective attention, the biased competition model has recently gained popularity as an account for the capacity of VWM (Franconeri, Alvarez, & Cavanagh, 2013; Shapiro & Miller, 2011). The general principle of the model is that items within the visual field compete for representation within the limited capacity of regions (aka content maps) in the visual cortex. These regions can be conceptualized as two-dimensional areas of the cortex with coherent spatial organization where the preferred stimuli of neurons change smoothly from one location to the next, e.g. area MT where neurons vary in motion direction selectivity (Albright, Desimone, & Gross, 1984). In regards to parallel consolidation, if two or more items are simultaneously represented in a relatively small region, the competition between these representations results in one (or possibly both) failing to propagate into VWM storage and being lost. Further, the loss in
resolution observed during parallel consolidation can be explained by the reduced signal to noise ratio of individual items as more are represented in the same region, i.e. as each signal acts as noise for all other signals.

According to this account, a number of factors moderate the degree of competition between items including the size of the receptive fields in visual areas, the number of items presented, item similarity, and item spatial proximity (Franconeri, et al., 2013; Kastner & Ungerleider, 2001). Indeed, we found that there is a positive relationship between the similarity of items and the likelihood of consolidation failure, but only when presented simultaneously (Rideaux & Edwards, 2016), consistent with a biased competition model. However, according to a biased competition framework, another factor that should influence competition is whether items are presented in the same or different visual hemifields, i.e. unilateral vs. bilateral hemifield presentation.

Visual information presented in the left and right hemifields is initially processed separately in the right and left hemispheres of the cortex, respectively (Dimond & Beaumont, 1971; Sperry, 1961). Better performance is observed on a number of tasks that require splitting attention between two or more locations when items are presented bilaterally, compared to unilaterally; this is referred to as a bilateral hemifield advantage (BHA). A BHA has been demonstrated for several tasks including letter identification (Banich & Belger, 1990), multiple object tracking (Alvarez & Cavanagh, 2005), enumeration (Delvenne, Castronovo, Demeyere, & Humphreys, 2011) and VWM item storage (Delvenne, 2005; Umemoto, Drew, Ester, & Awh, 2010). The advantage is thought to reflect a reduction in competition between items vying for cortical representation (Franconeri, et al., 2013; Pollman, Zaidel, & von Cramon, 2003; Sereno & Kosslyn, 1991). Thus, one way to investigate whether the capacity of parallel consolidation can be explained by biased competition is to determine whether a BHA exists for this process. That is, if items (simultaneously) presented unilaterally are subject
to more consolidation failure (due to competition/interference) than when presented bilaterally, this would be compelling evidence indicating biased competition as an account for the capacity of parallel consolidation.

This may explain the inconsistent findings surrounding parallel consolidation of orientation. Whereas in our previous studies we found a pattern of results suggesting parallel consolidation of orientation may be possible (Rideaux, et al., 2015; Rideaux & Edwards, 2016), the rate of consolidation failure found by Liu and Becker (2013) was so high (~50%) that it suggested observers were only capable of consolidating one of two items presented simultaneously. Importantly, while we always presented items in separate hemifields, they presented items in the same hemifield on half the trials. Thus, by presenting items unilaterally, they may have inadvertently selectively disadvantaged observers’ performance in the simultaneous condition, compared to the sequential condition.

Conversely, Mance et al., (2012) found no BHA for parallel consolidation of colour items on a matching task, suggesting that this may not have influenced the likelihood of consolidation failure of orientation. However, we found evidence of a positive correlation between item similarity and likelihood of consolidation failure, up to around 70° (Rideaux & Edwards, 2016). Quantitative comparisons between qualitatively difference features, e.g. colour and orientation, are challenging at the best of times. However, perceptual similarity can be compared by examining corresponding just noticeable differences (JNDs) across different features. The size of the JND relative to the physical range of a feature can then be used as an indication of the size of its perceptual space. By applying this method, one can see that the perceptual space of colour is considerably greater than that of orientation (or motion) (Foster & Ward, 1991; Nagi & Sanchez, 1990; Webster, De Valois, & Switkes, 1990; Witzel & Gergenfurtner, 2013). Thus, the relatively large perceptual space of colour, together with the high degree of
In summary, the information bottleneck model fails to account for recent developments regarding the nature of parallel consolidation and there is evidence to suggest that biased competition may explain these findings. While it is currently unclear whether a BHA exists for this process, its presence would provide convincing evidence for a biased competition account in addition to explaining the seemingly inconsistent findings within this area regarding the ability to consolidate orientation information in parallel. Thus, to investigate whether a BHA exists for parallel consolidation of orientation and motion direction, here we compare parallel consolidation of these features when presented unilaterally vs. bilaterally. Furthermore, we employ a recall task with a continuous response measure so that we can examine the type of errors resulting from any potential unilateral presentation disadvantage.

### 7.3. Experiment 1: A bilateral hemifield advantage for parallel consolidation

In order to further investigate the possibility that a biased competition model can account for the capacity of parallel consolidation, here we employ a recall task to examine whether a BHA exists for parallel consolidation of orientation and motion direction information.

#### 7.3.1. Method

#### 7.3.2. Observers
Twelve observers participated in the study (mean age, 22). All had normal or corrected to normal acuity and gave informed written consent to participate in the study. All observers were compensated $20/hour for their participation.

7.3.3. Apparatus

Experiments were run under the MATLAB (version R2013a) programming environment, using software from the PsychToolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on a Phillips Brilliance 202P4 CRT monitor that was driven by an NVIDIA graphics card in a host Dell computer. The monitor had a spatial resolution of 1024 x 768 pixels and a frame rate of 120Hz.

7.3.4. Stimuli

The stimuli and procedure were similar to that employed in our previous study (Rideaux & Edwards, 2016). A 2 × 2 experimental design was used: feature (orientation/motion direction) × hemifield presentation (unilateral/bilateral). The general presentation sequence consisted of a stimulus interval, followed by a cue, and then a response interval. In each stimulus interval two items were presented simultaneously (40 ms) followed by a mask (200 ms) to prevent further processing from iconic memory. This exposure duration has been shown to be the minimum required to consolidate a single item, or two in parallel (Becker, Miller, & Liu, 2013; Rideaux, et al., 2015). Items and masks were presented on the corners of a figurative square, centred on fixation, each point 8° visual angle from fixation. Items were presented in adjacent locations so that they were equidistant between trials. Items were presented pseudo-randomly, in a counterbalanced design, such that there were an equal number of trials where items were presented
unilaterally/bilaterally, and within these conditions an equal number where they were presented in the left/right and upper/lower visual fields.

The stimuli in the orientation condition were Gabors (contrast, 0.7; spatial frequency, 1 cycles/°; random phase) within a Gaussian envelope (4° radius) and the mask was pixel noise of random luminance levels with a uniform distribution (0 – 63 cd/m²) within a circular aperture (4.2° radius). In the motion direction condition stimuli consisted of 100 Gaussian blobs (0.3° radius), to allow sub pixel resolution movement, within a circular aperture (4° radius), which wrapped around when they reached the edge of the aperture. The blobs were displaced 0.082° each frame, resulting in a speed of 9.8°/s. The mask in this condition consisted of 300 Gaussian blobs within a circular aperture (4.2° radius), positioned randomly on each frame, creating a percept of dynamic noise. The orientation/direction of each pair of items were determined pseudo-randomly from between 0-179° and 0-359°, respectively, with the constraint that they must be separated by at least 15°.

The stimulus interval and cue were separated by 500 ms interval, where only the fixation cross was present. The cue consisted of a white circle presented for 500 ms at the location of one of the items, determined randomly. The cue was followed by a response interval consisting of either a Gabor, identical to those used in the stimulus interval, (orientation condition) or an arrow (length 6°) extending from fixation (direction condition). During the response interval the cursor was positioned at fixation and became visible, allowing the orientation/direction of the Gabor/arrow to be manipulated by moving the mouse. Examples of the presentation sequence are illustrated in Figure 7.1.
The background was grey (mean luminance, 12 cd/m\(^2\)) and the blobs in the motion condition were white (mean luminance, 63 cd/m\(^2\)). The observer sat 50 cm from the monitor, with their head supported on a chin rest.

7.3.5. Procedure

The observers’ task was to match the orientation/direction of the Gabor/arrow in the response interval to that of the cued item in the preceding stimulus interval. No duration limit was used to restrict responses, once the observer had moved the Gabor/arrow with the mouse to the orientation/direction they believed matched that of the cued item, they would left-click to indicate their response and initiate the next trial. Observers were instructed to maintain fixation throughout the presentation sequence and to remember both items in order to perform the task accurately.

Before the main experiment, observers spent approximately 15 min performing the task without recording data, in order to familiarize them with the stimuli/task. During this
initial stage, trials from each condition were randomly intermixed. In the main experiment trials from each feature condition were blocked. Four blocks were run for each feature. Blocks consisted of 120 trials, totalling 960 trials and an approximate testing duration of one hour per observer. Testing was split into two half hour sessions, reversing feature condition presentation order for even numbered observers.

7.3.6. Data analysis

For each trial, the offset (error) was calculated by subtracting the orientation/direction recorded from the observer’s response from that of the cued item. Initially, the variance of the offset was analysed for each participant. However, there are (at least) two sources of variability within the offsets, resulting from two types of trials. One where the observer successfully consolidates the cued item into VWM, resulting in a von Mises distribution of distribution of offsets with a mean ($\mu$) and standard deviation ($\sigma$) (Zhang & Luck, 2008). The other where they fail to consolidate the item and must guess (g), resulting in a uniform distribution. Thus, in order to evaluate whether an improvement in performance is due to a reduction in the guess rate or an increase in the resolution of the consolidated representations, a mixture model must be fit to the offset data to isolate these sources of variation. A model was fit to both the aggregate and individual offset data within each feature condition using a Markov Chain Monte Carlo (MCMC) method. Data analysis was performed using the MemToolbox (Suchow, Brady, Fougnie, & Alvarez, 2013).

7.3.7. Results

7.3.8. Raw offset data

The raw offset data for orientation and motion direction was analysed separately for variability (variance) using a one-way repeated measures analysis of variance
A main effect of presentation was found for motion direction, $F(1,11) = 37.4$ $p < .001$, and was approaching significance for orientation, $F(1,11) = 3.6$ $p = .08$, (Figs. 7.2a & 7.2b). This pattern of results indicates that the offsets between item and response orientation/direction were more variable for items presented unilaterally compared to items presented bilaterally. The analysis below was run to investigate the source of this variability.

**Figure 7.2.** Experiment 1 raw offset data. The grand-average offset between target and response orientation/direction. Error bars represent ±1 SEM.

### 7.3.9. Model fit

The Bayesian information criterion (BIC) was used to compare the fit of three types of mixed models to individuals’ data: standard mixture model (mixture model), variable precision model, and swap model. While a mixture model assumes precision remains constant, a variable precision model assumes precision is normally distributed and calculates its mean and standard deviation (Fougnie, Suchow, & Alvarez, 2012). In addition to partitioning sources of variance into guess rate and precision, a swap model isolates a third potential source of variation: responses made based on the orientation/direction of the non-target item (Bays, Catalao, & Husain, 2009). Direction information may be particularly vulnerable to these spatial binding errors (Tripathy & Barret, 2004). A mixture model was used as it was found to fit individual observer data...
better than the two alternative models (mixture model BIC scores were lowest for over 90% of data sets [supplementary material]). The rejection of these alternative models in favour of a mixture model is consistent with previous research on VWM consolidation (Liu & Becker, 2013; Miller, et al., 2014; Rideaux & Edwards, 2016).

Model fit was evaluated using Kolmogorov-Smirnov (KS) tests, confirming that the model fit the data well (97% of ps > .5; average KS statistic = .06). Model parameters for orientation and motion direction were analysed separately for guess rate (g) and standard deviation (σ), using a one-way repeated measures ANOVA. No main effects of presentation were found for standard deviation, (orientation) $F(1,11) = 0.17 \ p = .90$ and (direction) $F(1,11) = 0.19 \ p = .67$. In contrast, main effects for guess rate were found for both orientation and direction, $F(1,11) = 5.81 \ p = .03$ and $F(1,11) = 47.9 \ p < .001$, respectively (Figs. 7.3a & 7.3b). These results show that the source of error responsible for higher variability of offsets in the unilateral condition for both features is an increased guess rate, as opposed to increased standard deviation.

![Figure 7.3](image)

**Figure 7.3.** Experiment 1 model parameter analysis. The average (a) standard deviation (σ) and (b) guess rate (g) model parameters within unilateral and bilateral hemifield presentation conditions, for orientation and motion direction items. All error bars represent ±1 SEM.

### 7.3.10. Discussion

These results demonstrate a clear BHA for parallel consolidation of orientation and motion direction items. This is confirms that (at least some of) the poorer
performance observed by Liu and Becker (2013) when items were presented simultaneously, compared to the sequentially, was in due to presenting items unilaterally. The results also show that presenting items unilaterally, as opposed to bilaterally, increases the likelihood of consolidation failure, but does not reduce the resolution of encoded items, which is consistent with a biased competition account (Franconi et al., 2013). That is, items presented bilaterally are initially processed in different cortical hemispheres, reducing the extent to which they compete for representation. In contrast, by presenting items unilaterally, both items are initially processed in the same hemisphere and experience more competition, resulting in an increased likelihood of failing to consolidate one or both.

Although we found a BHA for parallel consolidation, the guess rate in the unilateral condition was still below that predicted by serial consolidation (.5), i.e. if only one item were consolidated on each trial. Thus, although it would seem unlikely given the difficult nature of consolidating two items (as indicated by the consolidation failure rate and anecdotal observer comments), given that more than one item can be consolidated in each hemifield, it may be possible to consolidate three items in parallel. Indeed, evidence from studies employing matching tasks suggest that parallel consolidation of three colour or motion direction items may be possible (Mance et al., 2012; Rideaux, et al., 2015). Furthermore, several motion studies indicate the limit of motion processing is between two and three, depending on how the signals are constructed (Edwards & Greenwood, 2005; Edwards & Rideaux, 2013; Greenwood & Edwards, 2006a, 2006b, 2009; Rideaux & Edwards, 2014). Given that the precise limit of parallel consolidation is unknown, with evidence pointing to a limit of either two or three items, Experiment 2 examines the possibility that three signals can be consolidated in parallel.
7.4. Experiment 2: The capacity of parallel consolidation

Although there are claims that the limit of parallel consolidation is two items (Miller, Becker, & Liu, 2014), there is partial evidence from both within (Mance et al., 2012; Rideaux et al., 2015) and outside (Greenwood & Edwards, 2009; Rideaux & Edwards, 2014) of VWM literature suggesting that parallel consolidation three items may be possible. However, despite this, examination of whether three orientation items can be consolidated in parallel, or investigation of parallel consolidation of three items of any feature using a continuous response measure, has not been conducted. Here we explicitly test whether three orientation or motion direction items can be consolidated in parallel using a continuous response measure, in order to evaluate the sources of error associated with increasing the number of items simultaneously presented from two to three.

7.4.1. Method

7.4.2. Observers

Ten observers participated in the study (mean age, 22). All had normal or corrected to normal acuity and gave informed written consent to participate in the study. All observers were compensated $20/hour for their participation.

7.4.3. Stimuli and procedure

The stimuli and procedure were similar to that employed in Experiment 1. However, to examine if three items can be consolidated in parallel, and if so, whether there is a further reduction in the resolution of encoded representations (between two and three items), a $2 \times 2$ experimental design was used: item feature (orientation/motion direction) $\times$ set size ($2/3$). Items and masks were presented at the corners of a figurative
triangle, centred on, and 8° from, fixation. Examples of the presentation sequence are shown in Figure 7.4.

**Figure 7.4.** An example of the stimuli used in Experiment 2. The top row illustrates an example of the presentation sequence in the orientation condition (set size 3) and the bottom row a presentation sequence in the motion direction condition (set size 2). The black arrows in the motion sequence have been added to indicate the direction of the blobs.

Trials from each condition were blocked, with trials in the set size two condition also blocked into one of the three item location configurations possible, i.e. location 1 & 2, 2 & 3, and 1 & 3. For each feature condition observers ran six blocks, these were randomly interleaved within a feature mega block. Blocks consisted of 120 trials, totalling 1440 trials and an approximate testing duration of two hours per observer. Testing was split into two one hour sessions, reversing feature condition presentation order for even numbered observers.

7.4.4. Results

7.4.5. Raw data offset

The data for each feature was analysed separately using a one-way repeated measures ANOVA. A main effect of set size was found for both orientation and motion,
$F(1,9) = 39.2 \ p < .001$ & $F(1,9) = 25.7 \ p = .001$, respectively. This indicates that the offset between the cued item and observers’ response orientation/direction was more variable when three items were presented, compared to two.

7.4.6. Model fit

Consistent with Experiment 1, a standard mixture model was fit to each participant’s data and KS tests were used to evaluate model fit (85% ps > .05; average KS statistic = .05). A one-way repeated measures ANOVA was used to analyse model parameters for each feature separately. Main effects of set size for standard deviation and guess rate were found for both orientation, $F(1,9) = 12.7 \ p = .006$ and $F(1,9) = 31.1 \ p < .001$, and direction, $F(1,9) = 28.7 \ p < .001$ and $F(1,9) = 90.0 \ p < .001$, respectively (Figs 7.5a & 7.5b). These results show that the increased variability in the set size three condition is due to both an increase in consolidation failure and standard deviation.

**Figure 7.5.** Experiment 2 model parameter analysis. The average (a) standard deviation ($\sigma$) and (b) guess rate ($g$) model parameters within set size 2 and 3 conditions, for orientation and motion direction. All error bars represent ±1 SEM.

Mixture model fit data best for all conditions, except for in the set size three/orientation condition, where swap model fit data best for 50% and mixture 40%. Initially, we analysed this condition using both models. The outcome was virtually identical for the standard deviation parameter. Further, the sum of the guess rate and swap rate found using the swap model was equivalent to the guess rate found using the mixture
model. Thus, for sake of comparing with other conditions we analysed this condition using a mixture model, while recognising that that a proportion of the guesses made in the set size 3 condition were likely the result of spatial binding errors.

7.4.7. Discussion

The guess rate in the three item condition for both features is around .33, which is the proportion of guesses predicted assuming two items were consolidated on each trial. This appears to be consistent with the interpretation that the capacity of parallel consolidation is two. However, three points which must be considered make the interpretation of the results less definitive.

First, given that in the corresponding set size two conditions the guess rate is around .1 -.15, it is not appropriate to assume that in the set size three condition that two items would always be consolidated. If we assume observers would have the same likelihood of consolidating two items in the both conditions, then the most conservative estimate of guess rate predicted by only consolidating two items in the three item condition would be the sum of the guess rate in the set size two condition (.1 -.15) and that predicted by this strategy (.33). Thus, to evaluate whether observers were able to consolidate more than two items in parallel, the estimate produced by the sum of these guess rates was compared to that found in the set size three condition. Paired t-tests revealed that the guess rate in the set size three condition was significantly better for both orientation, $t(9) = 4.7.4 \ p < .001$, and direction, $t(9) = 3.7 \ p = .005$, indicating that observers may have been able to consolidate three items in parallel on some of the trials. It could be argued that observers found it easier to consolidate two items when three were present, however, this is unlikely given that competition between items increases with the number of items presented simultaneously (Franconeri et al., 2013).
Second, although the storage capacity of VWM is around 3-4 items (Luck & Vogel, 1997), previous consolidation research shows that progressing from two to three items reduces performance (on a matching task), even when items are presented sequentially (Mance et al., 2012). Thus, some of the increased guess rate observed here in the set size three condition is likely due to storage decay and spatial binding errors, as opposed to consolidation failure. Indeed, at least for orientation we found evidence for this, where during the comparison of model fit the swap model was found to fit the majority of set size three data sets better.

Finally, the difference in precision found is also an indication that three items were being consolidated in parallel on some of the trials, and that as a result, they were encoded at a reduced resolution. We previously found that in addition to an increased likelihood of consolidation failure, another cost associated with parallel consolidation is a reduction in the resolution at which items are encoded. The results here suggest that the resolution is further reduced as the number of to-be-consolidated items is increased from two to three.

Given these considerations, it is difficult to make a definitive claim regarding whether parallel consolidation of three items is possible. However, a number of indicators point to the possibility that observers were capable of consolidating three items in parallel.

7.5. General discussion

The main findings of the current study are that there is a clear BHA for the parallel consolidation of orientation and motion direction items (Experiment 1), and that it may be possible to consolidate up to three of these items in parallel (Experiment 2). The
finding that items were more likely to be consolidated when presented bilaterally, compared to unilaterally, is consistent with a biased competition account of the capacity of parallel consolidation. That is, bilateral presentation resulted in less interference between the items as they competed for cortical representation. This also shows that the differential between sequential and simultaneous presentation conditions found by Liu and Becker (2013), which the authors interpreted as evidence for an inability to consolidate orientation information in parallel, was (at least partially) due to selectively disadvantaging performance in the simultaneous condition by presenting items unilaterally.

We previously claimed that an increase in consolidation failure for simultaneously (relative to serially) presented orientation items made interpretations regarding the ability to consolidate orientation in parallel uncertain, even though the increase was too small to be explained by a strict serial consolidation strategy (Rideaux & Edwards, 2016). The current results explain this small increase in consolidation failure, confirming that orientation can be consolidated in parallel. As we previously flagged, the finding that colour does not appear to be as susceptible to consolidation failure during parallel consolidation may be a reflection of the size of its perceptual space, which is larger than that of orientation (and motion direction).

In line with this, Mance et al., (2012) found no BHA for parallel consolidation of colour, which appears to be inconsistent with the results found here; however, it is consistent with previous studies that have demonstrated a BHA for recall of orientation but not for colour (Delvenne, 2005; Umemoto et al., 2010). Together, these findings point to structural differences in the neural networks where these features are represented in early visual areas, e.g. area V5/MT. Whereas motion direction and orientation are susceptible to a relatively high degree of interference, colour representations appear to be more robust. This may be explained by larger areas of cortical representation, narrower
tuning bandwidths or less lateral inhibition. Alternatively, previous research indicates that a BHA is only observed when task difficulty is high (Banich & Belger, 1990; Merola & Liederman, 1990), suggesting that parallel consolidation of colour is achieved more effortlessly than orientation or motion direction. However, these interpretations are not exclusive, the difficulty experienced in consolidating these features in parallel may be moderated by the degree of cortical interference.

While the results from Experiment 2 are ultimately inconclusive regarding the capacity of parallel consolidation, they indicate that if parallel consolidation of three items is possible, it is achieved at an even greater cost, both to resolution and likelihood of consolidation failure and spatial binding errors, than that associated with parallel consolidation of two items. This is consistent with a biased competition account, in that increasing the number of items also increases cortical interference, i.e. consolidation failure. Furthermore, the reduction in precision is also consistent with our previous findings that indicate that spreading of cognitive resources employed during consolidation results in items being encoded at a lower resolution (Rideaux & Edwards, 2016).

In conclusion, the current study proposes a framework, that is becoming increasing popular in explaining limitations of attention and VWM (Franconeri et al. 2013; Shapiro & Miller, 2011), upon which the capacity of parallel consolidation can be explained, i.e. biased competition. This is evidenced here by the presence of a BHA for parallel consolidation, but draws on a number of findings from previous research. Furthermore, we provide evidence suggesting that the limitation of this process may be higher than previous estimates, however further investigation is required to solidify this interpretation.
Chapter 8. Summary and final discussion

The broad aim of this thesis was to investigate the cost of parallel information processing within the human visual system. Towards this end, three key theoretical issues were identified and each addressed through a series of experiments. Because each empirical chapter has been presented as a stand-alone publication, specific details relating to the results of each experiment will not be repeated here. Rather, I will first summarize the main empirical findings, before considering their theoretical implications as a whole. A final conclusion will then be offered.

8.1. Summary of present findings

As stated throughout this thesis, while the timesaving benefit of parallel processing is clear, the cost is less well understood. A common initial approach to the study of parallel processing is to determine its capacity within a given system. This can provide both an understanding of its limitations and insight into its underlying mechanisms. For example, previous research has shown that the capacity of parallel
motion processing is dependent on the type of motion stimuli (i.e. three for global-motion and around five for form-specific motion), and additionally has demonstrated a general principle of parallel motion processing; that is, as the number of signals which are processed simultaneously increases so too does the signal intensity required to process each signal. However, due to the tasks employed to discern these limits, it remained unclear what this capacity reflects, i.e. what information is extracted at this level. In order to determine how the capacity of parallel processing varies as a function of the level of detail of the to-be-extracted information, I first sought to determine what information is extracted during parallel motion processing.

8.1.1. Parallel motion processing capacity as a function of information extraction

Previous studies have inferred the capacity of parallel motion processing, for global and form-specific motion, from observers’ capacity to discriminate between two intervals containing either \( n \) or \( n + 1 \) motion signals (Greenwood & Edwards, 2006; Edwards & Rideaux, 2013). However, relatively little information is required to perform this task; the observer does not even need to extract the precise number of items present in each interval, merely which interval has more or fewer. While the capacity to perform this discrimination reflects an important limitation of the parallel motion processing system, a logical next step is to determine whether this limit varies as a function of the complexity of information which is extracted. This possibility was examined in experiments outlined in Chapter 4. By requiring observers to respond to different aspects of a stimulus containing multiple motion signals, I determined that the resolution of parallel motion processing varies as a function of the complexity of to-be-extracted information. That is, while the capacity to discriminate between more or fewer signals is around five or six (Edwards & Rideaux, 2013), observers were unable to accurately
identify the actual number of signals present beyond four. Further, the ability to identify whether a particular motion direction was present, or to indicate the direction of the signals, was limited to displays containing three signals. These findings demonstrate that there is not a single hard-and-fast parallel processing limit, but rather a flexible trade-off between the complexity of the to-be-encoded information and the ability to represent that information.

8.1.2. The cost and capacity of parallel consolidation

Information is processed at multiple levels within the visual system, and as different cognitive processes are engaged, e.g. VSTM, the limitations imposed by these systems must also be considered. Thus, having established that the resolution of parallel motion processing varies as a function of complexity of the to-be-extracted information (i.e. the more complex the information, the lower the capacity of parallel processing), the second aim of the thesis was to determine whether there is a cost associated with parallel processing. Previous studies suggest that not all features can be consolidated in parallel - for instance, it has been reported that colour can while orientation cannot (Liu & Becker, 2013; Mance et al., 2012) - however, parallel consolidation of motion direction had not yet been examined. Thus, as a first step, experiments reported in Chapter 5 investigated whether motion direction can be consolidated in parallel. Evidence was found indicating that it was possible to consolidate direction information in parallel. Furthermore, we found that both the similarity between items and the facilitation of spatial attention influenced performance. That is, when the range of items was reduced, effectively increasing the similarity between items, parallel consolidation performance was selectively reduced. Additionally, it was demonstrated that presenting items in random (as opposed to fixed) spatial locations reduced performance across both conditions. Thus,
given these findings, we proceeded to re-investigate parallel consolidation of orientation, and found evidence suggesting that it may also be consolidated in parallel, contrary to previous claims (Becker et al., 2013; Liu & Becker, 2013).

Next, experiments outlined in Chapter 6 further examined whether a) these features could be consolidated in parallel and, if so, b) if there was a cost associated with this process which could potentially explain the previous findings. That is, both the selective reduction in performance for parallel consolidation observed when item similarity is increased and the seemingly inconsistent findings regarding the ability to consolidate orientation in parallel. Previously, this had been investigated using colour, and results had suggested that two colours could be consolidated in parallel at no cost (Becker et al., 2013). In examining this with motion direction and orientation, we confirmed that direction could be consolidated in parallel, consistent with our previous results, while the evidence for orientation was less conclusive. Furthermore, we demonstrated that there is a twofold cost associated with parallel consolidation of direction: firstly, the resolution at which items are encoded is reduced, and secondly, the likelihood of failing to consolidate one (or both) item/s is increased. We also found that the reduction in resolution was not due to spreading spatial attention over a larger area when attempting to consolidate two items in parallel, compared to one at a time (Castiello & Umiltà, 1992; Eriksen & Yeh, 1985), indicating that this is likely a result of spreading of (other) cognitive resources engaged during consolidation. Furthermore, we demonstrated that the increased rate of consolidation failure was related to the similarity between items presented simultaneously. This relationship is consistent with biased competition models of spatial attention and VSTM storage; that is, items with highest and lowest similarity resulted in the most consolidation failure (Franconeri et al., 2013).

The third aim of this thesis was to examine whether the cost associated with parallel processing can ultimately explain its capacity: that is, how many items can be
consolidated in parallel. To this end, experiments reported in Chapter 7 examined the capacity of this process and a potential account of this limitation. We had previously found that when items were presented simultaneously, the degree of similarity between items was related to the likelihood of consolidation failure, consistent with biased competition accounts of spatial attention and VSTM storage (Desimone & Duncan, 1995; Franconeri et al., 2013; Shapiro & Miller, 2011). According to this account, a number of factors, including item similarity, influence the interference between items competing for cortical representation. This model was first claimed to underlie spatial attention, but has now been proposed as the neural mechanism behind limited resource models of VSTM storage. For example, better performance on a number of visual tasks when items are presented in separate visual hemifields, as opposed to in the same hemifield - a BHA - is thought to reflect a reduction in interference between items vying for cortical representation (Franconeri et al., 2013). However, previous findings using colour items indicated no presence of a BHA for parallel consolidation (Mance et al., 2012), suggesting that the limitation of this capacity may be unrelated to biased competition. We found that a BHA existed for parallel consolidation of motion direction and orientation, and furthermore that only the likelihood of consolidation failure, not resolution of encoded items, was affected, consistent with a biased competition account of this limitation.

Finally, most estimates of parallel consolidation had indicated that no more than two items can be processed simultaneously (Mance et al., 2012; Miller et al., 2014). However, the pattern of results in these studies makes it difficult to draw conclusive claims regarding this capacity of two. Furthermore, consistent capacity limits of three (and in some instances five) from parallel motion processing studies (Greenwood & Edwards, 2006a, 2006b; Edwards & Rideaux, 2013) add to the possibility that the currently suggested capacity of parallel consolidation (2) may be underestimated. In explicitly evaluating whether observers were capable of consolidating three items in
parallel, as in previous studies, we found somewhat inconclusive evidence. However, a number of factors, including the further loss of resolution and significantly better performance than that predicted by a strategy where only two items are consolidated (based on performance in the two item condition), point to the possibility that (on at least some of the trials) observers were capable of consolidating three items. If this were the case, it is clear from the results that by attempting to increase the number of items consolidated in parallel, there is a further cost of reduced resolution and increased consolidation failure, which is consistent with our previous findings and the proposed biased competition account of the capacity.

8.2. Implications of the present findings

Results from the experiments described within this thesis have a range of implications for parallel processing of information within the human visual system. This section will present a discussion and synthesis of these implications.

8.2.1. Task demands and the capacity of parallel processing

Previous research demonstrated that a maximum of between three and six moving items could be processed simultaneously, depending on the type of motion signals (Greenwood & Edwards, 2006a, 2006b; Edwards & Rideaux, 2013). This could easily be interpreted as the ability to extract up to six motion directions in parallel, i.e. the speed/direction of six moving cars at a busy traffic intersection can all be processed simultaneously. However, given the task employed to discern this capacity, it is not clear whether this information is truly extracted. Indeed, the experiments reported in Chapter 4 demonstrate that while the presence of four or five distinct directions can be identified
simultaneously, the extraction of multiple motion directions is limited to three. This provides context to the previously found capacity and also indicates a principle of parallel processing that, at least within the area of multiple motion processing, had not yet been demonstrated. That is, that the limit of parallel processing varies as a function of the complexity of the items property being processed: the more complex the information being extracted, fewer items can be extracted in parallel. An important implication of this finding is that when determining processing limitations, or applying previously determined limits to a given situation, it is critical to consider task demands. This concept resonates with the conclusion drawn by Tripathy, Narasimham, & Barrett (2007) concerning local motion signals.

8.2.2. Parallel consolidation into visual short-term memory

Initially, consolidation of information into VSTM was thought to be limited to strictly serial processing (Huang et al., 2007). Recent developments showed that parallel consolidation into VSTM can be achieved with colour items, but it was suggested that orientation might be limited to serial processing (Liu & Becker, 2013; Mance et al., 2012). This is particularly interesting because it suggests that there may be something qualitatively unique about colour that allows it to be consolidated in parallel where other features cannot. However, since only two types of stimuli had yet been examined, before leaping to this conclusion, the next logical step was to determine whether features other than colour and orientation can be consolidated in parallel. The experiments detailed in Chapter 5 do precisely this, showing that motion direction, and possibly orientation, can be consolidated in parallel, contradicting previous claims. The importance of this finding extends beyond the demonstration that (at least) motion direction can be consolidated in parallel by demonstrating that features other than colour (and spatial location) are capable
of being encoded in parallel at this stage in processing. Thus, this suggests the strong possibility that multiple basic features are capable of being consolidated in parallel and that a common mechanism may be employed.

The timesaving benefits of parallel consolidation, over serial consolidation, are clear, i.e. it takes twice as long to consolidate two items serially as in parallel. Previous research suggests that there is no cost associated with consolidating items in parallel (Miller et al., 2014). Further, although we found some evidence for parallel consolidation of orientation, previous research indicates that this feature is limited to strictly serial processing (Liu & Becker, 2013). Thus, the experiments reported in Chapter 6 explicitly examine the errors associated with attempting to consolidate orientation and motion direction in parallel in order to confirm whether this is possible and, if so, what cost is associated with this process. In doing so, we confirm that motion direction, and possibly orientation can be consolidated in parallel, and that there is a twofold cost: items are encoded at a reduced resolution and the likelihood of failing to consolidate one (or both) item/s is increased. Thus, while there is a clear benefit of parallel processing, there is also a distinct cost. That is, by placing a greater load on the system, the representations encoded into VSTM are less precise, and the rate at which items fail to be stored entirely is increased, likely due to competitive interference. An implication of this is that, given there is a time-accuracy trade-off between parallel and serial processing (consolidation), the appropriateness of each method for any given situation is dependent on the relative importance of these factors.

It is likely that the two costs associated with parallel consolidation are driven by different mechanisms: spreading of cognitive resources used during VSTM consolidation results in lower resolution encoding while interference between items results in increased consolidation failure. This is evidenced by our finding the BHA for parallel consolidation modulates the likelihood of consolidation failure, but not precision. However, while it is
likely these are distinct mechanisms, it is unlikely that they operate independently. For instance, the resolution of items is likely to play a role in the likelihood of interference such that lower resolution items are subject to more interference. Items encoded at higher resolution are cortically represented by relatively narrower population response profiles (McAdams & Maunsell, 1999; Saproo & Serences, 2010; Treue & Martinez-Trujillo, 1999); these profiles are less likely to overlap, resulting in less interference (see Figure 8.1). Furthermore, it is likely that this is a unidirectional relationship, in that increased interference between items does not impact the resolution at which they are encoded. Further research is needed investigate this hypothesis by explicitly examining the relationship between these two factors.

![Figure 8.1](image)

Figure 8.1. An example of the relationship between the resolution of items and interference. The red and blue dashed lines represent neural population response profiles for motion directions at around 120° and 240°, respectively. When items are encoded at high resolution a) the profiles are narrow and do not overlap, whereas when encoded at low resolution, b) overlapping profiles can result in consolidation failure of one or both items.

There is considerable ongoing debate regarding the nature of VSTM storage, which can be reduced to the arguments for one of two types of models: discrete and continuous storage. Initially it was largely assumed that a discrete model could account for the storage capacity of VSTM; however, as investigatory methods became
increasingly sophisticated, allowing for more detailed examination of the items stored, a trade-off discovered between the number of items stored and the precision of each item led many agree that a continuous (aka limited resource) model best describes the capacity (Bays & Husain, 2008; Fougnie, Asplund, & Marois, 2010; Horowitz & Cohen, 2010; Ma, et al., 2014). Several researchers have extended this by suggesting an underlying neural mechanism of the limited resource model: biased competition (Franconeri et al., 2013; Shapiro & Miller, 2011).

Given the considerable functional overlap between consolidation and storage mechanisms of VSTM, our results, which indicate that a limited resource model can best account for the capacity of parallel consolidation, have clear implications for the ongoing debate surrounding storage. While it is feasible that consolidation and storage may operate using markedly different mechanisms (i.e. continuous and discrete), it seems more plausible that similar mechanisms are engaged, and that our results, in addition to a growing consensus (Ma, et al., 2014), support a limited resource account of VSTM storage. However, these operations have been linked to differential activation of cortical substrates, i.e. frontal/prefrontal cortex for consolidation (Curtis & D’Esposito, 2003; Passingham & Sakai, 2004) and regionally distributed areas for maintenance (Wager & Smith, 2003); thus, this trade-off could plausibly be localized to executive functions of VSTM, and not necessarily extend to retention.

Returning to VSTM consolidation, the pattern of results associated with the cost of parallel consolidation, i.e. the relationship between consolidation failure and item similarity, is likely an indication of the underlying mechanism that restricts this process. That is, the biased competition model, which has thus far been used to describe the capacity of spatial attention and VSTM storage, predicts that items presented simultaneously, as opposed to serially, compete for cortical representation, which can result in consolidation failure. Thus, experiments detailed in Chapter 7 were conducted
to further evaluate whether the biased competition model could be used to explain the capacity of parallel consolidation, and furthermore, to determine a precise estimate of this capacity. Our results were consistent with a biased competition account of parallel consolidation; that is, we found the presence of a BHA for parallel consolidation. Thus, this indicates that biased competition between items contributes to both the cost of parallel consolidation and also its capacity. Finally, while not entirely conclusive, this interpretation is consistent with our findings regarding the capacity of parallel consolidation. While observers may have been capable of consolidating three items in parallel, this could only be achieved at an even greater cost to encoding precision and consolidation likelihood; an outcome predicted by a limited resource/biased competition account.

To further investigate the capacity of parallel consolidation, with the aim of determining whether three items can be consolidated simultaneously, future research could use electroencephalogram (EEG) or magnetoencephalography (MEG) to measure the number of items stored after each simultaneous presentation. Recently, it was demonstrated that the amplitude of event-related potential (ERP) components, specifically the sustained posterior contralateral negativity (SPCN), is directly related to the number of items stored in VSTM (Jolicoeur, Brisson, & Robitaille, 2008; Robitaille, Grimault & Jolicoeur, 2009). Thus, comparison of the amplitude of the SPCN between conditions where observers are presented with two or three items simultaneously could be employed to physiologically evaluate whether more than two items can be consolidated in parallel. Similarly, magnetic resonance imaging (MRI) could also be used to address this question as an increased blood oxygenation level dependent (BOLD) response in the posterior parietal cortex is strongly correlated to VSTM load (Todd & Marois, 2004).
These findings have dramatic implications for the currently proposed information bandwidth model of VSTM consolidation (Becker, et al., 2013). The model claims that there is only one factor in the determination of parallel consolidation (the size of an item’s information bandwidth relative to a putative consolidation bottleneck), and that there is no cost of parallel consolidation to information for which this can be achieved. In contrast, we found that there is a twofold cost associated with this process, and that multiple factors (i.e. number of items, bilateral hemifield presentation and item similarity) influence the likelihood of items being consolidated. The information bandwidth model fails to account for this new evidence; however, as alluded to previously, the biased competition model fits the current findings well. It is challenging to discern the precise relationship between the two costs associated with parallel consolidation, and their relative contributions in determining the capacity on this process, from the current findings. However, given the current evidence, we propose that like VSTM storage and spatial attention, the biased competition model (at least partially) accounts for the cost and capacity of parallel consolidation into VSTM.

Biased competition may also explain why orientation, if it is consolidated in parallel, appears to be most susceptible to consolidation failure; that is, given its relatively small perceptual space (Foster & Ward, 1991; Webster, De Valois, & Switkes, 1990), compared to colour (Nagy & Sanchez, 1990; Witzel & Gegenfurtner, 2013), orientation is less robust to interference during dual representation at a critical stage of consolidation. While this argument appears to be lessened by the finding that direction is less susceptible to consolidation failure than orientation, and the two have a similar sized perceptual space (Clifford, 2002), the results from Chapter 6 regarding the resolution at which these features were encoded (relative to their physical ranges) suggest that overall the perceptual space of direction may actually be markedly larger than that of orientation.
In addition to being unable to draw conclusive interpretations regarding the precise capacity of parallel processing for motion direction, the current findings are also limited in their generalizability across features. That is, while we found consistent patterns of results for direction, it is possible that other features may be consolidated in a qualitatively different manner. In particular, previous findings for colour suggest that there is no cost associated with parallel consolidation of this feature; however, possible explanations for these findings have been discussed. Thus, further research is needed to investigate the possibility of qualitative differences in the way other features are consolidated in parallel to determine if a unifying model of parallel consolidation is appropriate.

8.3. Conclusions

The results of this thesis provide three broad conclusions regarding parallel processing within the human visual system. Firstly, the capacity of parallel processing, specifically parallel motion processing, is determined not only by the number of items but also the complexity of information which is extracted. Second, that there is a twofold cost associated with parallel consolidation of (motion direction and possibly orientation) information into VSTM: both the resolution at which items are encoded is reduced and the likelihood of consolidation failure is increased. Finally, the same mechanism that appears to underpin (part of) the cost of parallel consolidation can also explain its capacity: biased competition. Together these results provide important insight into parallel processing of information at multiple stages in the visual system, both in terms of cost and capacity.
References


PARALLEL PROCESSING IN THE HUMAN VISUAL SYSTEM


Appendices

Appendix A: Bayesian information criterion values for model comparison in Chapter 6, Experiment 1

Appendix B: Bayesian information criterion values for model comparison in Chapter 6, Experiment 2

Appendix C: Bayesian information criterion values for model comparison in Chapter 7, Experiment 1

Appendix D: Bayesian information criterion values for model comparison in Chapter 7, Experiment 2
### Appendix A: Bayesian information criterion values for model comparison in Chapter 6, Experiment 1

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Orientation: sequential</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2875.20</td>
<td>2882.75</td>
<td>2882.75</td>
<td>2882.75</td>
<td>-7.54</td>
<td>-7.54</td>
<td>-0.00</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2718.82</td>
<td>2725.83</td>
<td>2716.54</td>
<td>2723.40</td>
<td>-7.01</td>
<td>2.28</td>
<td>9.28</td>
<td>-4.58</td>
<td></td>
</tr>
<tr>
<td>3082.40</td>
<td>3089.94</td>
<td>3089.94</td>
<td>3089.94</td>
<td>-7.54</td>
<td>-7.54</td>
<td>-0.00</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>3060.82</td>
<td>3067.59</td>
<td>3067.23</td>
<td>3067.96</td>
<td>-6.77</td>
<td>-6.41</td>
<td>0.36</td>
<td>-7.14</td>
<td></td>
</tr>
<tr>
<td>2908.00</td>
<td>2915.54</td>
<td>2911.92</td>
<td>2915.54</td>
<td>-7.54</td>
<td>-3.92</td>
<td>3.62</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2929.14</td>
<td>2936.65</td>
<td>2935.59</td>
<td>2936.69</td>
<td>-7.50</td>
<td>-6.44</td>
<td>1.06</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2763.53</td>
<td>2771.07</td>
<td>2767.12</td>
<td>2771.07</td>
<td>-7.54</td>
<td>-3.60</td>
<td>3.94</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2798.96</td>
<td>2806.13</td>
<td>2806.50</td>
<td>2805.85</td>
<td>-7.18</td>
<td>-7.54</td>
<td>-0.36</td>
<td>-6.89</td>
<td></td>
</tr>
<tr>
<td>2889.79</td>
<td>2897.21</td>
<td>2895.74</td>
<td>2897.19</td>
<td>-7.42</td>
<td>-5.94</td>
<td>1.48</td>
<td>-7.39</td>
<td></td>
</tr>
<tr>
<td>2597.54</td>
<td>2605.08</td>
<td>2605.08</td>
<td>2605.08</td>
<td>-7.54</td>
<td>-7.54</td>
<td>-0.00</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2701.34</td>
<td>2708.88</td>
<td>2702.72</td>
<td>2708.87</td>
<td>-7.54</td>
<td>-1.38</td>
<td>6.16</td>
<td>-7.53</td>
<td></td>
</tr>
<tr>
<td><strong>Orientation: simultaneous</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2865.98</td>
<td>2873.52</td>
<td>2872.41</td>
<td>2872.02</td>
<td>-7.54</td>
<td>-6.43</td>
<td>1.11</td>
<td>-6.04</td>
<td></td>
</tr>
<tr>
<td>2784.07</td>
<td>2791.71</td>
<td>2789.26</td>
<td>2791.63</td>
<td>-7.64</td>
<td>-5.19</td>
<td>2.45</td>
<td>-7.56</td>
<td></td>
</tr>
<tr>
<td>3365.82</td>
<td>3371.17</td>
<td>3372.99</td>
<td>3373.36</td>
<td>-5.35</td>
<td>-7.17</td>
<td>-1.82</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>3279.17</td>
<td>3286.71</td>
<td>3286.66</td>
<td>3286.55</td>
<td>-7.54</td>
<td>-7.48</td>
<td>0.06</td>
<td>-7.38</td>
<td></td>
</tr>
<tr>
<td>3258.21</td>
<td>3263.93</td>
<td>3264.67</td>
<td>3265.03</td>
<td>-5.72</td>
<td>-6.46</td>
<td>-0.74</td>
<td>-6.82</td>
<td></td>
</tr>
<tr>
<td>3131.01</td>
<td>3138.55</td>
<td>3136.70</td>
<td>3138.55</td>
<td>-7.54</td>
<td>-5.70</td>
<td>1.84</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>3148.84</td>
<td>3156.38</td>
<td>3155.66</td>
<td>3156.07</td>
<td>-7.54</td>
<td>-6.82</td>
<td>0.72</td>
<td>-7.23</td>
<td></td>
</tr>
<tr>
<td>2868.51</td>
<td>2876.05</td>
<td>2865.25</td>
<td>2875.95</td>
<td>-7.54</td>
<td>3.26</td>
<td>10.80</td>
<td>-7.44</td>
<td></td>
</tr>
<tr>
<td>3029.93</td>
<td>3037.47</td>
<td>3035.79</td>
<td>3037.43</td>
<td>-7.54</td>
<td>-5.86</td>
<td>1.68</td>
<td>-7.50</td>
<td></td>
</tr>
<tr>
<td>2762.47</td>
<td>2770.01</td>
<td>2770.01</td>
<td>2769.55</td>
<td>-7.54</td>
<td>-7.54</td>
<td>0.00</td>
<td>-7.08</td>
<td></td>
</tr>
<tr>
<td>2807.99</td>
<td>2815.53</td>
<td>2812.70</td>
<td>2815.53</td>
<td>-7.54</td>
<td>-4.71</td>
<td>2.83</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td><strong>Direction: sequential</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1242.77</td>
<td>1249.62</td>
<td>1249.62</td>
<td>1249.62</td>
<td>-6.85</td>
<td>-6.85</td>
<td>-0.00</td>
<td>-6.85</td>
<td></td>
</tr>
<tr>
<td>2432.50</td>
<td>2439.84</td>
<td>2438.05</td>
<td>2438.63</td>
<td>-7.35</td>
<td>-5.55</td>
<td>1.80</td>
<td>-6.13</td>
<td></td>
</tr>
<tr>
<td>2438.05</td>
<td>2445.35</td>
<td>2444.91</td>
<td>2445.59</td>
<td>-7.31</td>
<td>-6.86</td>
<td>0.44</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2231.74</td>
<td>2239.28</td>
<td>2227.81</td>
<td>2234.32</td>
<td>-7.54</td>
<td>3.93</td>
<td>11.47</td>
<td>-2.58</td>
<td></td>
</tr>
<tr>
<td>2540.42</td>
<td>2547.96</td>
<td>2544.78</td>
<td>2547.96</td>
<td>-7.54</td>
<td>-4.36</td>
<td>3.18</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2851.34</td>
<td>2856.88</td>
<td>2857.81</td>
<td>2858.88</td>
<td>-5.54</td>
<td>-6.47</td>
<td>-0.93</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2807.99</td>
<td>2811.66</td>
<td>2815.22</td>
<td>2815.53</td>
<td>-3.67</td>
<td>-7.23</td>
<td>-3.56</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2784.67</td>
<td>2792.21</td>
<td>2789.94</td>
<td>2792.21</td>
<td>-7.54</td>
<td>-5.26</td>
<td>2.28</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2665.58</td>
<td>2673.12</td>
<td>2672.99</td>
<td>2673.12</td>
<td>-7.54</td>
<td>-7.41</td>
<td>0.13</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2602.19</td>
<td>2609.73</td>
<td>2608.23</td>
<td>2609.58</td>
<td>-7.54</td>
<td>-6.04</td>
<td>1.50</td>
<td>-7.39</td>
<td></td>
</tr>
<tr>
<td>2516.72</td>
<td>2524.26</td>
<td>2510.29</td>
<td>2522.42</td>
<td>-7.54</td>
<td>6.43</td>
<td>13.97</td>
<td>-5.70</td>
<td></td>
</tr>
<tr>
<td>2840.25</td>
<td>2847.68</td>
<td>2847.04</td>
<td>2847.78</td>
<td>-7.43</td>
<td>-6.79</td>
<td>0.64</td>
<td>-7.53</td>
<td></td>
</tr>
</tbody>
</table>
### Direction: simultaneous

<table>
<thead>
<tr>
<th></th>
<th>1221.82</th>
<th>1228.67</th>
<th>1228.67</th>
<th>1229.17</th>
<th>-6.85</th>
<th>-6.85</th>
<th>-0.01</th>
<th>-7.35</th>
</tr>
</thead>
<tbody>
<tr>
<td>2886.34</td>
<td>2893.69</td>
<td>2893.79</td>
<td>2893.79</td>
<td>-7.35</td>
<td>-7.45</td>
<td>-0.10</td>
<td>-7.45</td>
<td></td>
</tr>
<tr>
<td>2737.13</td>
<td>2744.67</td>
<td>2741.82</td>
<td>2744.67</td>
<td>-7.54</td>
<td>-4.69</td>
<td>2.85</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2493.38</td>
<td>2500.92</td>
<td>2499.10</td>
<td>2500.92</td>
<td>-7.54</td>
<td>-5.72</td>
<td>1.82</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2524.65</td>
<td>2532.00</td>
<td>2531.06</td>
<td>2532.19</td>
<td>-7.35</td>
<td>-6.40</td>
<td>0.94</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>3251.87</td>
<td>3259.41</td>
<td>3259.41</td>
<td>3259.40</td>
<td>-7.54</td>
<td>-7.54</td>
<td>-0.00</td>
<td>-7.53</td>
<td></td>
</tr>
<tr>
<td>3202.17</td>
<td>3206.21</td>
<td>3209.71</td>
<td>3209.71</td>
<td>-4.04</td>
<td>-7.54</td>
<td>-3.50</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2927.70</td>
<td>2933.76</td>
<td>2935.24</td>
<td>2935.24</td>
<td>-6.07</td>
<td>-7.54</td>
<td>-1.48</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2792.72</td>
<td>2800.26</td>
<td>2800.25</td>
<td>2800.26</td>
<td>-7.54</td>
<td>-7.53</td>
<td>0.02</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>2779.74</td>
<td>2786.65</td>
<td>2784.23</td>
<td>2782.09</td>
<td>-6.90</td>
<td>-4.49</td>
<td>2.41</td>
<td>-7.35</td>
<td></td>
</tr>
<tr>
<td>2568.58</td>
<td>2576.12</td>
<td>2570.93</td>
<td>2576.12</td>
<td>-7.54</td>
<td>-2.35</td>
<td>5.19</td>
<td>-7.54</td>
<td></td>
</tr>
<tr>
<td>3248.38</td>
<td>3252.14</td>
<td>3251.03</td>
<td>3245.53</td>
<td>-3.77</td>
<td>-2.65</td>
<td>1.11</td>
<td>2.85</td>
<td></td>
</tr>
</tbody>
</table>
### Appendix B: Bayesian information criterion values for model comparison in Chapter 6, Experiment 2

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Orientation: rand</strong></td>
<td>1437.23</td>
<td>1444.08</td>
<td>1443.60</td>
<td>1444.08</td>
<td>-6.85</td>
<td>-6.36</td>
<td>0.48</td>
<td>-6.85</td>
</tr>
<tr>
<td>sequential</td>
<td>1927.86</td>
<td>1934.81</td>
<td>1927.94</td>
<td>1934.80</td>
<td>-6.95</td>
<td>-6.08</td>
<td>0.67</td>
<td>-6.94</td>
</tr>
<tr>
<td></td>
<td>1880.59</td>
<td>1887.54</td>
<td>1886.06</td>
<td>1887.58</td>
<td>-6.95</td>
<td>-5.48</td>
<td>1.48</td>
<td>-7.00</td>
</tr>
<tr>
<td></td>
<td>1908.97</td>
<td>1915.73</td>
<td>1912.62</td>
<td>1915.95</td>
<td>-6.77</td>
<td>-3.66</td>
<td>3.11</td>
<td>-6.99</td>
</tr>
<tr>
<td></td>
<td>1871.58</td>
<td>1878.61</td>
<td>1878.17</td>
<td>1876.24</td>
<td>-7.03</td>
<td>-6.59</td>
<td>0.44</td>
<td>-6.66</td>
</tr>
<tr>
<td></td>
<td>1809.71</td>
<td>1816.36</td>
<td>1816.74</td>
<td>1816.74</td>
<td>-6.65</td>
<td>-7.03</td>
<td>-0.38</td>
<td>-7.03</td>
</tr>
<tr>
<td>sequential</td>
<td>1823.63</td>
<td>1830.53</td>
<td>1829.00</td>
<td>1829.76</td>
<td>-6.90</td>
<td>-5.37</td>
<td>1.53</td>
<td>-6.14</td>
</tr>
<tr>
<td></td>
<td>1964.24</td>
<td>1971.27</td>
<td>1971.27</td>
<td>1971.27</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1916.21</td>
<td>1922.57</td>
<td>1921.74</td>
<td>1921.61</td>
<td>-6.36</td>
<td>-5.53</td>
<td>0.83</td>
<td>-5.40</td>
</tr>
<tr>
<td></td>
<td>1936.91</td>
<td>1943.94</td>
<td>1940.57</td>
<td>1943.37</td>
<td>-7.03</td>
<td>-3.66</td>
<td>3.37</td>
<td>-6.46</td>
</tr>
<tr>
<td></td>
<td>1941.82</td>
<td>1948.49</td>
<td>1948.72</td>
<td>1948.81</td>
<td>-6.68</td>
<td>-6.91</td>
<td>-0.23</td>
<td>-6.99</td>
</tr>
<tr>
<td><strong>Orientation: fixed</strong></td>
<td>1456.31</td>
<td>1463.16</td>
<td>1460.65</td>
<td>1463.16</td>
<td>-6.85</td>
<td>-4.34</td>
<td>2.51</td>
<td>-6.85</td>
</tr>
<tr>
<td>sequential</td>
<td>1915.17</td>
<td>1921.78</td>
<td>1918.60</td>
<td>1922.16</td>
<td>-6.61</td>
<td>-3.43</td>
<td>3.18</td>
<td>-6.99</td>
</tr>
<tr>
<td></td>
<td>1882.60</td>
<td>1889.62</td>
<td>1889.83</td>
<td>1889.32</td>
<td>-6.82</td>
<td>-7.03</td>
<td>-0.21</td>
<td>-6.53</td>
</tr>
<tr>
<td></td>
<td>1921.12</td>
<td>1928.15</td>
<td>1924.21</td>
<td>1925.98</td>
<td>-7.03</td>
<td>-3.09</td>
<td>3.94</td>
<td>-4.86</td>
</tr>
<tr>
<td></td>
<td>1928.36</td>
<td>1934.95</td>
<td>1935.40</td>
<td>1935.39</td>
<td>-6.59</td>
<td>-7.03</td>
<td>-0.44</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1809.08</td>
<td>1815.62</td>
<td>1815.19</td>
<td>1814.28</td>
<td>-6.54</td>
<td>-6.10</td>
<td>0.44</td>
<td>-5.20</td>
</tr>
<tr>
<td>sequential</td>
<td>1855.49</td>
<td>1862.44</td>
<td>1860.82</td>
<td>1862.07</td>
<td>-6.95</td>
<td>-5.33</td>
<td>1.62</td>
<td>-6.59</td>
</tr>
<tr>
<td></td>
<td>1849.22</td>
<td>1855.80</td>
<td>1854.50</td>
<td>1854.93</td>
<td>-6.57</td>
<td>-5.28</td>
<td>1.29</td>
<td>-5.70</td>
</tr>
<tr>
<td></td>
<td>1949.69</td>
<td>1956.72</td>
<td>1956.72</td>
<td>1956.72</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1879.34</td>
<td>1886.37</td>
<td>1884.56</td>
<td>1886.09</td>
<td>-7.03</td>
<td>-5.22</td>
<td>1.81</td>
<td>-6.75</td>
</tr>
<tr>
<td></td>
<td>1854.12</td>
<td>1861.15</td>
<td>1856.23</td>
<td>1858.11</td>
<td>-7.03</td>
<td>-2.11</td>
<td>4.92</td>
<td>-3.99</td>
</tr>
<tr>
<td>sequential</td>
<td>1949.09</td>
<td>1956.12</td>
<td>1956.12</td>
<td>1956.12</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td><strong>Orientation: simultaneous</strong></td>
<td>1466.17</td>
<td>1472.17</td>
<td>1471.41</td>
<td>1473.02</td>
<td>-6.00</td>
<td>-5.25</td>
<td>0.75</td>
<td>-6.85</td>
</tr>
<tr>
<td></td>
<td>2016.72</td>
<td>2023.75</td>
<td>2023.50</td>
<td>2023.75</td>
<td>-7.03</td>
<td>-6.79</td>
<td>0.25</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1890.13</td>
<td>1897.05</td>
<td>1896.97</td>
<td>1895.49</td>
<td>-6.92</td>
<td>-6.84</td>
<td>0.08</td>
<td>-5.37</td>
</tr>
<tr>
<td></td>
<td>2015.35</td>
<td>2022.38</td>
<td>2022.38</td>
<td>2022.38</td>
<td>-7.03</td>
<td>-7.03</td>
<td>0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>2034.57</td>
<td>2041.51</td>
<td>2041.43</td>
<td>2041.60</td>
<td>-6.95</td>
<td>-6.86</td>
<td>0.08</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1868.06</td>
<td>1874.75</td>
<td>1875.10</td>
<td>1875.09</td>
<td>-6.69</td>
<td>-7.03</td>
<td>-0.34</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1772.86</td>
<td>1779.89</td>
<td>1779.31</td>
<td>1779.89</td>
<td>-7.03</td>
<td>-6.44</td>
<td>0.59</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1884.64</td>
<td>1891.67</td>
<td>1891.67</td>
<td>1891.67</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1941.49</td>
<td>1947.86</td>
<td>1948.52</td>
<td>1948.52</td>
<td>-6.37</td>
<td>-7.03</td>
<td>-0.66</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1952.30</td>
<td>1959.33</td>
<td>1959.33</td>
<td>1959.33</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td>-----------</td>
<td>------------</td>
<td>---------</td>
<td>-----------------------</td>
<td>--------------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
<td>--------</td>
</tr>
<tr>
<td>Direction: rand sequential</td>
<td>1524.45</td>
<td>1631.48</td>
<td>1631.48</td>
<td>1631.48</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1597.71</td>
<td>1604.69</td>
<td>1600.54</td>
<td>1603.48</td>
<td>-6.97</td>
<td>-2.83</td>
<td>4.15</td>
<td>-5.77</td>
</tr>
<tr>
<td></td>
<td>1979.30</td>
<td>1986.25</td>
<td>1986.33</td>
<td>1986.33</td>
<td>-6.95</td>
<td>-7.03</td>
<td>-0.08</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1750.26</td>
<td>1757.29</td>
<td>1757.29</td>
<td>1757.29</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1735.83</td>
<td>1734.31</td>
<td>1742.86</td>
<td>1742.86</td>
<td>1.52</td>
<td>-7.03</td>
<td>-8.55</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1945.07</td>
<td>1950.01</td>
<td>1952.10</td>
<td>1952.10</td>
<td>-4.94</td>
<td>-7.03</td>
<td>-2.09</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1845.99</td>
<td>1853.02</td>
<td>1841.63</td>
<td>1852.05</td>
<td>-7.03</td>
<td>4.36</td>
<td>11.39</td>
<td>-6.06</td>
</tr>
<tr>
<td></td>
<td>1778.76</td>
<td>1785.72</td>
<td>1785.79</td>
<td>1785.31</td>
<td>-6.96</td>
<td>-7.03</td>
<td>-0.07</td>
<td>-6.55</td>
</tr>
<tr>
<td></td>
<td>1746.38</td>
<td>1753.41</td>
<td>1752.70</td>
<td>1753.37</td>
<td>-7.03</td>
<td>-6.32</td>
<td>0.71</td>
<td>-6.99</td>
</tr>
<tr>
<td></td>
<td>1758.34</td>
<td>1765.37</td>
<td>1763.77</td>
<td>1765.37</td>
<td>-7.03</td>
<td>-5.44</td>
<td>1.59</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1723.78</td>
<td>1729.65</td>
<td>1724.46</td>
<td>1730.24</td>
<td>-5.87</td>
<td>-0.68</td>
<td>5.19</td>
<td>-6.47</td>
</tr>
<tr>
<td>Direction: fixed sequential</td>
<td>1618.49</td>
<td>1624.64</td>
<td>1624.56</td>
<td>1625.43</td>
<td>-6.15</td>
<td>-6.06</td>
<td>0.08</td>
<td>-6.93</td>
</tr>
<tr>
<td></td>
<td>1898.70</td>
<td>1904.08</td>
<td>1905.22</td>
<td>1905.16</td>
<td>-5.38</td>
<td>-6.52</td>
<td>-1.14</td>
<td>-6.46</td>
</tr>
<tr>
<td></td>
<td>1576.82</td>
<td>1583.88</td>
<td>1583.85</td>
<td>1584.00</td>
<td>-7.06</td>
<td>-7.03</td>
<td>0.02</td>
<td>-7.17</td>
</tr>
<tr>
<td></td>
<td>1910.50</td>
<td>1917.53</td>
<td>1917.18</td>
<td>1917.53</td>
<td>-7.03</td>
<td>-6.68</td>
<td>0.35</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1804.71</td>
<td>1811.47</td>
<td>1811.63</td>
<td>1811.27</td>
<td>-6.76</td>
<td>-6.92</td>
<td>-0.16</td>
<td>-6.55</td>
</tr>
<tr>
<td></td>
<td>1769.34</td>
<td>1766.12</td>
<td>1773.32</td>
<td>1776.37</td>
<td>3.21</td>
<td>-3.98</td>
<td>-7.19</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1877.50</td>
<td>1882.26</td>
<td>1884.52</td>
<td>1882.79</td>
<td>-4.76</td>
<td>-7.02</td>
<td>-2.26</td>
<td>-5.29</td>
</tr>
<tr>
<td></td>
<td>1801.60</td>
<td>1806.62</td>
<td>1808.63</td>
<td>1808.63</td>
<td>-5.02</td>
<td>-7.03</td>
<td>-2.01</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1748.08</td>
<td>1754.04</td>
<td>1755.11</td>
<td>1755.11</td>
<td>-5.96</td>
<td>-7.03</td>
<td>-1.07</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1775.88</td>
<td>1782.92</td>
<td>1779.41</td>
<td>1781.06</td>
<td>-7.03</td>
<td>-3.52</td>
<td>3.51</td>
<td>-5.18</td>
</tr>
<tr>
<td></td>
<td>1874.45</td>
<td>1881.48</td>
<td>1879.81</td>
<td>1881.48</td>
<td>-7.03</td>
<td>-5.36</td>
<td>1.67</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1653.19</td>
<td>1660.22</td>
<td>1660.22</td>
<td>1660.22</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td>Direction: simultaneous</td>
<td>1771.94</td>
<td>1778.93</td>
<td>1778.97</td>
<td>1778.97</td>
<td>-6.99</td>
<td>-7.03</td>
<td>-0.05</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1727.80</td>
<td>1734.83</td>
<td>1734.83</td>
<td>1734.83</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1900.78</td>
<td>1997.81</td>
<td>1997.81</td>
<td>1997.81</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1949.25</td>
<td>1954.78</td>
<td>1955.92</td>
<td>1956.28</td>
<td>-5.53</td>
<td>-6.66</td>
<td>-1.14</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>2072.00</td>
<td>2079.03</td>
<td>2079.03</td>
<td>2079.03</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1945.89</td>
<td>1952.97</td>
<td>1952.87</td>
<td>1952.92</td>
<td>-7.03</td>
<td>-6.96</td>
<td>0.05</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1943.65</td>
<td>1946.28</td>
<td>1950.68</td>
<td>1950.68</td>
<td>-2.63</td>
<td>-7.03</td>
<td>-4.40</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>1843.71</td>
<td>1849.41</td>
<td>1850.74</td>
<td>1850.74</td>
<td>-5.69</td>
<td>-7.03</td>
<td>-1.34</td>
<td>-7.03</td>
</tr>
<tr>
<td></td>
<td>2037.56</td>
<td>2044.60</td>
<td>2044.60</td>
<td>2043.91</td>
<td>-7.03</td>
<td>-7.03</td>
<td>-0.00</td>
<td>-6.34</td>
</tr>
<tr>
<td></td>
<td>1751.12</td>
<td>1757.79</td>
<td>1757.92</td>
<td>1758.15</td>
<td>-6.67</td>
<td>-6.80</td>
<td>-0.13</td>
<td>-7.03</td>
</tr>
</tbody>
</table>
Appendix C: Bayesian information criterion values for model comparison in Chapter 7, Experiment 1

<table>
<thead>
<tr>
<th>Condition</th>
<th>1. Mixture</th>
<th>2. Swap</th>
<th>3. Variable Precision</th>
<th>1 - 2</th>
<th>1 - 3</th>
<th>2 - 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Direction: unilateral</td>
<td>4413.4</td>
<td>4421.3</td>
<td>4420.7</td>
<td>-7.9</td>
<td>-7.3</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td>4211.5</td>
<td>4219.5</td>
<td>4209.3</td>
<td>-8</td>
<td>2.2</td>
<td>10.2</td>
</tr>
<tr>
<td></td>
<td>4327.9</td>
<td>4334.5</td>
<td>4334.4</td>
<td>-6.6</td>
<td>-6.5</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>4731</td>
<td>4738.9</td>
<td>4733.9</td>
<td>-7.9</td>
<td>-2.9</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>4584.5</td>
<td>4592.5</td>
<td>4583.3</td>
<td>-8</td>
<td>1.2</td>
<td>9.2</td>
</tr>
<tr>
<td></td>
<td>4968.4</td>
<td>4966.9</td>
<td>4976.4</td>
<td>1.5</td>
<td>-8</td>
<td>-9.5</td>
</tr>
<tr>
<td></td>
<td>4550.9</td>
<td>4558.3</td>
<td>4558.1</td>
<td>-7.4</td>
<td>-7.2</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>4910.1</td>
<td>4918</td>
<td>4918.2</td>
<td>-7.9</td>
<td>-8.1</td>
<td>-0.2</td>
</tr>
<tr>
<td></td>
<td>4586.7</td>
<td>4594.7</td>
<td>4592.6</td>
<td>-8</td>
<td>-5.9</td>
<td>2.1</td>
</tr>
<tr>
<td></td>
<td>5058</td>
<td>5065.7</td>
<td>5065.7</td>
<td>-7.7</td>
<td>-7.7</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>5207.9</td>
<td>5213.9</td>
<td>5215.9</td>
<td>-6</td>
<td>-8</td>
<td>-2</td>
</tr>
<tr>
<td></td>
<td>4046.3</td>
<td>4054.4</td>
<td>4046.9</td>
<td>-8.1</td>
<td>-0.6</td>
<td>7.5</td>
</tr>
<tr>
<td>Direction: bilateral</td>
<td>4459.8</td>
<td>4467.8</td>
<td>4467.7</td>
<td>-8</td>
<td>-7.9</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>4343.3</td>
<td>4351.2</td>
<td>4351.2</td>
<td>-7.9</td>
<td>-7.9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4262.1</td>
<td>4270.1</td>
<td>4268.1</td>
<td>-8</td>
<td>-6</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>4790.1</td>
<td>4798</td>
<td>4797</td>
<td>-7.9</td>
<td>-6.9</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>4262.9</td>
<td>4270.9</td>
<td>4270.8</td>
<td>-8</td>
<td>-7.9</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>5069.5</td>
<td>5077.5</td>
<td>5077.5</td>
<td>-8</td>
<td>-8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4472.9</td>
<td>4480.1</td>
<td>4480.9</td>
<td>-7.2</td>
<td>-8</td>
<td>-0.8</td>
</tr>
<tr>
<td></td>
<td>4888.7</td>
<td>4896.7</td>
<td>4896.7</td>
<td>-8</td>
<td>-8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4576.3</td>
<td>4584.3</td>
<td>4584.3</td>
<td>-8</td>
<td>-8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>5103.1</td>
<td>5111.1</td>
<td>5111.1</td>
<td>-8</td>
<td>-8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>5157.2</td>
<td>5164.5</td>
<td>5165.3</td>
<td>-7.3</td>
<td>-8.1</td>
<td>-0.8</td>
</tr>
<tr>
<td></td>
<td>4048.5</td>
<td>4056.5</td>
<td>4041.1</td>
<td>-8</td>
<td>7.4</td>
<td>15.4</td>
</tr>
<tr>
<td>Orientation: unilateral</td>
<td>4728.9</td>
<td>4736.5</td>
<td>4736.8</td>
<td>-7.6</td>
<td>-7.9</td>
<td>-0.3</td>
</tr>
<tr>
<td></td>
<td>4393.8</td>
<td>4401.7</td>
<td>4398</td>
<td>-7.9</td>
<td>-4.2</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td>4356.7</td>
<td>4364.2</td>
<td>4363.2</td>
<td>-7.5</td>
<td>-6.5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>4829.5</td>
<td>4837.4</td>
<td>4837.4</td>
<td>-7.9</td>
<td>-7.9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4722.1</td>
<td>4730</td>
<td>4730</td>
<td>-7.9</td>
<td>-7.9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4802.9</td>
<td>4810.9</td>
<td>4810.9</td>
<td>-8</td>
<td>-8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4501.7</td>
<td>4508.7</td>
<td>4509.7</td>
<td>-7</td>
<td>-8</td>
<td>-1</td>
</tr>
<tr>
<td></td>
<td>5051.7</td>
<td>5059.7</td>
<td>5059.7</td>
<td>-8</td>
<td>-8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>5123.6</td>
<td>5130</td>
<td>5131.3</td>
<td>-6.4</td>
<td>-7.7</td>
<td>-1.3</td>
</tr>
</tbody>
</table>
### Parallel Processing in the Human Visual System

<table>
<thead>
<tr>
<th></th>
<th>5358.2</th>
<th>5365.8</th>
<th>5366.2</th>
<th>-7.6</th>
<th>-8</th>
<th>-0.4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5358.2</td>
<td>5365.8</td>
<td>5366.2</td>
<td>-7.6</td>
<td>-8</td>
<td>-0.4</td>
</tr>
<tr>
<td></td>
<td>4428.9</td>
<td>4427.9</td>
<td>4428.9</td>
<td>-7</td>
<td>-8</td>
<td>-1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Orientation: bilateral</th>
<th>4633</th>
<th>4639</th>
<th>4640.9</th>
<th>-6</th>
<th>-7.9</th>
<th>-1.9</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4451.1</td>
<td>4459</td>
<td>4459</td>
<td>-7.9</td>
<td>-7.9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4347.3</td>
<td>4355.2</td>
<td>4350.4</td>
<td>-7.9</td>
<td>-3.1</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>4740.5</td>
<td>4747.7</td>
<td>4748.4</td>
<td>-7.2</td>
<td>-7.9</td>
<td>-0.7</td>
</tr>
<tr>
<td></td>
<td>4665.1</td>
<td>4669.1</td>
<td>4673</td>
<td>-4</td>
<td>-7.9</td>
<td>-3.9</td>
</tr>
<tr>
<td></td>
<td>4747.2</td>
<td>4755.1</td>
<td>4755.2</td>
<td>-7.9</td>
<td>-8</td>
<td>-0.1</td>
</tr>
<tr>
<td></td>
<td>4509.8</td>
<td>4517.2</td>
<td>4517.3</td>
<td>-7.4</td>
<td>-7.5</td>
<td>-0.1</td>
</tr>
<tr>
<td></td>
<td>5268.3</td>
<td>5275.9</td>
<td>5276.3</td>
<td>-7.6</td>
<td>-8</td>
<td>-0.4</td>
</tr>
<tr>
<td></td>
<td>5013.8</td>
<td>5021.8</td>
<td>5020.8</td>
<td>-8</td>
<td>-7</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>5147.6</td>
<td>5155.5</td>
<td>5155.5</td>
<td>-7.9</td>
<td>-7.9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>5147.6</td>
<td>5155.5</td>
<td>5155.5</td>
<td>-7.9</td>
<td>-7.9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>4484</td>
<td>4492</td>
<td>4491.5</td>
<td>-8</td>
<td>-7.5</td>
<td>0.5</td>
</tr>
</tbody>
</table>
### Appendix D: Bayesian information criterion values for model comparison in Chapter 7, Experiment 2

<table>
<thead>
<tr>
<th>Condition</th>
<th>1. Mixture</th>
<th>2. Swap</th>
<th>3. Variable Precision</th>
<th>1 - 2</th>
<th>1 - 3</th>
<th>2 - 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Direction, N = 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Mixture</td>
<td>4026.2</td>
<td>4034.1</td>
<td>4030.9</td>
<td>-7.9</td>
<td>-7.4</td>
<td>-2.5</td>
</tr>
<tr>
<td>2. Swap</td>
<td>3978.2</td>
<td>3983.1</td>
<td>3985.6</td>
<td>-4.9</td>
<td>-7.4</td>
<td>-5.3</td>
</tr>
<tr>
<td>3. Variable Precision</td>
<td>4024.1</td>
<td>4031.8</td>
<td>4026.5</td>
<td>-7.7</td>
<td>-2.4</td>
<td>5.3</td>
</tr>
<tr>
<td>1 - 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 - 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Direction, N = 3</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Mixture</td>
<td>4637.4</td>
<td>4645.3</td>
<td>4645.3</td>
<td>-9.7</td>
<td>-7.9</td>
<td>0</td>
</tr>
<tr>
<td>2. Swap</td>
<td>4324.6</td>
<td>4332.5</td>
<td>4332.3</td>
<td>-7.9</td>
<td>-7.7</td>
<td>0.2</td>
</tr>
<tr>
<td>3. Variable Precision</td>
<td>4451.8</td>
<td>4459.7</td>
<td>4459</td>
<td>-7.9</td>
<td>-7.2</td>
<td>0.7</td>
</tr>
<tr>
<td>1 - 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 - 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Orientation, N = 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Mixture</td>
<td>3091.6</td>
<td>3099.1</td>
<td>3098.8</td>
<td>-7.5</td>
<td>-7.2</td>
<td>0.3</td>
</tr>
<tr>
<td>2. Swap</td>
<td>4040.5</td>
<td>4045.3</td>
<td>4030.3</td>
<td>-4.8</td>
<td>10.2</td>
<td>15</td>
</tr>
<tr>
<td>3. Variable Precision</td>
<td>3848.2</td>
<td>3852.4</td>
<td>3855.2</td>
<td>-4.2</td>
<td>-7</td>
<td>-2.8</td>
</tr>
<tr>
<td>1 - 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 - 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Orientation, N = 3</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Mixture</td>
<td>4469.9</td>
<td>4457.9</td>
<td>4456.2</td>
<td>-7.9</td>
<td>-7.9</td>
<td>0</td>
</tr>
<tr>
<td>2. Swap</td>
<td>4372.3</td>
<td>4378.7</td>
<td>4378.7</td>
<td>-6</td>
<td>-6.4</td>
<td>-0.4</td>
</tr>
<tr>
<td>3. Variable Precision</td>
<td>4200.8</td>
<td>4205.2</td>
<td>4208.7</td>
<td>-4.4</td>
<td>-7.9</td>
<td>-3.5</td>
</tr>
<tr>
<td>1 - 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 - 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Orientation, N = 3</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Mixture</td>
<td>44733.6</td>
<td>4733</td>
<td>4733</td>
<td>10</td>
<td>-0.6</td>
<td>-10.6</td>
</tr>
<tr>
<td>2. Swap</td>
<td>4796.2</td>
<td>4771.4</td>
<td>4804</td>
<td>24.8</td>
<td>-7.8</td>
<td>-32.6</td>
</tr>
</tbody>
</table>
### Parallel Processing in the Human Visual System

<p>| | | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>4245.9</td>
<td>4253.5</td>
<td>4253.3</td>
<td>-7.6</td>
<td>-7.4</td>
<td>0.2</td>
</tr>
<tr>
<td>4726.1</td>
<td>4729.7</td>
<td>4734</td>
<td>-3.6</td>
<td>-7.9</td>
<td>-4.3</td>
</tr>
<tr>
<td>4188</td>
<td>4195.9</td>
<td>4182.5</td>
<td>-7.9</td>
<td>5.5</td>
<td>13.4</td>
</tr>
</tbody>
</table>