Mechanisms of Visual Feature Binding

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A thesis submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

Faculty of Science

The University of Sydney

2015

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Acknowledgements

First and foremost I would like to extend my sincerest thanks to my supervisor, Prof. Colin W. G. Clifford. I have been extremely fortunate to receive his expert help, guidance and patience on every step of this journey. Similarly, my profuse thanks go to my associate supervisor, Dr. Ryan T. Maloney. I cannot truly express in words how much both Colin and Ryan have helped and encouraged me, and how thankful I am in return.

I would also like to thank the other members of Colin's lab, both past and present, who have provided both their valuable assistance and time during my candidature at the University of Sydney. Thank you, Blake, Damien, Erin, Isabelle, Kiley, Matthew, Tamara, Tony, and Yumiko. I would also like to thank my associate supervisor Dr. Irina Harris, in addition to A Prof. Alex Holcombe, Dr. Mark Schira, Dr. Steven Most, Prof. David Alais, and his lab members, Garry, Emily and Shui for their time and for helpful discussions and questions. My thanks also go out to my lovely and wonderful friends (both offline and online), FT, KV, LL, MB, MM, and MP for being always willing to talk and share their opinions with me.

Finally, I would like to thank my family for all their love and support over the past few years. Specifically, my father, Mark, my mother, Evelyn, my brother, Joshua, and my grandparents, Olivia and Egidio as their encouragement and support has helped me immensely. This thesis is not only the culmination of four years worth of work, but also due to the love and respect I have

for science. The help of these people and countless others have enabled me to complete this challenging and rewarding thesis.

The research detailed in this thesis was financially supported by an Australian Research Council (ARC) Future Fellowship (C.W.G.C.; grant number FT110100150), a National Health and Medical Research Council grant (C.W.G.C.; grant number APP1027258), and the ARC Centre of Excellence in Vision Science.

Abstract

Visual feature binding is the method by which coherent objects and scenes are perceived. Advances in the science of perception have indicated that visual features such as colour, motion, and orientation are to some extent, processed separately in primate early visual cortex. However, the mechanism by which these features are integrated remains unclear. Phenomenologically, the process of binding features to form objects appears to be an efficient and automatic process. Some research also shows a high temporal resolution for binding features together, in addition to populations of neurons that jointly code for features. However, dominant theories of feature binding and the majority of the binding literature indicate that the feature binding process is severely limited by a relatively low temporal resolution, especially when compared to other perceptual properties such as feature detection.

To identify and resolve the discrepancy in the feature binding literature, I investigate the feature binding process and its inter-relationship with perceptual surface segregation. Surface segregation has been postulated as the method by which features can be rapidly bound together, giving them impression of a high temporal resolution. In Chapter 2, displays are used that alternate between two arrays of differently coloured, oppositely moving dots. The alternation frequency is modified in order to gauge the temporal resolution of binding. This is combined with surface segregation cues such as coherent motion, consistency of dot configuration, and colour. In Chapter 3, coloured, oriented gratings are used to investigate colour-orientation binding. Angular separation, spatial and temporal coincidence, and stimulus presentation

duration are varied. Across these experiments, a number of these surface segregation cues are manipulated in order to measure the corresponding effects on feature binding, perceptual interpretation of the stimulus, and its neural representation. The results of the psychophysical experiments indicate that feature binding, surface segregation, and temporal integration are inextricably linked. These findings are reinforced by data gathered through functional magnetic resonance imaging (fMRI) of human subjects. Both surface segregation and feature pairs were found to modulate neural activity in early visual cortex, providing evidence that similar neural substrates are recruited for both feature binding and surface segregation.

Overall, the two complementary sets of experiments using stimulus conjunctions of colour-motion and colour-orientation stimuli provide converging evidence and insight into the dynamics of the underlying binding mechanisms. A discussion of the implications of the research follows, concluding that rapidly formed surface representations can be maintained across presentation intervals by temporal integration. Attentional selection of one feature (e.g. orientation) can then be used to boost the response to the paired feature (colour) in order to identify and extract the correct feature pairing. Based on the known properties of the visual system, several potential neural mechanisms are proposed that are consistent with both the psychophysical and neural data, in addition to suggested future directions for the study of visual feature binding.

Declaration

I submit this thesis to the University of Sydney in fulfilment of the requirements for the degree of Doctor of Philosophy. The work presented in this thesis is original to the best of my knowledge, except where acknowledged in the text. Portions of this work have been presented at several conferences and submitted for publication in scientific journals as noted in Appendix A. I hereby declare that I have not submitted this material, either in full or in part, for a degree at this or any other institution.

List of Figures and Tables

Chapter 1. Introduction

1.1. Rationale

For many animals, the most efficient and accurate way of gathering information about the world is through visual perception. The ubiquitous nature of sight has driven the evolution of humans and shaped our behaviour, customs, and societal norms. However, despite the fundamental advantages that vision provides to nearly all animals, we often take the complexity of the viewing process for granted (Treisman, 1998). The brain is tasked with processing and interpreting a limitless combination of perceptual inputs (O'Reilly, 1998). Furthermore, perception must occur both in a timely manner using a finite amount of resources in order to ensure that any response to external stimuli is both appropriate and executed accurately (Von der Malsburg, 1995). Our attempts to model how biological vision interprets the visual scene, and subsequently replicate it through computer vision are currently being developed (Barrow & Tenenbaum, 1978).

The visual system solves several problems, one of which is the formation of accurate object representations. This is a non-trivial problem, as the visual inputs we receive are often incomplete and ambiguous (Klink, Van Wezel, & Van Ee, 2012). For example, a cluttered environment provides opportunities for several confounding factors to interfere with accurate perception of the visual scene. Occlusion of objects, similarity of visual attributes, and shared edges are all factors that must be considered when assessing a scene (Maunsell & Treue, 2006).

In scenes with moving or transparent objects, this process is further complicated. Nevertheless, phenomenologically it appears effortless as objects are separated and appropriately assigned their constituent edges, textures, colours, and spatial locations.

Our knowledge of how visual features such as colour, orientation, and directions of motion are bound together to form objects is still incomplete. We must first understand how visual feature binding occurs in order to comprehend visual perception as a whole.

1.2. Research aims and scope

Visual feature “binding” is the process by which basic features such as colour, motion, and orientation, are integrated together (Treisman & Gelade, 1980). Feature binding must occur in order to match our phenomenological experience of the world as an organised and unified one. Despite a large body of work surrounding this topic, a consensus as to how binding occurs in human vision remains unreached (Quinlan, 2003). As such, it is important to understand the circumstances where binding can both succeed and fail. Through the consideration of these cases, an overall theory of feature binding can be developed. Therefore, in this thesis I explore the properties of visual feature binding using complementary psychophysical and fMRI techniques. Functional MRI studies here investigate binding in the visual cortex, and as such the literature discussed in the following sections will be similarly focused.

The perception of colour-motion and colour-orientation feature conjunctions (or feature pairs) will be tested by manipulating several stimulus characteristics. By understanding the properties of feature binding in this manner, theories of binding can be developed that are consistent with both current and past research. Ultimately, integration of a complete theory of feature binding with the knowledge of other visual processes is necessary in order to form a complete theory of visual perception.

The goal of these experiments is not to explicitly test theories of feature binding. Further, as the experiments presented here are a small subset of many possible ways in which feature binding can be probed, the aim of the current thesis is not to present a complete theory of feature binding. Rather, the psychophysical and neuroimaging studies conducted here explore the characteristics and properties of feature binding, addressing a discrepancy in the literature regarding its temporal resolution. Specifically, the present thesis aims to test whether the feature binding process is a slow, late process or a rapid, early one. The implications of these results will be considered within various feature binding frameworks. It is hoped these results serve to guide future research and refinement of current behavioural and neural feature binding theories.

1.3. Organisation of the visual cortex and the resultant binding problem

1.3.1. Response properties of neurons

Electrophysiological studies of monkey primary visual cortex (V1) provided fundamental insights into the response properties of neurons in visual cortex (Albright, 1984; Dubner & Zeki, 1971; Hubel & Wiesel, 1961; Hubel & Wiesel, 1968; Maunsell & Van Essen, 1983b; Zeki, 1978a). The responses of each neuron, the majority of which are binocularly driven, were tied to visual stimulation within a small spatial location (Zeki, 1978b). Neurons increase their fire rate in response to greater stimulation of this specific area (Hubel & Wiesel, 1968). Surrounding this area was a zone that, when stimulated, suppressed the baseline firing rate of the neuron (Hubel & Wiesel, 1961). Together, these observations indicated that each neuron possessed a ‘receptive field’: an area in the visual field that neurons in the visual cortex monitored and responded to (Allman, Miezin, & McGuinness, 1985).

Furthermore, studies identified that a majority of neurons were selective towards one of several basic visual features, suggesting that the visual scene was decomposed for analysis (Albright, 1984; Dubner & Zeki, 1971; Horwitz & Albright, 2005; Hubel & Wiesel, 1968; Hubel, Wiesel, & Stryker, 1978; Johnson, Hawken, & Shapley, 2008; Maunsell & Van Essen, 1983b; Zeki, 1978b, 1993). These studies found neurons tended to favour one type of visual feature when located in their receptive field. For example, a neuron tuned to vertical orientations would exhibit rapid spiking behaviour in response to arrays of vertical bars. However, the firing rate of that same neuron was inhibited when presented with horizontal bars (Hubel & Wiesel, 1968). This suggested that the visual scene was broken down into its constituent features such as contours and edges during the initial processing, and that neurons exhibited a functional specificity.

Further single-cell studies revealed that V1, V2 and V3 of non-human primates contained many cells tuned to attributes from two or more visual features (Burkhalter & Van Essen, 1986; Gegenfurtner, Kiper, & Fenstemaker, 1996; Gegenfurtner, Kiper, & Levitt, 1997; Johnson et al., 2008; Leventhal, Thompson, Liu, Zhou, & Ault, 1995; Shipp, Adams, Moutoussis, & Zeki, 2009; Tamura, Sato, Katsuyama, Hata, & Tsumoto, 1996). For example, Leventhal et al. (1995) and others found that cells had dual selectivity for colour-motion, colour-orientation, and motion-orientation attributes in V1 and V2. V2 especially contained more double duty cells than V1 (Burkhalter & Van Essen, 1986; Gegenfurtner et al., 1996; Tamura et al., 1996). They conclude that the functional specificity of neurons may not be as clear as previously believed. This point will be discussed further in section 1.3.5.

1.3.2. Retinotopic and functional organisation of visual cortex

Studies indicate that a degree of functional organisation and specialisation exists in human visual cortex (Haxby et al., 1994; Hubel & Wiesel, 1968; McKeefry & Zeki, 1997; Ramachandran & Gregory, 1978; Van Essen & Zeki, 1978; Zeki, 1974; Zeki et al., 1991) (Figure 1.1, Figure 1.2a). In addition to the response specific behaviours of neurons, the overall architecture of the visual system suggests that visual features are processed with some degree of independence (Bartels & Zeki, 1998). For example, within V1 and V2 neurons tuned for individual features are grouped together in both monkeys (Hubel et al., 1978; Mishkin, Ungerleider, & Macko, 1983; Zeki, 1978a) and humans (Kim, Duong, & Kim, 2000; Larsson & Heeger, 2006; Savoy, 1987; Wandell, Dumoulin, & Brewer, 2007; Yacoub, Harel, & Uğurbil, 2008).

In V1, Livingstone and Hubel (1984) identified patches of strong cytochrome oxidase staining, termed ‘blobs’, containing neurons sensitive to colour (also see Sincich & Horton, 2005a). Many of these cells were tuned for both colour and luminance (Johnson, Hawken, & Shapley, 2001). Cells in the inter-blob areas were found to be sensitive to orientation and direction of motion (Livingstone & Hubel, 1984). The organisation of orientation-tuned neurons into columns was also identified (Hubel & Wiesel, 1974; Hubel et al., 1978). That is, the preferred orientation of neurons varied by small and systematic amounts when sampling from neurons across these columns.

In V2, the response properties of cells are dependent on their location within either the cytochrome oxidase-defined thick stripes, thin stripes, or interstripe regions (Sincich & Horton, 2005a; Tootell & Born, 1992; Zeki, 1993). Cells located in the thin stripes have been reported to receive inputs from blob cells in V1 (Sincich & Horton, 2005b), correlated with findings that these cells are receptive to colour (DeYoe & Van Essen, 1985; Tootell & Hamilton, 1989). Interblob regions in V1 project to both the thick stripes and interstripe regions, both of which contain orientation selective cells (Hubel & Livingstone, 1987; Sincich & Horton, 2002).

Two extrastriate examples of functional organisation are V4 and V5/MT+ (Roe et al., 2012; Van Essen & Maunsell, 1983). V4 was initially regarded as a key colour processing area, as several studies have demonstrated that V4 is highly receptive to colour stimuli (Heywood, Gadotti, & Cowey, 1992; Roe et al., 2012; Van Essen & Zeki, 1978; Zeki, 1983a, 1983b). Cells in V4 are organised such that cells responding to similar colours tend to be grouped together (Zeki, 1983c, 1993). However, V4 may be more specialised for processing form (Gegenfurtner & Kiper, 2003), as it was found that the majority of its cells are respond equally well to chromatic and achromatic stimuli (Schein, Marrocco, & De Monasterio, 1982). It is worth noting that caution must be taken when comparing monkey and human neurophysiology (Goodale & Milner, 1992; Larsson & Heeger, 2006). While areas V1, V2, V3 and MT are similar in both humans and monkeys (Orban, Van Essen, & Vanduffel, 2004), Heywood et al. (1992) provide evidence, for example, that the human and monkey homologues of V4 may not be functionally equivalent.

The connections between V1 and area MT (Shipp & Zeki, 1989) and recordings of MT in monkeys and its homological equivalent in humans, V5/MT+ (Albright & Desimone, 1987; Dumoulin et al., 2000; Garcia & Grossman, 2009), suggest it is specialised for motion processing. Cells in MT are organised with respect to their preferred direction of motion: sampling cells arranged in a parallel manner within MT, one would find a gradual shift in the motion selectivity of these neurons (Albright, 1984; Zeki, 1974, 1993). Further, Albright and Desimone (1987) report that MT is highly organised in terms of both receptive field size and position. In addition to neural analyses of monkeys, further evidence for the functionality of area MT come from human studies. Lesions to MT+ can induce motion blindness, termed cerebral akinetopsia (Beckers & Homberg, 1992; Van Oostende, Sunaert, Van Hecke, Marchal, & Orban, 1997; Zeki, 1991). In healthy subjects, transcranial magnetic stimulation (TMS) was used to disrupt healthy subjects’ V5/MT+, inducing temporary akinetopsia (Beckers & Homberg, 1992). This is discussed further in section 1.3.4.

Further evidence for modular processing of the visual scene can be observed in the organisation of early visual areas. V1, V2, V3 and V3AB can be retinotopically defined (Engel, Glover, & Wandell, 1997; Larsson & Heeger, 2006; Sereno et al., 1995; Tootell, Switkes, Silverman, & Hamilton, 1988; Van Essen & Zeki, 1978) (Figure 1.1). Retinotopic organisation is observed if the spatial and temporal configurations of visual stimulation correlate with neuronal patterns of activation (Grill-Spector & Malach, 2004; Larsson & Heeger, 2006). That is, in a retinotopically organised area, neurons in proximity are also more likely to respond to stimuli in the same part of the visual field. Using this principle, V1 to V3AB can be defined by their patterns of activation to a rotating wedge stimulus (Larsson & Heeger, 2006).

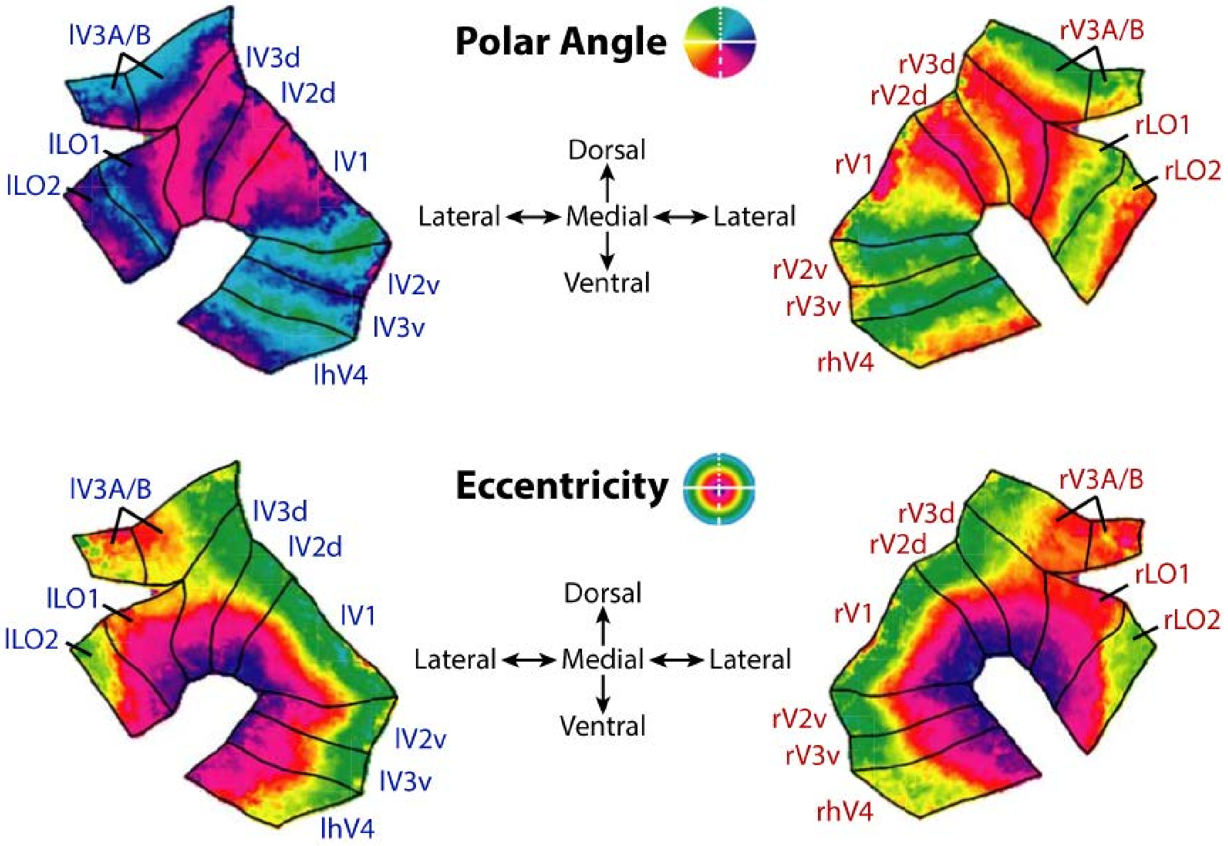

Figure 1.1. Retinotopic organisation of the visual cortex. Shown here is the cortical representation of polar angle (top) and eccentricity (bottom) averaged over 15 subjects. Areas belonging to left and right hemispheres are prefixed with a lowercase ‘l’ or ‘r’, respectively. The colour of the flattened representation indicates the rotation of the wedge (top) or the eccentricity of the circle (bottom) which best corresponds to the polar angle or eccentricity indicated by the small coloured circles next to the respective titles. From Larsson and Heeger (2006).

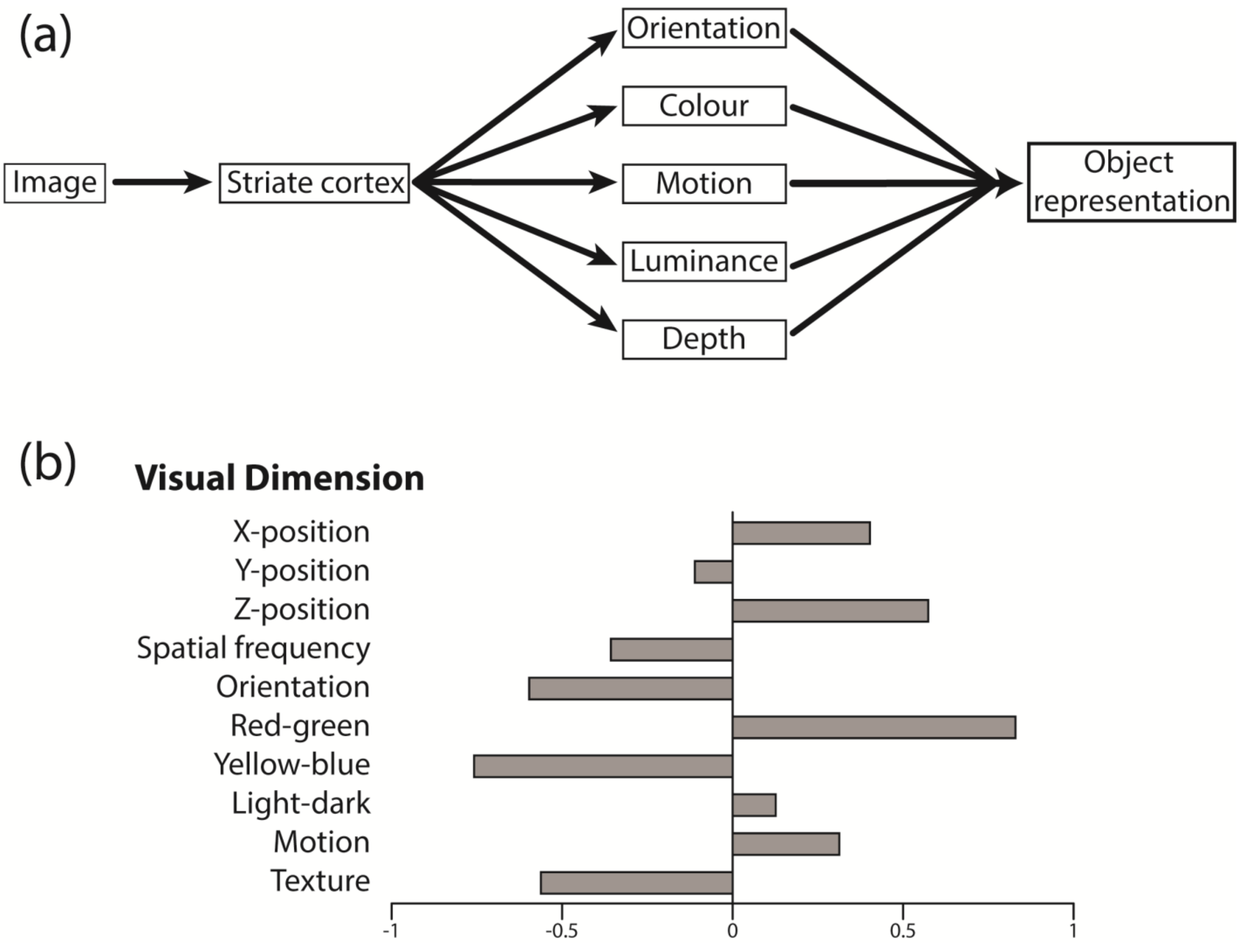

Figure 1.2. Two models of feature encoding. **(a)** Traditional models of the visual system assume images are broken down into constituent features for processing, before recombining these into object representations. **(b)** An integrated approach to image coding by Lennie (1998). Here, neurons code for several dimensions of an image, rather than coding for individual visual features. Adapted from Burr (1999).

1.3.3. The visual hierarchy

Further advances into the structure and functions of the visual cortex led to the idea that visual processing was executed in a structured and sequential manner (Felleman & Van Essen, 1991; Hubel & Livingstone, 1987; Van Essen & Maunsell, 1983) (Figure 1.2a). Neurons from areas later in the visual hierarchy have bigger receptive field sizes (Albright & Desimone, 1987; Felleman & Kaas, 1984; Felleman & Van Essen, 1987), and are located further from striate cortex (Zeki, 1993). While neurons earlier in the visual hierarchy processed simple aspects of stimuli, projections to later areas aggregated the responses of these neurons together. Neurons in these later areas also have more complex response profiles and respond to more complex figures – a trait not seen in early visual areas (Maunsell & Newsome, 1987; Tanaka, 1993). These areas are thus thought to be involved with the integration of information, coding features in a multidimensional fashion.

Furthermore, it was argued that the visual hierarchy was organised into two functionally specialised processing streams (Mishkin et al., 1983; Ungerleider & Haxby, 1994; Van Essen & Maunsell, 1983) (Figure 1.3). The dorsal pathway, containing area V5/MT+, is specialised for the localisation of objects in space, while the ventral pathway, containing V4, is associated with the identification of objects (Van Essen & Maunsell, 1983). Ungerleider and Mishkin (1982) argue that these two streams did the majority of processing before visual information was subsequently integrated at a later stage. However, an alternative view suggests that the functions of the ventral and dorsal pathways subserve perception and action respectively (Goodale &

Milner, 1992; Milner & Goodale, 2008). That is, while the ventral pathway is involved in explicit visual awareness of a scene, the dorsal pathway guides interaction with the visual scene. Perry and Fallah (2014) expand on this proposal, detailing how each stream may consolidate information into object representations.

Under any hierarchical framework like those described here, three modes of processing can be identified, defined by the relationships between neurons (Lamme & Roelfsema, 2000; Lamme, Super, & Spekreijse, 1998; Salin & Bullier, 1995; Van Essen & Maunsell, 1983) (Figure 1.4). Feedforward processing is the main mode by which information is transmitted through both dorsal and ventral streams in the visual hierarchy. Visual inputs arriving in V1 via the lateral geniculate nucleus of the thalamus rapidly proceed through V2, V3 and onward to higher areas (Lamme & Roelfsema, 2000) and serves as the primary method by which information is propagated. Feedback is the process by which higher areas send signals back to earlier areas for confirmatory analysis (Bouvier & Treisman, 2010b; Di Lollo, Enns, & Rensink, 2000), or to influence processing (Hochstein & Ahissar, 2002; Juan & Walsh, 2003), and operates on a longer timescale (Lamme et al., 1998). More on the role of feedback in feature binding is discussed in Section 1.5.4. Finally, lateral/horizontal connections link parallel areas together (Van Essen, Anderson, & Felleman, 1992). A large number of these horizontal connections exist: in monkey cortex 30% of all possible connections between areas are present (Felleman & Van Essen, 1991). These connections are thought to increase the flexibility of visual processing by providing a non-linear method of information sharing (Salin & Bullier, 1995; Van Essen et al., 1992).

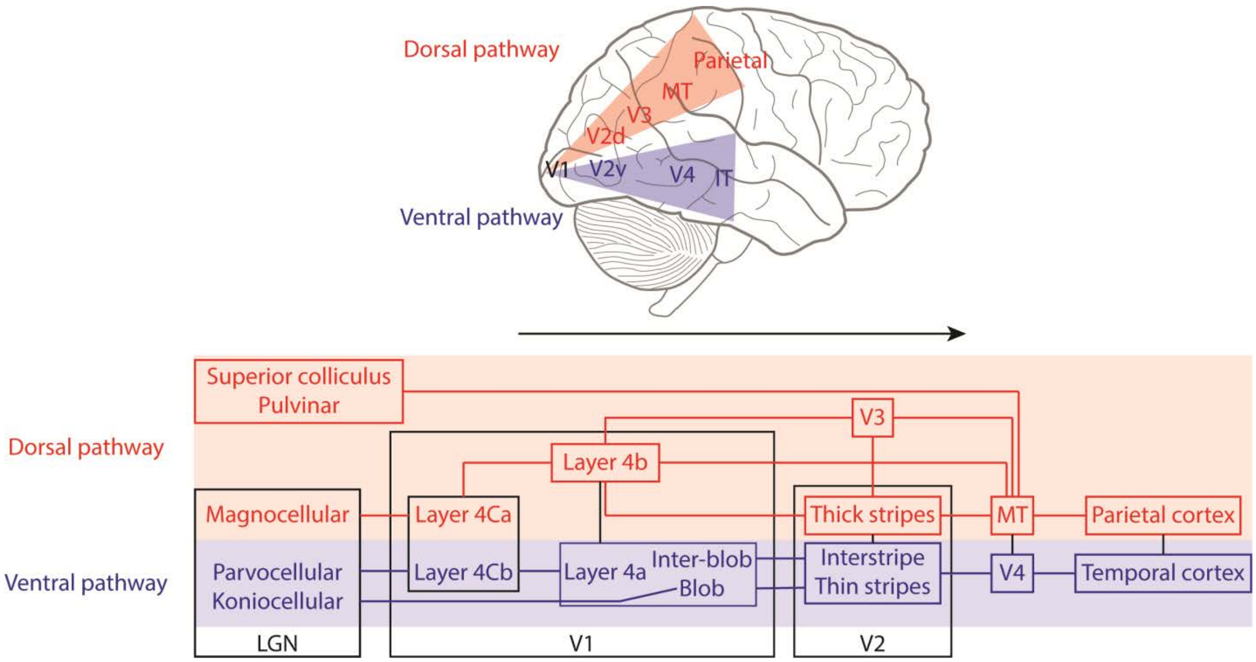

Figure 1.3 Organisation of dorsal and ventral processing streams. Schematic representation of the two main processing streams and their major connections in the visual cortex: the dorsal pathway (in red) and the ventral pathway (in blue). Red and blue lines indicate connections within a corresponding pathway, while black lines indicate parallel or lateral connections between pathways. Adapted from Lamme and Roelfsema (2000).

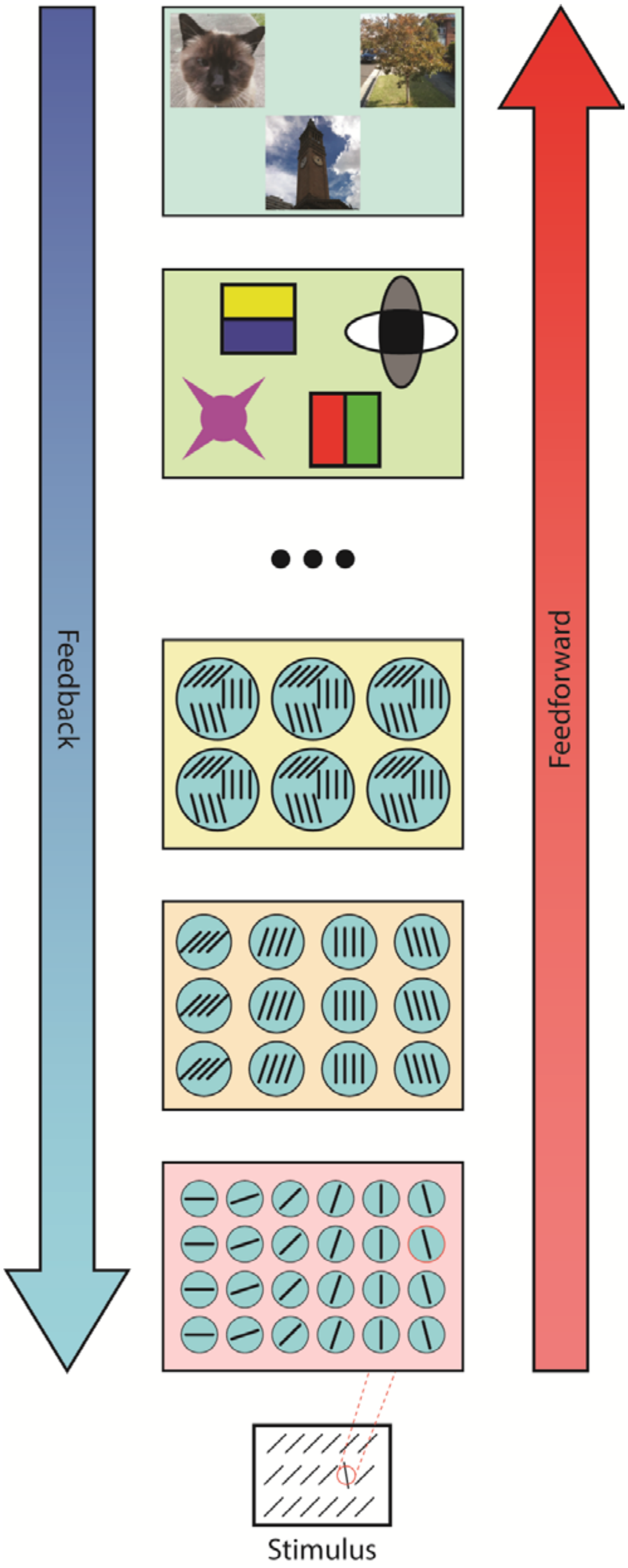
Feedback
Feedforward
Stimulus

Figure 1.4. Feedforward and feedback modes of processing. A graphical representation of increasingly complex representations of visual information is shown here. Feedforward processing involves having the real-world stimulus (white box) processed initially by early visual areas, represented by the lower, coloured boxes. Visual information at the earliest stage is represented through basic visual features (such as orientation in this example). These are subsequently integrated into more complex representations such as feature conjunctions and objects by higher areas. In the reverse process, feedback involves projections from higher areas sent to lower areas. Adapted from Hochstein and Ahissar (2002).

1.3.4. Neuropsychological evidence for the binding problem

Through their modular view of the brain, Zeki and Bartels (1998) maintain that an area that processes colours is what enables the awareness of colour. Therefore, they argue that the process of feature binding can be regarded as a “binding of consciousnesses” (also Zeki, 2003; Zeki & Bartels, 1999). Reported here are clinical studies of patients with localised damage to part of their visual cortex, causing specific visual processing deficiencies while leaving the rest of their vision relatively intact. The patients described here experience a selective ‘blindness’ towards a specific visual feature such as colour or motion (Grill-Spector & Malach, 2004; Zeki, 1990, 1991). Clinical studies such as these provide insight into the structure and function of the brain.

Cerebral achromatopsia results in patients either perceiving colours as less distinct, or losing the ability to see colour altogether (Setälä & Vesti, 1994; Victor, 1988; Zeki, 1990). A review by Meadows (1974) indicates that most cases of cerebral achromatopsia are caused by damage to the anterior, inferior portion of the visual cortex. A more recent review found that damage to the occipito-ventral region was common across a large number of studies (Bouvier & Engel, 2006). Bouvier and Engel (2006) assert that while this region is critical for processing colour, it is not exclusively responsible for colour vision. While Zeki (1990) reports that the vast majority of cerebral achromatopsia patients report seeing the world in grey, the performance of cerebral achromatopsia patients on colour tests such as the Farnsworth-Munsell 100-hue colour test can vary widely (Victor, 1988).

A rarer deficiency is cerebral akinetopsia, where patients report being unable to perceive moving objects (Zeki, 1991). Patients with cerebral akinetopsia describe their phenomenological experience of the world as a series of still frames and are unable to judge the positions of moving objects (Zeki, 1991). However, the motion perception ability and overall visual experience of akinetopsia patients varies widely (e.g. Baker, Hess, & Zihl, 1991; Newsome & Pare, 1988). For example, a patient with bilateral posterior brain damage was able to perceive motion in their peripheral vision, but not centrally (Zihl, Von Cramon, & Mai, 1983).

More directly indicative of a binding problem, some clinical studies indicate that localised damage to the visual cortex is associated with deficiencies in feature binding. An infarction in a patient's right posterior temporal region generated an inability to perceive form defined by motion (Cowey & Vaina, 2000). Critically, however, the ability to detect both form and motion individually was intact. Unilateral damage to the rostral pulvinar nucleus was associated with an inability to bind colour and form, with Ward, Danziger, Owen, and Rafal (2002) concluding that damage here resulted in an inability to correctly localise individual visual features.

Lesions to the posterior parietal cortex also appear to disrupt the feature binding process. One patient with bilateral parietal lesions was more likely to report a physically non-existent combination of features (Braet & Humphreys, 2009). The likelihood of this failure to bind paradoxically increased when the stimulus was presented for a longer period of time. In the same study, neurodisruption in the form of pulses of transcranial magnetic stimulation (TMS) applied to the same area in healthy control subjects also increased the rate at which illusory conjunctions were reported, providing converging evidence for the function of these parietal regions. Another patient with bilateral parietal occipital lesions was unable to correctly report shape-colour combinations, even when stimuli were freely viewed (Robertson & Treisman, 1995).

More evidence for a feature binding problem comes from those who suffer from Balint's syndrome (Bálint, 1909). Balint's syndrome occurs following bilateral parietal lesions and symptoms include optic ataxia, apraxia and severe difficulty binding features together (Friedman-Hill, Robertson, Desimone, & Ungerleider, 2003; Robertson, 2003; Robertson, Treisman, Friedman-Hill, & Grabowecky, 1997). Despite an ability to recognise objects, patients are unable to properly bind features together, such as shape and colour (Rafal, 2001; Robertson et al., 1997). Finally, participants with lesions to the right temporo-parietal cortex were significantly worse than healthy controls in identifying target letters presented among a rapid serial stream of distractors, indicative of a disruption in temporal feature integration. (Arend, Rafal, & Ward, 2011).

1.3.5. Evidence against modular processing

Alternate views of the visual system exist whereby processing in the visual cortex has an integrated, rather than modular, organisation (Gegenfurtner et al., 1996; Lennie, 1998; Leventhal et al., 1995; Van Essen et al., 1992). Lennie (1998) in particular argues that the visual cortex processes a scene in a holistic manner. A multi-dimensional representation of the visual scene is constructed by neurons with increasingly sparser representations (Burr, 1999; Lennie, 1998)

(Figure 1.2b). While he admits that, due to the weight of evidence, MT is most likely the primary motion processing area, there is evidence to support his claim that other areas of the visual cortex have some role in processing all visual attributes of a scene.

Certainly, the functional organisation of the visual cortex is not as clearly defined or as well-understood as initially thought (Leventhal et al., 1995). Studies indicate that a proportion of cells in V4 are tuned to visual attributes other than colour (Ghose & Daniel, 1997; Hinkle & Connor, 2002; Tolias, Keliris, Smirnakis, & Logothetis, 2005). Cells found within early areas of the visual cortex are also less homogenous than initially believed (Gegenfurtner et al., 1996; Leventhal et al., 1995). It was also found that chromatic signals can modulate responses in MT, suggesting colour can affect judgements of speed (Seidemann, Poirson, Wandell, & Newsome, 1999).

Furthermore, the fact remains that the visual cortex is highly interconnected - even between dorsal and ventral processing streams (Gegenfurtner & Kiper, 2003; Grill-Spector & Malach, 2004; Konen & Kastner, 2008; Lehky & Sereno, 2007; Maunsell & Van Essen, 1983a). The large amount of horizontal connections may indicate that visual processing occurs in a distributed, sparsely-coded manner. (Lamme et al., 1998; Salin & Bullier, 1995; Van Essen et al., 1992).

1.4. Neuroimaging of feature binding in human early visual cortex

1.4.1. Correlates of perceived feature conjunctions

Functional magnetic resonance imaging (fMRI) has enabled feature binding to be studied in human visual cortex using a blood oxygen level dependent (BOLD) response (Grill-Spector & Malach, 2004; Logothetis & Wandell, 2004). The blood oxygenation level of a particular location in the brain is a complex and indirect measure of neural activity (Vazquez & Noll, 1998; Wandell, 1999), that also jointly reflects the volume of cerebral blood present and the associated oxygen consumption (Logothetis & Wandell, 2004). Fluctuations in the BOLD signal are recorded across regions of interest, while participants view various feature conjunctions. Multivariate decoding techniques such as support vector machines (SVM) (Joachims, 1999) can then be used to analyse the large amounts of data generated by the BOLD response (Formisano, De Martino, & Valente, 2008; Karl J Friston, Frith, Frackowiak, & Turner, 1995; Seymour & Clifford, 2012; Seymour, Clifford, Logothetis, & Bartels, 2009; Seymour, Clifford, Logothetis, & Bartels, 2010; Tong & Pratte, 2012). SVMs analyse and compare the differences between patterns of activity for each type of presented stimuli. Sufficiently different patterns indicate that differential responses to the stimuli are occurring. By observing patterns of neural activity across a large area, an impression of the underlying neural coding can be gained (Logothetis & Wandell, 2004).

Using multivariate fMRI techniques, previous studies have demonstrated that feature pairs such as colour-motion (Bouvier & Treisman, 2010a; Seymour, Clifford, et al., 2009; Zhang, Qiu, Zhang, Han, & Fang, 2014), colour-orientation (Sumner, Anderson, Sylvester, Haynes, & Rees, 2008), colour-form (Seymour et al., 2010), and motion-stereoscopic depth (Seymour & Clifford, 2012) are coded in conjunction as early as V1 in humans. The majority of these studies also find that activity modulation to feature conjunctions occur in V2, V3, V3AB and V4. Portions of the parietal cortex were differentially modulated when participants performed a feature binding task where conjunctions were either distributed in space or presented sequentially. Here, the parietal cortex was more active during the spatial task (Shafritz, Gore, & Marois, 2002). Through neuroimaging, the evidence indicates that feature binding involves a number of cortical visual areas.

1.4.2. Correlates of perceptual misbinding

Neural correlates of perceptual misbinding have recently been observed (Kanai, Sereno, & Vincent, 2010; Zhang et al., 2014). Both studies used a display where differently-coloured dots were exclusively paired with a direction of motion in the centre portion of the stimulus (e.g. red dots moving up and green dots moving down) while the reverse pairing was present in the periphery (Wu, Kanai, & Shimojo, 2004). When fixating on a central cross, dots in the periphery appeared to match the colour-motion pairing in the centre. Using this stimulus in an fMRI study, it was found that patterns of BOLD modulated by stimuli in the periphery were more consistent with the perceived rather than the physical colour-motion pairing (Kanai et al., 2010; Zhang et al., 2014). The activity of V2 reflected the misbound percept rather than the physical stimulus.

1.5. Proposed solutions to the feature binding problem

1.5.1. Early coding of feature conjunctions

The research described in the previous sections provided several possible accounts of how visual features are processed. However the method by which these features are subsequently integrated still remains unclear. One possible method is through the dense coding of feature pairs by conjunction detectors in early visual cortex (Bowers, 2009). Several psychophysical studies provide evidence for early processing of feature pairs (e.g. Blaser, Papathomas, & Vidnyánszky, 2005; Favreau, Emerson, & Corballis, 1972; Holcombe & Cavanagh, 2001). It was previously mentioned in Section 1.3.1 that some single unit studies found that many neurons in V1 and V2 are selective for more than one visual attribute (Burkhalter & Van Essen, 1986; Gegenfurtner et al., 1996; Johnson et al., 2008; Leventhal et al., 1995; Shipp et al., 2009; Tamura et al., 1996). Furthermore, the discussed fMRI evidence also indicates that feature conjunctions are represented in early visual cortex (Bouvier & Treisman, 2010a; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003; Seymour & Clifford, 2012; Seymour, Clifford, et al., 2009; Seymour et al., 2010; Sumner et al., 2008). Therefore, it could be argued that features are bound during this early stage by means of conjunction detectors. This theory is a simple solution to the binding problem which avoids the problems associated with a central integrator, it also raises several serious issues worth considering (Plaut & McClelland, 2010).

From a physiological point of view, efficiency is a key argument against the idea of low-level feature conjunctions (Von der Malsburg, 1999). If low-level neurons are acting as specialised conjunction detectors, an infinite number of neurons would be required to process the endless number of feature combinations that are possible (O'Reilly, 1998). Moreover, unless features remain unbound in the periphery, conjunction detectors would be needed throughout the visual field as neurons within early visual cortex tend to have small receptive fields (Rolls & Deco, 2002; Zeki, 1978b).

Another issue with the prospect of early feature binding is that it is mostly inconsistent with the psychophysical literature discussed in Section 1.7. If conjunction detectors function as a feature binding mechanism at an early stage, then conjunction pop-out and high temporal resolutions for perceiving feature conjunctions should be observed just as for the detection of features (Desimone & Duncan, 1995). However, we find that the temporal resolution of feature binding is comparatively slower when compared with other visual processes such as feature identification, flicker detection and surface segregation, which are all known to be early, rapid processes (Bodelón, Fallah, & Reynolds, 2007; Holcombe, 2009; Keesey, 1972; Møller & Hurlbert, 1996; Nakano & Kaiser, 1992; Sajda & Finkel, 1995; Treisman & Gormican, 1988). It appears that even if features are coded in conjunction in early visual cortex, this does not necessarily translate into awareness.

1.5.2. Late, central integration

From our current knowledge about the properties and function of the visual hierarchy (discussed in Section 1.3.3), it seems plausible that visual feature binding may be a process occurring later in the visual hierarchy. Neurons here tend to have both increasingly complex response properties and larger receptive fields (Felleman & Kaas, 1984; Maunsell & Newsome, 1987). As these areas tend to receive input from multiple sources (Grill-Spector & Malach, 2004; Maunsell & Van Essen, 1983a; Van Essen & Maunsell, 1983), it follows that the modular processing of visual features may be bound together at a higher stage of processing (Arend et al., 2011; Shafritz et al., 2002; Treisman, 1998). The physiological evidence presented in Section 1.3.4 supports this idea, as damage to visual areas higher in the visual hierarchy results in either an inability to bind certain feature pairs, or an increase in illusory conjunctions (Arend et al., 2011; Braet & Humphreys, 2009; Cowey & Vaina, 2000; Robertson & Treisman, 1995; Ward et al., 2002).

Conjunction perception can be driven by top-down attentional processes, whereas feature perception is mostly exogenously driven (Treisman & Gelade, 1980; Treisman & Sato, 1990). Reaction times and error rates for conjunction detection are generally higher than feature perception, even in healthy subjects, coinciding with the longer processing times associated with higher-order processes (Holcombe, 2009). More psychophysical evidence along these lines is discussed in Section 1.7.

1.5.3. Neuronal synchrony

Explicit neural mechanisms of feature binding have also been proposed (Von der Malsburg, 1994). Neural synchrony is the idea that features belonging to the same object are coded through synchronous firing of neurons, typically within the gamma frequency range (30-100 Hz) (Elliott & Müller, 1998; Usher & Donnelly, 1998). That is, neurons responsive to features belonging to a single object synchronise their rate of action potential firing, serving as a temporal "tag". While synchronous activity has been detected throughout the visual cortex, the precise function that it plays remains unclear (Usrey & Reid, 1999). Nevertheless, some evidence indicates that monkey visual cortex is able to synchronize neuronal fire at approximately 40 Hz when observing feature conjunctions (Eckhorn, Frien, Bauer, Woelbern, & Kehr, 1993; Elliott & Müller, 1998; Tallon-Baudry & Bertrand, 1999). Higher cortical areas are receptive to gamma-band firing, suggesting that these areas may play a role in integrating or "reading out" the synchronised neural signals (Singer, 1999).

However, evidence for neuronal synchrony is not robust (Shadlen & Movshon, 1999). Several studies have demonstrated that synchronised firing of neurons to feature conjunctions is not reliable (Palanca & DeAngelis, 2005; Thiele & Stoner, 2003). Von der Malsburg (1995) argues that perhaps not all types of binding require synchronous activity. However, he concedes that the temporal coding of conjunctions has the distinct disadvantage of being a time consuming process. That is, given the small amount of time to perceive a conjunction, neurons are limited to a small number of temporal channels in which the conjunction can be coded (Von der Malsburg, 1995).

1.5.4. Re-entrant processes

More recently, re-entrant processing has been thought to play a critical role in feature binding, and visual awareness in general (Bouvier & Treisman, 2010b; Di Lollo et al., 2000; Koivisto & Silvanto, 2012; Pascual-Leone & Walsh, 2001; Rothenstein, Rodriguez-Sanchez, Simine, & Tsotsos, 2008) (Figure 1.4). After an initial pass through the visual system, feature conjunction hypotheses are generated (Bouvier & Treisman, 2010b). Later visual areas must ensure these are accurate using a feedback process, whereby earlier areas with a higher spatial resolution confirm or reject this hypothesis (Bouvier & Treisman, 2010b; Koivisto & Silvanto, 2012).

Bouvier and Treisman (2010b) demonstrate this idea using a colour-orientation binding task. Given a set of 6 objects composed of an orthogonal set of one coloured line and one white line, one of these objects was cued using 4 surrounding dots. This display was presented for 75ms, after which all items except the 4 dot cue disappeared. Out of the six items, subjects were instructed to report both the orientation and colour of the cued item. The persisting dots serves as a type of visual mask, known as object substitution masking, where the lingering dot mask disrupts perception without actually overlapping the masked stimulus (Enns & Di Lollo, 1997). Participants were significantly worse at reporting the conjunction when the dots persisted compared to when they did not. However, when participants were tested on feature identification, performance was unimpaired. Bouvier and Treisman (2010b) suggest that due to the timecourse of re-entrant processing (also see Koivisto & Silvanto, 2012), object substitution masking disrupts the feedback process – the hypothesis generated by the feedforward sweep is different to the on-screen stimulus at the time of feedback, thus disrupting the feature binding process (Bouvier & Treisman, 2010b; Di Lollo et al., 2000; Rothenstein et al., 2008).

1.5.5. Feature integration theory

Feature integration theory (FIT) is a prominent conceptualisation of how features may be bound together. Proposed by Treisman and Gelade (1980), they reasoned that features are integrated at a later stage in the visual stream by recruiting higher areas to do the ‘binding’ (also Treisman & Sato, 1990). In this two-stage model, features are initially represented on individual, topographic feature maps. A top-down driven attentional process (conceptualised as a ‘spotlight’ of focus) would then search these maps, bringing feature pairs that are spatially coincident under this spotlight to visual awareness. In effect, attention acts as a filter for the information reaching consciousness (Cavanagh, He, & Intriligator, 1999; He, Cavanagh, & Intriligator, 1996). From this, a key prediction was made that unless feature pairs were attended to, they remained unbound.

FIT accounted for much of the then-current literature, making it a highly influential model. Experiments where manipulations to attention were made supported this claim (Allen, Baddeley, & Hitch, 2006; Allen, Hitch, & Baddeley, 2009; Brown & Brockmole, 2010; Fougnie & Marois, 2009; Golomb, L’Heureux, & Kanwisher, 2014; Robertson, 2003), detailed further in Sections 1.7.1 and 1.7.2. However, Section 1.7.3 and onwards provides compelling evidence against a strictly attention-based theory of feature integration, instead suggesting that there is also an autonomous, bottom-up component to feature binding.

1.5.6. Guided search

Both the successes and shortcomings of FIT motivated the creation of alternate frameworks and mechanisms by which features are bound. For example, the guided search model (Wolfe, 1994, 2007; Wolfe, Cave, & Franzel, 1989) proposes a two-stage process for feature binding. Parallel processes first parse basic visual features in a rapid manner, the outcome of which then guides attention to the appropriate spatial locations. In the most recent version of the guided search model, Wolfe (2007) modifies the guiding map to a set of weights summed from both bottom-up and top-down processes to account for more recent psychophysical evidence.

1.5.7. Object files

Under the object files framework, feature binding is conceptualised as a process enabling the perception of objects (Hommel, 1998, 2004; Kahneman, Treisman, & Gibbs, 1992). Each physical object is represented by a temporary network of activations, which links together basic visual features (Kahneman et al., 1992; Wolfe & Bennett, 1997). This network acts as a spatially and temporally limited ‘file’, that allows rapid access of all linked attributes (Hommel, 2004). In order for an object file to represent an object, it must be both cohesive and have a singular boundary (Mitroff, Scholl, & Wynn, 2004). The distinction is made between the relatively long time it takes to generate a new file when compared to updating or accessing an already open file (Egeth & Yantis, 1997; Kahneman et al., 1992). This is because creating a new file may involve assigning salient, coincident features with a pointer or marker, and any overlap in features can cause interference when opening the object file (Hommel, 2004).

1.6. Does a binding problem exist?

1.6.1. Di Lollo's argument

Di Lollo (2012) argues that there may not be a binding problem at all. Recent advances in neuroimaging techniques (Grill-Spector & Malach, 2004; Mukamel & Fried, 2012), in addition to some psychophysical data, lead him to this conclusion. In Sections 1.6.2 and 1.6.3, a treatment of evidence for and against his position is discussed. He argues that there is no need for a feature binding mechanism, as a visual scene is processed entirely by re-entrant mechanisms. Thus, he asserts, features are never 'unbound' invalidating the initial premise for the binding problem.

Di Lollo (2012) points out that there is a large number of competing feature binding theories, that he claims stem from efforts to solve a non-existent problem. Indeed, there are many proposed solutions to the feature binding problem (Quinlan, 2003), some of which are reviewed in Section 1.5. However, in the author's opinion, the existence of a wide variety of theories is more indicative of an ever evolving landscape of literature, as is the case with most emerging concepts in science.

1.6.2. Discussion of neural data

As discussed in Section 1.5.1, it has been proposed that feature binding occurs as early as V1 and V2 (Bartels, 2009), in part due to the discovery that neurons are able to code for a conjunction of visual features (Burkhalter & Van Essen, 1986; Gegenfurtner et al., 1996; Johnson et al., 2008; Leventhal et al., 1995; Shipp et al., 2009; Tamura et al., 1996). This might seem to circumvent the need for a feature binding mechanism altogether. However, there is evidence to suggest that conjunction detectors in V1 are not sufficient to dismiss the binding problem. Psychophysical experiments demonstrate that adaptation to invisible stimuli causes low-level effects, despite participants being unaware of the adapting stimuli (Blake & Fox, 1974; He & MacLeod, 2001; Maruya, Watanabe, & Watanabe, 2008; Shady, MacLeod, & Fisher, 2004). Furthermore, neural imaging studies demonstrate that activity in V1 is not necessarily an indicator of perceptual awareness (Crick & Koch, 1995; Gur & Snodderly, 1997; Lamme, Supèr, Landman, Roelfsema, & Spekreijse, 2000; Tong, 2003; M. Watanabe et al., 2011). Therefore, even if conjunctions are represented in V1, the binding problem remains as to how these representations are to be decoded and integrated into objects for visual perception.

Evidence supporting the presence of a binding problem also exists in human imaging studies. Correlates of misbound features have be found in human visual cortex (Kanai et al., 2010; Zhang et al., 2014), suggesting binding is a real problem and is not processed on the scale of individual neurons. Multivariate classification both within and beyond striate cortex of perceived feature conjunctions (Seymour & Clifford, 2012; Seymour, Clifford, et al., 2009; Seymour et al., 2010; Sumner et al., 2008; Zhang et al., 2014) indicates that feature binding extends throughout the visual cortex. The neurological studies presented in Section 1.3.4 further indicate that a role exists for higher areas in the visual hierarchy: damage to these areas can disrupt the binding process while still allowing feature perception to occur (Arend et al., 2011; Braet & Humphreys, 2009; Cowey & Vaina, 2000; Robertson & Treisman, 1995; Ward et al., 2002). Taken together, these studies are more indicative that the binding process involves the whole visual cortex, and if this process is disrupted, features may remain in their unbound state.

1.6.3. Discussion of behavioural data

Di Lollo (2012) argues that binding occurs within early visual cortex, which is known to have a high spatiotemporal resolution (Zeki, 1993). However, this assertion must be consolidated with the measured low temporal resolution of feature conjunction perception (Bodelón et al., 2007; Holcombe, 2009; Moutoussis & Zeki, 1997a). A low temporal resolution may be more in line with his proposal of re-entry as a binding mechanism, as the timecourses of these two processes are similar (Bouvier & Treisman, 2010b; Koivisto & Silvanto, 2012). Regardless, the low resolution results from a distinct cost in binding features, which is not present during feature identification (Clifford, Holcombe, & Pearson, 2004; Seymour, McDonald, & Clifford, 2009). This cost manifests itself as a failure to bind in demanding psychophysical tasks, such as the tasks eliciting illusory conjunctions described in Section 1.7.2 (Ashby, Prinzmetal, Ivry, & Maddox, 1996; Chastain, 1982; Cohen & Ivry, 1989; Prinzmetal & Keysar, 1989; Treisman & Schmidt, 1982).

In his argument, Di Lollo (2012) states that, rather than a cost associated with feature binding, erroneous conjunction perception results from an incorrect observer expectation biasing perceptual hypotheses. Take the case where one fails to bind an arbitrary set of features, while still clearly perceiving individual features (e.g. Moutoussis & Zeki, 1997a). Rather than an incorrect observer expectation, which *a priori* should not exist with arbitrary pairs of features (Holcombe & Clifford, 2012), errors in feature binding seem more consistent with a feature binding mechanism requiring both time and resources in order to perceive conjunctions.

A subset of psychophysical studies, detailed in Section 1.7.6, seem to demonstrate that feature binding can occur under conditions of rapid alternation between feature pairs (Clifford, Spehar, & Pearson, 2004; Holcombe, 2001; Holcombe & Cavanagh, 2001; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002), suggesting the involvement of an early process. This apparent discrepancy in the feature binding literature is a central focus of the present thesis, and the experimental work presented in Chapters 2 and 3 represents an attempt at its resolution, discussed further in Chapter 4.

1.7. Psychophysical evidence for a binding problem

1.7.1. Visual search

The visual search paradigm was highly influential in shaping feature binding theories such as FIT. In a typical visual search task, participants searched arrays of objects for either an unique feature or conjunction of features (e.g. a target red circle among green circles, red squares, and green squares) (Nakayama & Silverman, 1986; Poisson & Wilkinson, 1992; Robertson, 2003; Treisman & Gelade, 1980; Treisman & Sato, 1990; Wang, Cavanagh, & Green, 1994; Wolfe, 1994; Wolfe et al., 1989). The amount of non-target distractors varied on each trial, and search slopes were calculated based on how quickly participants found the target as a function of the number of distractors.

Reaction times remained constant during feature search, independent of the number of distractors present in the trial (Desimone & Duncan, 1995; Poisson & Wilkinson, 1992; Treisman & Gelade, 1980; Wang et al., 1994) . However, reaction times varied linearly with the number of distractors during conjunction search. That is, as the number of distractors increased, participants spent longer searching the display for the target (Nakayama & Silverman, 1986; Poisson & Wilkinson, 1992; Treisman & Gelade, 1980; Treisman & Sato, 1990). The results of these experiments were explained within a framework whereby an attentional spotlight “scanned” the individual feature maps. While searching an individual feature map was a serial process, combining features across maps was not. Attention is a spatially limited process, and as such, a serial search across both a larger array and distractors with features similar to the target increased search times (Treisman & Gelade, 1980).

1.7.2. Illusory conjunctions

Identified by Treisman and Schmidt (1982), an illusory, or misbound, conjunction is a conjunction of features bound at random that is perceived, but not physically present (Cohen & Ivry, 1989; Holcombe & Cavanagh, 2001; Kanwisher, 1991). For example, if a red circle and blue square are simultaneously presented for a brief amount of time while an observer's attention is occupied elsewhere, it is possible that a blue circle and red square may be reported instead of the correct feature pairing (Treisman & Schmidt, 1982). While reports of both shape and colour were accurate, perception of the specific combination of attributes was disrupted. This demonstrated of how feature binding can fail when attention is not present to bind features together. Another method of disrupting attention was through rapid serial visual presentation (RSVP) tasks, whereby a rapid serial stream of distractors and targets was presented (Intraub, 1989; McLean, Broadbent, & Broadbent, 1983). A larger amount of information presented over a shorter period of time increased the likelihood of participants reporting an illusory conjunction (Chun & Potter, 1995).

A different type of illusory conjunction has been identified under conditions of binocular rivalry. Square-wave gratings of different colours were presented dichoptically at the same retinal coordinates in each eye (Hong & Shevell, 2006, 2009; Maloney, Lam, & Clifford, 2013). Each of these gratings also varied in a second visual feature for each eye, such as orientation, motion, or rotation. In addition to the binocular rivalry of the stimulus, occasionally attributes of the gratings would combine to form one containing a combination of colours in both eyes, combined with the second visual feature of one of the gratings. In this way, a feature combination was generated that was not physically present (Hong & Shevell, 2006, 2009; Maloney et al., 2013).

Another type of task takes advantage of limitations in the spatial resolution of the visual system. Several studies found that illusory conjunctions are more likely to occur when distractors are placed closer together (Ashby et al., 1996; Chastain, 1982; Cohen & Ivry, 1989; Prinzmetal & Keysar, 1989). In short, these tasks demonstrated that binding can fail when the spatial resolution of attention is exceeded (Intraub, 1989; McLean et al., 1983). Combined with the neurological data presented in Section 1.5.2, illusory conjunctions may occur due to uncertainty of the spatial location of the features (Ashby et al., 1996). This contrasts sharply with the high spatial resolution of low level areas (Zeki, 1993), and indicates that features must be bound elsewhere.

1.7.3. Colour contingent after-effects

The McCollough effect is a type of colour contingent after-effect, and occurs after adapting to a display alternating between, for example, a red horizontal grating and a green vertical grating (Held & Shattuck, 1971; McCollough, 1965). Subjects reported the white portions of a black and white test grating tinged with red when oriented vertically, and tinged with green when oriented horizontally. A similar effect also occurs when colour is paired with motion (Favreau et al., 1972; Mayhew & Anstis, 1972). These after-effects are thought to be a low level or early process resulting from the suppressed responses of one of two competing populations of conjunction neurons (Dodwell & Humphrey, 1990; Favreau et al., 1972; G. K. Humphrey & Goodale, 1998; P. D. Jones & Holding, 1975; McCollough, 1965; Murch, 1976). Despite their feature-specific requirements, a lack of interocular transfer suggests the involvement of low-level monocularly responsive cells (Coltheart, 1973; Favreau et al., 1972; Mayhew & Anstis, 1972; McCollough, 1965).

Similar to the results observed using single-feature after-effects (e.g. Gibson & Radner, 1937; He & MacLeod, 2001; Rajimehr, 2004), several studies have demonstrated orientation and motion contingent chromatic adaptation even when the stimulus conjunction was not consciously perceived (Blaser et al., 2005; Houck & Hoffman, 1986; G. K. Humphrey & Goodale, 1998; Vul & MacLeod, 2006). These low level after-effects are indicative of combined feature processing at an early stage (G. K. Humphrey & Goodale, 1998). If visual features were being processed completely independently of one another, one would expect no motion after effects associated with a particular colour. However, a lack of awareness of the adapting stimulus indicates that there are several steps involved for feature conjunctions to reach awareness.

1.7.4. Incorrect feature integration despite attention

There have also been demonstrations of stimuli generating incorrect feature pairings despite the presence of attention (Wu et al., 2004; Zhang et al., 2014). For example, Wu et al. (2004) used a stimulus containing red and green dots assigned opposite directions of motion. When these dots were presented in the periphery with no central stimuli, conjunction identification was accurate. However, when additional red and green dots were displayed in the centre with the reverse colour-motion pairing, this additionally reversed the perception of dots in the periphery. Participants were explicitly told to attend to the peripheral dots while maintaining a central fixation. Yet despite this, responses to the binding task were significantly biased in favour of the central dot pairing (Wu et al., 2004). This is a result difficult to resolve with FIT, and may require additional explanation focused on crowding, the limited resolution of extra-foveal vision, and contextual spreading of cues (Balas, Nakano, & Rosenholtz, 2009; Levi, Klein, & Aitsebaomo, 1985; Whitney & Levi, 2011).

1.7.5. Perceived temporal asynchrony of simultaneously presented features

When a stimulus exhibits a physical change in two visual attributes simultaneously, a corresponding perceptual synchronicity is not always experienced. This perceived temporal asynchrony is argued to be indicative of the modular nature of visual processing (Moutoussis & Zeki, 1997b; Zeki & Bartels, 1998). A perceived asynchrony suggests that individual features reach awareness at different times. A likely reason for this is due to different processing times of each type of visual feature – a consequence of modularity at some level during feature processing (Zeki, 2001).

Demonstrations of perceptual asynchronies exist for many feature pairings such as colour-motion (Arnold, 2005; Arnold & Clifford, 2002; Arnold, Clifford, & Wenderoth, 2001; Aymoz & Viviani, 2004; Barbur, Wolf, & Lennie, 1998; Clifford, Spehar, et al., 2004; Johnston & Nishida, 2001; Linares & López-Moliner, 2006; Moutoussis & Zeki, 1997a, 1997b), colour-form (Aymoz & Viviani, 2004; Moutoussis & Zeki, 1997b; Viviani & Aymoz, 2001), colour-orientation (Clifford, Arnold, & Pearson, 2003), and form-motion (Aymoz & Viviani, 2004; Viviani & Aymoz, 2001). Lending support to this idea are findings from Arnold and Clifford (2002), which indicate that a reduction in perceived colour-motion asynchrony occurs when dots alternated between more similar directions of motion. It indicates that perceptual asynchrony may in part be affected by inhibitory activity within distinct processing areas (Arnold & Clifford, 2002). Furthermore, the same features reliably lead others: viewing colour and motion stimuli such as colour reliably preceding motion (Arnold et al., 2001). Linares and López-Moliner (2006) note that there is a small but significant masking effect in these displays as one feature pair is replaced by the other. However, they stress the majority of the measured asynchrony between colour and motion is due to differences in processing.

Interestingly, several results appear to run counter to the modular processing account of temporal asynchrony (Bedell, Chung, Ogmen, & Patel, 2003; Enns & Oriet, 2004; Nishida & Johnston, 2002). For example, Nishida and Johnston (2002) found that the observed colour-motion asynchrony varied with temporal alternation frequency (Also see Arnold & Clifford, 2002 for colour-orientation). This discrepancy is also highlighted by counterintuitive results which provide evidence for both a perceived temporal asynchrony but also accurate judgements of simultaneity. Clifford et al. (2003) found that simultaneous changes of feature pairs were accurately reported despite a paradoxical 50ms perceptual bias in favour of colour compared to orientation when subjects were required to pair events demarked by those same changes. Similarly, Holcombe and Cavanagh (2008) found that colour-motion asynchrony could be negated using an exogenous attention cue. Participants viewed 10 arrays of dots alternating in colour and motion. When a ring was flashed around an array, participants were able to accurately report the colour and motion pairing.

1.7.6 Surface selection and feature binding

Several experiments provide evidence for an object-based account of selection by attention, where the grouping of objects with similar attributes can guide attention (Treisman, 1982). In these experiments, one set of rotating coloured dots is initially presented (e.g. a red array of dots rotating clockwise). A second set of dots appears on-screen superimposed upon the first, with different colour and rotation attributes (green dots moving anticlockwise). One surface exogenously attracted attention by translating briefly before continuing to rotate (Reynolds, Alborzian, & Stoner, 2003), and subjects reported which of the two surfaces translated. As only 50% of the dots contained on one surface translated, the optimal strategy involved attending to the whole surface rather than individual dots. In this way, attentional cuing of one of the two surfaces improves performance, demonstrating that attention can be focused on objects, and not just spatial locations (Valdes-Sosa, Cobo, & Pinilla, 2000). A follow-up to this experiment identified and removed the confound of surface duration, as it was predicted that participants may have adapted to the first surface present (Stoner & Blanc, 2010). The overall findings of these studies corroborates the Reynolds et al. (2003) object-based account of attention (Stoner & Blanc, 2010).

The attentional selection of a surface can support feature binding in certain cases. This is evident in several experiments which demonstrate feature binding can occur in displays that rapidly alternate between pairs of features (typically colour-orientation or colour-motion pairings). For example, when a display alternates between a red grating tilted left and a green grating tilted right, accurate conjunction perception is supported even at alternation frequencies up to 16 Hz (Holcombe & Cavanagh, 2001). Under this arrangement, it was reported that both feature conjunctions were perceived simultaneously. Curiously, when the same feature pairs are spatially separated (that is, orientation separate from colour), the observed temporal resolution of feature binding is lowered, approaching previously observed estimates of 3 Hz (Holcombe, 2009).

A similar study used red discs superimposed on one of two orthogonally-oriented alternating gratings (Suzuki & Grabowecky, 2002). Identification of the colour-orientation pairing was possible at approximately 13.5 Hz. Suzuki and Grabowecky (2002) demonstrate that a rapidly alternating stimulus can be grouped by temporal phase, effectively segmenting each feature pair into separate surfaces. As surface segregation is a rapidly occurring process (Møller & Hurlbert, 1996; Sajda & Finkel, 1995), even high alternation frequencies can support conjunction perception when features are spatially coincident.

A similar result was observed in displays that alternated between two differently-coloured and oppositely moving sets of dots (Moradi & Shimojo, 2004). However, while the colour-motion conjunction was discriminable at the highest (15 Hz) and lowest frequencies (1.4 Hz) tested, performance around 5 Hz fell to chance. This was a seemingly paradoxical result, as a lower temporal frequency necessitates a longer conjunction presentation time of each set of dots, which should increase performance. In subsequent experiments, Moradi and Shimojo (2004) demonstrated that surface segregation may play a role in conjunction perception, similar to displays of colour and orientation (Holcombe & Cavanagh, 2001; Sajda & Finkel, 1995).

Using a 2 Hz temporal alternation frequency, Clifford, Spehar, et al. (2004) used a stimulus where one set of dots temporally alternated in colour and motion attributes simultaneously. A significant processing asynchrony was observed when the change in attributes of all dots occurred simultaneously – that is, 100% of the dots changed from, for example, red-left to green-right. However, the measured asynchrony was almost eliminated by shifting the phase by 180° in 50% of the dots. In doing so, the display now contained both feature conjunctions simultaneously. A similar result was achieved when the phase of each dot was randomised, producing a motion transparent display (Kanai, Paffen, Gerbino, & Verstraten, 2004). One possible explanation is that the simultaneous presence of both motion (Adelson & Movshon, 1982; Masson, Mestre, & Stone, 1999) and colour (Edwards & Badcock, 1996; Mitchell, Stoner, Fallah, & Reynolds, 2003; Stoner & Blanc, 2010; Valdes-Sosa et al., 2000) attributes facilitates surface segregation, thus enhancing perception of the stimulus. When motion signals are imbalanced at a local level, motion transparency is perceived (Qian, Andersen, & Adelson, 1994), suggesting that a global motion percept is built from local signals (Kanai et al., 2004).

1.8. The present thesis

The focus of this thesis is on identifying and understanding the mechanisms of feature binding using the types of displays discussed in Section 1.7.6. Both neurological and psychophysical experiments provide evidence for fast and slow feature binding mechanisms (Section 1.5). This apparent discrepancy in the literature merits clarification. A late binding mechanism would predict binding to fail at rapid alternation frequencies. Yet under certain conditions, conjunction discrimination at high alternation frequencies can be accurate (Clifford, Spehar, et al., 2004; Holcombe, 2001; Holcombe & Cavanagh, 2001; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002). While these results are in line with a fast feature binding mechanism, this in turn fails to account for the observed specific binding deficiencies occurring at frequencies around 5 Hz in some displays (Moradi & Shimojo, 2004) but not others (Holcombe & Cavanagh, 2001). The apparent discrepancy in these results suggests these stimuli may be engaging different but poorly understood mechanisms. Neither a fast nor slow feature binding mechanism in their current forms can provide a complete account of these results. Thus, in order to remedy the current situation, the focus of the present thesis investigates the dynamics of feature binding, in the hopes of elucidating the underlying processes.

Chapter 2. Dynamics of Colour-Motion Binding

2.1. Introduction

Vision research is currently expanding at a rapid pace. A large number of discoveries regarding how animals process visual inputs have been made using both psychophysical techniques and neural imaging. In particular, Chapter 1 discussed that the currently available evidence is heavily weighted towards the idea of a binding problem. That is, there exists a mechanism which parses and integrates visual features together in a way that represents reality. However, despite this work, a comprehensive model of feature binding has yet to account for the results generated by a multitude of feature binding studies. In this chapter, the spatial and temporal characteristics that influence the binding of colour and motion are explored in order to investigate the temporal resolution of the binding process. By understanding whether feature binding is a comparatively fast or slow process will in turn provide a greater understanding of the underlying processes that drive visual feature integration.

2.1.1. The temporal resolution of colour-motion binding

Psychophysical evidence indicates that a limited window exists in which the visual system can resolve the spatial and temporal coincidences of features (Holcombe, 2009; Moradi & Shimojo, 2004; Quinlan, 2003; Treisman, 1996; Treisman & Schmidt, 1982). The temporal resolution of feature binding is necessarily limited by the processing of individual features in addition to ascertaining their spatiotemporal coincidence (Bodelón et al., 2007). Thus, the binding of visual features is generally considered to be a relatively slow process (e.g. Treisman, 1996, 1998; Treisman & Gelade, 1980) with a perceptual limit close to 3 Hz for a stimulus alternating between two sets of features (Holcombe, 2009). However, a subset of studies have found that accurate feature conjunction discrimination appears to exist well beyond these established temporal limits (Clifford, Spehar, et al., 2004; Holcombe & Cavanagh, 2001; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002). Given the extremely short epochs used in these studies (33 ms or less) it seems unlikely that feature binding, as it is currently understood, could occur at this timescale.

One common observation across studies that found a high temporal resolution for feature binding (Clifford, Spehar, et al., 2004; Holcombe & Cavanagh, 2001; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002) is the perception of conjunction stimuli as stable and persistent transparent surfaces, a phenomenological quality that has been identified under different stimulus conditions as “temporal transparency” (Holcombe, 2001) or “persistent surface segregation” (Moradi & Shimojo, 2004). Upon viewing a stimulus, for example, that rapidly alternates between two different pairs of visual attributes simultaneously (e.g. leftwards motion paired with red and rightwards motion paired with green), subjects report seeing both sets of features simultaneously as distinct and transparent surfaces (Clifford, Spehar, et al., 2004; Holcombe, 2001; Holcombe & Cavanagh, 2001; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002).

When two spatially superimposed fields of differently-coloured, translating dots are presented simultaneously and are perceived as transparent, Moradi and Shimojo (2004) found that the perceptual pairing of colour with motion is almost perfect. This result held across a range of presentation conditions, such as when the dot fields were interleaved with blank periods of the same duration as the presentation of the stimuli. However, when the two dot fields were instead presented in an alternating manner over time (that is, never simultaneously: see Figure 2.1a), the accuracy of the colour-motion conjunction discrimination broke down in a surprising manner. Interestingly, when alternations occurred between dot fields at frequencies where they were more likely to be perceived as transparent surfaces (i.e. around 15 Hz, Holcombe, 2001), the observed conjunction discrimination was highly accurate and indistinguishable from discrimination in the condition where both RDKs were simultaneously present on the screen. Conversely, at a range of intermediate temporal frequencies (around 3-8 Hz), conjunction discrimination accuracy diminished to near-chance levels. Finally, ceiling conjunction discrimination was observed at very low temporal frequencies (less than 3 Hz). Here, the discrimination could easily be performed, in principle, within a single stimulus half-cycle, owing to the longer stimulus presentation period associated with the lower temporal alternation (Moradi & Shimojo, 2004; Nishida & Johnston, 2002).

The variation in the results obtained where dot fields were presented alternately or transparently presents an apparent paradox that can be broken down into issues of computational time and complexity. One might naïvely assume that binding colour and motion might be a computationally simpler process in the alternating stimulus, when only one field of dots is presented at a single point in time (Von der Malsburg, 1999). Viewing this display, only one pair of features must be instantaneously “bound”, as opposed to when both fields of dots are present simultaneously (as in the transparent condition; Clifford, 2010). Within the alternating display, higher alternation frequencies should also increase task difficulty as there is less time available to process the on-screen feature conjunction (Bodelón et al., 2007; Seymour, McDonald, et al., 2009). Moreover, both perceptual and neural asynchronies between colour and motion processing should drastically worsen conjunction discrimination at high alternation frequencies (Arnold, 2005; Arnold & Clifford, 2002; Clifford et al., 2003; Lo & Zeki, 2014; Moutoussis & Zeki, 1997a; Nishida & Johnston, 2002). Nevertheless, Moradi and Shimojo (2004) demonstrated that an increase in alternation frequency beyond 5 Hz paradoxically improved discrimination on the conjunction task.

2.1.2. Surface segregation as a method of feature binding

The non-monotonic function for conjunction discrimination generated by the alternating stimuli used in these experiments could indicate that different aspects or mechanisms of visual feature binding are operating at the two opposite ends of the temporal spectrum (i.e. the high and low frequencies) (Holcombe, 2001, 2009; Moradi & Shimojo, 2004). For example, at low alternation frequencies, typical binding processes would be active that are able to identify and pair colour and motion attributes within the relatively long presentation periods afforded by the low alternation frequency (Karlsen, Allen, Baddeley, & Hitch, 2010; Treisman, 1996; Treisman & Gelade, 1980; Treisman & Kanwisher, 1998; Von der Malsburg, 1999). Meanwhile, high alternation frequencies may have facilitated the perceptual grouping of the display into two motion-defined surfaces. This chapter explores the idea that surface segregation through the grouping of similar visual attributes can be a key aspect of parsing the visual scene (Stoner & Albright, 1996; Watt & Phillips, 2000).

The stimulus characteristics that are related both to surface segregation and accurate colour-motion binding are explored across a range of alternation frequencies. In doing so, it is assumed that if a conjunction stimulus is perceived as a transparent surface, it must by definition be perceptually segregated from at least the background, if not the background plus another transparent surface (Watamaniuk, Flinn, & Stohr, 2003). At high alternation frequencies, motion-defined surfaces are temporally integrated across presentations (Farrell, Pavel, & Sperling, 1990) and perceived as coherent transparent fields for the entire stimulus duration, enhancing perceptual accuracy. Visual persistence is a likely mechanism for the stability of this percept, as it acts over a short temporal window (Coltheart, 1980; Mezrich, 1984; Shioiri & Cavanagh, 1992). The relationship between temporal integration and visual persistence (Farrell, 1984) is discussed further in Experiment 7A.

Accurate conjunction perception is associated with the perceptual segregation of a stimulus into distinct, transparent surfaces (Clifford, Spehar, et al., 2004; Holcombe & Cavanagh, 2001; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002). While the perception of surface transparency can improve the binding of colour with motion (Arnold, 2005; Clifford, Spehar, et al., 2004; Moradi & Shimojo, 2004; but see also Wu et al., 2004 for a case of colour misbinding in motion transparency), the question remains as to why this is the case. Studies using a stimulus introduced in Valdes-Sosa et al. (2000), whereby participants have to detect a motion change in one of two sets of differently coloured, oppositely rotating dots, provides insight (Section 1.7.6). It was concluded that the perceptual decomposition of a bi-vectorial motion display into transparent surfaces allows attention to be allocated to the features of each surface (Stoner & Blanc, 2010; Valdes-Sosa et al., 2000).

Stimulus manipulations that promote the perception of surface transparency may therefore facilitate the attentional selection of a single surface. In doing so, these manipulations provide insight into how conjunction discrimination can be improved at high temporal frequencies (Clifford, Spehar, et al., 2004; Moradi & Shimojo, 2004). For example, Moradi and Shimojo (2004) demonstrated that the addition of irrelevant, moving grey dots to their coloured random-dot motion displays resulted in enhanced conjunction discrimination at the intermediate alternation frequencies (3-8 Hz) where discrimination would otherwise be poor. These dots may have facilitated surface segregation, by enhancing the motion contrast between conjunction pairs (Lankheet & Palmen, 1998; Nothdurft, 1993; Regan & Beverley, 1984; Treisman & Kanwisher, 1998). It is likely that perceptual segregation of transparent surfaces is somehow facilitating the feature binding process at these rapid time scales (Moradi & Shimojo, 2004). Perceptual segregation of conjunction stimuli into transparent surfaces at higher temporal frequencies may afford the visual system a sufficient amount of time in which feature binding can occur, in spite of the very rapid temporal alternations of the stimulus (Clifford, 2010; Clifford, Spehar, et al., 2004; Moradi & Shimojo, 2004).

2.1.3. Neurophysiological evidence for feature binding and surface segregation

Several studies have investigated the neurophysiological basis of both feature binding. It is known that neurons in primate early visual cortex selectively respond to basic visual features such as colour and motion (Felleman & Van Essen, 1991; Livingstone & Hubel, 1988; Mishkin et al., 1983; Zeki, 1978a; Zeki et al., 1991). Further research has revealed that many neurons respond selectively to more than one type of feature (Burkhalter & Van Essen, 1986; Johnson et al., 2008; Leventhal et al., 1995). However, while the activity profile of populations of neurons may encode basic features, the processes by which this information is correctly decoded and integrated are still largely unknown.

The study of motion transparency in the visual cortex, however, may provide some clues as to how the perception of transparency interacts with the feature binding process. When presented with bi-vectorial motion stimuli, neurons in anaesthetised monkey V1 tend to respond to motion in their preferred direction, regardless of the presence of an overlapping field of dots moving in a different direction (Qian & Andersen, 1995; Snowden, Treue, Erickson, & Andersen, 1991). In contrast, the responses of V5/MT neurons are suppressed when shown the same stimuli (McDonald, Clifford, Solomon, Chen, & Solomon, 2014; Snowden et al., 1991). Human fMRI studies have demonstrated that transparent motion inhibits activity in the V5/MT+ complex in a similar manner (Garcia & Grossman, 2009; Heeger, Boynton, Demb, Seidemann, & Newsome, 1999; Muckli, Singer, Zanella, & Goebel, 2002). Activity in V5/MT+ may be responsible for the perceptual interpretation of a stimulus as two transparent surfaces (Castelo-Branco et al., 2002;

McDonald et al., 2014; Muckli et al., 2002; Snowden et al., 1991). Here, temporal integration of the activity of direction-selective neurons across the stimulus alternation periods would result in a stable, continuous percept through which feature pairs can be parsed and extracted.

2.1.4. Aims of this chapter

In this chapter, the specific temporal and spatial characteristics of colour-motion binding are explored through surface segregation in order to ascertain the temporal resolution of the feature binding process. Colour-motion displays are manipulated to one of two ends. Moradi and Shimojo (2004) found that conjunction discrimination at intermediate temporal frequencies could be improved with the addition of irrelevant, non-target dot fields (both moving and stationary), that provided no information about the target feature conjunction. They argue that this improvement (in spite of the increased complexity of the stimulus) was due to the irrelevant dots acting as surface segregation cues. This line of reasoning is followed in Experiments 1A-3A, which supplement the segregation of dot fields at intermediate alternation frequencies where conjunction discrimination is typically poor. In doing so, the stimulus characteristics of the additional dots are explored in order to ascertain the reason behind the improvement in conjunction discrimination. In Experiments 4A-7A, stimulus manipulations are employed to disrupt the surface segregation process at high alternation frequencies, which are predicted to reduce conjunction discrimination. Through manipulations of known aspects of surface segregation (such as the consistency of stimulus attributes or interference with visual persistence), a reduction in conjunction discrimination exclusively at high alternation frequencies should be observed if feature binding is dependent dependence on perceptual transparency.

To conclude the chapter, Experiments 8A-10A investigate if the perceptual experience of transparency in bi-vectorial motion is matched by modulation of activity in early visual areas across temporal alternation frequency. However, changes in neural activity between stimuli presented at high and low alternation frequencies may be attributed to alternation frequency rather than the percept of transparency. Thus, two display types were tested at two different alternation frequencies: one that alternates between two sets of dots in a sequential manner and a spatially interleaved display that appears transparent independent of frequency. Sequential and spatially interleaved stimuli are predicted to produce similar activity at higher frequencies, where they both generate the impression of motion transparency. At lower frequencies however, the spatially interleaved stimulus should continue to appear transparent while the sequential stimulus will not. A corresponding difference in neural activity is therefore expected in the form of a display type (sequential/spatially interleaved) by alternation frequency interaction effect, matching the perceptual experience of motion transparency.

2.2. General methods

2.2.1. Subjects

In this chapter’s experiments, informed written consent was obtained from all psychophysical subjects (age range: 22-46). All subjects were experienced psychophysical observers. While the author and other experimenters participated in these studies and were not naïve to the experimental manipulations, they were unaware of the order in which each condition was presented. All subjects had normal or corrected-to-normal visual acuity, normal trichromacy, and were free of psychiatric/neurological illness. The experimental protocol was approved by the University of Sydney Human Research Ethics Committee.

2.2.2. Apparatus

All experiments were conducted under the same conditions. Subjects sat at a viewing distance of 57 cm from a gamma-corrected ViewSonic Graphics Series G90f CRT monitor (36 cm × 27 cm) with a vertical refresh rate of 60 Hz and resolution of 1024 × 768 pixels. Gamma correction took place using a ColourCal colourimeter. Luminance and chromaticity were measured for each gun from minimum (0) to maximum intensity (255) in steps of 17. Uncalibrated, values increasing from 0 to 255 generate a different, non-linear luminance function for each gun. Once this is measured however, the luminance output of each gun can be corrected, with the aim of linearising the luminance output. Once calibrated, the value input for any gun will be directly proportional to the luminance generated. This calibration ensured that stimuli were generated in a manner where their constituent colours were both controlled and balanced.

Stimuli were generated through Matlab (R2010a 7.10; The Mathworks, Natick, MA) and the Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997) on a PC with an Intel Core i7-2600 CPU, 3.4 GHz processor and an AMD Radeon HD 6450 display adapter. Experiments were run in a light and sound-proof testing booth. Subjects responded using a standard Dell keyboard.

2.2.3. Visual stimuli

For this series of experiments, stimulus design was based on Moradi and Shimojo (2004) (see Figure 2.1a). Two 'target' random dot kinematograms (RDKs) with a luminance of 28 Cd/m^2, presented against a black background, were generated at the beginning of each trial: one contained orange dots (CIE: $x = 0.43$, $y = 0.45$), and the other blue dots ($x = 0.21$, $y = 0.25$). These colours were chosen using DKL colour space (Derrington, Krauskopf, & Lennie, 1984) to ensure that the load on the opponent colour channels was balanced and they summed to grey ($x = 0.29$, $y = 0.33$). Where additional RDKs were used, these had the same stimulus characteristics as the target RDKs, except for colour. All dots had adjusted colours based on a minimum flicker paradigm described in section 2.2.4 (Walsh, 1953) conducted individually by each subject, to ensure colours were subjectively equiluminant at approximately 28 Cd/m^2.

The RDKs consisted of dots with a Gaussian 'blob' profile ($\sigma = 0.042°$ of visual angle) and distributed evenly throughout an annular window with a minimum distance of 0.7° from any other dot. 11.8% of the total viewing area was filled with dots, giving a density of 3.7 dots/deg^2. RDKs were randomly assigned opposite rotations each trial and constantly rotated at a rate of

60° s^{-1} (equivalent to 0.167 Hz) while on screen. The average dot speed within the RDKs was 4.8° of visual angle per second.

The annulus containing the RDK had a raised cosine luminance profile with an outer radius of 6.3° of visual angle, inner radius of 2.8° and 0.8° of smoothing at both inner and outer edges. The total area of the ring was 98 deg^2. At the centre of the annulus was a grey fixation cross with a height and length of 0.4° and line width of 0.07°. A white and grey fixation ring with a diameter of 1.4° and width of 0.5° encircled this cross. The annulus was used to minimise tracking eye movements that might otherwise result from dots passing close to fixation; rotational movement balanced motion energy across the display, in addition to avoiding transients caused by dots leaving and entering the annulus.

2.2.4. Design and procedure

Most experiments employed both spatial and temporal manipulations of these stimuli using a within-subjects factorial design. Within a single trial, alternated between RDKs would occur at one of several temporal frequencies (1.67, 2.5, 3.33, 5, 7.5 and 15 Hz). Frequencies were chosen to divide equally into the stimulus duration, 1200 ms to ensure an equal presentation of both the orange and blue RDKs. These frequencies were combined with a number of display types. The total duration of each trial was 1700 ms, which included 250 ms masks presented immediately before and after the stimulus. The mask was a static superposition of both orange and blue dots generated in an identical fashion to the stimulus. It was used to avoid any unwanted transients caused by the sudden onset and offset of the stimulus.

Unless otherwise stated, subjects completed 40 trials for each display type and alternation frequency combination, divided equally into five runs. Within runs, each display type was counterbalanced for onset colour and colour-motion conjunction. Subjects' task was a colour-motion ‘binding’ judgement where the rotation direction of the orange RDK (clockwise or counterclockwise) was reported on each trial using a standard keyboard. Subjects were instructed to maintain fixation upon the central cross for the duration of each trial.

Before the commencement of the experiments, subjects calibrated the orange and blue dots using a minimum flicker paradigm (Walsh, 1953). This was done in order to achieve subjective equiluminance between these colours, minimising any uncontrolled differences between the stimuli. As luminance is a strong factor in the salience of a stimulus (Nothdurft, 2002), it is important that both blue and orange dots had the same subjective brightness. Subjects were presented with one set of static dots with otherwise identical characteristics to the experimental stimuli described above. The colour of the dots alternated at 15 Hz from the orange and blue values used across these experiments. Subjects were instructed to modify the luminance of the blue dots until they experienced a minimal amount of flicker. This procedure was completed 7 times with a starting value of the blue dots jittered around 28 ± 0.5 Cd/m^2. The average selected luminance across the 7 trials was computed and saved for use in each of these experiments, with each subject having a unique luminance value.

2.2.5. Data analysis

Data were analysed first in Matlab (R2010a 7.10; The Mathworks, Natick, MA), and then using IBM SPSS Statistics 20 for Windows. Conjunction discrimination was coded as the proportion of correct responses across all 5 experimental runs. These data were subjected to a two-way repeated-measures ANOVA with planned polynomial contrasts. Subjects were treated as a random factor and the independent variables of the experiment (e.g. angular separation and temporal alternation frequency) as fixed factors. Where main effects, interactions, and the trends associated with each were significant in the ANOVA, the outcomes of planned, Bonferroni-corrected polynomial contrasts up to a degree of 3 (cubic) were reported. If comparison between individual data points needed to be made, Bonferroni-corrected paired-samples t-tests were used.

2.3. Experiment 1A: Discrimination of colour-motion conjunctions with additional, moving dots

2.3.1. Rationale

Surface segregation appears to support accurate conjunction perception at high alternation frequencies (15 Hz), but not at intermediate frequencies (5 Hz) (Moradi & Shimojo, 2004). In the first set of experiments 1A-3A, additional dots are used to enhance feature binding by facilitating surface segregation at intermediate alternation frequencies. Additional dots are manipulated across several stimulus characteristics. In this way, the specific stimulus characteristics that support feature binding can be observed, while keeping the total colour-motion information present in a display constant. In this first experiment, moving additional RDKs with varying colour and dot configuration cues are tested.

2.3.2. Experimental methods

2.3.2.1. Subjects

Informed written consent was obtained from seven experienced psychophysical subjects (4 male; age range 20-43).

2.3.2.2. Visual stimuli

On each trial, two target RDKs were generated with the characteristics described in the general methods: one always orange, and the other always blue (Figure 2.1a). These were assigned opposite rotations and presented within an annulus. Rotation of RDKs were maintained even when not currently on-screen. In the control display, only one RDK was present on-screen at any point in time (Figure 2.1b). In the non-control conditions, two additional RDKs were added to the display with the same temporal alternation frequency and duty cycle as the target RDKs (Figure 2.1b). These additional RDKs had the same characteristics as the target RDKs such as dot shape, size, and density. In these displays, any point in time had two RDKs present on-screen: the rotating target and an oppositely rotating, additional RDK.

These displays were conceptually similar to those employed by Moradi and Shimojo (2004), who used two sparse, grey RDKs superimposed on their target RDKs, both always present, and translating in opposite directions. Even though these additional, irrelevant dots added to the complexity of the displays, conjunction discrimination was nevertheless improved. Moradi and Shimojo (2004) suggest that this was because the additional dots acted as a cue to segregation of the target surfaces, ensuring both leftwards and rightwards motion was always present in the stimulus display. Here, additional RDKs are manipulated in ways predicted to enhance surface segregation. If the hypothesis of Moradi and Shimojo (2004) is correct, a corresponding increase in conjunction discrimination should also be observed.

2.3.2.3. Design and procedure

This experiment was a 5 ‘display type’ by 6 ‘temporal alternation frequency’ (1.67, 2.5, 3.33, 5, 7.5 and 15 Hz) within-subjects factorial design. The basic control display in this experiment (Figure 2.1c - 'Control') was a display that alternated between orange and blue RDKs (target RDKs) with opposite rotations, such that a single colour-motion combination was on screen at any single point in time (Figure 2.1b).

The other four display types were various modifications of this control display (Figure 2.1b) using additional RDKs with variations in appearance, determined by the combination of two attributes which were predicted to enhance surface segregation: colour and configuration.

Variations to these were independent of each other, and determined if the additional RDKs were either the same or different to the preceding target RDK.

The four display types (in addition to the ‘control’ display) were (see Figure 2.1c):

i. ‘Grey, different configuration’ – here the additional RDKs differed from the target RDKs in both colour and configuration, meaning that the display alternated between two moving grey RDKs in addition to the target RDKs.

ii. ‘Coloured, different configuration’ – as with the ‘grey, different configuration’, but the additional RDKs were coloured orange and blue. When the orange target RDK was present on screen, the blue additional RDK would also be present, and likewise the blue target RDK was presented with the orange additional RDK.

iii. ‘Grey, same configuration’ - here the additional RDKs were of a different colour, but the same configuration as target RDKs. In this, the appearance of the display was that of two continuously-present RDKs, which both shifted between moving colour and static grey alternately such that only one coloured RDK was present at any one time.

iv. ‘Coloured, same configuration’ – as both target and additional RDKs of the same colour had matching configurations, this display appeared as if both target RDKs were present on-screen, simultaneously for the duration of the trial. As such, there was no effect of alternation frequency on the perceptual interpretation of this display.

These four permutations of same/different dot configuration and same/grey colour were tested, in addition to the control display. Subjects were instructed to ignore the additional RDKs (when present) and simply respond by reporting the direction of rotation of the orange RDK. Our aim in doing so was to determine which, if any, of these aspects of the additional/irrelevant RDKs might serve to improve conjunction discrimination at intermediate temporal alternation frequencies.

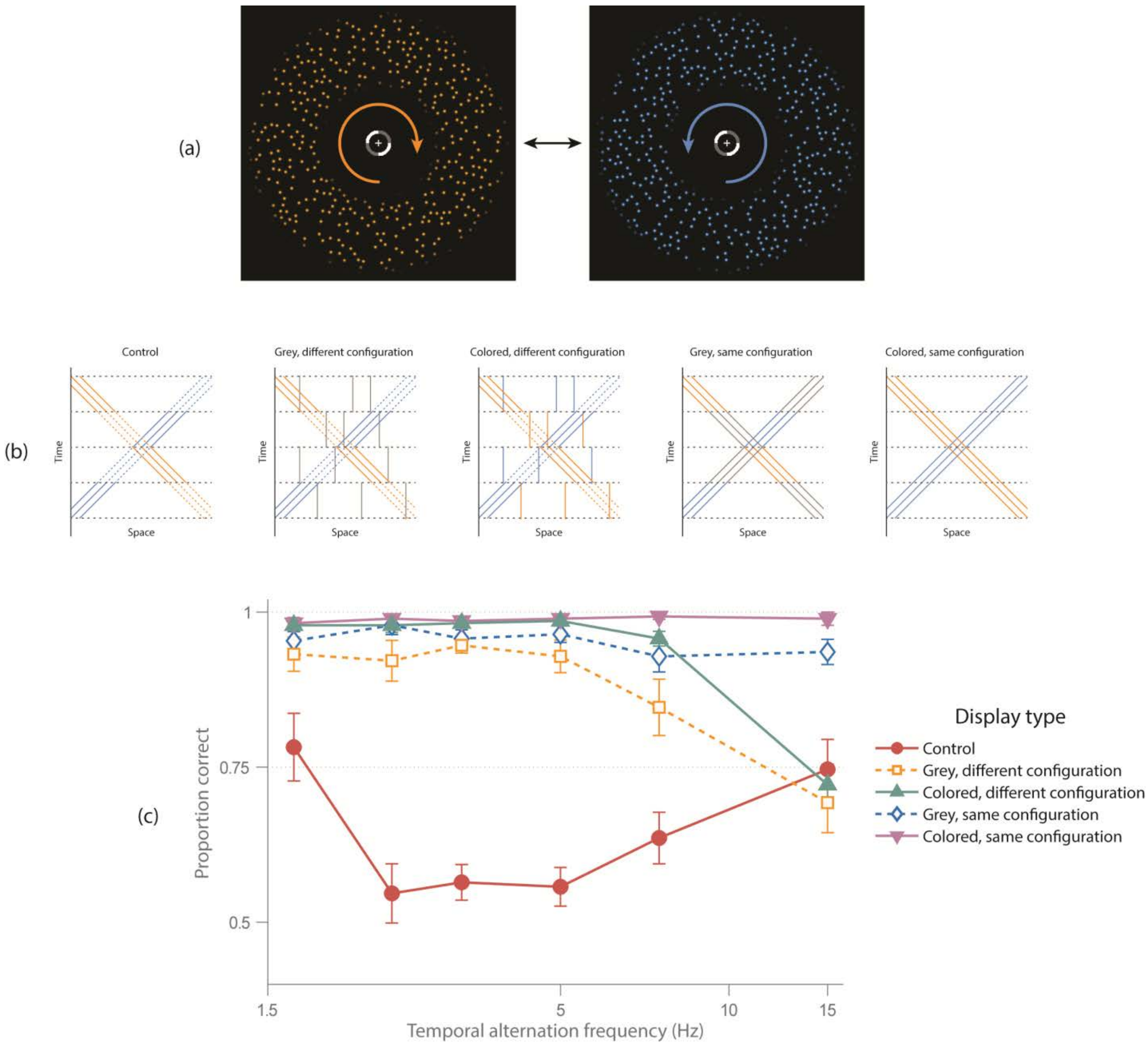

Figure 2.1. Stimulus design and results of Experiment 1A. **(a)** Representation of the control stimulus used in Experiment 1A. Orange and blue RDKs were generated and assigned opposite rotations. Alternation between RDKs occurred at one of several temporal alternation frequencies and while off-screen, RDKs continued to rotate. **(b)** Schematic space-time plots of each display type in Experiment 1A. Additional RDKs were added to the display such that in the non-control conditions, two RDKs were present on-screen simultaneously. Time is shown on the *y*-axis while rotation of RDKs across space is indicated by the *x*-axis. Dotted black horizontal lines indicate half the

temporal alternation period: when the orange target RDK is replaced by blue, or blue by orange. Each RDK is represented by 3 lines, the colour of the lines indicating which RDK the dots belong to (orange, blue, or grey). Solid lines indicate that the RDK is currently visible while dotted lines indicate the RDK is invisible, and serve to describe the trajectory of the RDK while it is off-screen. **(c)** Mean conjunction discrimination on the colour-motion binding task (*n*=7) for each display type, across temporal alternation frequency. Error bars denote ±1 between-subject standard errors.

2.3.3. Results and discussion

Averaged over each display type, temporal alternation frequency had a clear effect on conjunction discrimination ($F_{5,30} = 9.49$, $p < 0.001$; Figure 2.1c). However, the way in which alternation frequency affected discrimination interacted with display type to produce a varied distribution of the data ($F_{20,120} = 11.97$, $p < 0.001$). At all frequencies except the highest tested (15 Hz), it appears that adding an additional pair of alternating RDKs to the display significantly improves conjunction discrimination, even when discrimination is averaged over temporal frequency ($F_{4,24} = 104.58$, $p < 0.001$). Consistent with the conclusions Moradi and Shimojo (2004), an additional set of dots appears to facilitate the segregation of the target RDKs into separate surfaces.

To further elaborate on this, statistical tests were performed on each non-control display type after averaging across first colour and then dot configuration. In this way, conjunction discrimination could be compared across both colour and configuration. When display types were grouped over colour (that is, the average results of both display types containing coloured additional dots compared to those with grey dots), there was an overall main effect on conjunction discrimination ($F_{1,6} = 9.83$, $p = 0.02$). When additional dots were the same colour as the corresponding target dots, conjunction discrimination was significantly improved. A similar main effect was found when comparing the results of conditions with the same dot configuration to those with a different configuration ($F_{1,6} = 13.96$, $p = 0.01$). However, no significant interaction effects were detected in these comparisons. As dot configuration provided no additional colour-motion information, and nevertheless improved conjunction discrimination, evidence supporting the role of surface segregation in feature binding is provided.

Interestingly, the conjunction discrimination generated by both ‘different configuration’ display types remains at ceiling across most alternation frequencies, but is then reduced at the highest alternation frequency. This is contrasted against the ‘same configuration’ display types, which remain at ceiling across all alternation frequencies. When additional RDKs have a different configuration of dots, they are unused at the highest alternation frequency and subsequently serve only to add noise to the already-segregated target RDKs. In this way, the configuration of the additional RDKs appears to disrupt surface segregation, which is not seen in the ‘same configuration’ conditions at high alternation frequencies, suggesting dot configuration is a strong surface segregation cue.

Overall, these results suggest that additional RDKs can improve conjunction discrimination by means of facilitating surface segregation. Both colour and dot configuration can be cues to surface segregation (Adelson & Movshon, 1982; Masson et al., 1999; Snowden & Verstraten, 1999; Stoner & Blanc, 2010; Treisman & Kanwisher, 1998; Valdes-Sosa et al., 2000), which can influence the way in which a stimulus is perceived. The incorporation of additional coloured dots increased the redundancy of the stimulus which may have positively affected conjunction discrimination. It is however, telling that dot configuration generated a similar (if not greater) increase in conjunction discrimination, a difference further emphasised in Experiment 2A. These stimulus manipulations generated a result that would only be expected if there was a relationship between how target and additional RDKs were perceived. In this case, both sets of RDKs were linked through surface segregation, with each target and the corresponding additional RDK integrated into a representation of a single surface. In this way, both colour and dot configuration cues can serve to improve conjunction discrimination, especially at alternation frequencies where feature binding would otherwise not be possible.

However, the addition of colour to these moving, additional RDKs brings a confound in that it enhances the cues to colour-motion conjunction compared to the control display. This is addressed in the design of Experiment 2A which removes the motion of the additional RDKs while keeping the other stimulus manipulations the same as Experiment 1A. In doing so, any extra conjunction cues provided by these additional RDKs are removed (as RDKs no longer rotate) while otherwise keeping the colour and configuration cues identical to Experiment 1A. The overall implications of the stimulus manipulations used across Experiments 1A and 2A are subsequently discussed.

2.4. Experiment 2A: Discrimination of colour-motion conjunctions with additional, stationary dots

2.4.1. Rationale

In Experiment 1A, additional RDKs were added to an alternating colour-motion display, in order to enhance surface segregation. This in turn improved conjunction discrimination, suggesting that colour-motion conjunction discrimination is facilitated when surface representations can be appropriately formed. While colour and dot configuration, both surface segregation cues, significantly improved discrimination, a remaining question is the effect of motion on perceptual segregation. As consistent motion is another cue that can influence surface segregation and integration (Adelson & Movshon, 1982; Masson et al., 1999; Snowden & Verstraten, 1999; Treisman & Kanwisher, 1998), Experiment 2A removes the motion of the additional RDKs such that they remain static while on-screen. In effect, to produce a representation of two surfaces, integration over moving and static RDKs must take place. In contrast to Experiment 1A, surface formation here should at least be partially weaker due to the inconsistent motion between target and additional RDKs. Therefore, by comparing the results of Experiments 1A and 2A, the effect of motion on surface segregation and conjunction discrimination can be assessed.

2.4.2. Experimental methods

2.4.2.1. Subjects

Informed written consent was obtained from seven experienced psychophysical subjects (4 male; age range 20-43).

2.4.2.2. Visual stimuli

Experimental stimuli were similar to Experiment 1A to facilitate a comparison of results between these experiments (Figure 2.1a and Figure 2.2a). However, here the target RDKs did not move while off-screen (Figure 2.2b). This had the result of an RDK appearing in the same position in which it disappeared. In order to reflect this, additional RDKs no longer rotated while on-screen. When visible, additional RDKs were static, and only rotated while invisible.

2.4.2.3. Design and procedure

This experiment was a 5 ‘display type’ by 6 ‘temporal alternation frequency’ (1.67, 2.5, 3.33, 5, 7.5 and 15 Hz) within-subjects factorial design. In addition to the control condition, which contained no additional RDKs, there were four other display types, similar to those described in Experiment 1A. That is, the additional RDKs added to these display types varied in colour and configuration:

The four display types (in addition to the ‘control’ display) were (see Figure 2.2b):

i. ‘Grey, different configuration’ – here the additional RDKs differed from the target RDKs in both colour and configuration, meaning that the display alternated between two moving grey RDKs in addition to the target RDKs.

ii. ‘Coloured, different configuration’ – as with the ‘grey, different configuration’, but the additional RDKs were coloured orange and blue. When the orange target RDK was present on screen, the blue additional RDK would also be present, and likewise the blue target RDK was presented with the orange additional RDK.

iii. ‘Grey, same configuration’ - here the additional RDKs were of a different colour, but the same configuration as target RDKs. In this, the appearance of the display was that of two continuously-present RDKs, which both shifted between moving colour and static grey alternately such that only one coloured RDK was present at any one time.

iv. ‘Coloured, same configuration’ – this display was the same as the control display, where the two RDKs underwent alternations between periods of motion and rest, except in this display they remained visible when motionless. So while the orange RDK was undergoing rotation, the blue RDK was also present on-screen, though at a fixed position. The dot configuration in the two RDKs did not change.

These four permutations of same/different dot configuration and same/grey colour were tested, in addition to the control display.

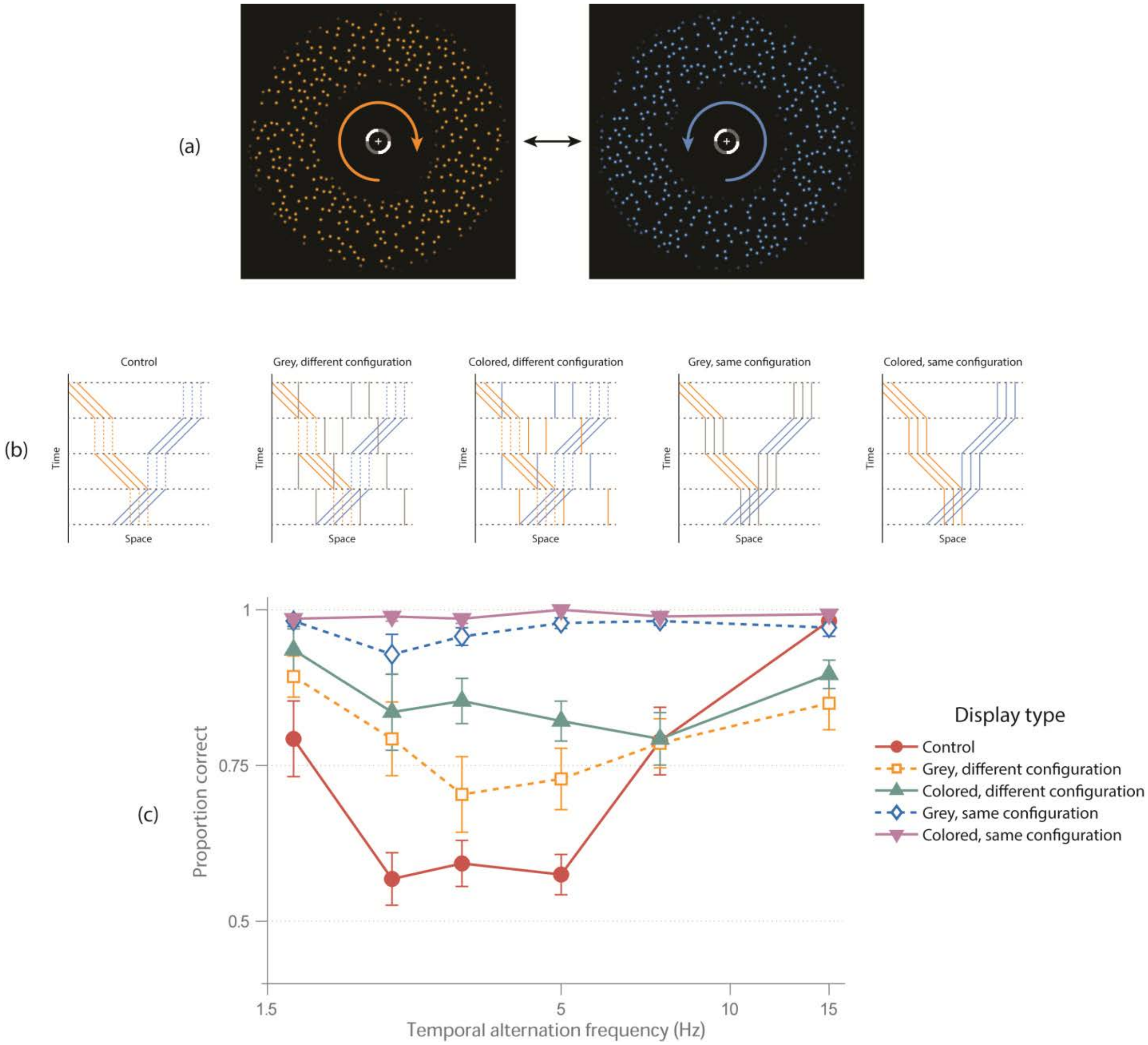

Figure 2.2. Stimulus design and results of Experiment 2A. (a) Representation of the control stimulus used in Experiment 2A, where alternations between orange and blue RDKs occurred at one of several alternation frequencies. **(b)** Schematic space-time plots of the display types in Experiment 2A. Conventions are the same as in Figure 2.1. Importantly, all additional RDKs and off-screen target RDKs were stationary, represented by vertical lines. **(c)** Mean conjunction discrimination on the colour-motion binding task (*n*=7) for each display type, across temporal alternation frequency. Error bars denote ±1 between-subject standard errors.

2.4.3. Results and discussion

Figure 2.2c displays the results of Experiment 2A. A two-way repeated measures ANOVA revealed main effects of display type ($F_{4,24} = 46.79$, $p < 0.001$) and temporal alternation frequency (main effect: $F_{5,30} = 13.11$, $p < 0.001$; quadratic trend: $F_{1,6} = 37.44$, $p = 0.001$). Alternation frequency affected conjunction discrimination in the same manner as the control condition in Experiment 1A: conjunction discrimination was better at the highest and lowest frequencies tested, and near chance around 5 Hz. In this experiment, the control display also displayed this trend best, a result supported by Moradi and Shimojo (2004).

The addition of any type of non-target RDK generally increased conjunction discrimination ($F_{20,120} = 8.75$, $p < 0.001$), when compared to the control display. Paradoxically, this was the case even when dots were grey and with a different configuration, thereby providing no information about the colour and motion attributes of the target RDK (main effect of display type: $F_{1,6} = 10.13$, $p = 0.019$; quadratic interaction: $F_{1,6} = 20.50$, $p = 0.004$). This result helps clarify the findings of Moradi and Shimojo (2004). In their experiment, they continuously displayed two superimposed grey RDKs with opposite motions (translating left and right) while alternations took place between two target RDKs with opposite motions (again, translating left and right) and different colours. Despite the low density of the grey RDKs (5% of the target RDKs), the continuous presence of these RDKs significantly increased conjunction discrimination at intermediate temporal frequencies compared to a display lacking the additional dots (Moradi & Shimojo, 2004).

Statistically, the results show a very robust effect of dot configuration in the additional RDKs on conjunction discrimination in this experiment, irrespective of whether the dots were a neutral grey, or the same colour as the target RDKs. That is, when RDKs had a matching configuration, conjunction discrimination was significantly better compared to a non-matching configuration ($F_{1,6} = 32.25$, $p = 0.001$). Colour also had a significant effect, whereby conjunction discrimination was higher when the additional RDKs were coloured compared to grey ($F_{1,6} = 22.03$, $p = 0.003$), although this was a smaller effect compared to configuration (Figure 2.2c). This result is supported by several other studies involving attention-based segregation of two rotating, differently-coloured RDKs (Mitchell et al., 2003; Stoner & Blanc, 2010; Valdes-Sosa et al., 2000). In these studies, discriminating a change in motion of one of two RDKs was only weakly affected by colour cues. It is possible that the continued presence of each RDK across the alternating periods of motion and rest in the ‘same configuration’ display types helped promote their perception as persistent surfaces, regardless of whether they lost their colour (i.e. changed to grey) or not while stationary. These studies support the idea that if the dot fields are segregated into moving surfaces early during processing, the appropriate allocation of colour to each surface becomes simple (Moradi & Shimojo, 2004), even if the surface loses its colour during periods of rest.

This is in contrast to the ‘different configuration’ display types, where the additional, stationary RDKs were of a different random configuration to those undergoing rotation, potentially “interrupting” surface segregation each time they appeared. Yet in these display types, conjunction discrimination was still improved at intermediate frequencies compared to the control condition. It is however possible that the presence of these additional RDKs still promoted surface segregation through motion contrast. Motion contrast has been demonstrated to be important in the segregation of surfaces (Lankheet & Palmen, 1998; Nothdurft, 1993; Regan & Beverley, 1984). That is, the opposing motion of the target RDK against the stationary RDKs (coloured or otherwise) could potentially enhance its salience, encouraging more accurate conjunction discrimination.

A comparison between Experiments 1A and 2A reveals that in terms of their effects on conjunction discrimination, display types are better grouped by configuration rather than by colour. In both experiments, ‘same configuration’ display types produced ceiling conjunction discrimination across all temporal alternation frequencies tested. In contrast, the removal of motion from the additional RDKs lowered conjunction discrimination in the ‘different configuration’ display types over all alternation frequencies. This matches the dip in discrimination in Experiment 1A for the ‘different configuration’ display types at the highest alternation frequency. These two results indicate that static, additional RDKs make the stimulus more difficult to interpret when compared to the equivalent ‘same configuration’ display types, subsequently reducing conjunction discrimination. If the target and additional RDKs share the same dot configuration, this difficulty can be overcome, suggesting that the pattern of the dots, or the texture of the surface, is a powerful surface segregation cue (Snowden & Verstraten, 1999).

2.5. Experiment 3A: Discrimination of colour-motion conjunctions with additional, vertically moving dots

2.5.1. Rationale

In Experiments 1A and 2A, the surface segregation cues of colour, dot configuration, temporal alternation frequency and specifically, coherent motion were tested. Both moving and static additional RDKs affected conjunction discrimination. However, to thoroughly test the effects of motion on surface segregation, Experiment 3A introduces additional RDKs with different directions of motion to the target RDKs, rather than a lack of motion. Conjunction discrimination may be affected if additional RDKs have a different direction of motion to the target RDKs, as the motion cue used to segregate surfaces will not be temporally consistent. This prediction is tested here using RDKs with linear (rather than radial) motion.

2.5.2 Experimental methods

2.5.2.1. Subjects

Informed written consent was obtained from seven experienced psychophysical subjects (4 male; age range 20-43).

2.5.2.2. Visual stimuli

The stimuli used in this experiment were similar to those in Experiments 1A. Here however, target dots translated horizontally instead of rotating (Figure 2.3a). Dots with linear motion were used as it was easier to add additional RDKs with a different direction of motion to the target RDKs. If rotating dots were used, additional RDKs that expanded or contracted may have generated confounds associated with a non-uniform direction of motion and the perceptual interpretation of the stimulus. That is, expanding/contraction of dots may give a sense of depth that would otherwise not be present in a display using linear motion, further complicating the interpretation of the results.

2.5.2.3. Design and procedure

This experiment was a 5 ‘display type’ by 6 ‘temporal alternation frequency’ (1.67, 2.5, 3.33, 5, 7.5 and 15 Hz) within-subjects factorial design. The five display types were (Figure 2.3b):

i. ‘Control LR’ – Only target dots were present in this display. Alternations between orange and blue RDKs translating in opposite directions (left and rightward movement) were displayed. While invisible, dots continued to translate left (or right) at the same speed. ‘LR’ is used here to indicate that only horizontal motion occurs.

ii. ‘Same LR’ – In this condition, coloured, target dots were replaced by moving grey, additional dots with the same spatial configuration, moving in the same directions as the targets (left and right). As such, there were always two RDKs on-screen simultaneously: one coloured and one grey.

iii. ‘Same UD’ – Similar to the ‘Same LR’ condition, except the grey additional dots translated vertically while on-screen. That is, on one particular trial, the orange target RDK would be replaced by grey dots moving upwards, and the blue RDK replaced by grey dots moving downward. The direction of motion of the additional dots were assigned independently. In this condition, invisible target RDKs would also match the associated on-screen grey RDK with regard to direction of motion. ‘UD’ is used here to indicate the presence of vertical motion: in both the additional RDKs and the off-screen behaviour of the target RDKs.

iv. ‘Different UD’ – Like the ‘Same UD’ display, grey dots with vertical movement replaced target RDKs. Here however, additional RDKs had a different dot configuration to the preceding target RDK.

v. ‘Control UD’ – This display did not contain any additional RDKs, but RDKs moved upward (or downward) while invisible. On a single trial, orange dots would (for example) move exclusively downward while on-screen, while blue dots would move upward. Two control conditions were used to assess if the off-screen behaviour of dots was also affecting conjunction discrimination.

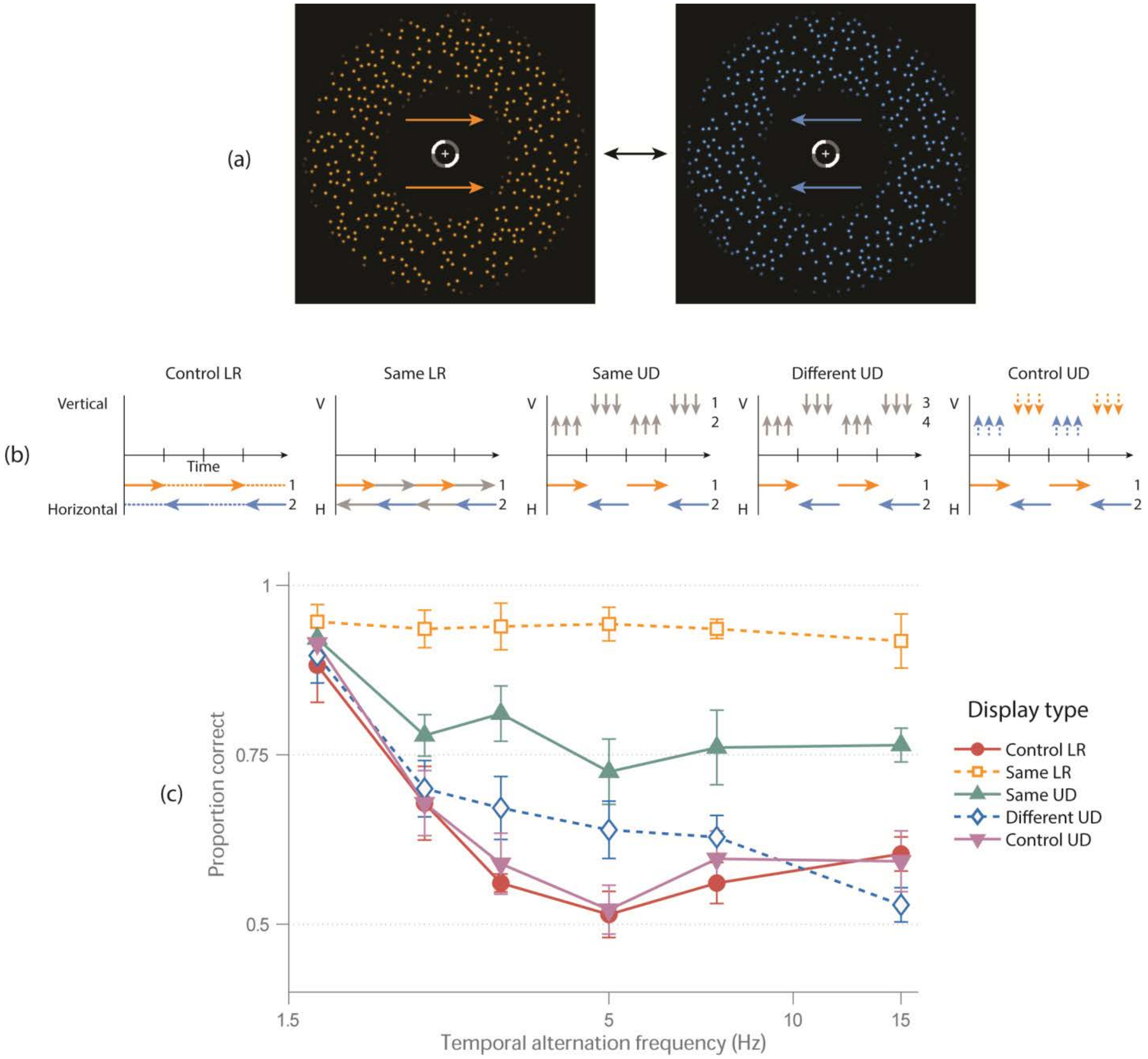

Figure 2.3. Stimulus design and results of Experiment 3A. (a) Representation of the base stimulus used in Experiment 3A. Orange and blue RDKs were generated and assigned opposite horizontal motions. Alternation between RDKs occurred at one of several temporal alternation frequencies and while off-screen, RDKs continued to move. **(b)** Dot motion characteristics of each display type in Experiment 3A. Additional RDKs were added to the display such that in the non-control conditions, two RDKs were always present on-screen simultaneously: one coloured and one grey. Time is shown on the *x*-axis, with each notch in the axis representing half the alternation

frequency, and the point at which the on-screen RDKs switch. The movement of each RDK (indicated by an arrow) across space is indicated by the direction of the arrow and its position on the *y*-axis. Arrow colours indicate the colour of the corresponding RDK, and a solid arrow indicates an on-screen RDK, while the dotted arrows indicate the behaviour of a currently invisible RDK. Small numbers next to the associated line indicate if an RDK shares the same dot configuration as another RDK. Only where numbers match, do RDKs share the same configuration. For example, in the ‘Same UD condition’, target RDKs move horizontally while the two additional grey RDKs move vertically, in opposite directions. Note that any differences in dot configuration are not represented here **(c)** Mean conjunction discrimination on the colour-motion binding task (*n*=7) for each display type, across temporal alternation frequency. Error bars denote ±1 between-subject standard errors.

2.5.3. Results and discussion

The results of Experiment 3A are displayed in Figure 2.3c. Significant main effects of both display type ($F_{4,24} = 35.76$, $p < 0.001$) and temporal alternation frequency ($F_{5,30} = 20.57$, $p < 0.001$) were observed. Specifically, averaged over display type, conjunction discrimination tended to decrease linearly as alternation frequency increased ($F_{1,6} = 31.01$, $p = 0.001$). Overall, it appears that, similar to Experiments 1A and 2A, the addition of any RDK can improve conjunction discrimination, even when they were horizontally translating.

Interestingly, there was a significant display type by alternation frequency interaction ($F_{20,120} = 4.75$, $p < 0.001$). Conjunction discrimination at low alternation frequencies was at ceiling regardless of display type, meaning the effects of any stimulus manipulations would be observed at higher frequencies. This was qualified by significant linear trend, indicating that as alternation frequency increased, the differences in conjunction discrimination between display types also increased ($F_{1,6} = 50.97$, $p < 0.001$). Specifically, conjunction discrimination remained consistently high when both dot configuration and direction of motion matched the target RDKs. Discrimination was impaired when additional RDKs had the same configuration, but a different direction of motion. However, feature binding remained consistently above chance across all alternation frequencies tested. Finally, when additional RDKs had both a different dot configuration and direction of motion to the target, conjunction discrimination was only marginally higher than the control conditions at all but the lowest alternation frequency (1.67 Hz).

Motion has been identified as a surface segregation cue in the literature (Lankheet & Palmen, 1998; Snowden & Verstraten, 1999; Watamaniuk et al., 2003). When directions of motion are more distinct, subjects are more likely to perceive multiple surfaces. Likewise, directions of motion closer together are more likely to be integrated together. The conclusions of this experiment support this, as a clear distinction was apparent between the condition where additional RDKs moved in the same direction as the target RDKs (‘same LR’) compared to those that did not (‘same UD’ and ‘different UD’). Thus, across Experiments 1A to 3A, it can be concluded that motion is a direct determinant regarding the strength of surface segregation, which in turn affected conjunction discrimination. When target and additional RDKs share the same motion, conjunction discrimination is high. However, discrimination drops when additional RDKs do not have the same motion as the target, whether that be because the additional RDKs are not moving, or because they are moving in a different direction to the target RDKs.

2.6. Experiment 4A: Effects of dot speed and off-screen behaviour on colour-motion conjunction discrimination

2.6.1. Rationale

In Experiments 1A and 2A, a distinct difference in conjunction discrimination between each control condition was observed ($F_{1,4} = 16.35$, $p = 0.007$). This different is most evident at the higher alternation frequencies, where temporal transparency occurs. In Experiment 1A, RDKs continue to rotate even while off-screen, whereas in Experiment 2A, RDKs stop rotating once off-screen. The differences in dot behaviour between experiments give rise to two possible explanations for the observed differences in conjunction discrimination. The first is that the motion path (continuous movement or static) of RDKs may be affecting conjunction discrimination. However, an alternative explanation is that, averaged over the total stimulus duration, the RDKs in Experiment 2A travel half the distance when compared to Experiment 1A. The averaged stimulus characteristics are an important consideration because at high temporal frequencies, where differences in conjunction discrimination are most prominent, RDKs are averaged over several temporal cycles. Thus, Experiment 4A aims to disentangle the relationship between off-screen behaviour and overall RDK rotation speed in order to investigate the differences in conjunction discrimination between Experiments 1A and 2A.

2.6.2. Experimental methods

2.6.2.1. Subjects

Informed written consent was obtained from seven experienced psychophysical subjects (4 male; age range 20-43).

2.6.2.2. Visual stimuli

Stimuli were based on the control conditions of Experiments 1A and 2A. Speed was varied such that these displays could either contain dots rotating at same speed in all previous experiments (‘full speed’), or half that speed (‘half speed’).

2.6.2.3. Design and procedure

This experiment had a 4 ‘display type’ by 6 ‘temporal alternation frequency’ (1.67, 2.5, 3.33, 5, 7.5 and 15 Hz) within subjects factorial design. The display types could be further broken down into a 2 ‘speed’ (full, half) by 2 ‘off-screen behaviour’ (moving, stopping) design. Dots that stop moving while not visible travel a total distance of half that in a display where they continue to move while off-screen. Thus, display types could be compared both across total distance covered and off-screen behaviour type, in order to determine which, if any, of these factors are responsible for the significantly increase conjunction discrimination in Experiment 2A’s control compared to Experiment 1A.

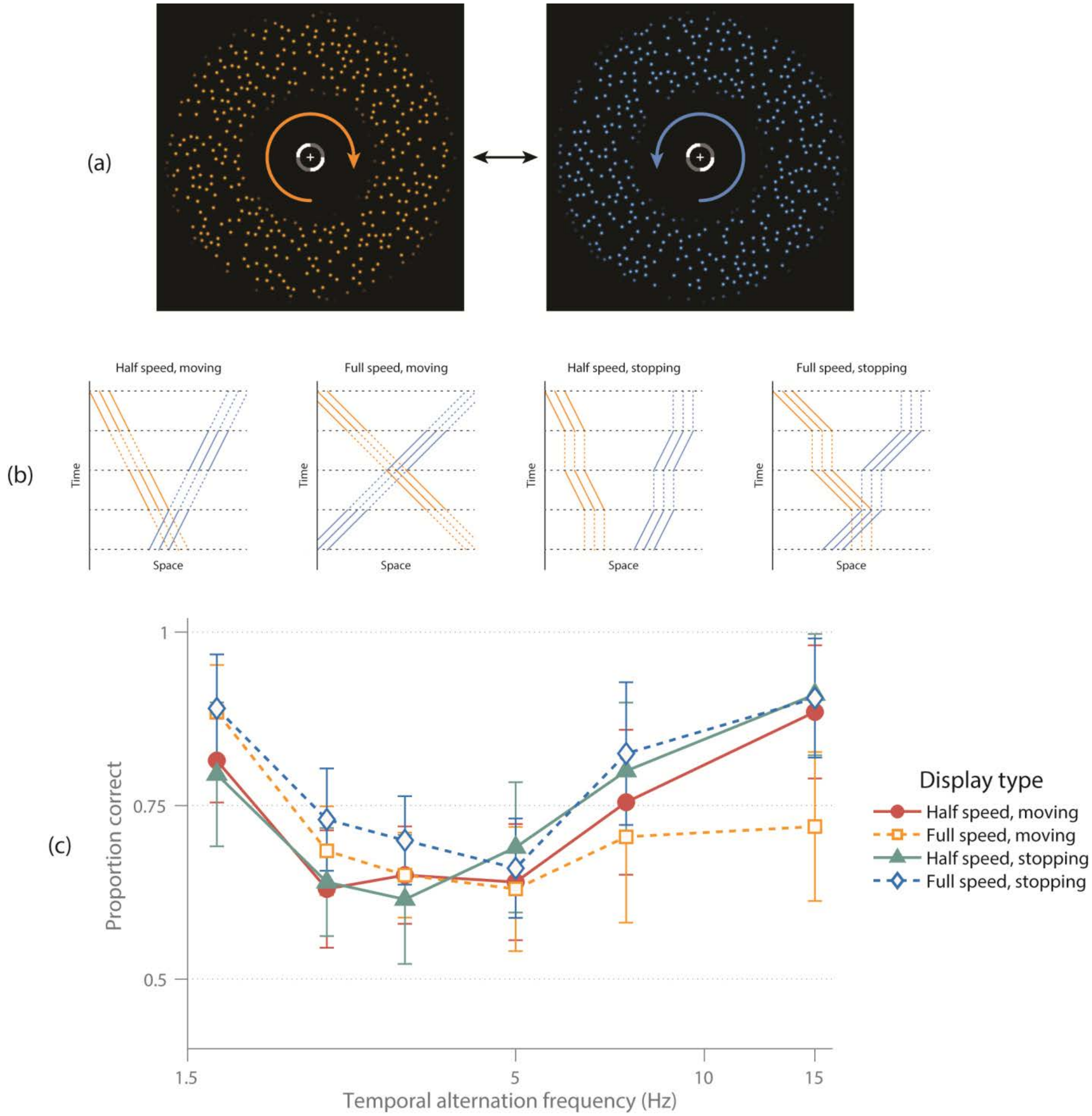

Figure 2.4. Stimulus design and results of Experiment 4A. (a) Representation of the stimulus used in Experiment 4A, where alternations between orange and blue RDKs occurred at one of several alternation frequencies. **(b)** Space-time plots of the display types in Experiment 4A. Conventions are the same as in Figure 2.1. It is important to note that the ‘full speed, moving’ and ‘full speed stopping’ display types are identical to the control conditions in

Experiments 1A and 2A respectively. **(c)** Mean conjunction discrimination on the colour-motion binding task (*n*=7) for each display type, across temporal alternation frequency. Error bars denote ±1 between-subject standard errors.

2.6.3. Results and discussion

The results of Experiment 4A are displayed in Figure 2.4c. Any main effects of display type, averaged over temporal alternation frequency, did not reach significance here ($F_{3,12} = 2.90$, $p = 0.079$). However, the main effect of frequency was still present on conjunction discrimination ($F_{5,20} = 2.27$, $p = 0.087$), generating a set of results that, when averaged over display type, had a quadratic trend ($F_{1,4} = 11.06$, $p = 0.029$).

There was no significant overall display type by alternation frequency interaction effect ($F_{15,60} = 1.75$, $p = 0.065$). However, the repeated measures analysis was subsequently applied to display types grouped by matching attributes. That is, results from display types with full speed ('full speed, moving' and 'full speed, stopping') were averaged together and compared against the average of the half speed conditions. Similarly, conditions with the same dot behaviour were averaged together and a comparison was made between the 'stopping' and 'moving' display types. While a significant interaction effect was only present when comparing the rotation speed of the dots ($F_{1,4} = 8.84$, $p = 0.041$), after Bonferroni correcting for two separate ANOVAs on non-independent sets of data (with significance now at $p < 0.025$), the statistical test is no longer significant.

Overall, this experiment did not find significant evidence to support either the speed or dot behaviour hypothesis regarding the differences in conjunction discrimination between the control conditions of Experiments 1A and 2A. Excluding the possibility of any significance effects due to random variation (i.e. a type 1 error), the results of this experiment indicate that the most likely explanation for the differences is a practice effect. As Experiment 1A and 2A shared the same subjects, it is possible that an increased familiarity with the stimulus allowed more accurate conjunction perception.

2.7. Experiment 5A: Discrimination of alternating colour-motion conjunctions with varying off-screen behaviour

2.7.1. Rationale

In the previous experiments (1A-3A), it was ascertained that surface segregation was able to support feature binding at intermediate temporal alternation frequencies. The reverse approach is now taken, with Experiments 5A-7A designed to investigate if a disruption of surface segregation at high alternation frequencies can cause a corresponding impairment in conjunction discrimination. Through a manipulation of the motion, dot configuration consistency or visual persistence of the display, surface segregation can be disrupted. Importantly, however, the temporal characteristics and colour-motion information contained in the display remain constant in order to isolate surface segregation as the factor supporting feature binding at high alternation frequencies. In the first of these experiments, Experiment 5A aims to determine if the same perceptual segregation was also influencing the temporal transparency percept present at high alternation frequencies through the use of motion and configuration consistency cues. Temporal transparency, by necessity, involves temporal integration of the stimulus over multiple presentation intervals. Thus, a reduction in conjunction discrimination through these manipulations by varying the temporal consistency of RDKs between presentation intervals – but only at high alternation frequencies – should be observed if a relationship exists between feature binding and perceptual transparency.

2.7.2. Experimental methods

2.7.2.1. Subjects

Informed written consent was obtained from five experienced psychophysical subjects (4 male; age range 20-28).

2.7.2.2. Visual stimuli

Stimuli similar to the control displays of Experiments 1A and 2A were used (Figure 2.5a). However, the relationships within and between dot configurations across temporal alternations were manipulated in order to disrupt the perceived transparency of the stimulus. This was in the form of differing behaviours in each display type during the periods when an RDK was not visible (i.e. off-screen). 5 display types were employed with various adjustments to the behaviour of the RDKs across presentations, all illustrated in Figure 2.5b.

2.7.2.3. Design and procedure

This experiment had a 5 ‘display type’ by 6 ‘temporal alternation frequency’ (1.67, 2.5, 3.33, 5, 7.5 and 15 Hz) within subjects factorial design. The 5 display types were (Figure 2.5b):

i. ‘Stopping’: This was a display that alternated between orange and blue RDKs (target RDKs) with opposite rotations, such that a single colour-motion combination was on-screen at any single point in time. This was a display identical to the control condition of Experiment 2A. As an example, the 5 Hz sequential presentation consisted of the orange RDK rotating for 100 ms, followed by the blue RDK for 100 ms, and so on until 1200 ms had elapsed. While an RDK was off-screen, it did not continue to rotate. Furthermore, the configuration of dots between the two RDKs was always different unless otherwise noted.

ii. 'Moving': As with the Stopping display, except that here RDKs continued to rotate while off-screen. This display is identical to the control display in Experiment 1A. Furthermore, it is essentially the same as the alternating display from Moradi and Shimojo (2004) except here the RDKs followed rotational instead of linearly translating motion trajectories.

iii. 'Randomising': RDKs appeared at a new, random angular position when arriving on-screen (although the configuration of the dots in each RDK was the same). While the angular position of the RDK was randomised, the shift was always more than a rotation of 60° but less than 270°. This set of angles was chosen to prevent any meaningful correlations of dot patterns, which may have resulted in the perception of the dots moving forward to backward.

iv. 'Resetting and unpaired': RDKs reset back to their initial angular position when appearing on-screen. Note that in this and the ‘resetting and paired’ display types (see below), the RDKs exhibited no net motion when averaged across a full trial.

v. 'Resetting and paired': This display had the same behaviour as the 'Resetting and unpaired' display, but here the dot configurations of the orange and blue RDKs were identical and yoked in position, such that a single set of dots oscillated between two directions of motion and two colours, with the change in the 2 attributes occurring at the same point in time (i.e. a phase difference of 0°). This display type is comparable to those from previous experiments investigating perceptual asynchrony between colour and motion (e.g. Amano, Johnston, & Nishida, 2007; Arnold, 2005; Arnold & Clifford, 2002; Bedell et al., 2003; Clifford, Spehar, et al., 2004; Holcombe & Cavanagh, 2008; Linares & López-Moliner, 2006; Moutoussis & Zeki, 1997a).

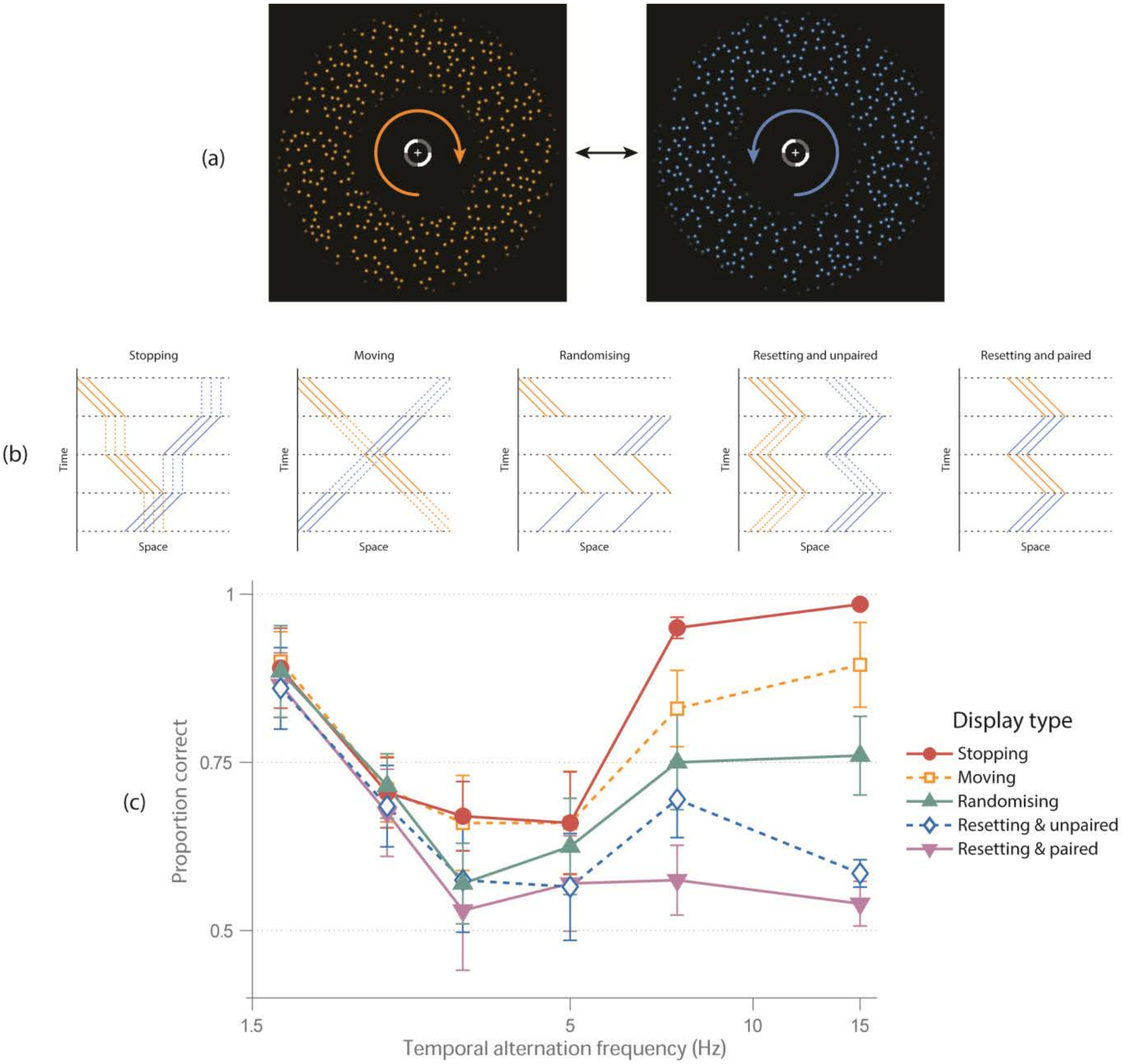

Figure 2.5. Stimulus design and results of Experiment 5A. (a) Representation of the stimulus used in Experiment 5A, where alternations between orange and blue RDKs occurred at one of several alternation frequencies. **(b)** Schematic space-time plots of the display types in Experiment 5A. Conventions are the same as in Figure 2.1. The ‘moving’ and ‘stopping’ display types are identical to the control conditions in Experiments 1A and 2A respectively. **(c)** Mean conjunction discrimination on the colour-motion binding task (*n*=5) for each display type, across temporal alternation frequency. Error bars denote ±1 between-subject standard errors.

2.7.3. Results and discussion

Experiment 5A aimed to test the stimulus characteristics that cause accurate conjunction discrimination to break down at high temporal alternation frequencies. These results are given in Figure 2.5c. A 2-way repeated measures ANOVA revealed main effects of both display type ($F_{4,16} = 33.30$, $p < 0.001$) and temporal frequency ($F_{5,20} = 9.66$, $p < 0.001$). The main effect of temporal alternation frequency exhibited a significant quadratic trend ($F_{1,4} = 10.87$, $p = 0.03$), in agreement with previous experiments (1A-4A). As frequency increased in the range of 1.67 to 5 Hz, a corresponding drop in conjunction discrimination occurred. As the presentation interval of each feature pair shortened, there was less time available in which to bind colour and motion features together. However, at 7.5 and 15 Hz, conjunction discrimination was overall increased.

There was also a significant display type by frequency interaction ($F_{20,80} = 6.87$, $p < 0.001$). Display type manipulations only affected conjunction discrimination at alternation frequencies where previous work indicates the perception of multiple transparent surfaces is supported (i.e. higher than 5 Hz; Holcombe, 2001; Moradi & Shimojo, 2004; T. Watanabe & Cavanagh, 1993). That is, no significant interaction was observed between display type as a function of alternation frequency between 1.67 and 5 Hz ($F_{12,48} = 0.94$, $p = 0.52$). Critically, however, between 5 and 15 Hz, display type interacted with alternation frequency to affect conjunction discrimination in a graded fashion ($F_{8,32} = 7.33$, $p < 0.001$). This may be due to the way in which motion across alternations affected the temporal integration of each dot field. In both the ‘moving’ and ‘randomising’ conditions, the configuration of each RDK upon reappearance had changed.

Furthermore, this is in correspondence with the relative conjunction discrimination between the ‘moving’ and ‘randomising’ display types. There was a larger distance between the disappearance and reappearance positions of the dots in the ‘randomising’ display than in the ‘moving’ display. In the ‘moving’ display, dots continued their rotation during the half-cycle where they were invisible (and the other RDK was visible). Motion coherence across alternations was affected to different degrees in all but the ‘moving’ display as the varying off-screen behaviour may have reduced the efficiency of the temporal integration (Lankheet & Palmen, 1998; Snowden & Verstraten, 1999; Watamaniuk et al., 2003).

In display types where dots exhibited no net motion when averaged across a full stimulus cycle (the two display types where RDKs reset their angular positions while off-screen: ‘resetting and unpaired’ and ‘resetting and paired’), conjunction discrimination was reduced to near chance as alternation frequency increased. Averaged over time, dot motion was no longer an effective method by which to differentiate between RDKs, therefore reintroducing the problem of correctly identifying temporally coincident feature pairs (Treisman, 1996). As each RDK is no longer perceptually segregated, binding fails, indicating that feature binding has a low temporal resolution. Small but significant differences existed between both ‘resetting’ display types (display type main effect: $F_{1,4} = 37.94$, $p = 0.004$). However, the difference between these two display types was significant only at 7.5 Hz (multiple comparisons using Bonferroni corrected, paired samples t-tests: $F_4 = 16.00$, $p = 0.016$).

In previous studies, stimulus arrangements much like the ‘resetting and paired’ display have been used to provide evidence for asynchronies in the processing of colour and motion (Amano et al., 2007; Arnold, 2005; Arnold & Clifford, 2002; Bedell et al., 2003; Clifford, Spehar, et al., 2004; Holcombe & Cavanagh, 2008; Linares & López-Moliner, 2006; Moutoussis & Zeki, 1997a). In one example, Moutoussis and Zeki (1997a) had a single set of dots oscillate between upwards and downwards motion and red and green colour, and subjects reported which direction was paired with which colour. They varied the relative phase of the change between colour and motion attributes, such that a phase difference of 0° meant that the change in colour and motion was perfectly simultaneous, a phase difference of 90° meant that the change in colour occurred at the midpoint of the dots’ excursion, and so on. In this way, they determined that subjects were most likely to report an exclusive colour-motion pairing when the change in colour lagged behind the change in motion by about 80 ms, suggesting that colour had an advantage over motion in terms of processing speed (Moutoussis & Zeki, 1997a).

Measured perceptual asynchronies of the sort identified by Moutoussis and Zeki (1997a) have largely been found to disappear under conditions where the dot displays are perceived as transparent (Clifford, Spehar, et al., 2004), and their interpretation of the results has been the focus of some scrutiny (see, for example, Amano et al., 2007; Arnold & Clifford, 2002; Bedell et al., 2003; Clifford, 2010; Nishida & Johnston, 2002). In the present study, conjunction discrimination was generally poor for both the ‘resetting and unpaired’ and ‘resetting and paired’ conditions at frequencies greater than 2.5 Hz. This suggests that the specific resetting action of the motion (i.e. the RDK returning back to its initial angular starting position with each onset period) is degrading conjunction discrimination, irrespective of whether there is one or two random dot configurations presented over time. As each RDK exhibits motion in both directions (the on-screen motion in the ‘correct’ direction and the apparent motion in the opposite direction caused by the resetting behaviour), segregation of each RDK on the basis of motion is now more difficult. The associated decrease in conjunction discrimination in these display types is consistent with the idea that the perception of surface transparency promotes more accurate conjunction discrimination (Moradi & Shimojo, 2004). While this point was not directly tested with a perceptual report of transparency (as in Experiment 9A), it may be that the absence of the transparency percept, rather than the ostensibly asynchronous processing of colour and motion, that accounts for the poorer conjunction discrimination at the higher frequencies tested here.

2.8. Experiment 6A: Discrimination of simultaneously presented colour-motion conjunctions with varying off-screen behaviour

2.8.1. Rationale

In Experiment 5A, the effects of altering motion coherence (within target RDKs) and dot configuration (between target RDKs) demonstrated that a disruption of perceptual surface segregation causes feature binding to fail, but only where binding is supported by surface segregation (at high alternation frequencies). In this experiment, the same experimental manipulations are repeated but with both target RDKs present on-screen simultaneously. Presentations of RDKs are interleaved with blank periods of an equal amount of time, during which the off-screen behaviour of each RDK occurs (moving, stopping, randomising, resetting). In this way, the amount of colour-motion information and the regularity at which it is presented also remains constant between Experiments 5A and 6A. As RDKs are now presented simultaneously, which produces a display that appears similar to temporal transparency, conjunction discrimination is expected to remain high over the frequency range that does not support temporal transparency. Within the frequency range supporting temporal transparency, conjunction discrimination is expected to decrease in the same way as the display types in Experiment 6A. Here, the temporal integration across RDK presentations should be equally disrupted by motion coherence manipulations.

2.8.2. Experimental methods

2.8.2.1. Subjects

Informed written consent was obtained from five experienced psychophysical subjects (4 male; age range 20-28).

2.8.2.2. Visual stimuli

Stimuli were used with identical parameters (and off-screen behaviours) as Experiment 5A. Here however, the display alternated between a period where both RDKs were presented simultaneously and a black period where no RDK was present (Figure 2.6a). These periods were always of the same length as each other, chosen to alternate at one of several alternation frequencies.

2.8.2.3. Design and procedure

This experiment had a 5 ‘display type’ by 6 ‘temporal alternation frequency’ (1.67, 2.5, 3.33, 5, 7.5 and 15 Hz) within subjects factorial design. The 5 display types were the same as in Experiment 5A, except here, RDKs were presented at the same time and alternated with blank periods (Figure 2.6b):

i. ‘Stopping’: a display that alternated between simultaneously presented orange and blue RDKs (target RDKs) with opposite rotations, and blank periods. When RDKs were visible, both colour-motion combinations were present simultaneously. The RDKs in this display had identical off-screen behaviours to that of the control condition of Experiment 2A. Furthermore, dot configurations between the two RDKs were always independent, except for condition (v).

ii. 'Moving': As with the ‘Stopping’ display, except that here RDKs continued to rotate while off-screen. This display had RDKs with off-screen behaviours identical to the control display in Experiment 1A, except that RDKs were presented simultaneously.

iii. 'Randomising': RDKs appeared at a new, random angular position when arriving on-screen (although the configuration of the dots in each RDK was the same). Again, shifts in rotation while off-screen were always between 60° and 270°.

iv. 'Resetting and unpaired': RDKs reset back to their initial angular position when appearing on-screen. Note that in this and the ‘resetting and paired’ display types (see below), the RDKs exhibited no net motion when averaged across a full trial.

v. 'Resetting and paired': This display had the same behaviour as the 'Resetting and unpaired' display, but here the dot configurations of the orange and blue RDKs were spatially matched. That is, for each orange dot, there was a blue dot travelling in the opposite direction in close spatial proximity as orange and blue RDKs had identical spatial configurations (as in Qian et al., 1994).

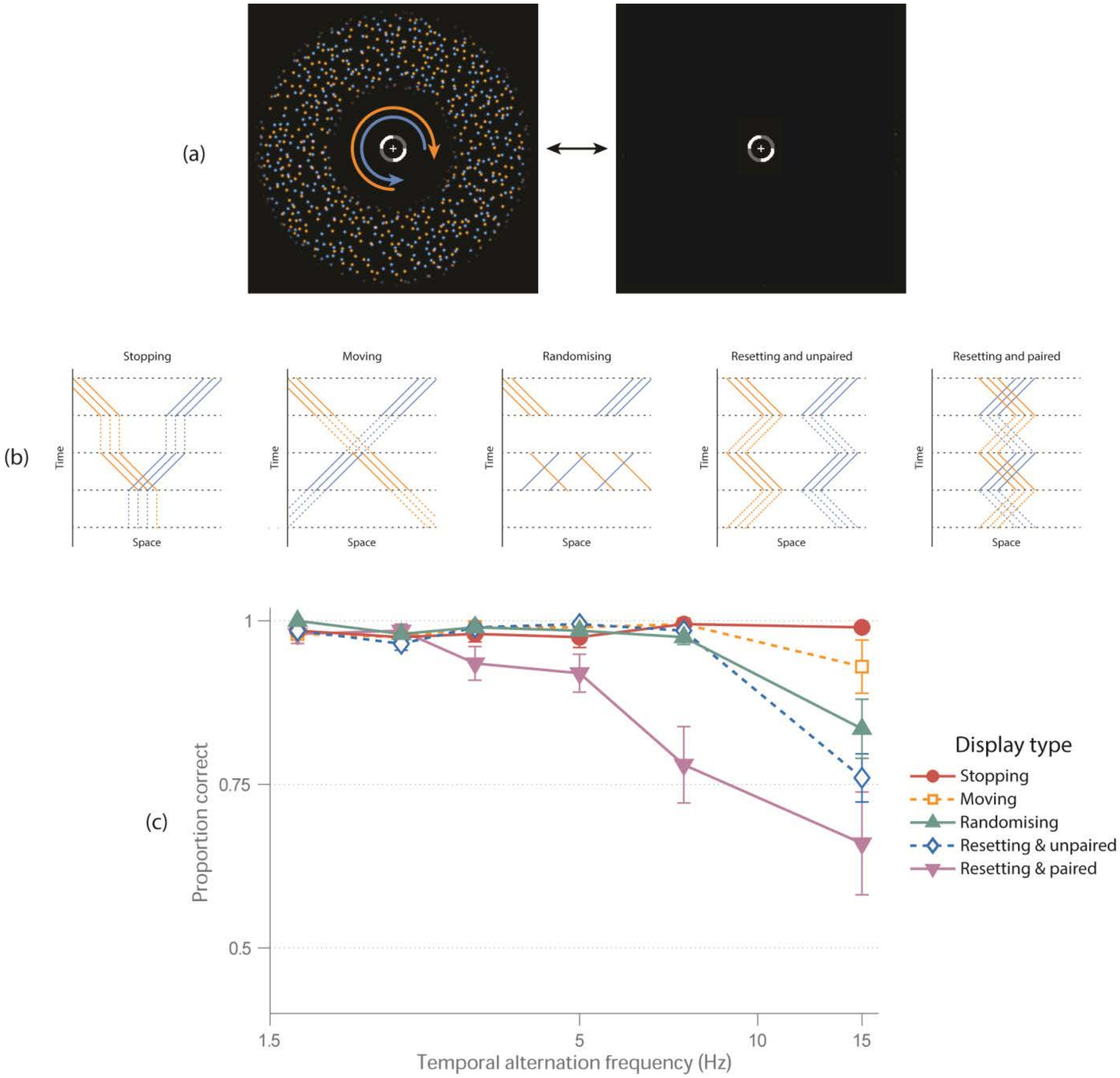

Figure 2.6. Stimulus design and results of Experiment 6A. (a) Representation of the stimulus used in Experiment 6A, where orange and blue RDKs were displayed simultaneously, and interleaved with blank periods at one of several alternation frequencies. **(b)** Space-time plots of the experimental display types. Conventions are the same as in Figure 2.1. RDK off-screen behaviours and dot configuration relationships between RDKs are identical to the corresponding conditions in Experiment 6A. **(c)** Mean conjunction discrimination on the colour-motion binding task

(*n*=5) for each display type, across temporal alternation frequency. Error bars denote ±1 between-subject standard errors.

2.8.3. Results and discussion

Averaged over temporal alternation frequency, display type had a significant effect on conjunction discrimination ($F_{4,16} = 13.58$, $p < 0.001$). Interestingly, the conjunction discrimination generated by each display type at 15 Hz is ordered in the same way as in Experiment 5A. That is, in both experiments, conditions where dot motion was predictable and consistent (‘stopping’ and ‘moving’) had higher conjunction discrimination than those that did not. Alternation frequency also had an overall effect on conjunction discrimination ($F_{5,20} = 19.26$, $p < 0.001$) which would not usually be expected when conjunction pairs are presented simultaneously (for example in Experiment 8A or Moradi & Shimojo, 2004). That conjunction discrimination decreases linearly with an increase in alternation frequency ($F_{1,4} = 19.00$, $p = 0.012$) demonstrates that the display type manipulations were successful in impairing temporal integration at high alternation frequencies.

Like Experiment 5A, display type and alternation frequency interacted significantly ($F_{20,80} = 9.55$, $p < 0.001$). This manifested as a linear increase in conjunction discrimination differences between display types as alternation frequency increased ($F_{1,4} = 59.68$, $p = 0.002$). That is, at lower alternation frequencies, conjunction discrimination was high and approximately equal among display types. However, as alternation frequency increased into the range facilitating temporal integration, conditions with lower motion coherence across presentations generated lower conjunction discrimination.

In comparing the results of Experiments 5A and 6A, the differences between both ‘resetting’ conditions should be observed. Whereas in Experiment 5A the difference in conjunction discrimination between these two display types was minimal, here in Experiment 6A this difference is considerably larger ($F_{1,4} = 9.18$, $p = 0.039$). The reason for this is most likely the way dots were spatially paired while still being simultaneously presented. In Experiment 5A, the ‘resetting and paired’ condition is perceptually interpreted as a single set of dots alternating in both motion and colour. Here however, dots are paired spatially such that each orange dot has a corresponding blue dot in close spatial proximity. Crowding may come into play in such a display, especially as RDKs are not presented centrally (Balas et al., 2009; Levi, 2008; Põder, 2006; Põder & Wagemans, 2007; Whitney & Levi, 2011). Thus, the sharper decrease in conjunction discrimination in this display type may be due to both the resetting behaviour (at high frequencies) and crowding (at intermediate to high frequencies).

Together, the results of Experiments 5A and 6A demonstrate that manipulations to motion coherence and dot configuration disrupt feature binding at high alternation frequencies in qualitatively similar ways. This was irrespective of RDK presentation as sequential or simultaneous. As the greatest differences in conjunction discrimination occurred only at high alternation frequencies, it suggests these manipulations did not directly affect the capacity to identify temporally coincident feature pairs. Rather, the perceptual interpretation of the stimulus was affected by disrupting temporal integration. This manifested as a decrease in conjunction discrimination at higher alternation frequencies as the low temporal resolution feature binding process relies on the temporal integration over successive presentations of a single RDK.

2.9. Experiment 7A: Discrimination of colour-motion conjunctions with varying background colour

2.9.1. Rationale

Experiments 5A and 6A demonstrated that disruption of temporal integration at high alternation frequencies could occur by manipulating motion coherence and dot configuration cues. This in turn affected perceptual surface segregation, which was associated with lowered conjunction discrimination. This experiment follows a similar rationale by investigating the role of visual persistence in temporal integration. The visual system is known to integrate over short temporal intervals (Di Lollo, 1980; Di Lollo & Wilson, 1978; Georgeson, 1987; Snowden & Braddick, 1991; Watamaniuk & Sekuler, 1992). Even within the retina, temporal integration of 0.3 to 640 ms intervals can take place (Barlow, 1958; Graham & Margaria, 1935). The necessity of temporal integration has already been demonstrated in previous experiments (1A-6A), but its relationship with visual persistence remains unclear (Dixon & Di Lollo, 1994). Experiment 7A investigates if the visual persistence of an RDK plays a role in the temporal integration found at high alternation frequencies.

2.9.2. Experimental methods

2.9.2.1. Subjects

Informed written consent was obtained from six experienced psychophysical subjects (5 male; age range 25-29).

2.9.2.2. Visual stimuli

Two random dot kinematograms (RDKs) were presented against a coloured background within the annulus. Outside the annulus, the background colour was black. One RDK was comprised of orange dots, and the other contained blue dots, both with a luminance of 29 Cd/m^2. Within the annulus, RDK backgrounds could either be orange, blue, or grey, and had a luminance of 23 Cd/m^2.

The RDKs consisted of circular dots with hard edges (that is, no Gaussian smoothing was applied) and a diameter of 0.32°. Unlike the other experiments in this chapter, dots had a hard edge was used to ensure exactly 2 colours per RDK: the dot colour and the background colour (rather than a smoothed gradient from dot colour to background). In this way, colour addition between alternating RDKs could be controlled precisely. Dots were distributed evenly throughout an annular window with a minimum distance of 0.7° from any other dot. On average, 11.8% of the total viewing area was filled with dots, giving a density of 3.7 dots/deg^2.

2.9.2.3. Design and procedure

This experiment had a 3 ‘display type’ by 8’ temporal alternation frequency’ (1.25, 2.5, 3.75, 5, 7.5, 10, 15, and 30 Hz) within-subjects factorial design. The 3 display types used in this experiment were as follows:

The ‘grey background’ display type (Figure 2.7a) in this experiment was used as control. The display alternated between orange and blue RDKs (target RDKs) with opposite rotations, such that a single colour-motion combination was on-screen at any single point in time. This display was similar to those previously used, except the space between the dots of both orange and blue RDKs (within the annulus) was filled with dark grey. In all display types, RDKs always rotated, even while not visible.

In the ‘same background’ display type (Figure 2.7b), the orange RDK had a background of dark orange, and the blue RDK had a dark blue background (hence, the label ‘same’ was used as the background and dots shared the same colour, but not luminance). Here, dot and background colours were calibrated such that the dots of the orange RDK and the background of the blue RDK would sum to the same grey as the reverse combination (blue dots on an orange background). See the general methods in Chapter 3 (and Figure 3.1) for an in-depth description of the colour calibration process used for this experiment. In previous experiments, visual persistence of an RDK would take place against a black background, meaning that orange and blue RDKs could still be easily distinguished. In such a case, it is difficult to say whether the processes of surface segregation, visual persistence, or a combination of the two are affecting conjunction discrimination. Thus, this condition aims to remove the perceptual advantage of visual persistence by having dots of an RDK persist on matched coloured background. That is, dots from the orange RDK would persist on the dark blue background of the blue RDK, creating a set of perceptually grey dots. Blue dots persisting on the dark orange background would perceptually produce dots of the same shade of grey, rendering them indistinguishable. Thus, low conjunction discrimination here at high alternation frequencies could be attributed to the effects of visual persistence, as the colour-motion pairing would be masked, but importantly, the perception of two surfaces would remain intact. As demonstrated in Experiment 9A, colour appears to be a relatively minor surface segregation cue.

Finally, the ‘different background’ display type (Figure 2.7c), consisted of the orange RDK presented against a dark blue background (and likewise, a blue RDK on a dark orange background). This condition was designed with two considerations. The first is that at higher alternation frequencies, the rapidly alternating colours of the background in the ‘same background’ condition may impact conjunction discrimination. This condition is therefore used to observe the effects of a background that changes colour on conjunction discrimination. However, in order to minimise the impact of differently coloured backgrounds on visual persistence, adding the dot colour of one RDK to the background of the other does not mask the colour-motion pairing. Although the colours used in both ‘same’ and ‘different’ background display types are identical, (and thus at high alternation frequencies both will sum to dark grey), in this condition the dots themselves will be distinguishable even at high alternation frequencies (see the transparent percept column in Figure 2.7a-c)

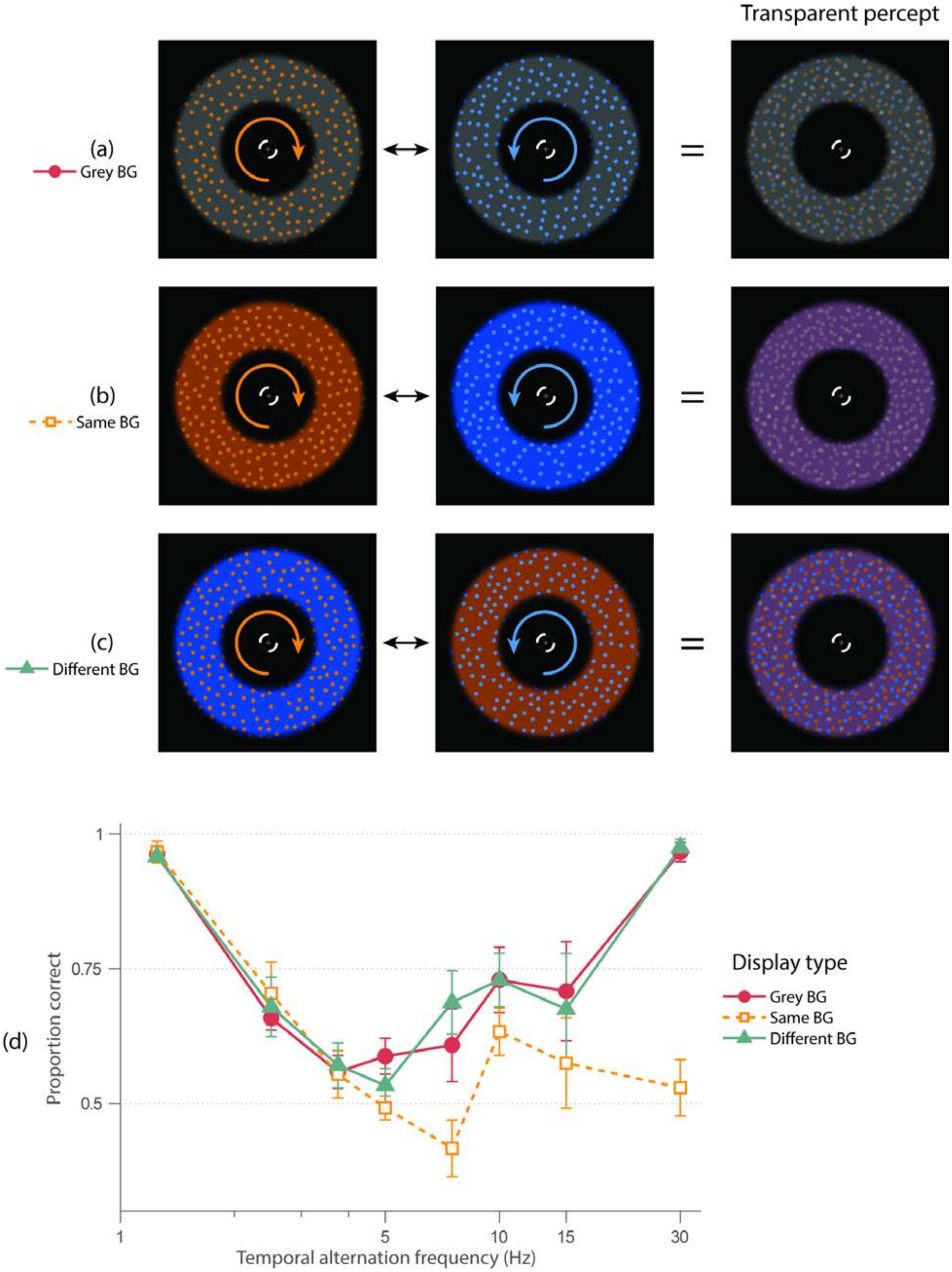
Transparent percept
(a)
Grey BG
(b)
Same BG
(c)
Different BG
(d)
Proportion correct
1
0.75
0.5
1
5
10
15
30
Temporal alternation frequency (Hz)
Display type
Grey BG
Same BG
Different BG

Figure 2.7. Stimulus design and results of Experiment 7A. (a)-(c) Representations of the 3 display types used in Experiment 7A: ‘grey’ background, ‘same’ background, and ‘different’ background display types respectively. All dots were subjectively calibrated for subjective isoluminance, as were the background colours. The third column is the sum of the two RDKs, and serves as a representation of how they would be perceived under conditions of temporal transparency/visual persistence. **(a)** The ‘grey’ background condition had the same grey background applied to both the orange and grey RDKs. **(b)** The ‘same’ background condition had a dark orange background applied to the orange RDK, and a dark blue background applied to the blue RDK. In this condition, the addition of any RDK’s dot colour to the background of the other RDK would generate the same grey colour. **(c)** The ‘different’ background condition had the colour opposite to the dot colour applied to the respective background for each RDK (i.e. dark blue background for orange dots and dark orange background for blue dots). **(d)** Mean conjunction discrimination on the colour-motion binding task ($n=6$) for each background type, across temporal alternation frequency. Error bars denote ±1 between-subject standard errors.

2.9.3. Results and discussion

The aim of Experiment 7A was to determine if visual persistence was supporting high conjunction discrimination in colour-motion displays. In the same background condition, RDK backgrounds were calibrated in such a way that dots of one RDK persisting on the background of the other would result in an indistinguishable set of grey dots, negatively affecting conjunction discrimination. However, if the addition of a coloured background caused low conjunction discrimination, both the same and different background display types would generate similar patterns of data.

The results of this experiment are displayed in Figure 2.7d. Background type had an overall effect on conjunction discrimination, averaged across alternation frequency (two-way repeated measures ANOVA; $F_{2,4} = 56.36$, $p = 0.001$). Temporal alternation frequency also significantly affected conjunction discrimination ($F_{7,14} = 14.64$, $p < 0.001$), with the pattern of data described best by a significant quadratic trend ($F_{1,2} = 2417.14$, $p < 0.001$). That is, averaged across display type, accurate conjunction discrimination was present at both the lowest and highest frequencies tested (1.25 and 30 Hz respectively). However, discrimination was reduced to chance around 5 Hz, similar to the patterns of data present in this chapter’s experiments.

Of specific interest in this experiment was the significant interaction between display type and alternation frequency ($F_{14,28} = 4.77$, $p < 0.001$). From the data, it is clear that while each display type produced similar conjunction discrimination at low alternation frequencies, differences in discrimination are greater between background types at frequencies from 10 Hz onwards where temporal transparency occurs. Specifically, conjunction discrimination for the same background display remains at chance, and was significantly different to the grey background condition ($F_{1,5} = 54.29$, $p < 0.001$). This is in comparison to the differences in discrimination between the grey and different background display types, which do not differ significantly over the 5-30 Hz frequency range ($F_{1,5} = 0.09$, $p = 0.776$).

There are definite links between visual persistence, apparent motion, and temporal integration (Farrell, 1984; Green, 1986). Several factors affect visible persistence such as luminance and duration (Dixon & Di Lollo, 1991). Specifically, as duration decreases, the effective time of a persistent afterimage increases (Dixon & Di Lollo, 1991; Hogben & Di Lollo, 1985). Consistent with these findings, differences between display types were most apparent at higher alternation frequencies. Farrell et al. (1990) also found that with regard to stroboscopic motion, persistence increases as the duration between stimulus appearances decreases. In this experiment, RDKs always rotated at the same rate. This means that a higher alternation frequency resulted in a smaller spatial distance between disappearance and reappearance, increasing visual persistence.

One potential confound addressed by the results of this experiment is that the poorer colour contrast in the same background display may adversely affect perception of the correct rotation. However, if this was the driving factor behind these results, one would expect lowered conjunction discrimination across all temporal alternation frequencies tested for this display type. However, this was not evident in the frequency range of 1.25-5 Hz, where all display types generated similar conjunction discrimination. The interaction effect between display type and frequency is better explained by the effect of visual persistence. While persistence occurs on a brief timescale (Dixon & Di Lollo, 1991; Hogben & Di Lollo, 1985), the higher alternation frequency results in a shortened period of time in which an RDK is off-screen. The more rapid appearances and disappearances mean that persistence occurs more often, and for a greater proportion of the time when an RDK is not present.

The nature of this visual persistence (Coltheart, 1980; Shioiri & Cavanagh, 1992) is still a matter for speculation, with Moradi and Shimojo (2004) suggesting it is probably a form of iconic memory trace (Neisser, 2014; Sperling, 1960). Di Lollo and Wilson (1978) present results that indicate visual persistence is a result of the earliest stages of temporal integration. Dixon and Di Lollo (1994) find that the temporal relationship between closely-presented stimuli is preserved and expressed through temporal integration. The relationship between rapidly presented stimuli can be described by a model whereby sustained activation of stimuli generate persistence while non-overlapping activity inhibits it (Groner, Bischof, & Di Lollo, 1988). In this experiment, however, the persistence of each RDK is masked by the other. While still present, RDKs can no longer be distinguished through persistence alone. In line with this, Dixon and Di Lollo (1994) suggest that visual persistence extends the duration of briefly present stimuli in order to provide enhanced perception.

This experiment is also comparable in stimulus design to the results of that in Holcombe and Cavanagh (2001) and the experiments of Chapter 3. Holcombe and Cavanagh (2001) developed a colour-orientation stimulus whereby alternations took place between two orthogonal and oppositely coloured gratings. Like this experiment, the addition of the orange and blue colours from each grating summed to grey, masking the colour-orientation pairing at high alternation frequencies. Holcombe and Cavanagh (2001) found that conjunction discrimination was reported with at least 75% accuracy for all frequencies up to 16 Hz. Beyond this, however, conjunction discrimination of colour-orientation falls to chance while discrimination of colour-motion stimuli remains consistently at ceiling. This experiment accounts for the discrepancy: the perception of stimuli presented at high alternation frequencies are affected by visual persistence, but are usually not designed to have RDKs sum together in a manner independent of the colour-orientation conjunction.

The results of this experiment make a distinction between the ways in which each RDK is segregated. Specifically, the effect of visual persistence here suggests that while RDKs are segregated, they cannot completely be isolated. That is, each RDK is perceptually overlayed over the other in an additive manner. If the surface segregation process stored completely independent surface representations at a consciously accessible level, the attributes of an individual representation would be clear. However, despite a high alternation frequency and the unambiguous colour and motion features of each RDK, conjunction discrimination was still poor in the same background display. It follows then, that the perceptual interpretation of the stimulus is not only dependent on temporal integration, but also on the temporal resolution of individual feature detectors such as colour and motion and the way that persistence occurs in visual system.

2.10. Experiment 8A: Discrimination of alternating and simultaneous colour-motion conjunctions

2.10.1. Rationale

The next set of experiments, 8A-10A, are designed to investigate the relationship between stimulus presentation, alternation frequency, perceptual interpretation and neural activity. Three different measures are taken of the same stimulus. In Experiment 8A, an objective measure is taken of the stimuli whereby colour-motion binding task accuracy is measured as per Experiments 1A-7A. Experiment 9A uses a subjective measure, in which subjects report their perceptual interpretation of the stimulus. Finally, Experiment 10A investigates patterns of neural data in early visual cortex associated with viewing this stimulus in order to examine the relationship between perceptual interpretation and neural activity. First, Experiment 8A investigates the spatial and temporal parameters that drive accurate conjunction discrimination, with regard to surface segregation.

2.10.2. Experimental methods

2.10.2.1. Subjects

Informed written consent was obtained from 5 experienced psychophysical subjects (3 male; age range 24-46). The same subjects participated in Experiment 10A.

2.10.2.2. Visual stimuli

In addition to a display similar to previous experiments (specifically, the control condition in Experiment 2A), a new type of display was employed. The spatially interleaved display (Figure 2.8a) simultaneously presented both RDKs across concentric, logarithmically-spaced annuli, or strips. Strips were used here instead of overlaying both RDKs (like in Experiment 6A) to prevent a doubling of dot density and to avoid dots of different colours physically overlapping. Strips were designed such that one containing orange dots rotating in one direction were flanked on either side by strips of blue dots rotating in the opposite direction.

Strip width increased linearly with radius from 0.15° to 0.39° for each of the 10 strips present in each display. Each strip alternated between orange and blue at the specified alternation frequencies. Annular strips were used in order to balance local motion cues and perceived flicker with the sequential presentation while avoiding dots physically overlapping. In this way, dot density was kept constant between the sequential and spatially interleaved conditions. As has been observed previously (Clifford, Spehar, et al., 2004) under this arrangement, separate strips from the same RDK were readily combined into a coherent whole such that two transparent RDKs were perceived.

2.10.2.3. Design and procedure

This experiment had a 2 ‘display type’ (sequential/spatially interleaved) × 6 ‘alternation frequency’ (1.67, 2.5, 3.33, 5, 7.5 and 15 Hz) within-subjects design. Both display types were present an equal amount of times in each experimental run, but interleaved randomly. Subjects were instructed to report the colour-motion pairing.

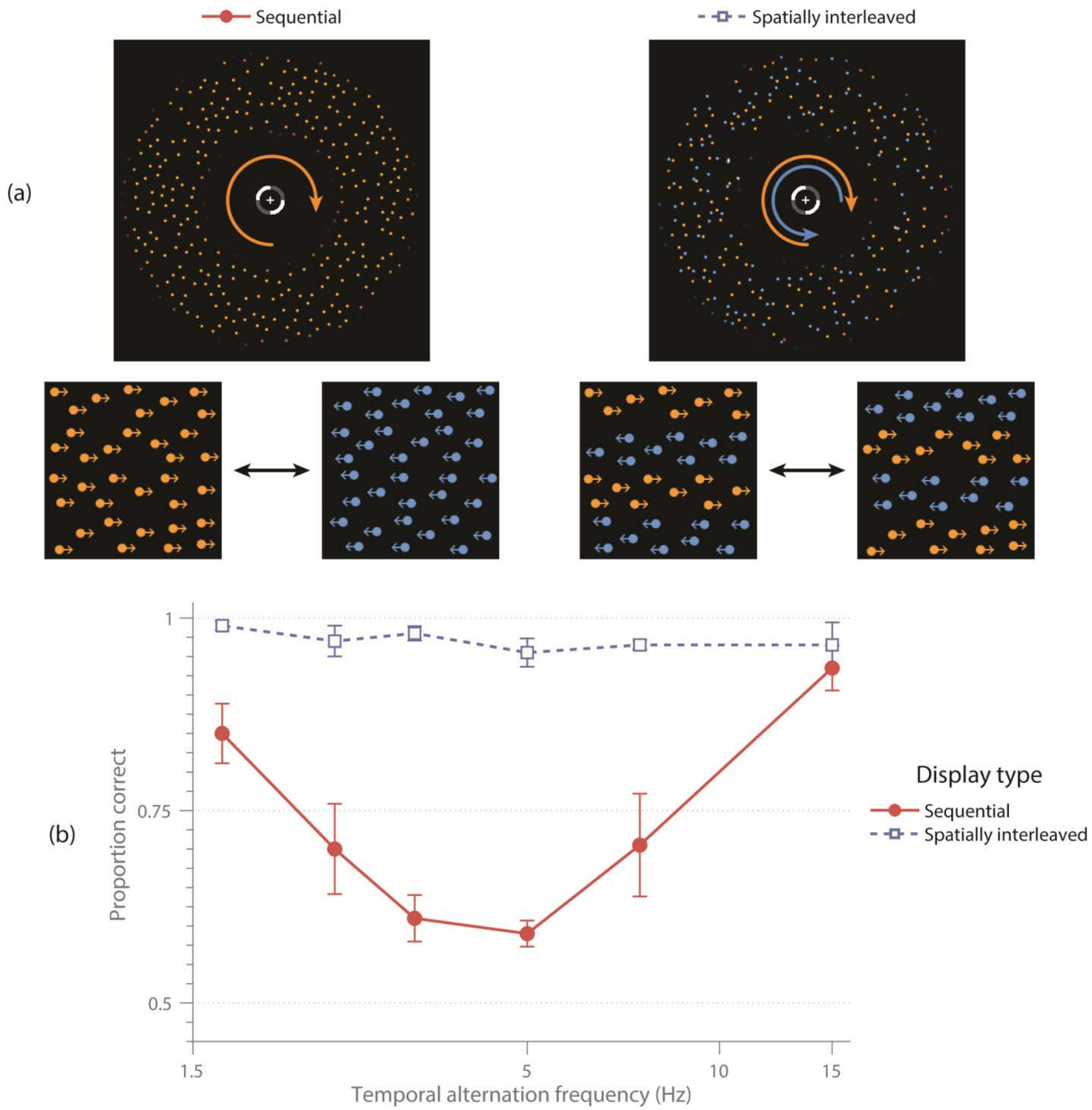

Figure 2.8. Stimulus design and results of Experiment 8A. (a) Representation of both display types used in this experiment. Black arrows denote alternation, while coloured arrows attached to dots indicate the rotation direction within a single portion of the stimulus. The left portion of **(a)** represents the sequential display. Here, only one colour and one rotation direction was on-screen at a time. This display was identical to the control condition in

Experiment 2A. The right portion of **(a)** represents the spatially interleaved display. While the specific colour-motion pairing remains the same as the sequential display (in this example), both colours and motions were present simultaneously in concentric, alternating strips. Alternations between colour and motion occurred within those strips as demonstrated in the figure. **(b)** Mean conjunction discrimination on the colour-motion binding task (*n*=5) for each display type, across temporal alternation frequency. Error bars denote ±1 between-subject standard errors.

2.10.3 Results and discussion

This experiment investigated the temporal dynamics of two different display types with regard to visual feature binding. Main effects of both display type ($F_{1,4}$ = 171.07, $p < 0.001$) and alternation frequency ($F_{1,4}$ = 8.11, $p = 0.001$) were present (Figure 2.8b). Critically, a significant quadratic presentation by frequency interaction was observed ($F_{1,4}$ = 84.60, $p = 0.001$). While conjunction discrimination in the spatially interleaved conditions was at ceiling across all alternation frequencies, discrimination in the sequential display decreased, and then increased across alternation frequency (Moradi & Shimojo, 2004). As both display types had the same dot density, local motion cues, and alternation period, the difference in conjunction discrimination can therefore be attributed to an interaction between display type and frequency.

The spatially interleaved stimulus was designed to appear transparent regardless of alternation period, supported by a non-significant linear trend for the spatially interleaved condition (repeated measures GLM; $F_{1,3}$ = 0.01, $p = 0.93$). A clear quadratic trend, however, was present in the sequential display data ($F_{1,4}$ = 107.97, $p < 0.001$). Conjunction discrimination was close to ceiling in the sequential display at the highest (15 Hz) and lowest (1.67 Hz) alternation frequencies, and approached chance as alternation frequency approached 5 Hz.

The segregation of the two RDKs into transparent surfaces in both the sequential (at high frequencies) and spatially interleaved display types (at all frequencies) may involve motion opponency at the early stages of visual processing (H. Jones, Grieve, Wang, & Sillito, 2001;

Lindsey & Todd, 1998), and/or an imbalance of local motion cues (Qian et al., 1994). At this high frequency, visual persistence may also contribute to the perceived transparency of the sequential condition, as explored in Experiment 7A (Coltheart, 1980; Di Lollo & Wilson, 1978; Dixon & Di Lollo, 1991; Farrell, 1984; Farrell et al., 1990; Mezrich, 1984; Shioiri & Cavanagh, 1992). Despite the serial presentation of RDKs, if presentation intervals occur within a sufficiently short temporal window (Shioiri & Cavanagh, 1992) both RDKs may appear to persist simultaneously, producing the percept of simultaneous, transparent and distinct surfaces. At alternation frequencies around 5 Hz, individual colour-motion presentations were too short to identify and bind features together, and discrimination was near chance (see also Moradi & Shimojo, 2004). At these frequencies, the RDKs may mask each other. Unlike the high frequency conditions, the stimulus duration here exceeded the time course of visible persistence, preventing the perception of motion transparency (Coltheart, 1980; Shioiri & Cavanagh, 1992).

Conjunction discrimination in the sequential display steadily improved with a reduction in the alternation frequency below 5 Hz. While only one surface was now perceived at a time, a longer alternation period enabled features to be bound within a single presentation (Moradi & Shimojo, 2004; Nishida & Johnston, 2002). Feature binding is believed to be a relatively slow process (Treisman & Gelade, 1980). Therefore, without surface segregation, a long presentation period is required to reliably perceive feature pairings (Holcombe, 2009; Treisman, 1996, 1998; Treisman & Gelade, 1980). Together, these results suggest that either a high alternation frequency or simultaneous presentation, as in the case of the spatially interleaved condition, is necessary to enable stable transparent surface segregation (Moradi & Shimojo, 2004).

2.11. Experiment 9A: Subjective interpretations of coloured, moving dots

2.11.1. Rationale

In Experiment 8A, it was demonstrated that both the presentation of the RDKs and the temporal alternation frequency at which they are displayed affected conjunction discrimination. While Experiments 1A-8A provided objective, experimental evidence that surface segregation can support visual feature binding, the effect of display type and alternation frequency on the subjective interpretation of colour-motion stimuli is now investigated. Experiment 9A investigates the perception of the stimuli used in Experiment 8A in order to determine if the perception of multiple surfaces is linked to feature binding ability.

2.11.2. Experimental methods

2.11.2.1. Subjects

Informed written consent was obtained from 4 experienced psychophysical subjects (3 male; age range 24-33).

2.11.2.2. Visual stimuli

Stimuli were identical to Experiment 8A (Figure 2.8a) in that both sequential and spatially interleaved stimuli were used. However, in 3 of the 6 experimental runs, RDKs were grey in order to match the stimuli used in Experiment 10A.

2.11.2.3. Design and procedure

This experiment had a 2 ‘display type’ (sequential/spatially interleaved) × 6 ‘alternation frequency’ (1.67, 2.5, 3.33, 5, 7.5 and 15 Hz) within-subjects design. Here, participants made two separate subjective judgements on the properties of the stimulus after the trial had ended. Participants first reported the number of surfaces they perceived simultaneously in each trial (one or two), and then indicated the display type of the trial (sequential or simultaneous).

A key point of difference was that, unlike the number of runs and trials used in all previous experiments (detailed in the general methods) here subjects completed 6 runs of the subjective judgement task, for a total of 576 trials overall. 3 runs used orange and blue coloured dots, and the other 3 replaced both orange and blue dots with mean luminance grey dots that were matched to the stimulus in Experiment 10A. Further details are presented in the methods of Experiment 10A.

2.11.3. Results and discussion

Figure 2.9 displays the results of this experiment. There is a clear difference in subjective interpretation between sequential and spatially interleaved display types in Figure 2.9a. The significant effect of alternation frequency on condition identification ($F_{1,3} = 55.51$, $p < 0.001$) is correlated with the reported number of surfaces. That is, as alternation frequency increased, participants were more likely to report that they distinguished two surfaces, when averaged over display type ($F_{1,3} = 235.47$, $p = 0.001$). Furthermore, there was a significant display type by frequency interaction effect, averaged across both coloured and grey display types ($F_{1,3} = 229.46$, $p = 0.001$) such that only the sequential display produced a varying percept as a function of alternation frequency. The presence of both motions in the spatially interleaved display generated the impression of two continuously present surfaces, which then enabled the colour-motion pairings to be isolated and identified in the binding task of Experiment 8A. This also occurred for the sequential display, but exclusively at high frequencies where it also produced the percept of two simultaneous surfaces.

The identification of each display as a sequential or segregated display decreased linearly as alternation frequency increased (Figure 2.9b; $F_{1,3} = 168.80$, $p = 0.001$). This indicates that sequential and spatially interleaved conditions tended to be less distinguishable at higher alternation frequencies. The difficulty of this task was directly correlated to the perception of multiple motion-defined surfaces (Figure 2.9a): higher accuracy was associated with motion-defined surface segregation. Matched conjunction discrimination between the display conditions and the subjective judgement task suggests an equivalence in perception between the sequential and spatially interleaved display types at higher temporal frequencies. Discrimination in the sequential display type matched that of the interleaved display at 15 Hz, coinciding with the maximal value on the surface judgement task where participants perceived all displays as most transparent.

No significant differences between colour and grey display types were observed in the sequential display ($F_{1,3} = 0.44$, $p = 0.55$), or the interleaved display ($F_{1,3} = 1.85$, $p = 0.27$), and furthermore, no significant differences in the identification of display types were found ($F_{1,3} = 0.15$, $p = 0.72$). That no differences or interactions between colour and grey display types were found in either subjective tasks suggests the stimuli of Experiments 8A, 9A, and 10A resulted in very similar perceptions of transparent motion. This is important, as Experiment 10A examines the neural response associated with surface segregation (using grey RDKs), linking back to the psychophysical experiments of this chapter.

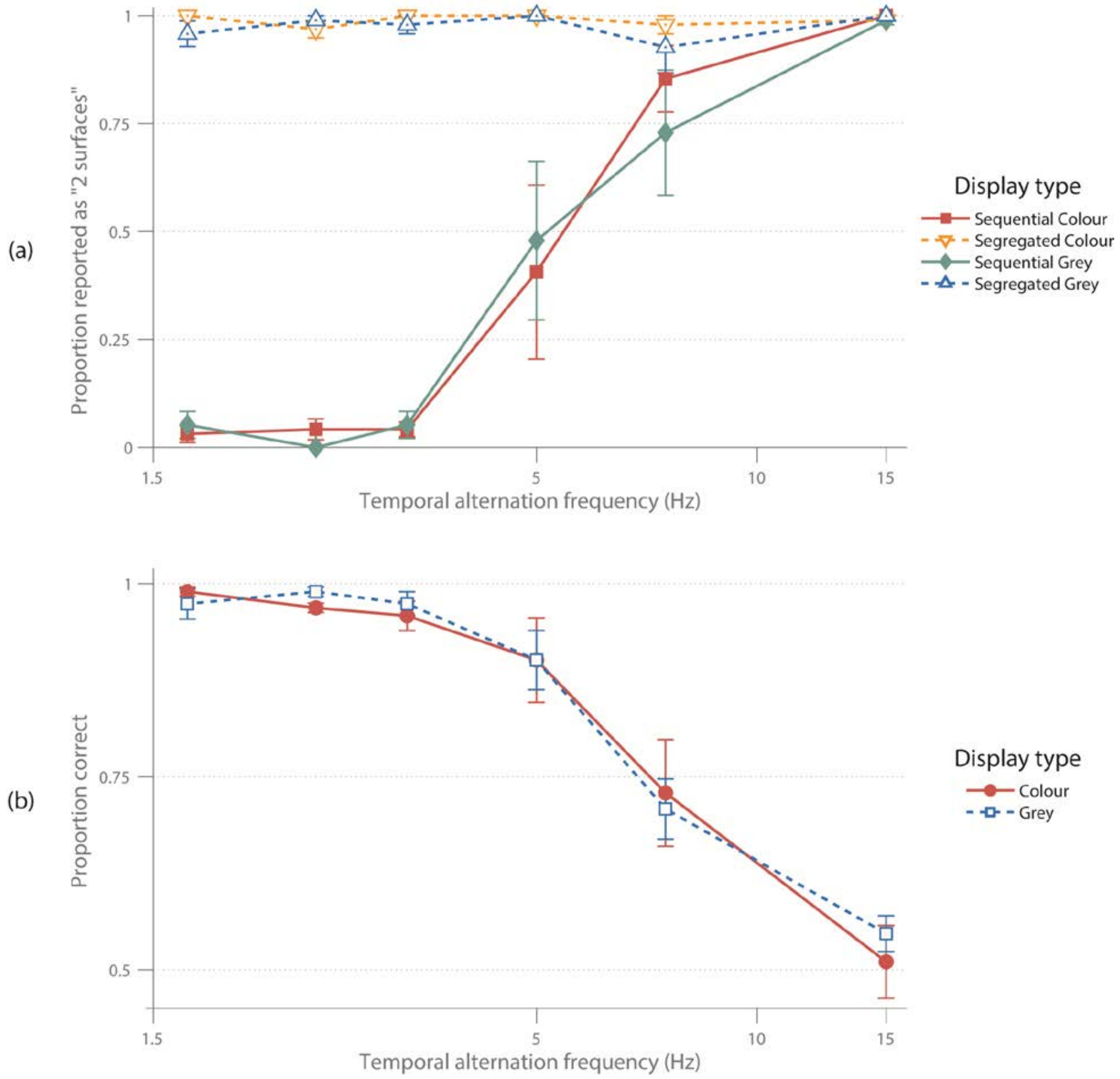

Figure 2.9. Results of Experiment 9A. (a) Mean proportion of each display type, across temporal alternation frequency, reported as ‘2 surfaces’. Display types using both grey dots and coloured dots are represented. **(b)** Mean proportion of responses correctly identifying display type (*n*=5) for both coloured and grey display types, across temporal alternation frequency. In both **(a)** and **(b)**, error bars denote ±1 between-subject standard errors.

2.12. Experiment 10A: Observing correlates of motion transparency in human early visual cortex

2.12.1. Rationale

Having observed that both display type and alternation frequency interact to generate a perception of one or two surfaces in Experiments 8A and 9A, the neural activity of the underlying processes are subsequently investigated. The aim here is to investigate if the perceptual experience of transparency in bi-vectorial motion is matched by modulation of activity in early visual areas. Changes in neural activity between stimuli presented at high and low alternation frequencies may be attributed to alternation frequency rather than the percept of transparency. Therefore, the spatially interleaved display is used as a comparison to the sequential display as it appears transparent independent of frequency as determined in Experiment 9A. Sequential and spatially interleaved stimuli are predicted to produce similar patterns of activity at higher frequencies, where they both generate the impression of motion transparency. At lower frequencies however, the spatially interleaved stimulus should continue to appear transparent while the sequential stimulus will not. A corresponding difference in neural activity is therefore predicted, with a display type (sequential/spatially interleaved) by alternation frequency interaction manifesting in a way that matches the perceptual experience of motion transparency.

2.12.2. Experimental methods

2.12.2.1. Subjects

The same 5 experienced psychophysical subjects (3 male, age range: 25-46) as in Experiment 8A took part in this experiment. All subjects have had previous experienced being scanned in this manner. Visual corrections in the MRI scanner took the form of prescription squash goggles. The experimental protocol was approved by the University of Sydney Human Research Ethics Committee.

2.12.2.2. Apparatus

Data were collected using a Philips Achieva 3T TX scanner (Philips, Amsterdam) with a whole head coil. A field-echo echo-planar imaging (FEEPI) pulse sequence was used to acquire T_2*-weighted functional MR images of blood oxygenation level-dependent (BOLD) contrast. The FEEPI protocol was defined according to the following parameters: time to echo (TE) = 32 ms, time to repetition (TR) = 3000 ms, flip angle = 90°, field of view = 69 × 192 × 192 mm, matrix = 128 × 128, voxel size = 1.5 mm (isotropic). The images were acquired in 46 interleaved ascending slices (1.5 mm thickness) in a tilted coronal plane that covered the entire occipital cortex as well as a portion of the posterior parietal and temporal lobes. In addition to the functional scans, a whole-head structural MR image (voxel size = 1 mm isotropic) was obtained for each subject within each experimental scanning session for co-registration purposes, using a turbo field echo protocol for optimal grey and white matter contrast.

Stimuli were generated on a Dell Precision M4400 laptop with an nVidia Quadro FX 1700M display adapter and displayed on an MR-compatible “BOLDscreen” liquid crystal display (Cambridge Research Systems) via a fibre optic DVI cable. The BOLDscreen had a resolution of 1920 × 1200 pixels, a refresh rate of 60 Hz and a mean luminance of 147.9 Cd/m^2 and was calibrated with measurements obtained via a PR-670 SpectraScan spectrophotometer (Photo Research Inc.). Images were viewed at a total distance of 121.5 cm through a rear-facing first surface mirror mounted upon the head coil, giving a viewing angle of 15.2° (0.013° per pixel). The subjects’ behavioural responses during scanning were collected via an MR-compatible LU400-PAIR Lumina response pad (Cedrus, San Pedro, CA).

2.12.2.3. Visual stimuli

Stimuli were identical to the grey RDKs used in Experiment 9A. That is, grey dots replaced both blue and orange dots in the stimuli of Experiment 8A and 9A. In addition to this, no mask was used between stimulus presentations. Previous studies have demonstrated that colour is a somewhat effective surface segregation cue (Croner & Albright, 1997; Edwards & Badcock, 1996; Perry & Fallah, 2012). As this was an investigation into motion-defined surfaces, the stimuli presented here aimed to minimise the effects of other visual features that could potentially demarcate the two RDKs, confounding the fMRI results. Grey RDKs were therefore used to ensure the observed results were purely due to differences in the motion directions of these RDKs. The results of the subjective judgement task in Experiment 9A indicate that there were no significant differences in the way participants perceived motion transparency between the coloured stimuli used in the primary psychophysical experiment and greyscale stimuli used in this experiment.

2.12.2.4. Design and procedure

This experiment was a 2 ‘stimulus display type’ (sequential/spatially interleaved RDK presentation) × 2 ‘temporal alternation frequency’ (5 and 15 Hz) within-subjects block design. These alternation frequencies were chosen for the fMRI experiment as they had optimal temporal characteristics for maximizing the perceptual difference between the stimulus display types, based on the binding task results of Experiment 8A and the subjective interpretation data of Experiment 9A.

Stimuli were presented in counterbalanced blocks of 15 s, aligned with 5 volume acquisitions (3000 ms each). In each block, 5 repetitions of stimuli (2500 ms) and fixation (500 ms) were presented. This was done in order to keep presentation durations comparable to the psychophysical task. Here, stimuli had a 500 ms raised cosine contrast ramp on and off instead of a static mask. As there was no colour-motion conjunction present in this stimulus, a static stimulus mask as per all previous experiments was unnecessary and may have decreased the signal to noise ratio. Block order was counterbalanced both between and within runs. Stimulus blocks were presented in groups of four, with 15 second fixation-only blocks between them. Each condition was presented 4 times per run, for a total of 21 blocks per run. Runs lasted for 315 seconds, and participants viewed 12 runs in total.

To control for attention and fixation, subjects performed an attentionally-demanding dimming task throughout each run (Figure 2.10). In order to confirm that subjects were fixating and keeping their spatial attention directed at the fixation spot, mutual information analysis was performed in order to determine the correlation between stimulus and response. In the centre of the display, the fixation cross alternated between black and grey on average every 1500 ms, jittered randomly by ± 500 ms. Subjects indicated (by holding down one of the two buttons on the response pad) the current state of the fixation cross (dimmed or not dimmed). Button press data was used to quantify participants’ ability to maintain fixation during their time in the scanner.

Button-press data for the attention task at fixation are displayed in Figure 2.10 and were assessed using a mutual information (MI) analysis, given by Equation 1:

$$MI = \sum_{r,s} p(s)\, p(r \mid s) \log_2 \frac{p(r \mid s)}{p(s)} \tag{1}$$

where $p(r)$ is the probability of a response, $p(r|s)$ is the probability of a response given the stimulus, and MI is expressed in bits of information. Response data were time-shifted with respect to the timecourse of the fixation cross luminance change in order to find the lag (approximating reaction time) at which the maximal amount of mutual information was provided. Mutual information was then converted to efficiency, given by Equation 2:

$$Efficiency = \frac{100 \times MI}{H(s)} \tag{2}$$

where *H*(*s*) is the entropy of the stimulus display train, defined in Equation 3 as:

$$H(s) = -\sum_{s} p(s)\log_{2} p(s) \tag{3}$$

Efficiency denotes the degree to which the stimulus predicts the response, with a higher efficiency indicating a better correspondence between stimulus and response time courses, reflecting appropriate fixation and spatial attention directed towards the fixation spot.

Measured at a resolution of 60 Hz, the minimum efficiency in a single run averaged across subjects was 48.9% (SD = 16.2%), and the maximum was 74.4% (SD = 3.3%). Minimum efficiencies were well above chance, suggesting subjects were fixating and attending to the fixation task across all runs of the study. Mean efficiency averaged across all runs ranged from 46.9% to 69.6% between subjects. If subjects were responding at random, an efficiency close to 0% would be expected.

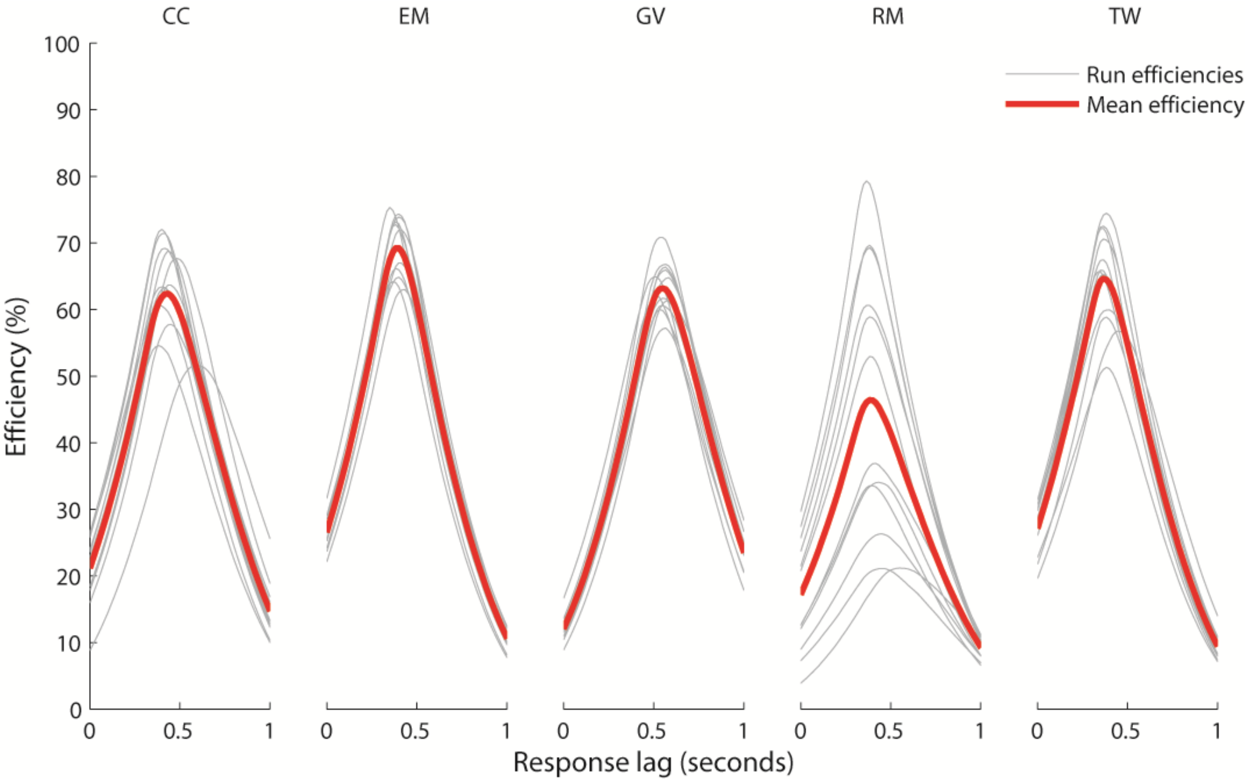

Figure 2.10. Individual run and mean efficiencies on the fixation task. Fixation task efficiency (*n*=5) is presented on a per-subject basis. Thin grey lines indicate the efficiency score for one subject on one run. Red lines indicate the mean efficiency for one subject averaged over 12 runs. The locations of the peak mean efficiency on the x-axis represent subjects' mean reaction times.

2.12.2.5. Retinotopic mapping/definition of ROIs

In prior scanning sessions, both functional and high-resolution anatomical scans were acquired for each subject. An average anatomical image was prepared consisting of whole-head sagittal and transverse images (voxel size = 1 mm isotropic) and a higher-resolution partial coronal image (voxel size = 0.75 mm isotropic) of the caudal brain to maximize anatomical detail in the occipital lobes. Before averaging, the images were aligned using normalized mutual information-based coregistration, inhomogeneity corrected (Manjon et al., 2007), and normalized according to their peak white matter intensities and resampled (where necessary) to a voxel size of 0.75 mm (isotropic). The average anatomical image of each subject was then segmented using the automatic algorithms of ITK-SNAP (www.itksnap.org; Yushkevich et al., 2006) and mrGray (Teo, Sapiro, & Wandell, 1997), supplemented with careful manual editing.

Functional scans were obtained of subjects viewing clockwise/counter clockwise rotating wedges and expanding/contracting ring stimuli as described in Wandell et al. (2007). Data were coregistered through SPM5 (www.fil.ion.ucl.ac.uk/spm/software/spm5/; K J Friston, Ashburner, Kiebel, Nichols, & Penny, 2007) and organized into ROIs. The maximal activations of each voxel to the wedge stimuli was then used to generate a polar angle map of the visual cortex using the best-fitting sinusoid for the time course of each voxel (Larsson & Heeger, 2006). From this map, visual areas were manually defined in mrVista (white.stanford.edu/software).

Functionally defined early visual cortex was delineated for each subject using the nomenclature and criteria of Wandell et al. (2007) and Larsson and Heeger (2006), in the same manner as previous studies from this laboratory (e.g. Supplementary Figure 1 in Mannion, McDonald, & Clifford, 2010). According to this scheme, areas V1-V3 and hV4 share a foveal representation at the occipital pole, whereas V3A and V3B (which were not separated in this analysis) share a dorsal foveal representation and border the dorsal portion of V3. Area hV4 was defined as a hemifield representation of the contralateral visual field bordering the ventral portion of V3 (Goddard, Mannion, McDonald, Solomon, & Clifford, 2011). In separate localizer scans, area V5/MT+ was localized as a region of lateral visual cortex in the ascending limb of the inferior temporal sulcus responding to coherently moving versus static random dot stimuli presented at low contrast (Dumoulin et al., 2000).

2.12.2.6. Analysis

Neural activity was measured in retinotopically-defined striate (V1) and extrastriate visual cortex (V2, V3, V3AB, and hV4). Multivariate pattern analysis (MVPA) techniques were used to decode display types (sequential and spatially interleaved) at each alternation frequency. This allowed us to probe the neural representation perceptual segregation under conditions where segregation was reliably reported (as measured in the subjective judgement task of Experiment 9A), compared to those where it was not. To determine whether the classifier could decode the display type from a given visual area reliably above chance, 1-sample *t*-tests were performed on the mean decoding performance across the four stimulus conditions for the five subjects.

A generalized linear model (GLM) contrast of fixation vs. all stimulus blocks was first performed, using SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5/). Only those voxels within each ROI that gave a significant response ($p < 0.05$, 1-tailed, uncorrected) to the stimulus over baseline in the t-map of activations were selected for further multivariate analyses (see below). Note that this contrast is orthogonal to those between the stimulus conditions of interest.

The multivariate analysis grouped BOLD responses in each stimulus condition by colour-orientation conjunction. For each voxel, the time series of responses to each conjunction in a stimulus block within each run was z-scored (fixation blocks were not used in the analysis) and a response to each conjunction computed as the mean of the z-scores from the 5 corresponding TRs within a single block. A linear support vector machine (SVM) as implemented in SVMLight (Joachims, 1999; C parameter set to 1.0) compared the difference in the patterns of activation for each visual area between the sequential and spatially interleaved display types for a single alternation frequency. 11 runs were used as training data, and the 12th was used as a test. For each visual area and each subject, this process was repeated 12 times such that all permutations of test and training assignments were run.

Reported classifier performance accuracies for each subject were the average decoding performance across the 12 permutations, and these were compared against chance performance (50%) using one-sample t-tests to establish significance. For the data presented in Figure 2.11, the 99th percentile of the null distribution was used to allow for Bonferroni correction over $n=5$ regions of interest for each subject. All results found to be significant using one-sample t-tests were confirmed to be significant at $p < 0.05$ using this method.

2.12.3. Results and discussion

The aim of Experiment 10A was to probe the neural substrates correlated with motion-defined surface perception. By altering only the temporal properties of the stimuli, the formation of motion-defined surfaces was affected, and this corresponded with activity in V1 and subsequent areas. All but one of the display type and frequency combinations (the 5 Hz sequential display) were perceived as two surfaces rotating in opposite directions, as evidenced by the data in Experiment 9A. Thus, a presentation by frequency interaction in this experiment was also expected. This was indeed what was found in the univariate analysis (Figure 2.11a). A repeated measures GLM (uncorrected) was used to assess the data for each visual area. Significant interaction effects in visual areas V1 ($F_{1,4} = 46.59$, $p = 0.002$), V2 ($F_{1,4} = 34.27$, $p = 0.004$), V3 ($F_{1,4} = 19.10$, $p = 0.012$), V3AB ($F_{1,4} = 14.31$, $p = 0.019$) and hV4 ($F_{1,4} = 9.55$, $p = 0.037$) but not V5/MT+ ($F_{1,4} = 0.05$, $p = 0.84$) were found. Univariate activity in early visual cortex was found to vary differently across frequencies for display type. This specific presentation by frequency interaction suggests that, similar to the psychophysical data, activity in early visual areas modulate with respect to the conscious perception of motion-defined surface segregation.

The present univariate effects were examined in further detail using multivariate pattern analysis (Figure 2.11b). Specifically, the goal here was to determine if the 15 Hz sequential and spatially interleaved display type could be identified on the basis of the elicited patterns of activity in each visual area. The SVM classifier maximised the chances of detecting an effect, such as differences in BOLD signal patterns or activation which may not be evident in the univariate analysis. One-sample *t*-tests were used to assess the performance of the SVM in distinguishing display type for each visual area. At 5 Hz, a one-sample uncorrected *t*-test found significantly above-chance display type classification classify conditions significantly using patterns of activity from almost all areas (V1: $F_4 = 55.77$, $p = 0.002$; V2: $F_4 = 95.85$, $p = 0.001$; V3: $F_4 = 13.97$, $p = 0.020$; V3AB: $F_4 = 28.97$, $p = 0.006$; V5/MT+: $F_4 = 18.93$, $p = 0.012$) bar hV4 ($F_4 = 7.62$, $p = 0.051$). However, high decoding performance here is not surprising, given the large differences in the intensity of the univariate response between display types. At the 15 Hz alternation frequency, the SVM was only able to classify conditions significantly above chance in area V3AB ($F_4 = 34.521$, $p = 0.004$). The majority of visual areas examined appeared to respond similarly to sequential and spatially interleaved display types at 15 Hz despite the physical differences between them. This indicates that similar activity between conditions in the univariate analysis was not due to different patterns of activation simply averaging out to the same overall level of activity. Rather, it can be concluded that not only the overall level of activation, but the patterns of activation in early visual areas mirror our perception of motion-defined surfaces.

Neurons in monkey primary visual cortex respond to the presence of their preferred direction independent of transparency (Qian & Andersen, 1995; Snowden et al., 1991). Qian et al. (1994) propose that motion transparency is due to unbalanced local motion cues at the spatial resolution of V1. However, this alone would not account for the display type by frequency interaction effect found in this study. The distribution of local motion signals within the stimuli was identical in both display types across time. Given the temporal integration properties and small receptive field sizes of neurons in V1, a difference in activity at a local level between display types is not necessarily expected (Snowden et al., 1991). As motion transparency necessitates an integration of motion signals across at least a significant portion of the display, any differences in frequency-dependent activation between conditions and motion transparency more likely arise due to interactions with areas containing larger receptive fields (Dubner & Zeki, 1971; Stoner & Blanc, 2010). In this way, the modulation of activity in early visual areas here may be reflective of not just low-level spatiotemporal filtering (Foster, Gaska, Nagler, & Pollen, 1985; Gegenfurtner et al., 1996; Leventhal et al., 1995) but also feedback from higher-level areas (Bouvier & Treisman, 2010b; Sajda & Finkel, 1995; Stoner & Blanc, 2010). However, the present results do not allow us to test this speculation.

It is important to consider both the spatial and temporal properties of visual neurons (Foster et al., 1985; Gegenfurtner et al., 1996; Leventhal et al., 1995), as it is their interaction that generates the perception of motion transparency within the specific range of parameters measured here. The higher amplitude response to the spatially interleaved display type may be a result of the greater motion contrast within this condition (Heeger et al., 1999; Shulman, Schwarz, Miezin, & Petersen, 1998; Tynan & Sekuler, 1984), as some cells will have receptive fields crossing the borders of the concentric motion strips. These cells would be expected to contribute differently to the population response sampled with fMRI compared with their response to the spatially uniform RDKs in the sequential display, especially at lower alternation frequencies. Some neurons in macaque V1, for instance, show significant centre-surround organisation that bears a strong comparison to similar mechanisms in V5/MT and may have a role in extracting motion contrast information (H. Jones et al., 2001). Regardless of the precise underlying mechanism, the differences in the fMRI responses represent the result of the spatiotemporal filtering of the stimuli by populations of visual cortical neurons, and this is correlated with the perception of transparent motion.

Previous studies have found that the perception of motion transparency modulates activity in V5/MT+ (Garcia & Grossman, 2009; Heeger et al., 1999; Muckli et al., 2002; Treue, Hol, & Rauber, 2000). In this experiment, V5/MT+ demonstrated a consistent multivariate result, but no significant univariate interaction. Overall activity in V5/MT+, averaged over display type, decreased from 5 to 15 Hz, which is consistent with the operation of dynamic inhibitory processes. A combination of large receptive fields (Albright & Desimone, 1987; Dubner & Zeki, 1971) and mutual inhibition from opposing directions of motion (Qian et al., 1994; Stoner & Blanc, 2010) could account for this result, as pooling of local motion signals sampled from V1 would result in little net motion. Despite a lack of univariate modulation, patterns of activity enabled differential decoding of display type at 5Hz but not 15 Hz in V5/MT+, highlighting the value of performing the more sensitive multivariate analyses in addition to the conventional univariate ones. Together with the univariate result, this suggests that V5/MT+ may play a role in coding surface segregation in a way that is independent of overall levels of activity.

An interesting observation is that V3AB was the only area to produce above chance decoding of display type at 15 Hz. This may indicate that V3AB is receptive to the physical motion of the stimulus at timescales of less than 70 ms. Both V3A and V3B have been found to modulate strongly when motions from individual objects are perceptually grouped together in a transparent fashion (Caplovitz & Tse, 2010). V3B also includes portions of the Kinetic Occipital (KO) region, which responds more strongly to spatially segregated than transparent motion (Van Oostende et al., 1997). This evidence is consistent with the suggestion that V3AB is sensitive to the fine temporal structure in the 15 Hz displays used here.

In a previous study of visual feature binding, Seymour, Clifford, et al. (2009) were able to decode colour-motion conjunctions in human visual cortex as early as area V1 using a multivariate pattern analysis similar to the one used here. They used a transparent motion stimulus in which oppositely moving sets of dots were presented simultaneously with different colours. Presenting stimuli in this way with different colour-motion pairings ensured that the display types could not be decoded based on the presence or imbalance of any particular visual feature. Here, activity in early visual cortex was correlated with the perception of motion-defined surface transparency. This supports the notion that the results of Seymour, Clifford, et al. (2009) reflect the decoding of representations of differently coloured surfaces, rather than local colour-motion conjunctions.

In summary, activity in early visual areas correlated with the percept of motion-defined surface transparency, which in turn can support feature binding at high alternation frequencies. Corresponding trends to Experiments 2.10 and 2.11 were found in both univariate and multivariate analyses, revealing neural correlates of surface transparency in visual cortical areas as early as V1. That is, comparisons of activity between sequential and spatially interleaved display types at 15 Hz revealed minimal differences. In contrast, there were large differences between display types at 5 Hz, where the spatially interleaved display still looked transparent while the spatially interleaved display did not. Together, early visual areas are implicated in the perception of motion transparency, which in turn plays a major role in visual feature binding. These results are consistent with the idea that bound features are coded as surfaces in V1 and subsequent visual areas.

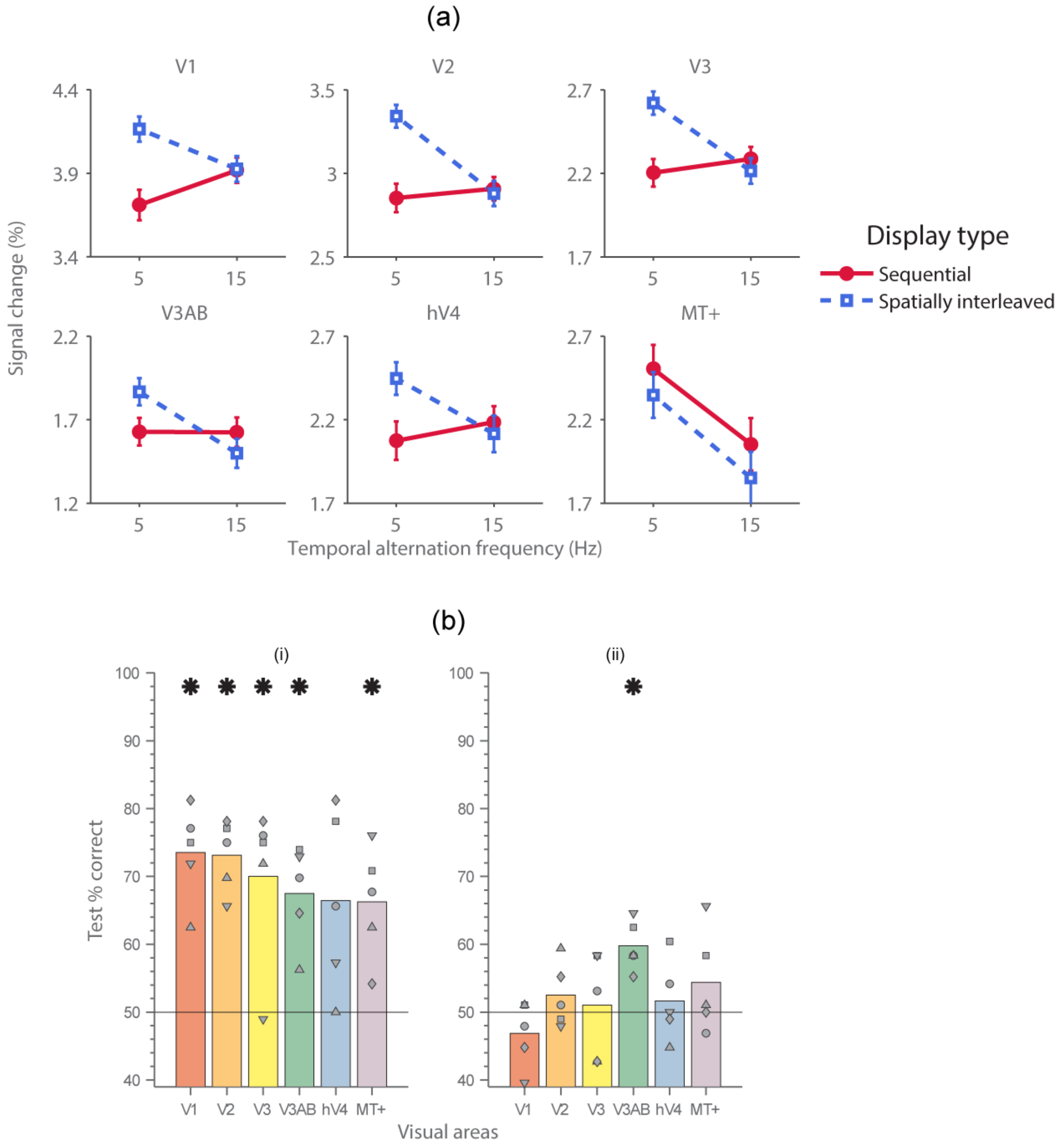

Figure 2.11. Univariate and multivariate fMRI results of Experiment 10A. (a) Average change in univariate BOLD responses of early visual areas across all participants (*n*=5) relative to fixation blocks. Note that each plot has identical *y*-axis scales, but different ranges. Error bars indicate ±1 between-subject standard errors. **(b)** Average

performance of a support vector machine (SVM) classifier distinguishing between sequential and spatially interleaved display types at **(i)** 5 Hz, and **(ii)** 15 Hz. Bars indicate average performance in decoding conditions while small grey icons indicate classifier performance for individual participants in each visual area. Asterisks denote significantly greater classification (all $p < 0.05$) than chance (50% indicated by the black horizontal line) across participants.

2.13. Chapter Discussion

A significant number of studies find that accurate feature conjunction discrimination can occur at high alternation frequencies (Clifford, Spehar, et al., 2004; Holcombe & Cavanagh, 2001; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002). However, the suggestion that a high temporal resolution for feature binding exists cannot account for the large majority of literature which instead indicates that feature binding is a slow process (see Holcombe, 2009; Quinlan, 2003; Singer & Gray, 1995; Treisman, 1996; Tsal, 1989). Here, surface segregation is offered as an alternate hypothesis, in order to account for this discrepancy. Moradi and Shimojo (2004) demonstrated that persistent surface segregation can facilitate colour-motion binding in alternating random dot displays. In this series of experiments, the stimulus characteristics related to surface segregation were explored in depth to determine if the addition and removal of segregation cues corresponded with accurate conjunction discrimination. In effect, it is demonstrated that the perceptual interpretation of the stimulus can bypass the relatively slow temporal resolution of feature binding.

2.13.1. Surface segregation can support colour-motion binding at intermediate frequencies

In the first three experiments, 1A-3A, colour-motion display types varied in alternation frequency. These displays were coupled with additional dots that varied in colour, dot configuration, and motion in order to enhance conjunction discrimination at intermediate frequencies, where discrimination is typically poor. By manipulating over multiple surface segregation cues in a parametric manner, corresponding increases in conjunction discrimination would be observed if surface segregation could support accurate feature binding. Experiments 5A through 7A took the opposite approach: by manipulating the motion coherence, dot configuration and persistence of colour-motion displays, the surface segregation already present due to high alternation frequencies could be disrupted. In this way, an investigation of the dependence of conjunction discrimination on perceptual segregation at high alternation frequencies could be conducted. Finally, Experiments 8A to 10A investigated the interaction between the spatial and temporal relationships between target RDKs, and the corresponding locus of processing within the human visual cortex. This was assessed in three ways (conjunction discrimination, subjective interpretation, and neural activity of early visual areas) in order to provide a comprehensive investigation of colour-motion feature binding within the visual system.

In Experiments 1A-3A, the continued presence of a given configuration of dots (e.g. the ‘same configuration’ display types) allowed for near-ceiling conjunction discrimination even at intermediate alternation frequencies (2.5 – 5 Hz), independent of the associated colour retention of the additional RDKs (i.e. changed to grey). There was, however, a marked difference in the conjunction discrimination between Experiment 1A and 2A in conditions where additional RDKs contained a different configuration of dots relative to the target RDKs. The display types in Experiment 2A also facilitated conjunction discrimination compared to the control condition (where RDKs disappeared during periods of rest, meaning only one was present on-screen at any one time), albeit to a lesser extent than the “same configuration” display types. However, in

Experiment 1A, discrimination between same and different configuration conditions were comparable at all but the highest alternation frequency tested. The difference in motion between these experiments (i.e. additional RDKs were either rotating or static) indicates that coherent motion across target and additional RDKs provides a consistent feature which enables the temporal integration over the trial duration by the visual system.

Motion is further noted as a surface segregation cue after a comparison across these 3 experiments. Where additional RDKs moved in the same direction as the target RDKs (Experiment 1A), overall higher levels of conjunction discrimination were produced compared to when additional RDKs were static (Experiment 2A) or moving in a different direction (Experiment 3A). While motion contrast is a factor in surface segregation, Experiment 3A demonstrated it was not enough to simply have the additional RDK contain motion. Rather, a comparison between these experiments across display types with identical colour and configuration attributes (that is, display types containing grey RDKs of the same or different configuration) reveals that the direction of motion between target and additional RDKs must be shared in order to produce the highest amount of conjunction discrimination through surface segregation (Bravo, 1998; Sekuler, 1990; Treue et al., 2000). Over the three surface segregation cue dimensions tested (colour, configuration, and motion), the results all indicate that surface representations that remain consistent over time are perceived more distinctly.

2.13.2. Disrupting temporal integration at high alternation frequencies also affects conjunction discrimination

In Experiments 5A and 6A, motion was also used to affect surface segregation, but this time at high alternation frequencies where conjunction discrimination was at ceiling. Using a similar rationale to the motion differences between Experiments 1A-3A, the off-screen behaviour of target RDKs was modified to affect motion consistency – that is, the predictability of the motion trajectory of target RDKs while off-screen was manipulated. In both these experiments, it was demonstrated that less consistent RDK motion was associated with lower conjunction discrimination, as a consequence of a disrupted surface segregation percept. At high alternation frequencies, temporal integration must take place in order to perceive persistent surface representations. By removing the motion coherence of RDKs across cycles (the ’randomising‘ and ’resetting’ display types), a key surface segregation cue was removed, thus rendering each target RDK perceptually less distinct. In turn, the impaired conjunction discrimination at higher frequencies demonstrated that surface segregation was necessary for accurate feature binding to occur at these high alternation frequencies.

Experiment 7A assessed the effects of visual persistence on conjunction discrimination at high alternation frequencies. The stimulus display here would otherwise be predicted to facilitate surface segregation, as each RDK had distinct and consistent colour and motion attributes. However, the overall perceptual interpretation of the stimulus was disrupted due to the temporal limitations of colour identification, indicating that visual persistence plays a role in interpreting a stimulus with a high alternation frequency. Here, temporal integration over short time intervals is expressed as visual persistence (Di Lollo, 1980; Di Lollo & Wilson, 1978; Georgeson, 1987; Snowden & Braddick, 1991; Watamaniuk & Sekuler, 1992). Several studies make the case for a difference between ‘physical’ persistence, where a persistent image is indistinguishable from a physically-present counterpart, and ‘informational persistence’, which is likened to a higher-order, fading trace of visual data (Badcock & Lovegrove, 1981; Bowling & Lovegrove, 1981; Di Lollo, 1984). The results of this experiment are consistent with the experience of visual persistence as physical, suggesting the involvement of low-level processes in accurately perceiving rapidly alternating stimuli.

2.13.3. Surface segregation is represented in human early visual cortex

Experiments 8A to 10A investigated the relationship between feature binding, surface segregation and the corresponding neural activity generated by two types of colour-motion displays. The first display type was where RDKs were presented sequentially as per the control condition of Experiments 1A-3A. In Experiment 9A, it was determined that the sequential display was perceived as transparent only at high alternation frequencies. The second display type was composed of two spatially interleaved RDKs. Experiment 9A demonstrated that the spatially interleaved display appeared transparent over all the tested alternation frequencies. Specifically at low alternation frequencies, for the interleaved display to appear transparent, local coherent motion must be spatially integrated for the perception of global motion to occur (A. T. Smith, Snowden, & Milne, 1994; Watamaniuk & Sekuler, 1992). Therefore, small radial strips were used to ensure subjects perceived the spatially interleaved display as two coherent surfaces (Clifford, Spehar, et al., 2004).

Display type and alternation frequency interacted such that at low alternation frequencies, only the spatially interleaved display was perceived as transparent. However, both sequentially and interleaved displays were perceived as transparent at high alternation frequencies. This interaction was also reflected in the results of Experiment 8A. Here, conjunction discrimination was high across all alternation frequencies tested for the spatially interleaved display. In the sequential display however, conjunction discrimination varied with alternation frequency such that conjunction discrimination was poor at 5 Hz, but accurate at high alternation frequencies. With a correspondence between temporal transparency and conjunction discrimination established, Experiment 10A sought to investigate how the neural response of early visual areas varied with perceptual segregation. Both display types were presented at 5 and 15 Hz, which were predicted to interact in a way similar to Experiments 8A and 9A.

Experiment 10A revealed a univariate interaction effect in early visual cortex of humans. The overall response levels of areas V1, V2, V3, V3AB and hV4 were modulated by the stimulus such that at 15 Hz, similar response magnitudes were observed for each display type, which diverged at 5 Hz. Multivariate decoding of display type produced a similar set of results, where decoding was above chance at 5 Hz for all areas except hV4, where the perceptual differences between display types was maximal. However at 15 Hz, where both display types were perceived as transparent, only V3AB produced above chance decoding. Together, univariate and multivariate results suggest that early visual cortex can code for the perception of surfaces rather than the physical stimulus, which in turn is associated with accurate feature binding.

Single-cell neurophysiology and neuroimaging studies provide some clues to the neural substrate of colour-motion feature binding and its possible relationship with surface transparency, as reported in these experiments. Cells have been detected in non-human primate visual cortex from V1 to V5/MT that exhibit a degree of selectivity for both colour and motion (Albright, 1984; Dubner & Zeki, 1971; Gegenfurtner et al., 1996; Gegenfurtner et al., 1997; Horwitz & Albright, 2005; Hubel & Wiesel, 1968; Leventhal et al., 1995; Maunsell & Van Essen, 1983b; Shipp et al., 2009; Zeki, 1978a, 1978b). Furthermore, human functional magnetic resonance imaging (fMRI) studies have found evidence for the coding of both correctly-perceived/bound and misbound colour-motion conjunctions in early visual cortex (Bouvier & Treisman, 2010a; Seymour, Clifford, et al., 2009; Zhang et al., 2014).

2.13.4. Temporal integration generates persistent surface representations, enhancing colour-motion binding

Considering that these experiments used stimuli matched for both temporal characteristics and colour-motion attributes, some general conclusions can be made which unify the obtained results. Manipulations of stimulus characteristics produced variations in conjunction discrimination at intermediate and high alternation frequencies. The ways in which these characteristics were altered primarily serve as cues in the perception of persistent, transparent surfaces (e.g. motion coherence and configuration) (Adelson & Movshon, 1982; Baylis & Driver, 1992; Bergen & Landy, 1991; Masson et al., 1999; Snowden & Verstraten, 1999; Treisman & Kanwisher, 1998). This is consistent with past research, demonstrating consistent and coherent surface segregation cues enhancing the perception of transparent surfaces can in turn promote accurate feature binding (Clifford, Spehar, et al., 2004; Moradi & Shimojo, 2004). While a high temporal alternation frequency is a surface segregation cue in itself (Clifford, Spehar, et al., 2004; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002), the addition of other surface cues in these experiments demonstrate that perceptual segregation can also occur at intermediate alternation frequencies. Overall, these results suggest that feature binding at intermediate and high frequencies may be contingent on the generation of stable and segregated percepts through integration of temporally consistent visual features.

Naïvely, the addition of surface segregation as another, intermediate step in the binding process would seem to lower the overall maximum temporal resolution at which feature pairs can be accurately perceived. However, it is precisely because surface segregation is a rapid and automatic process (Driver, Baylis, & Rafal, 1992; Julesz, 1984; Kahneman et al., 1992) that conjunction discrimination can occur at high temporal alternation frequencies. For example, Lamme (1995) recorded responses in primary visual cortex of awake macaques while they viewed a display of static dots which sometimes contained a small patch of translating dots. The resulting separation between figure and ground was associated with a response enhancement of neurons with receptive fields within the moving patch, occurring 30-40 ms after movement first started. Importantly, this response was independent of any orientation or direction selectivity, suggesting a role for early visual cortex in surface segregation. Activity in early visual cortex from V1 to V5/MT+ is also known to be associated with surface segregation in humans (Experiment 10A; Caplovitz & Tse, 2010; Ferber, Humphrey, & Vilis, 2003, 2005; Van

Oostende et al., 1997). However, the specific visual persistence associated with motion-based perceptual segregation may occur at a later stage of visual processing, specifically in the lateral occipital complex (Ferber et al., 2003, 2005).

Temporal integration enables a representation of each RDK to be built over successive stimulus presentations (Brockmole, Wang, & Irwin, 2002; Di Lollo, 1980; Eriksen & Collins, 1967), giving rise to a transparent percept. The experiments in this chapter demonstrate that the perceptual segregation of a stimulus is required for accurate feature binding at both intermediate and high alternation frequencies. A specific mechanism for this is discussed in Chapter 4 concerning the selection of a single visual feature, boosting the response to the associated feature through neurons that jointly code for multiple features (Burkhalter & Van Essen, 1986; Gegenfurtner & Kiper, 2003; Johnson et al., 2008; Leventhal et al., 1995). The attentional selection of a single surface may be involved in identifying the correct relationships between feature pairs (Stoner & Blanc, 2010; Treisman, 1969; Valdes-Sosa et al., 2000), which would be a conclusion supported by human fMRI data (O'Craven, Downing, & Kanwisher, 1999).

2.13.5. Modelling the colour-motion binding decision making process

An unresolved question that arises from these results is the way in which the appropriate colour (and motion) is assigned to a persistent surface representation once it is formed. Here, this is in part addressed by modelling how the visual system might interpret alternating colour-motion stimuli. By modelling the two-choice perceptual decision process in the basic, two target RDK display (for example, the ‘control’ display in Experiment 2A (Figure 2.2c) and the identical ‘stopping’ display of Experiment 5A (Figure 2.5c), qualitatively similar results to experiments in this chapter can be generated (Figure 2.12a). The aim here is to provide a neurally plausible and parsimonious account for the pattern of results observed here, obviating the need to render multiple stages of feature integration operating at different timescales. However, it is important to note that this model does not represent an attempt to exhaustively model all aspects of the data presented in this chapter; rather it is an attempt to provide a simple method for the processing of conjunction information, upon which predictions can be built and tested. Future investigations into the temporal dynamics of visual feature binding, and its relationship to surface transparency, could benefit by building upon the basic computational approach offered here.

The model is an accumulator model of the general form described in detail in several papers (P. L. Smith & Ratcliff, 2004; P. L. Smith & Vickers, 1988) (see also Ratcliff and Smith (2004), for a review of sequential-sampling models of two-choice perceptual discrimination of this sort). Models of this general class are neurally-principled (Levinson, 1966; P. L. Smith, 2010) and have proven quite successful in recent years in describing both the behavioural and neurophysiological aspects of simple two-choice perceptual decisions (e.g. Gold & Shadlen, 2007; Huk & Shadlen, 2005; Palmer, Huk, & Shadlen, 2005; Ratcliff, Hasegawa, Hasegawa, Smith, & Segraves, 2007; P. L. Smith, Ellis, Sewell, & Wolfgang, 2010). Two independent random-walk processes are used here (one representing evidence for the rotation of the orange RDK, and the other for blue) to describe the accumulation of sensory evidence (Figure 2.12b-d). Evidence for the two choices accumulates to a response criterion, or threshold, when the corresponding RDK is present on-screen. The first threshold to be reached by the accumulated evidence terminates the process, triggering the decision and the appropriate behavioural response.

Independent equations define the accumulation and decay of evidence. When an RDK is on-screen, evidence for the corresponding colour-motion pairing is increased. Across time, evidence is increased by a random value drawn from a Gaussian distribution, generating a roughly linear increase (on average) in evidence over time. For the period of time from the onset of the RDK to the current time, the amount of evidence accumulated is given in Equation 4:

$$\mathrm{E(T) = E(\,T_c) + \sum_{i=T_c}^{T} X_i} \tag{4}$$

Where E is the evidence accumulation value, T is a brief interval of time (16.67 ms here, corresponding to the display refresh rate), T_c is the time at which the display most recently changed from one RDK to the other. X_i is a number drawn randomly from a Gaussian distribution with a mean of 0.0405 and standard deviation of 0.005. These values were obtained by hand to provide the same qualitative form as the experimental data. All numerical values here are expressed as a proportion of the evidence accumulation threshold. In Figures 2.12b-d, this threshold has been arbitrarily set to a value of 1.0.

During the accumulation of evidence for the on-screen RDK, evidence for the off-screen RDK decays in an accelerating manner towards zero. In order to specify a decay towards zero, the decay formula is contingent on the sign of the previous and current evidence values. For the vast majority of cases where evidence is a positive value, this decay formula is given in Equation 5:

$$E(T) = E(T-1) - {Y_i}^{1+T-T_c} \tag{5}$$

Where Y_i is a number drawn randomly from a Gaussian distribution with a mean of 0.0044 and standard deviation of 0.005. If this sign (e.g. from positive to negative) changes from $E(T\text{-}1)$ to $E(T)$, the value of T_c is set to the current T and the sign of Y changes. If the amount of evidence gathered exceeds the threshold, evidence accumulation and decay ceases, and the correct response is made. If the threshold is not reached, a guess is made at the end of each trial. The exponent in the second term on the right hand side of Equation 2 increases over time from an initial value of one, corresponding to accelerating decay. These two processes, a linear accumulation and an accelerating decay, interact to determine a quadratic pattern of conjunction discrimination as a function of temporal alternation frequency similar to that obtained in Experiments 1A and 2A (Figures 2.1c and 2.2c). That is, accurate conjunction discrimination occurs at the lowest and highest alternation frequencies tested, with chance conjunction discrimination occurring at an intermediate range of frequencies (2.5 to 7.5 Hz).

At low alternation frequencies, evidence accumulation reaches threshold before the switch between orange and blue RDKs, i.e. within the first half cycle of the stimulus. Therefore, on most trials, the decay of evidence does not occur and conjunction discrimination is accurate (Figure 2.12b). However, intermediate frequencies provide presentation intervals long enough that the decay process equals or exceeds that of evidence accumulation (Figure 2.12c). Furthermore, a single interval is not long enough for evidence accumulation to reach threshold. This results in guesses for the large majority of the trials around 5 Hz, leading to chance conjunction discrimination. At high alternation frequencies, on average, evidence accumulation exceeds that of decay at a rate great enough to reach the response threshold before the termination of the stimulus (Figure 2.12d), as decay is modelled as an accelerating process. Modelling the perceptual decision of the binding task employed here thus provides a parsimonious way to describe the pattern of conjunction discrimination as a function of temporal alternation frequency without developing distinct binding mechanisms that operate on rapid or slow time scales (Blaser et al., 2005; Bodelón et al., 2007; Holcombe, 2001, 2009; Holcombe & Cavanagh, 2001; Nishida & Johnston, 2002; Treisman & Gelade, 1980).

While this is not an attempt to model all the display manipulations tested across the 10 experiments described here, this basic computational framework allows for some speculation on the processes that determined the pattern of conjunction discrimination for the other display types. For example, Experiments 1A-3A explored the qualities (namely, colour, configuration, and motion) of additional (yet irrelevant) dot surfaces that generally improve conjunction discrimination at intermediate frequencies, whilst not affecting it at high frequencies. It was shown that the presence of such additional dot surfaces during periods of target RDK motion influences the persistence of transparent surface representations to different degrees based on their stimulus characteristics, which in turn facilitates conjunction discrimination (Moradi & Shimojo, 2004). In the model, this persistence might allow for an extended time in which evidence can be accumulated, while also limiting the amount of evidence decay, as there is a reduction in the duration in which a single colour-motion feature pair is perceived to be off-screen. However, accumulation rates during this period of time must also be tempered with regard to any differences in attributes between target and additional RDKs, as similar colour or motion attributes would generate inhibitory activity within the visual cortex.

Experiments 5A, 6A, and 7A manipulated the off-screen behaviour and persistence of the dots in order to disrupt accurate conjunction discrimination at high alternation frequencies. Within this range of frequencies, producing a correct response is heavily reliant on the balance between evidence accumulation and decay. Compared to the ‘moving’ and ‘stopping’ display types present in Experiments 5A and 6A, where RDK movement is coherent across alternations, the decay of evidence could conceivably be accelerated in the ‘resetting’ display types, consistent with a weakened representation of the RDKs as persistent, transparent surfaces. Decay could be further enhanced if RDKs share the same dot configuration, as the perceptual difference between each RDK would be lessened, causing confusion. In Experiment 7A’s ‘same background’ condition, visual persistence causes both orange and blue RDKs to appear identical. This can be modelled by a small interval after each alternation in which the level of accumulated evidence remains static. This would effectively simulate the effects of visual persistence having a large effect at high alternation frequencies (where alternation, and thus persistence, occurs more often) while leaving conjunction discrimination at lower frequencies consistently high.

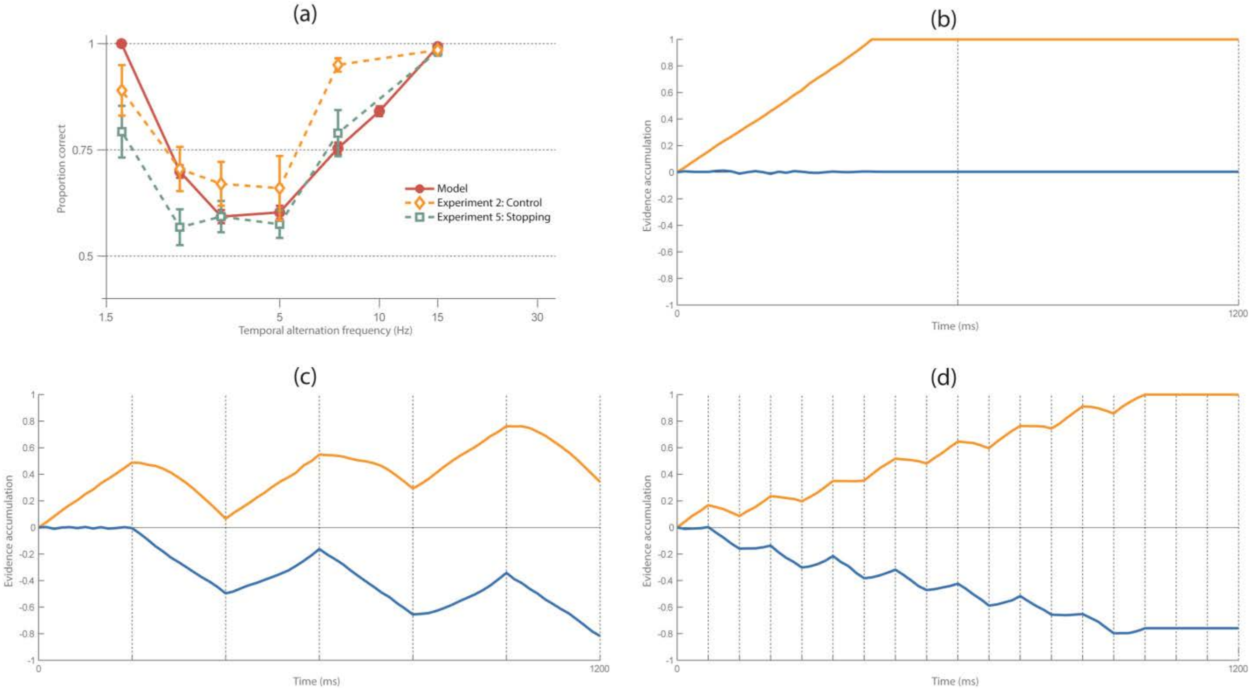

Figure 2.12. Averaged sample model data and single trial evidence accumulation time courses. (a) Mean conjunction discrimination of a data simulation (red circles) averaged over 1000 trials per data point. Error bars denote ±1 standard errors within each alternation frequency. Yellow and green dotted lines are the data from identical conditions where RDKs did not rotate while invisible: the control display in Experiment 2A and the 'stopping' display type in Experiment 5A, respectively. These data are re-plotted for the sake of comparison with the model simulation. **(b)-(d)** Example evidence accumulation time courses for a single trial at 1.67, 5 and 15 Hz, respectively. Blue and orange coloured lines indicate the evidence accumulation for the rotation direction of the respectively coloured RDK. Note that the y-axis is in arbitrary units, beginning at a starting point of 0 (no evidence for a colour-motion conjunction) and spanning from -1 to 1 at which point, the model makes a decision. Orange and blue lines necessarily diverge as the respective RDKs are assigned opposite rotations. Vertical dotted black lines indicate the half-period of the stimulus, i.e. a change from the orange to the blue RDK, or from blue to orange. Note that the x-axis is the same scale in panels **(b)-(d)**, corresponding to the experimental stimulus duration used throughout this chapter (1200 ms).

2.13.6. Conclusions

The experiments presented here clarify the suggestion that feature binding may be an early or otherwise rapid process (Blaser et al., 2005; Bodelón et al., 2007; Holcombe, 2009; Holcombe & Cavanagh, 2001; Maloney et al., 2013; Rousselet, Fabre-Thorpe, & Thorpe, 2002). Previously, the dissociation within the feature binding literature has resulted in the suggestion that more than one feature binding mechanism exists, each with a different temporal resolution. However, the results here can be accounted for in terms of a single but flexible binding mechanism. Taking into account the limitation of a low temporal resolution, both psychophysical and modelling results support the idea that the feature binding process can extract information from rapidly formed persistent surface representations. In this way, surface segregation effectively circumvents the relatively low resolution of feature binding by providing an extended temporal window in which the binding process can act (Holcombe, 2009; Quinlan, 2003; Treisman, 1996; Treisman & Schmidt, 1982). During this time, the visual system appears to organise feature pairs into rapidly formed surface representations (Moradi & Shimojo, 2004). These representations may assist in the attentional selection of a single feature, e.g. motion, which subsequently boosts the response to the paired colour. However, if these representations are not available, accurate conjunction discrimination is reliant on binding based on temporally coincident cues within a single presentation of a feature pair.

Chapter 3. Dynamics of Colour-Orientation Binding

3.1. Introduction

Within the visual system, basic features such as colour and orientation are encoded by the activity profile of populations of neurons (Zeki, 1978a; Zeki et al., 1991). While many neurons in early visual cortex appear to be selective for multiple features (Burkhalter & Van Essen, 1986; Johnson et al., 2008; Leventhal et al., 1995), a wealth of behavioural evidence indicates that a binding problem nonetheless exists (Bodelón et al., 2007; Clifford, 2010; Holcombe, 2009; Moradi & Shimojo, 2004; Quinlan, 2003; Treisman, 1996; Treisman & Schmidt, 1982; Wu et al., 2004). The visual system must take into account both the spatial location and the temporal coincidence of features in order to accurately represent objects composed of a combination thereof. This process of feature binding is considered to be relatively slow, necessitating multiple stages of processing (Bodelón et al., 2007; Holcombe, 2009; Treisman, 1996).

3.1.1. The locus and temporal resolution of colour-orientation binding

Surprisingly, Holcombe and Cavanagh (2001) presented findings contrary to this prevailing view using coloured, oriented gratings. They used a stimulus that rapidly alternated over time between two orthogonally-oriented and differently-coloured square-wave gratings presented in the same spatial location (Bodelón et al., 2007; Holcombe, 2001, 2009; Holcombe & Cavanagh, 2001; Suzuki & Grabowecky, 2002) (Figure 3.1b). Under this arrangement, they found a high temporal resolution for feature binding, contrasting with previous measures of feature binding (Bodelón et al., 2007; Holcombe, 2009; Treisman, 1996). Holcombe and Cavanagh (2001) argue that the observed high temporal resolution is indicative of early coding of feature pairs in the visual system. Without such a process, they argue that each feature combination would be lost to the later visual processes that have a lower temporal resolution (also see Blaser et al., 2005; Favreau et al., 1972). However, if feature binding occurs at an early stage of processing, this must be reconciled with evidence suggesting that binding appears to be a comparatively slow process (Bodelón et al., 2007; Holcombe, 2009; Quinlan, 2003; Treisman, 1996; Treisman & Schmidt, 1982).

Chapter 2 described how the “temporal transparency illusion” (Holcombe, 2001) can occur using colour-motion displays similar to those from Moradi and Shimojo (2004). A number of characteristics enabled the perceptual segregation of the stimulus, which in turn supported accurate conjunction discrimination. Here it is demonstrated that a similar result can be achieved using colour-orientation stimuli. When a stimulus alternates rapidly between two pairs of features (e.g. an orange, left-tilted grating with a blue, right tilted one), a paradoxical visual illusion occurs. During temporal transparency, subjects report perceiving gratings simultaneously as distinct and transparent (Holcombe & Cavanagh, 2001), despite an absence of static transparency cues (Holcombe, 2001). Under these conditions, the combination of colour and orientation features belonging to each surface can be accessed simultaneously, while remaining readily distinguishable, even at temporal alternation frequencies up to 19 Hz (Holcombe & Cavanagh, 2001).

The measured high temporal resolution may be associated with surface segregation (Møller & Hurlbert, 1996; Sajda & Finkel, 1995) rather than that of feature binding. Experiments in the previous chapter demonstrate that the accurate feature binding observed under conditions of temporal transparency is instead tied to the generation of persistent representations of feature pairs (Clifford, Spehar, et al., 2004; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002). Persistent segregation only occurred through a combination of surface segregation cues that supported accurate conjunction discrimination at high temporal frequencies. The combination of stimulus manipulations that were used affected conjunction discrimination in a way that tended to support surface segregation. Importantly, conjunction discrimination was affected only at intermediate frequencies and higher where surface segregation was also predicted to support feature binding. Providing an account consistent with past research, the conclusions of the previous chapter indicate that the feature binding process may attentionally select persistent representations of features when these are available in order to determine the correct feature pairing. Thus, when surface representations can be formed for the duration of the trial, the slower binding process is then afforded sufficient time in which to identify and extract feature pairs (Moradi & Shimojo, 2004).

3.1.2. A distinction between neural correlates of perceived and non-perceived feature conjunctions

As mentioned previously, early visual cortex appears to jointly code for more than one feature. This has been found both in single-cell recordings (Burkhalter & Van Essen, 1986; Johnson et al., 2008; Leventhal et al., 1995) and fMRI data (Bouvier & Treisman, 2010a; Seymour & Clifford, 2012; Seymour, Clifford, et al., 2009; Seymour et al., 2010; Sumner et al., 2008; Zhang et al., 2014). These studies consistently find that visual feature conjunctions are represented as early as primary visual cortex (V1). However, while the activity profile of populations of neurons may encode basic features, the processes by which this information is correctly decoded and integrated are still largely unknown.

A challenging prospect when investigating the neural correlates of feature binding is disentangling the perception of feature conjunctions from their simple presence in the stimulus. This is an important distinction when identifying brain regions that correlate with binding per se (Whitney, 2009; Zhang et al., 2014). Previous research has indicated that invisible features are represented in early visual cortex including orientation (Haynes & Rees, 2005; He et al., 1996), motion (Moutoussis & Zeki, 2006), and flicker (Gur & Snodderly, 1997; Jiang, Zhou, & He, 2007); adaptation to invisible features and conjunctions has also been observed (Blaser et al., 2005; Houck & Hoffman, 1986; G. K. Humphrey & Goodale, 1998; Vul & MacLeod, 2006). Therefore, it is important to identify if the neural activity associated with feature binding is reflective of the physical stimulus alone, or if early visual areas can also be modulated by the conscious perception of a feature conjunction.

3.1.3. Experimental aims

In this chapter, the inter-relationship between surface segregation and the binding of colour with orientation is probed, with a focus upon the idea that the surface segregation process mediates conjunction discrimination at high temporal alternation frequencies. In this series of experiments, the temporally alternating, coloured gratings that were employed by Holcombe and Cavanagh (2001) are manipulated. Namely, several surface segregation cues such as the angular separation between the gratings (Holcombe & Cavanagh, 2001; Kawabe & Miura, 2004; Nothdurft, 1991; T. Watanabe & Cavanagh, 1996), temporal alternation rate and spatial coincidence are varied. If colour-orientation binding relies on surface segregation, manipulations of the stimulus should see conjunction discrimination rise and fall accordingly. An fMRI experiment was subsequently conducted using adapted experimental stimuli in order to probe the responses of early visual areas to perceived feature conjunctions.

In the psychophysical “binding” task, subjects discriminated the colour-orientation conjunction of coloured, oriented gratings. Unlike the colour-motion stimulus however, the impairment in conjunction discrimination at temporal alternation frequencies around 5 Hz is not immediately apparent using orthogonally oriented colour-orientation stimuli. A reduction of the angular separation of the gratings revealed that conjunction discrimination again became poor at 5 Hz when surface segregation is weakened. Further experiments were designed to clarify what factors affect the perceptual segregation of the stimuli as transparent, superimposed surfaces in order to influence conjunction discrimination.

3.2. General methods

3.2.1. Subjects

Informed written consent was obtained from all psychophysical subjects (age range: 22-46), who were experienced psychophysical observers. . This included the author of the thesis and two other experimenters involved in the study. While the author and experimenters were not naïve to the experimental manipulations, they were unaware of the order in which each condition was presented. All subjects had normal or corrected-to-normal visual acuity, normal trichromacy, and were free of psychiatric/neurological illness. The experimental protocol was approved by the University of Sydney Human Research Ethics Committee.

3.2.2. Apparatus

All experiments were conducted under the same conditions. Subjects sat at a viewing distance of 57 cm from a gamma-corrected ViewSonic Graphics Series G90f CRT monitor (36 cm × 27 cm) with a vertical refresh rate of 60 Hz and resolution of 1024 × 768 pixels. Gamma correction was achieved with measurements made using a Cambridge Research Systems ColourCal colorimeter.

Stimuli were generated through Matlab (R2010a 7.10; The Mathworks, Natick, MA) and the Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997) on a PC with an Intel Core i7-2600 CPU, 3.4 GHz processor and an AMD Radeon HD 6450 display adapter. Experiments were run in a light and sound-proof testing booth. Subjects responded using a standard Dell keyboard.

3.2.3. Visual stimuli

All experiments in this chapter employed variations on two temporally alternating square wave gratings. Unless otherwise stated, gratings had standardised characteristics across all experiments. Gratings had a spatial frequency of 0.84 cycles per degree of visual angle, and were presented at one of five angular separations: 5°, 10°, 15°, 20°, or 90° (orthogonal). For example, a 5° angular separation saw each grating rotated by ±2.5° from vertical.

Gratings were always presented within an annular region (inner radius = 2.21°; outer radius = 12.08°) against a mean-luminance grey background (of 26 Cd m^{-2}). Contrast at the edges of the annulus was ramped with a raised cosine luminance profile of 0.84°. A single trial contained alternating blue (CIE: x = 0.24, y = 0.28) and orange (CIE: x = 0.33, y = 0.36) gratings. For each grating, one spatial half-cycle was light blue or orange (29 Cd m^{-2}), while the other spatial half cycle was dark blue or orange (23 Cd m^{-2}). The centre of the annulus contained a small fixation cross of 0.4° × 0.4° , encircled by a black and white fixation ring (diameter = 1.4°).

The dark blue and orange and light blue and orange colours were defined using DKL space (Derrington, Krauskopf, & Lennie, 1984), and were calibrated individually for each subject prior to the experiment such that all combinations of blue and orange summed subjectively to a shade of grey (CIE: x = 0.28, y = 0.31) in order to avoid discrimination biases due to imbalanced colour saturation (Holcombe & Cavanagh, 2001). Calibration involved two steps, performed separately for the light and dark colour pairs: subjective equiluminance calibration using a minimum motion stimulus (Figure 3.1a; Anstis & Cavanagh, 1983), and a colour matching task using 30 Hz temporally alternating gratings (Figure 3.1b). During luminance calibration, subjects viewed a repeating series of 4 square wave, vertical gratings. These had their phases shifted by (in order) 0°, 90°, 180°, and 270°. The 0° and 180° gratings consisted of counter-phase orange and blue strips of the same physical luminance, while the 90° and 270° gratings were monochrome gratings containing black and white strips. The stimulus rapidly alternated at one of 8 temporal alternation frequencies (1.25, 2.5, 3.75, 5, 7.5, 10, 15, and 30 Hz) between these gratings always in the same order. The spatial phases of the monochrome gratings were thus offset by 90° with respect to the coloured gratings. The resulting perception was, for example, if orange appeared subjectively brighter than the blue, subjects would perceive apparent motion rightwards (demonstrated in Figure 3.1a), and the opposite would occur if blue appeared brighter than orange. Subjects were instructed to adjust the luminance of the blue colour until it generated the minimum amount of apparent motion. This procedure was repeated 6 times, with a small amount of inter-trial jitter around ± 0.5 Cd/m^2 in the blue luminance for both light and dark colour calibration. Upon completion, light and dark luminance values were calculated by averaging together the recorded values together.

These luminance values were stored for each subject and subsequently used in the colour calibration procedure (Figure 3.1b). Subjects adjusted the light blue colour by varying it along the yellow-violet axis. Subjects were instructed that their perceptual impression of the stimulus should appear similar to that in the lower portion of Figure 3.1b: that is, 3 shades of grey should be discernible while fixation on the central cross was maintained. In doing so, when the sum of light orange and dark blue equalled that of light blue and dark orange, colour-orientation conjunctions were no longer visible in the sum of the gratings. The overall perception of the stimulus was that, when calibrated properly, an achromatic plaid was observed, such that the particular colour-orientation combination could not be resolved (Figure 3.1b). This task was performed to remove any subjective differences in chromaticity between blue and orange gratings. Any subjective differences in chromaticity would affect perception of the stimulus at all alternation frequencies. This could in turn bias a subject's responses such that the correct conjunction would be reported, but due to an artefact of the stimulus, rather than an experimental manipulation.

3.2.4. Design and procedure

In all experiments unless otherwise stated, subjects performed a colour-orientation 'binding' task where they reported the tilt (leftwards or rightwards) associated with the orange grating. Where the angular separation between gratings were varied, 5 values were used (5°, 10°, 15°, 20°, and 90°). Otherwise, gratings were orthogonal. Where temporal alternation frequency was varied, 8 different frequencies were employed (1.25, 2.5, 3.75, 5, 7.5, 10, 15, and 30 Hz) (Experiment 4B also used a 6 Hz temporal frequency for a total of 9 frequencies, however). Temporal alternation frequencies were chosen such that they divided evenly into 60 Hz. Stimulus duration was 800 ms, including a 250 ms raised cosine contrast ramp at the beginning and end of each trial to eliminate onset and offset transients.

A subject would view all conditions in an experiment, as all employed a within-subjects factorial design. Subjects performed 5 repeat runs and were allowed breaks between runs. Within a run, each possible combination of varied stimulus attributes was repeated 8 times (randomly interleaved) for a total of 40 trials per condition. Furthermore, trials within runs were counterbalanced for the onset grating and colour-orientation pairing. Prior to performing the feature binding task, subjects completed a practice run with auditory feedback to familiarise themselves with the task. During the actual experiment, subjects reported the tilt (leftwards or rightwards) of the orange grating in an unspeeded manner (with no auditory feedback) at the end of each trial using a standard keyboard while maintaining fixation on the central cross.

3.2.5. Data analysis

Data were analysed first in Matlab (R2010a 7.10; The Mathworks, Natick, MA), and then using IMB SPSS Statistics 20 for Windows. Conjunction discrimination was coded as the proportion of correct responses across all 5 experimental runs. These data were subjected to a two-way repeated-measures ANOVA with planned polynomial contrasts. Subjects were treated as a random factor and the independent variables of the experiment (e.g. angular separation and temporal alternation frequency) as fixed factors. Where main effects, interactions, and the trends associated with each were significant in the ANOVA, the outcomes of planned, Bonferroni-corrected polynomial contrasts up to a degree of 3 (cubic) were reported. If comparison between data points needed to be made, Bonferroni-corrected paired-samples *t*-tests were used.

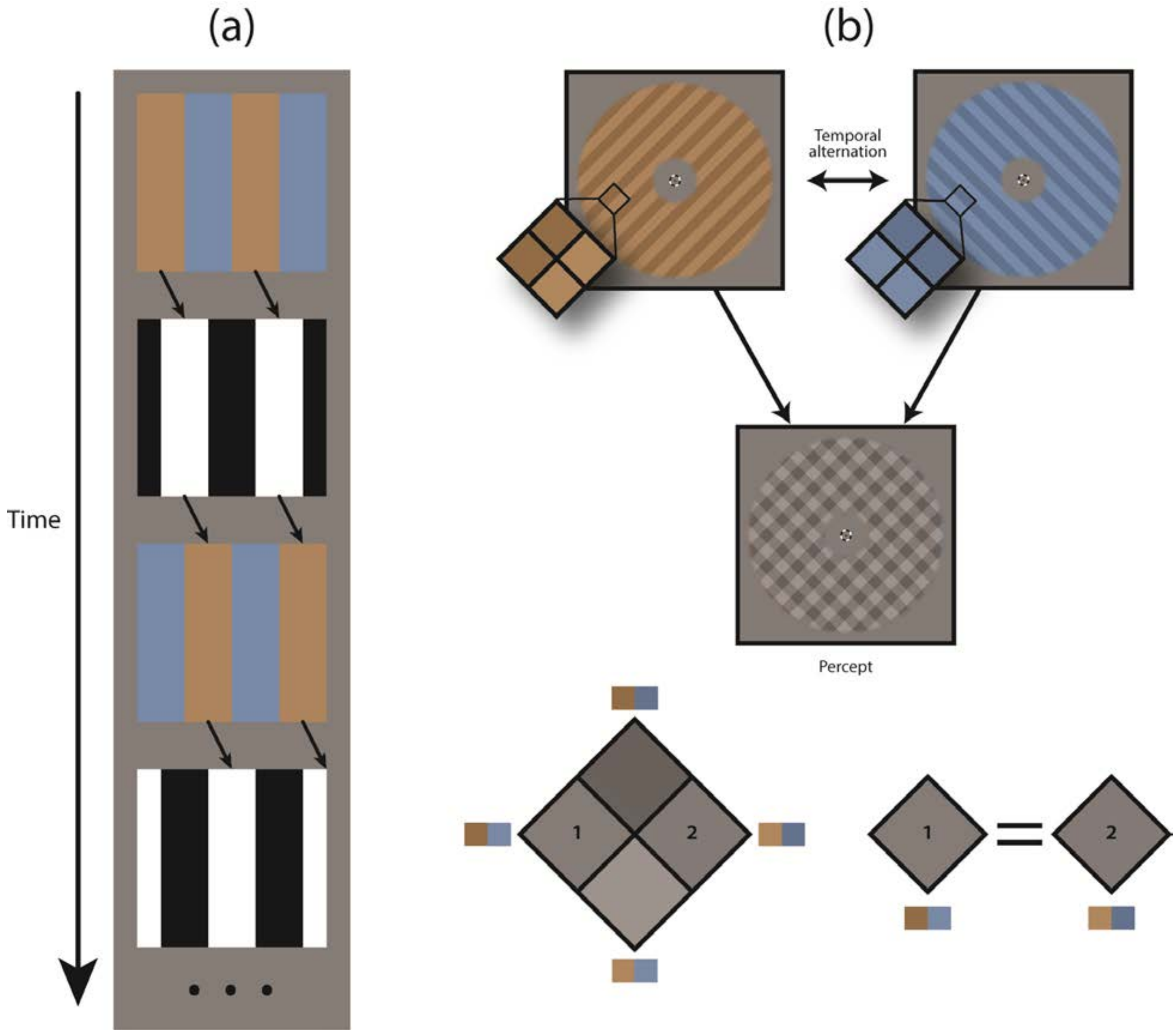

Figure 3.1. Minimum motion and colour calibration designs. **(a)** Representation of the minimum motion task used in finding the equiluminance point between light orange and light blue (and similarly, dark orange and dark blue). From top to bottom, the phases of these gratings were 0°, 90°, 180°, and 270°. If the subjective luminance of orange and blue was unbalanced, this would manifest as apparent motion, as indicated by the small black arrows. A difference in luminance between orange and blue colours would cause the coloured grating to appear more similar to the achromatic grating. This increased correspondence between gratings, coupled with the shifts in phase, means that the sequence outlined in the figure is more likely to be perceived as a moving grating (Green, 1986). For

example, if orange appears lighter than blue, the orange and white bars of each grating will generate apparent motion (moving right in this example). The blue and dark bars would be similarly correlated in this example, also moving to the right. However, if the orange and blue colours are subjectively equiluminant both orange and blue are equally likely to be matched with the light luminance strip, which will not create a strong sense of motion. **(b)** Representation of the colour calibration task. 30 Hz alternation between the orange and blue square wave grating (top) generated an impression of a flickering, monochrome grating. The bottom portion of the image demonstrates the task goal. To correctly calibrate the display, subjects adjusted the light blue colour such that the combination of dark orange and light blue (panel 1) generated a perceptually identical grey to the combination of light orange and dark blue (panel 2).

3.3. Experiment 1B: Discrimination of feature conjunctions using coloured, oriented gratings

3.3.1. Rationale

In their original study, Holcombe and Cavanagh (2001) used coloured square-wave gratings that were oriented orthogonally to one another (see also Bodelón et al., 2007; Holcombe, 2001; Suzuki & Grabowecky, 2002). Here, it was reasoned that narrowing this angular separation might cause the rapid colour-orientation binding normally enabled by temporal transparency to break down. This is because a smaller separation between the gratings should impair the perception of the gratings as distinct surfaces (Nothdurft, 1991; T. Watanabe & Cavanagh, 1996). Thus, it is predicted that at higher alternation frequencies, a reduction in angular separation between gratings will be associated with lowered conjunction discrimination.

3.3.2. Experimental methods

3.3.2.1. Subjects

Six experienced psychophysical subjects (4 male; age range 22–29), participated in this experiment.

3.3.2.2. Visual stimuli

The grating display contained two temporally-alternating, square wave gratings (Holcombe & Cavanagh, 2001) presented at one of five angular separations (Figure 3.2a): 5°, 10°, 15°, 20°, or 90° (orthogonal). For example, a 5° angular separation saw each grating rotated by ±2.5° from vertical.

3.3.2.3. Design and procedure

This experiment employed a 5 ‘angular separation’ (5°, 10°, 15°, 20°, and 90°) × 8 ‘temporal alternation frequency’ (1.25, 2.5, 3.75, 5, 7.5, 10, 15, and 30 Hz) within-subjects factorial design. Subjects performed a colour-orientation ‘binding’ task where they reported the tilt (leftwards or rightwards) of the orange grating (Figure 3.2a).

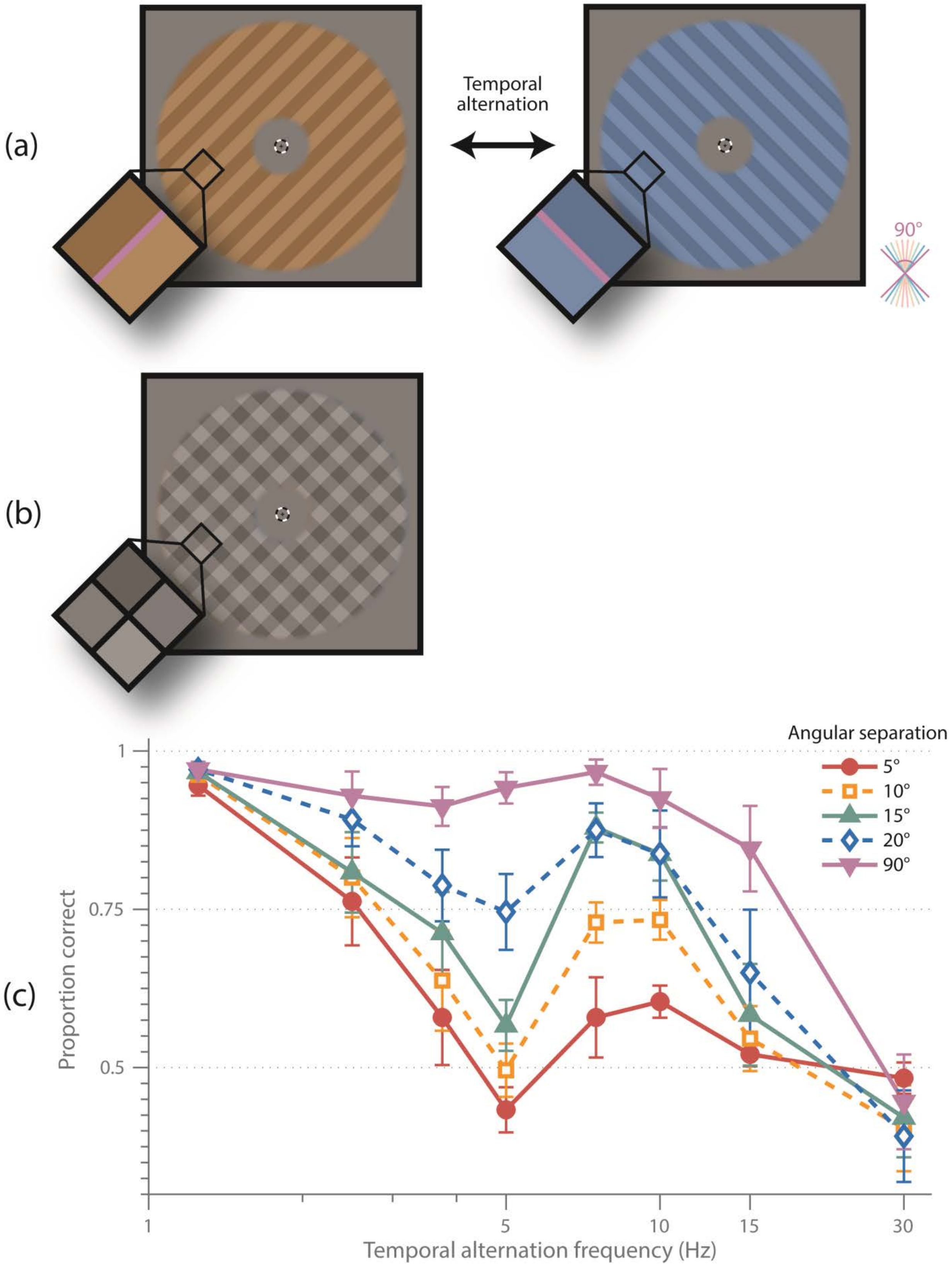
(a)
Temporal alternation
90°
(b)
(c)
Angular separation
5°
10°
15°
20°
90°
Proportion correct
1
0.75
0.5
1
5
10
15
30
Temporal alternation frequency (Hz)

Figure 3.2. Stimulus design and results of Experiment 1B. (a) An orange square-wave grating tilted in one direction was temporally alternated at the same spatial location with a blue grating tilted in the opposite direction. Gratings were presented at one of 5 angular separations (90° in this example; shown in purple). **(b)** Orange and blue gratings were calibrated such that they summed physically to an achromatic plaid (Holcombe & Cavanagh, 2001), wherein the colour-orientation pairing information was lost. The plaid's appearance was independent of the colour-orientation pairing. **(c)** Mean colour-orientation conjunction discrimination across subjects (*n*=6) as a function of both the angular separation and the temporal alteration frequency. Error bars denote ±1 SEM.

3.3.3. Results and discussion

The aim of Experiment 1B was to identify the role of surface segregation in supporting accurate conjunction discrimination at high temporal alternation frequencies. Overall, the pattern of results in Figure 3.2c suggests that a combination of cues important in surface segregation are needed to facilitate accurate conjunction discrimination at high alternation frequencies. Specifically, both angular separation and temporal alternation frequency appear to have combined and systematic effects on conjunction discrimination (Clifford, Spehar, et al., 2004; Moradi & Shimojo, 2004; Nothdurft, 1991; T. Watanabe & Cavanagh, 1996).

Across temporal alternation frequency, an increase in conjunction discrimination was unsurprisingly associated with an increase in angular separation (two-way repeated-measures ANOVA with planned polynomial contrasts, linear trend: $F_{1,5} = 47.32$, $p < 0.001$; Figure 3.2c). This result is more likely due to a weakened surface segregation percept however, rather than the higher task difficulty associated with the discrimination of similar orientations. Experiments 2B (and 7B) are designed to verify this hypothesis.

Across all angular separations, the selective impairment in conjunction discrimination at 5 Hz reveals a transition in the way that binding occurred (main effect of temporal frequency; linear trend: $F_{1,5} = 43.79$, $p = 0.001$; and cubic trend: $F_{1,5} = 17.19$, $p = 0.009$). An increase in alternation frequency from 1.25–5 Hz corresponded with a decrease in conjunction discrimination. At very low alternation frequencies, feature binding can (in principle) occur within a single presentation of a conjunction stimulus. But as an increase in frequency necessitates a shorter grating presentation, task difficulty should therefore increase due to the limited time by which a single conjunction stimulus can be sampled by the visual system.

However, it was found that conjunction discrimination improved from 5–10 Hz, the range of frequencies facilitating temporal transparency (Holcombe, 2001). In this range, the attributes of each grating are temporally integrated at the level of surface representations across the full trial duration. This creates stable representations of each grating in the form of perceptually transparent surfaces (Suzuki & Grabowecky, 2002). Access to these representations over a period exceeding individual grating presentations provides a sufficient temporal window within which feature binding can act (Clifford, Holcombe, et al., 2004; Moradi & Shimojo, 2004). However, from 10–30 Hz, surface segregation fails, and conjunction discrimination falls to chance levels as gratings combine perceptually to form a grey plaid (Figure 3.2b). Combined with the non-foveal stimulus presentation, a high alternation frequency masked the colours present in the display in a way that produced a percept where individual gratings were no longer distinguishable.

Temporal alternation frequency affected conjunction discrimination non-monotonically for each angular separation (quadratic interaction: $F_{1,5} = 69.35$, $p < 0.001$). At frequencies around 5 Hz, when surface segregation is impaired by small angular separations (Nothdurft, 1991; T. Watanabe & Cavanagh, 1996), conjunction discrimination is similarly affected. This suggests that accurate conjunction discrimination around alternation frequencies of 5 Hz and higher is reliant on surface segregation. From 2.5–5 Hz, a smaller angular separation interacted with the shorter grating presentation duration at these frequencies to interfere with the formation of orientation-defined surfaces, decreasing conjunction discrimination. This effect was most pronounced at 5 Hz, where discrimination was clearly lowered as a function of angular separation. However, as frequency increased from 5–30 Hz, the difference in conjunction discrimination across angular separation was reduced as temporal transparency appeared to mitigate the effects of small angular separations on conjunction discrimination.

Thus, at high alternation frequencies (5 to 15 Hz), surface segregation appears to play a necessary role in feature binding. Furthermore, the impairment of performance at intermediate frequencies suggests that the temporal transparency illusion is driven by a number of surface cues that reduce the ambiguity of the stimulus: in this case, angular separation and temporal alternation frequency (Clifford, Holcombe, et al., 2004; Moradi & Shimojo, 2004; Nothdurft, 1991; T. Watanabe & Cavanagh, 1996). If accurate conjunction discrimination at, for example, 10 Hz, was instead due to a rapid binding mechanism (Holcombe & Cavanagh, 2001), it would be expected that conjunction discrimination could only improve at lower alternation frequencies. Instead, a disproportionately larger decrease at 5 Hz than at 10 Hz was observed when angular separation was reduced, suggesting that feature binding can occur by extracting feature pairs from surface representations when these representations are available. In order to confirm the relationship between surface segregation and conjunction discrimination, Experiment 2B sought to determine the correspondence between the current stimulus manipulations and subjective judgements of surface segregation.

3.4. Experiment 2B: Subjective interpretations of coloured, oriented gratings

3.4.1. Rationale

Experiment 2B identifies the relationship between binding task performance and subjective impressions of surface segregation. Subjects reported whether the same stimuli used in Experiment 1B appeared transparent or not. In this way, the subjective, perceptual interpretation of the stimulus could be determined. In combination with the results from Experiment 1B, this allowed a direct relationship between the objective conjunction discrimination measures of Experiment 1B and subjective judgements of surface segregation to be established.

3.4.2. Experimental methods

3.4.2.1. Subjects

Nine subjects participated in Experiment: 2 experimenters, including the author plus 7 naïve subjects (4 male, age range 22-28).

3.4.2.2. Visual stimuli

Stimuli identical to those used in Experiment 1B were presented (Figure 3.2a).

3.4.2.3. Design and procedure

Subjects reported whether they saw the display according to one of three categories: “Sequential”, “Transparent”, or a “Plaid”. Subjects were instructed beforehand on the meaning of each response. “Sequential” was reported when subjects experienced the stimulus as discrete, successive presentations of the individual gratings. “Transparent” was reported when subjects perceived both gratings as simultaneously present, but still individually distinguishable (Holcombe, 2001; Holcombe & Cavanagh, 2001; Suzuki & Grabowecky, 2002). Finally, “Plaid” was reported when subjects were no longer able to distinguish individual gratings and instead perceived a single plaid (Figure 3.1b). When making judgements, subjects were instructed to ignore stimulus flicker or colour saturation, and instead focus on the sequential or simultaneous appearance of the gratings.

The focus of this experiment was the range in which the experimental stimulus was subjectively perceived as transparent. Thus, data were coded and are presented here as the mean proportion of “Transparent” responses for each condition. “Sequential” and “Plaid” responses were combined, as both responses represented a lack of transparent perception.

3.4.3. Results and discussion

This experiment aimed to identify the relationship between the perceptual interpretation (Figure 3.3) and conjunction discrimination (Figure 3.2c) of the colour-orientation stimulus. Across angular separations, reports of perceptual surface segregation of the stimulus rose most rapidly after 5 Hz and peaked at 10 Hz. Within the range of 5-30 Hz the perception of transparency rose and fell in the same manner as the conjunction discrimination measured in Experiment 1B (main effect of temporal frequency: $F_{7,56} = 4.91$, $p < 0.001$, cubic trend: $F_{1,3} = 58.28$, $p < 0.001$). Below 5 Hz, stimuli were generally reported as “Sequential”, while at 15 Hz and above, “Plaid” was reported most often. Overall, the transition in perception from a sequentially-presented display to transparent surfaces was identified at around 5 Hz, matching the alternation frequency where conjunction discrimination broke down across angular separation in Experiment 1B.

Across temporal frequency, angular separation appeared to have no effect on the transparency of the stimulus (non-significant main effect of angular separation: $F_{4,32} = 1.23$, $p = 0.317$). A significant interaction effect was present in the data ($F_{28,224} = 2.77$, $p < 0.001$). However, a quadratic interaction effect where differences in conjunction discrimination between angular separation first increased and then decreased across alternation frequency was not found ($F_{1,8} = 3.11$, $p = 0.77$). The observed interaction most likely stems from subtle effects in stimulus interpretation, which was not the main focus of this experiment. On inspection of the data, it appears that at 90° angular separation, the proportion of ‘Transparent’ responses was not at ceiling, even at the peak of the curve, unlike some of the other separations. It can only be speculated upon, but this result may be due to a rivalling type of percept where perceptual dominance rivals between both gratings (Brascamp, Van Ee, Pestman, & Van Den Berg, 2005; Leopold & Logothetis, 1999; Mamassian & Goutcher, 2005).

Together, Experiments 1B and 2B highlight two distinct temporal frequency ranges where accurate conjunction discrimination is possible: less than 5 Hz and around 10 Hz, suggesting a direct relationship between surface segregation and conjunction discrimination. Therefore, two further stimulus displays were devised in Experiments 7B and 8B in order to isolate the processes driving conjunction discrimination at each frequency range.

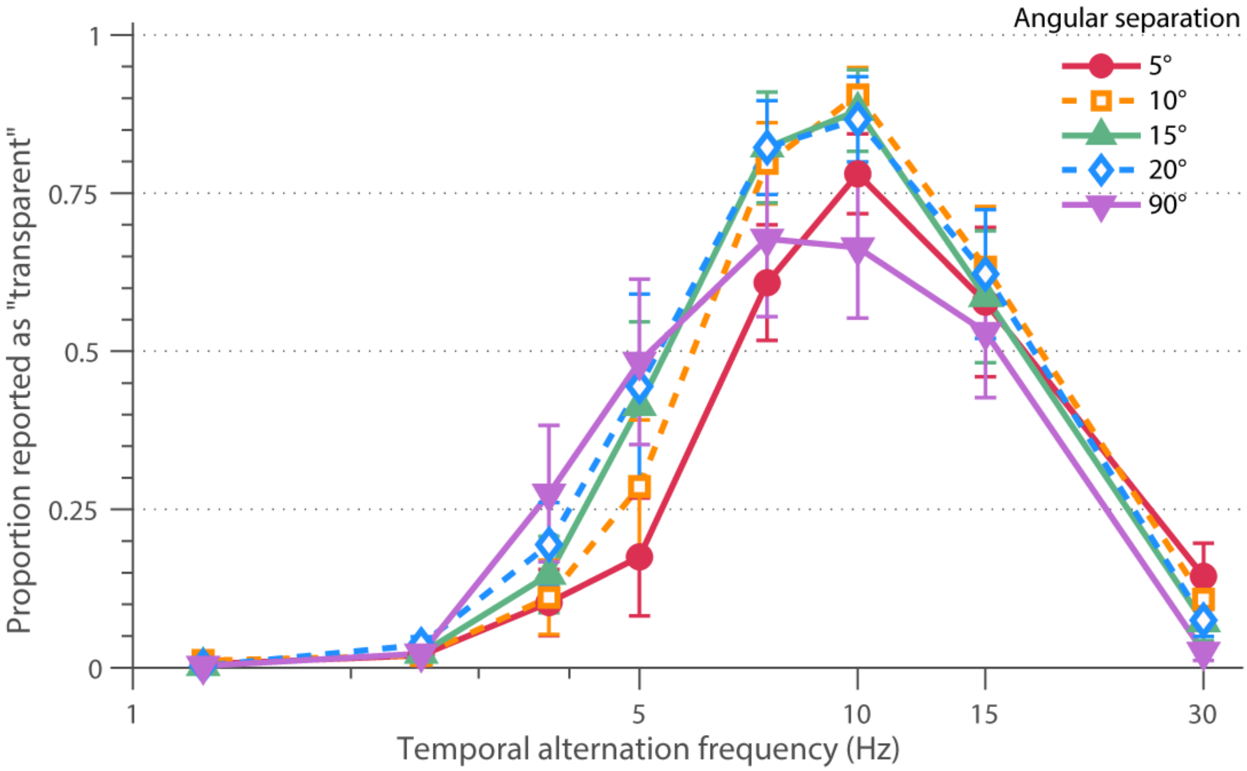

Figure 3.3. Results of Experiment 2B. Mean proportion of "Transparent" responses across subjects (*n*=9) as a function of both the angular separation and the temporal alternation frequency. Error bars denote ±1 between-subject standard errors.

3.5. Experiment 3B: Perceptual asynchrony of colour and orientation

3.5.1. Rationale

Discussed in Chapter 1, the asynchronous perception of various visual features is one source of difficulty in accurately perceiving conjunctions. Across Experiments 1B, 7B and 8B, the difficulty of the conjunction discrimination task varied across alternation frequency, angular separation or both. As such, it is concluded that the manipulation of these surface segregation cues has an effect on feature binding. However, psychophysical evidence for a perceptual colour-orientation asynchrony exists (Clifford et al., 2003; Moutoussis & Zeki, 1997a). Furthermore, it is also known that variations in temporal alternation frequency (Nishida & Johnston, 2002) and differences in angular motion (Arnold & Clifford, 2002) can also affect the perceived asynchrony of colour and motion features. Therefore, perhaps the perceived asynchrony between colour and orientation features may also be contributing to the difficulty of the colour-orientation binding task. This effect may be masked due to either a large angular difference or a high temporal alternation frequency. However, in Experiment 1B at 5 Hz where conjunction discrimination is markedly stratified according to angular separation, perceptual asynchrony may be serving as a confounding factor to the acquired results.

To test this hypothesis, the relative phase between changes in colour and orientation attributes is shifted (see Moutoussis & Zeki, 1997a). If perceptual asynchrony is affecting task difficulty, an offset change in colour compared to orientation should increase conjunction discrimination.

However, if there is no influence of perceptual asynchrony, conjunction discrimination should remain constant regardless of the colour-motion phase offset at lower angular separations.

3.5.2. Experimental methods

3.5.2.1. Subjects

5 experienced psychophysical observers (4 male, age range 25-29) participated in this Experiment.

3.5.2.2. Visual stimuli

This stimulus used a temporal alternation frequency of 5 Hz in all display conditions, but was otherwise the same grating condition as in previous experiments (Figure 3.4a). Here, the phase at which colour and orientation changed was varied in steps of 30° (Figure 3.4b), in addition to angular separation (Figure 3.2a). A 0° shift in phase corresponded to a simultaneous change in colour and orientation attributes, (e.g. an orange leftward tilted grating would instantaneously swap to a blue, rightward tilted grating). At 5 Hz with a monitor refresh rate of 60 Hz, a 30° shift in phase affected the stimuli such that a grating’s colour changed 1 frame later than its orientation. At a phase shift of 180°, colour and orientations again changed simultaneously, but the conjunction pairing was reversed such that in the previous example, orange is now paired with a rightward tilt (and blue with left).

3.5.2.3. Design and procedure

This experiment was a 5 ‘angular separation’ (5°, 10°, 15°, 20°, 90°) by 12 ‘phase shifts’ (0° to 330° in steps of 30°) within subjects factorial design. Subjects completed 5 runs, each containing 8 repeats of each frequency-phase shift combinations presented in a random order. Subjects were instructed to respond by keypress to each stimulus and report the tilt of the orange grating.

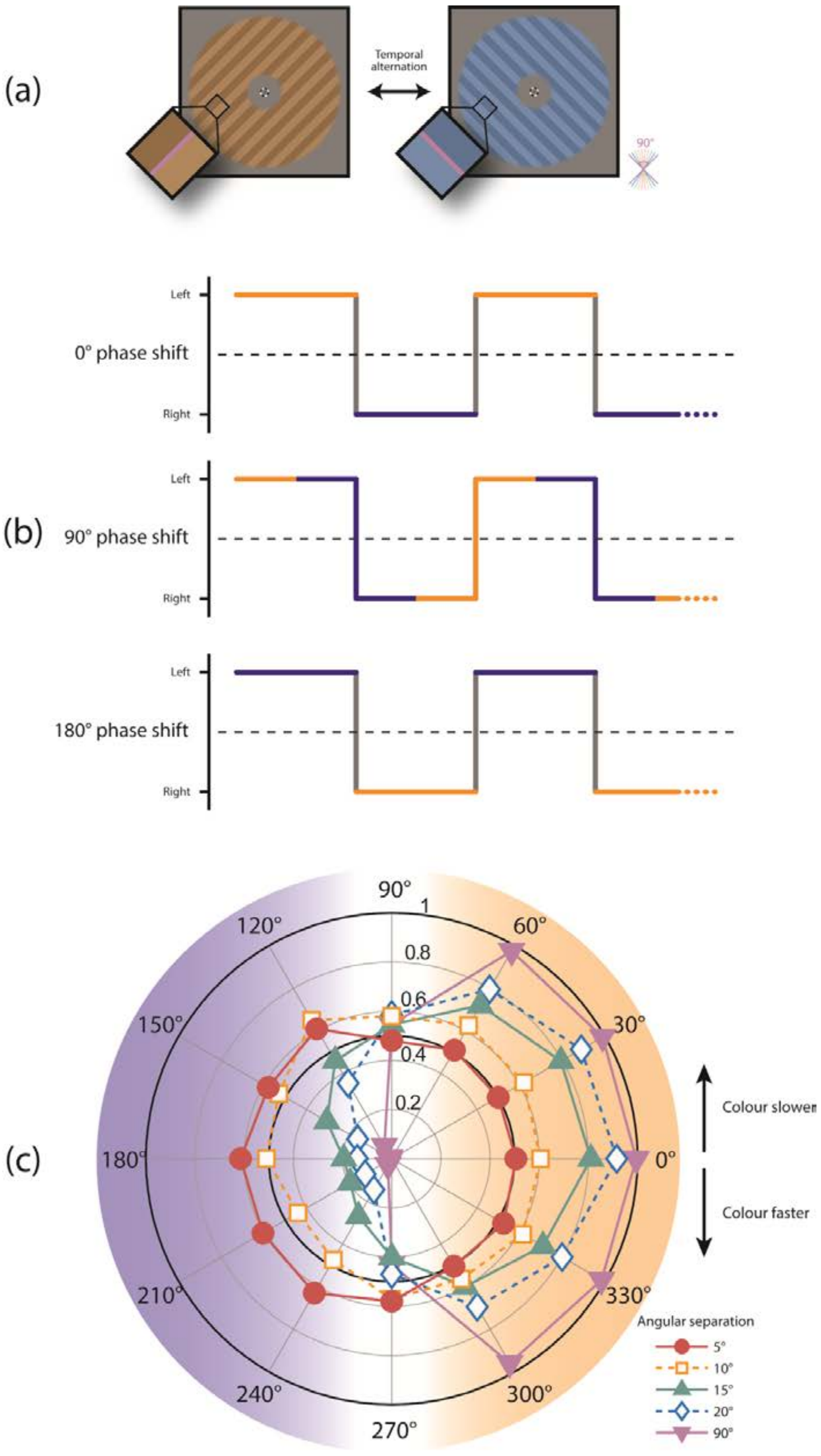
(a)
Temporal alternation
90°
(b)
Left
0° phase shift
Right
Left
90° phase shift
Right
Left
180° phase shift
Right
(c)
90°
120°
60°
150°
30°
180°
0°
210°
330°
240°
300°
270°
1
0.8
0.6
0.4
0.2
Colour slower
Colour faster
Angular separation
5°
10°
15°
20°
90°

Figure 3.4. Stimulus design and results of Experiment 3B. **(a)** Representation of the stimulus. **(b)** Demonstration of the phase shift in orientation with respect to colour. In this example, orientation is shifted to change later than colour, until the colour- orientation pairing is reversed. All permutations of colour and orientation offsets were tested. **(c)** Mean colour-orientation conjunction discrimination across subjects (*n*=5) as a function of both the angular separation and the phase shift between colour and orientation. Error bars are not shown in this figure for clarity, and can instead be found in Table 3.1. Symbols closer to the outside of the circle indicate a higher proportion of responses for the orange grating tilted left. Symbols closer to the middle of the circle represent a higher proportion of responses for the blue grating tilted left. The left side of the plot (300°-60°) indicates that the majority of left-tilted grating frames were orange. Similarly, the right side of the plot (120°-240°) indicate the majority of left-tilted frames were blue. The inner solid black circle indicates a proportion correct of 0.5 – where the number of responses for orange and blue were equal. Symbols closer to this line indicate chance conjunction discrimination. However, as 90° and 270° phase shifts have an equal number of orange and blue grating frames tilted to the left, chance conjunction discrimination at these phase shifts were expected. The black arrows to the right of the graph indicate if colour changed before or after the closest change in orientation.

Table 3.1.

Between-subject standard errors for each condition in Experiment 3B

Relative Phase (°)	Angular separation (°)				
	5	10	15	20	90
0	0.056	0.038	0.049	0.044	0.005
30	0.053	0.057	0.067	0.032	0.010
60	0.078	0.061	0.080	0.070	0.016
90	0.050	0.057	0.037	0.048	0.042
120	0.048	0.021	0.022	0.059	0.026
150	0.046	0.099	0.068	0.068	0.006
180	0.032	0.054	0.023	0.067	0.006
210	0.017	0.042	0.020	0.043	0.006
240	0.025	0.076	0.081	0.053	0.015
270	0.020	0.064	0.052	0.042	0.064
300	0.057	0.048	0.048	0.091	0.028
330	0.097	0.051	0.062	0.065	0.010

3.5.3. Results and discussion

Overall, the results of this experiment replicated that of Experiment 1B (at the phases of 0° and 180°; Figure 3.2c). However, while a small amount of evidence for an asynchrony was observed, this was not consistent at the lowest two (5° and 10°) angular separations where discrimination was the poorest (Figure 3.4c). That is, conjunction discrimination was predicted to be more accurate (i.e. peak) at a phase shift of 0° and 180°, where colour and tilt were exclusively paired. From 0° onwards, discrimination progressively lowered, reaching chance at 90°, where the pairing of orange-left was present for the same amount of time as orange-right. This conjunction discrimination minimum was also expected, and found from the phase range of 180° to 270°.

If perceptual asynchrony was resulting in poor conjunction discrimination, a shift in the way the radial data is oriented would be observed. A shift of a greater magnitude should be associated with a lower angular separation where the maximum and minimum discrimination would not be aligned along the 0°-180° line, where colour and orientation had exclusive pairings, as the phase shifted stimulus would compensate for any perceptual asynchrony.

To analyse the data, the CircStat toolbox for Matlab was used (Berens, 2009). The tests applied here are detailed in Berens (2009). First, Rayleigh's test for non-uniformity was applied to the data at each angular separation. This test assesses if the data is significantly distributed in a non-uniform fashion (i.e. is not circular). For 5° and 10°, this analysis did not reach significance (p = 0.33 and p = 0.22, respectively). However, for separations of 15°, 20° and 90°, the data here were found to significantly deviate from a uniform distribution (all $p < 0.001$). Next, the mean direction of the data was calculated. For angular separations of 5° and 10°, the direction of the data peaked at a phase shift of 201° and 36° respectively. However, as separations of 5° and 10° separations were circular, these phase shift values represent random noise in the mainly circular distribution. For separations of 15°, 20°, and 90°, the peak of the data was found at phase shifts of 16° (27ms of orientation leading colour), 10° (17ms), and 3° (5ms) respectively. Confidence intervals for these values were less than ± 0.3°, indicating these were significantly different from a phase shift of 0°.

From previous studies, a slight rotation of the data towards vertical indicates that, at best, perceptual asynchrony may play a very minor role in the difficulty of the colour-orientation binding tasks presented in this chapter. However, it is important to consider the values here were obtained using a 60 Hz monitor. This resolution limits the accuracy of the measured asynchrony to ±16 ms, meaning that only the obtained asynchronies of 15° and 20° will fall outside a phase shift of 0°. There was no asynchrony observed here for an angular separation 90°, which did not replicate the findings of Clifford et al. (2003). They found a small but significant asynchrony between colour and orientation which was highest at the lowest alternation frequency tested, 1 Hz (with colour leading by approximately 50 ms), which may account for the differences in observed asynchronies. Furthermore, in their experiment, they used a monitor with a 100 Hz refresh rate which provided increased measurement accuracy.

3.6. Experiment 4B: Discrimination of colour-orientation conjunctions within a single presentation

3.6.1. Rationale

An evidence-accumulation model of the colour-motion binding process was introduced in the previous chapter discussion (Section 3.12), which described the perceptual binding as a choice made after accumulating enough sensory evidence over the temporal window in which the stimulus was displayed. The idea of gradually acquiring evidence for the correct feature combination over time is further explored in Experiments 4B and 5B. In Experiment 1B, it was demonstrated that surface segregation supports accurate conjunction discrimination in the 7.5-15 Hz frequency range. Given this, a remaining question is regarding the timescale of feature conjunction awareness. That is, can conjunction discrimination occur rapidly, within the initial presentations of a grating, or is it only over the course of the trial that evidence accumulates for a feature conjunction? Considering the timescale at which surface representations are formed will provide insight into the underlying nature of the binding process.

Here, only a single stimulus cycle is displayed on each trial, meaning that the trial duration of a more rapid alternation frequency was shorter than a slower alternation. If surface representations can be formed immediately, a similar pattern of results should be observed as in Experiment 1B for each angular separation. However, if surface segregation instead occurs gradually over time, conjunction discrimination should steadily increase as the alternation frequency decreases (and hence trial duration increases).

3.6.2. Experimental methods

3.6.2.1. Subjects

4 experienced psychophysical observers (all male, age range 25-29) participated in this experiment.

3.6.2.2. Visual stimuli

Identical stimuli and angular separations were used as in Experiment 1B (Figure 3.5a). However, as each grating was only shown once per trial, temporal alternation frequencies did not need to divide equally into 60 Hz. Therefore, frequencies of 1.25, 2.5, 3.75, 5, 6, 7.5, 10, 15 and 30 Hz were used. These frequencies corresponded to stimulus presentation durations of (excluding the stimulus mask) 33, 67, 100, 133, 167, 200, 300, 400, and 800 ms respectively. The previously unused frequency of 6 Hz was used to provide an intermediate frequency between 5 Hz (producing chance-level discrimination) and 7.5 Hz (supporting high discrimination).

Further, as it was possible that visual persistence could bias the conjunction discrimination of subjects, especially at higher alternation frequencies, a mask was used at the beginning and ends of each stimulus presentation. A 266 ms mask was used, rapidly displaying 8 chequered patterns in succession. These checks were the same as those used in Experiments 8B and 9B, as they had the advantage of containing the same colours as the gratings, without the associated colour-orientation information. These checks were always presented in an order that prevented any colour-orientation information from being integrated across presentations.

3.6.2.3. Design and procedure

Subjects completed 5 runs, each containing 8 repeats of each frequency-angular separation combination,presented in a random order. In total, subjects completed 1800 trials. Subjects were instructed to respond by keypress to each stimulus and report the orientation of the orange grating.

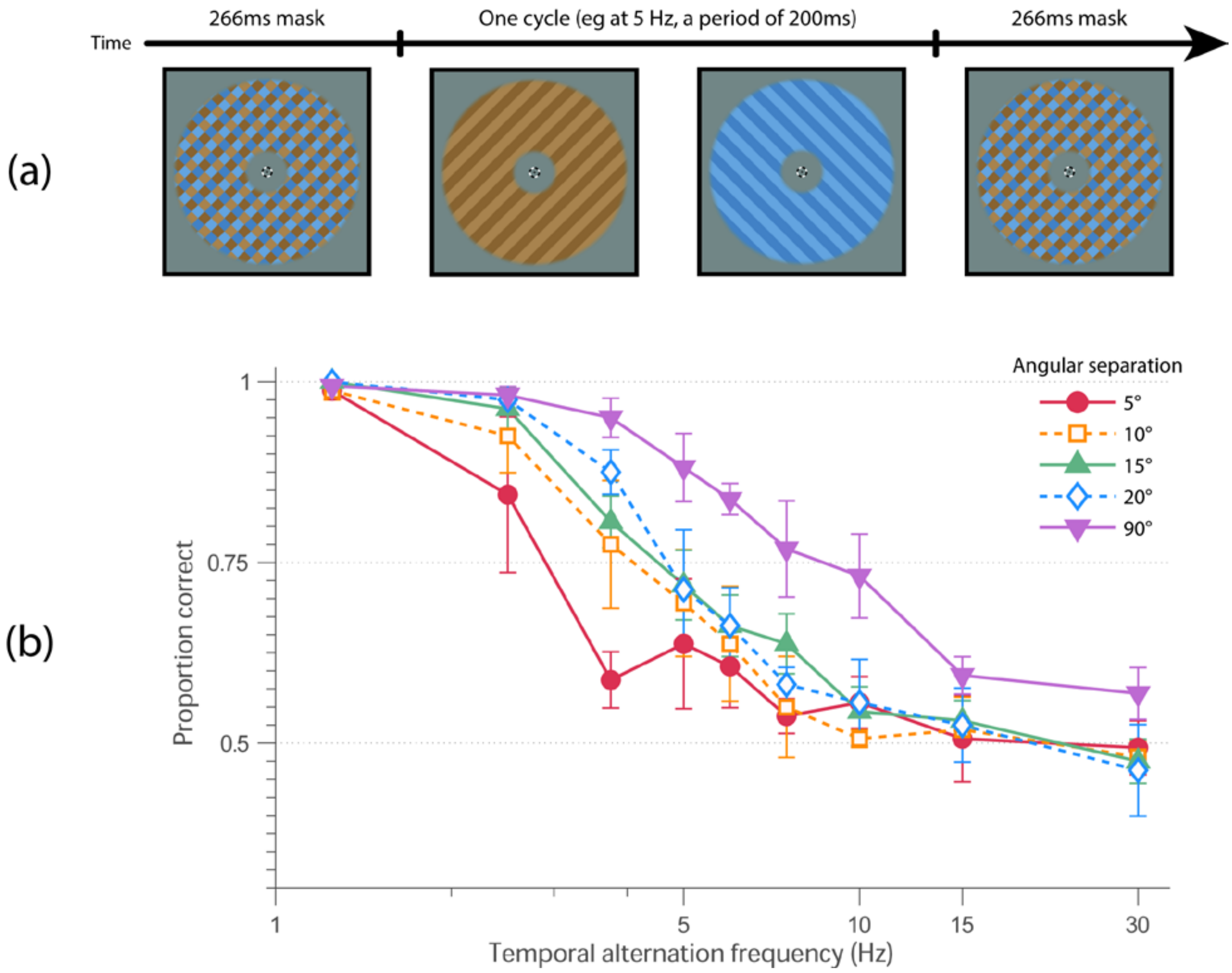

Figure 3.5. Stimulus design and results of Experiment 4B. (a) Stimulus trials always began and ended with a check mask containing the four colours used in the gratings. The duration of the mask remained the same, although the overall trial duration varied with temporal alternation frequency. After the mask, a grating of one colour was presented, followed by a grating of the other colour. Each grating was presented only once, with presentation durations varying according to the temporal alternation frequency being tested. For example, during the 5 Hz condition, completion of a full period took 200ms to complete. Therefore, both orange and blue gratings were presented for 100 ms each. **(b)** Mean colour-orientation conjunction discrimination across subjects (*n*=4) as a function of both the angular separation and the temporal alteration frequency. Error bars denote ±1 SEM.

3.6.3. Results and discussion

Across temporal alternation frequency, angular separation differentially affected conjunction discrimination (Figure 3.5b; $F_{4,12} = 13.56$, $p < 0.001$). Similar to previous experiments, an increased angular separation was associated with an overall improvement in conjunction discrimination (linear trend: $F_{1,3} = 15.86$, $p = 0.028$). The main effect of alternation frequency ($F_{8,24} = 29.10$, $p < 0.001$) is best qualified by the significant linear trend ($F_{1,3} = 121.95$, $p = 0.002$). That is, an increase in alternation frequency was associated with poorer conjunction discrimination as there was less time available in which to bind colour and orientation features together.

Angular separation interacted with alternation frequency to modify at what point conjunction discrimination fell to chance ($F_{32,96} = 1.85$, $p = 0.012$). That is, a larger angular separation approached chance at a higher alternation frequency. Furthermore, a higher angular separation was associated with a shallower conjunction discrimination slope. At lower alternation frequencies, conjunction discrimination was high and relatively similar across angular separations. However, as alternation frequency increased, a lower angular separation was associated with a sharper decline in conjunction discrimination. Therefore, it appears that when angular separation is higher, conjunction discrimination is not only more reliable, but also more rapid. Presumably, when surface segregation cues are less ambiguous, the feature conjunction can be extracted more rapidly.

Performance across all angular separations was at chance from 15-30 Hz. Despite the aforementioned rapid surface segregation, these results seem to suggest that repeated stimulus cycles are required at high alternation frequencies to allow for temporal integration. This hypothesis is tested in the following experiment, 5B, at a frequency that supports temporal integration (7.5 Hz), and one that does not (5 Hz).

3.7. Experiment 5B: Discrimination of colour-orientation conjunctions with increasing presentation durations

3.7.1. Rationale

In Experiment 1B, stimuli were displayed with a presentation period of 800 ms for all alternation frequencies, which allowed for accurate conjunction discrimination at 7.5 Hz, but not at 5 Hz. However, Experiment 4B demonstrated that conjunction discrimination at both 5 and 7.5 Hz are very similar across all angular separations. In order to explore the temporal dynamics of the surface segregation process, the number of stimulus cycles was varied at these two alternation frequencies: 5 and 7.5 Hz to provide several intermediate presentation periods between that of Experiment 4B and Experiment 1B. If surface segregation is possible at 7.5, but not 5 Hz, a corresponding pattern of results should be observed that matches Experiments 1B and 4B. That is, while 5 and 7.5 Hz stimuli produced similar conjunction discrimination at the lowest presentation period, increasing this period should only increase discrimination for the 7.5 Hz stimulus in order to match the results of Experiment 1B.

3.7.2. Experimental methods

3.7.2.1. Subjects

4 experienced psychophysical observers (all male, age range 25-29) participated in this experiment.

3.7.2.2. Visual stimuli

Stimuli used were similar to those used in Experiment 3B. Here, however, alternation frequency was fixed at either 5 Hz (Figure 3.6a) or 7.5 Hz (Figure 3.6b). The total presentation duration of the stimulus was instead varied and tested in conjunction with 5 angular separations (5°, 10°, 15°, 20°, 90°). The check mask used in Experiment 4B was presented here for 266 ms at the beginning and end of each trial.

3.7.2.3. Design and procedure

This experiment had a 5 ‘angular separation’ (5°, 10°, 15°, 20°, 90°) by 4 ‘presentation duration’ within subjects factorial design. For the 5 Hz alternation frequency condition, these presentation durations were 200, 400, 600, and 800 ms, corresponding to 1, 2, 3 and 4 full stimulus cycles respectively. 800 ms was used as it was the standard trial duration used in Experiment 1B (and onwards). For the 7.5 Hz alternation frequency condition, presentation durations were 133, 267, 400, and 800 ms corresponding to 1, 2, 3 and 6 stimulus repeats.

Subjects performed a colour-orientation binding task whereby they responded to the orientation of the orange grating. Subjects completed 10 experimental runs in total: 5 runs at a frequency of 5 Hz and another 5 at 7.5 Hz. Within runs, alternation frequency was not varied.

3.7.3. Results and discussion

Figure 3.6 displays the results of this experiment. At the 5 Hz temporal alternation frequency condition, there is a clear stratification of conjunction discrimination by angular separation (Figure 3.6a; $F_{4,12} = 30.72$, $p < 0.001$). Further, across presentation duration, a greater angular separation resulted in overall higher conjunction discrimination ($F_{1,3} = 131.64$, $p = 0.001$). While presentation duration had an overall effect on conjunction discrimination over angular separation ($F_{3,9} = 5.52$, $p = 0.02$), the corresponding linear trend did not reach significance ($F_{1,3} = 8.11$, $p = 0.065$). Furthermore, no significant interaction between angular separation and presentation duration was detected ($F_{12,36} = 1.88$, $p = 0.07$).

Comparatively, significant main effects and interactions were found at an alternation frequency of 7.5 Hz (Figure 3.6b). A larger angular separation was associated with higher conjunction discrimination across presentation duration (main effect: $F_{4,12} = 40.10$, $p < 0.001$; linear trend: $F_{1,3} = 161.58$, $p = 0.001$). Across angular separation, a main effect of presentation duration was evident ($F_{3,9} = 26.28$, $p < 0.001$), such that an increase in presentation duration resulted in a significant improvement in conjunction discrimination (linear trend: $F_{1,3} = 182.03$, $p = 0.001$). Angular separation and presentation duration interacted to affect conjunction discrimination

($F_{12,36} = 4.89$, $p < 0.001$). Improvements in conjunction discrimination as a function of increasing presentation duration occurred more rapidly for larger angular separations.

Together, these results suggest that the effect of presentation duration on conjunction discrimination depend on the temporal integration afforded by a longer presentation time, which in turn may be associated with surface segregation. At 5 Hz, discrimination only slightly improves when presentation duration is lengthened. Here, the alternation frequency cannot alone support surface segregation. Thus, conjunction discrimination remains relatively stable across presentation duration; temporal integration is not occurring, thus rendering the increased presentation duration ineffectual. At 5 Hz, if accurate conjunction discrimination is to occur, it happens within the first stimulus cycle, i.e. at 125ms. Given an unambiguous surface segregation cue like an orthogonal angular separation, surface segregation can occur rapidly.

At 7.5 Hz, where conjunction discrimination is not at ceiling, a longer presentation duration positively affects conjunction discrimination in all but the 5° angular separation. Experiment 1B demonstrated that the 7.5 Hz frequency supports both surface segregation and temporal integration, as evidenced by the increase in discrimination from 5 to 7.5 Hz. Thus, it follows that a longer presentation duration will increase conjunction discrimination here. The extended duration may allow for a higher amount of temporal integration of the stimuli, which in turn enhances the segregation of the display into individual surfaces.

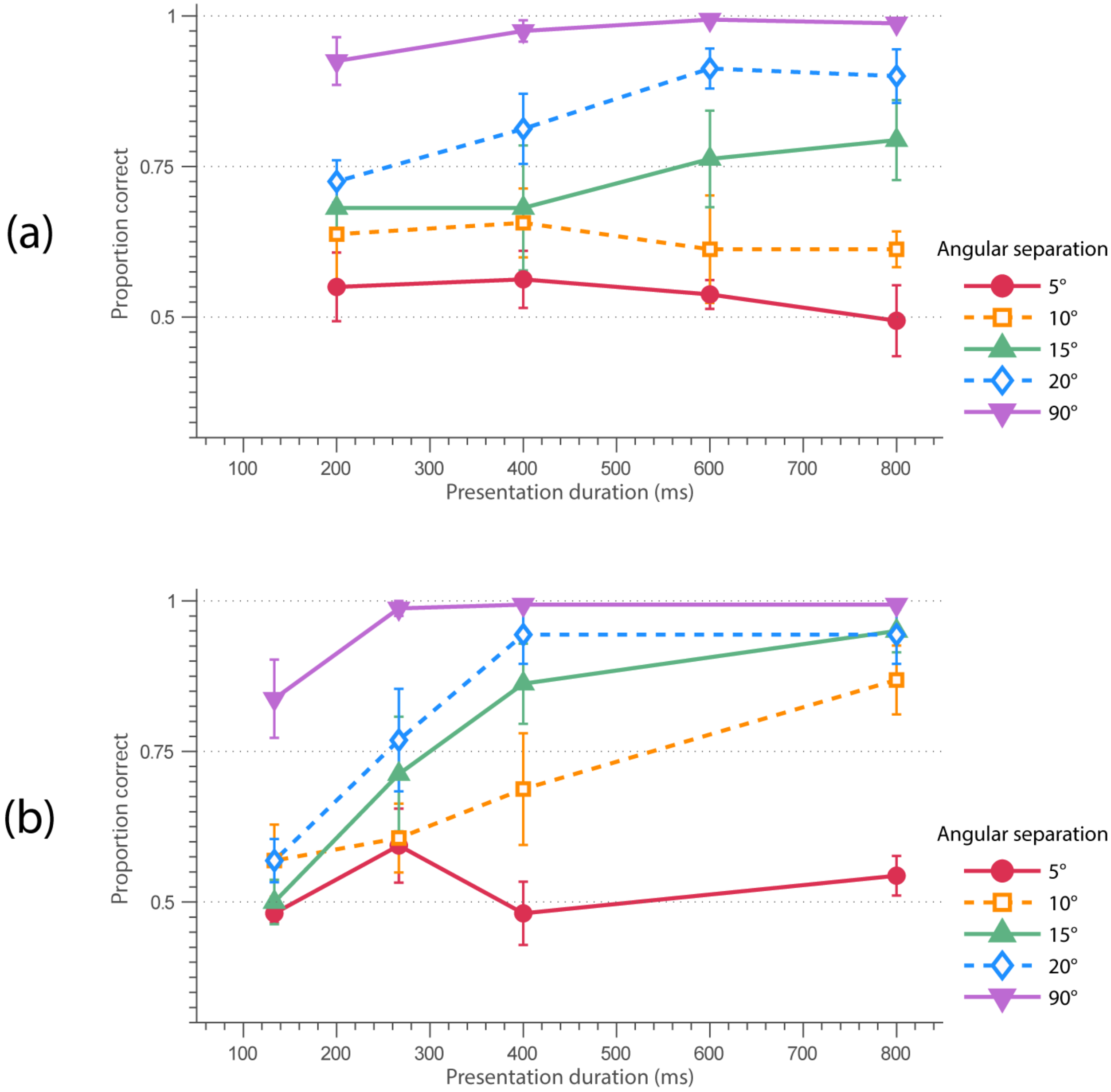

Figure 3.6. Results of Experiment 5B. Mean colour-orientation conjunction discrimination across subjects (*n*=4) at a temporal alternation frequency of **(a)** 5 Hz and **(b)** 7.5 Hz. Discrimination is expressed as a function of both the angular separation and the presentation duration of the stimulus. Error bars denote ±1 SEM.

3.8. Experiment 6B: Discrimination of motion-orientation conjunctions

3.8.1. Rationale

The general trend across Experiments 1B to 5B was that an orthogonal pair of gratings allows for highly accurate conjunction discrimination in a manner independent of the temporal alternation frequency. Conversely, colour-motion displays presented at a 5 Hz alternation frequency generate chance conjunction discrimination, as demonstrated in Experiments 1A-3A and Moradi and Shimojo (2004). The differences in conjunction discrimination between the two displays could be attributable to either motion or orientation. A potential hypothesis is that a large angular separation may permit rapid and accurate surface segregation even when paired with motion. This is tested using a novel motion-orientation binding task, removing any colour-based surface segregation cues (Experiment 9A; Edwards & Badcock, 1996; Mitchell et al., 2003; Stoner & Blanc, 2010; Valdes-Sosa et al., 2000). If a large angular separation can facilitate surface segregation, accurate conjunction discrimination should be observed at 5 Hz. Conversely, a specific 5 Hz deficiency as per the experiments in Chapter 2 would indicate that motion has a stronger bearing on the perceptual interpretation of a stimulus.

3.8.2. Experimental method

3.8.2.1. Subjects

5 experienced psychophysical observers (4 male, age range 25-29) participated in this experiment.

3.8.2.2. Visual stimuli

Square wave gratings were used with identical spatial characteristics to previous experiments (Figure 3.7a). However, both gratings were composed of alternate light and dark grey strips instead of orange and blue. These gratings were assigned opposite tilts and directions of motion on a trial-by trial basis. Furthermore, these pairings were independent across trials such that the left-tilted grating was equally likely to be moving left or right. Temporal alternation between gratings occurred at one of several frequencies, and while on-screen, a grating translated in the assigned direction.

3.8.2.3. Design and procedure

This experiment had a 5 ‘angular separation’ (5°, 10°, 15°, 20°, 90°) by 8 ‘temporal alternation frequency’ (1.25, 2.5, 3.75, 5, 7.5, 10, 15, and 30 Hz) within subjects factorial design. Subjects performed a motion-orientation binding task whereby they reported the motion direction of the right tilted grating. As there was a potential to confuse responses (as orientation and motion were both defined in terms of left and right), subjects performed a practice run with auditory feedback. Subjects completed 5 runs (not including the practice run), with 40 repeats for each angular separation and alternation frequency combination distributed equally across the 5 runs.

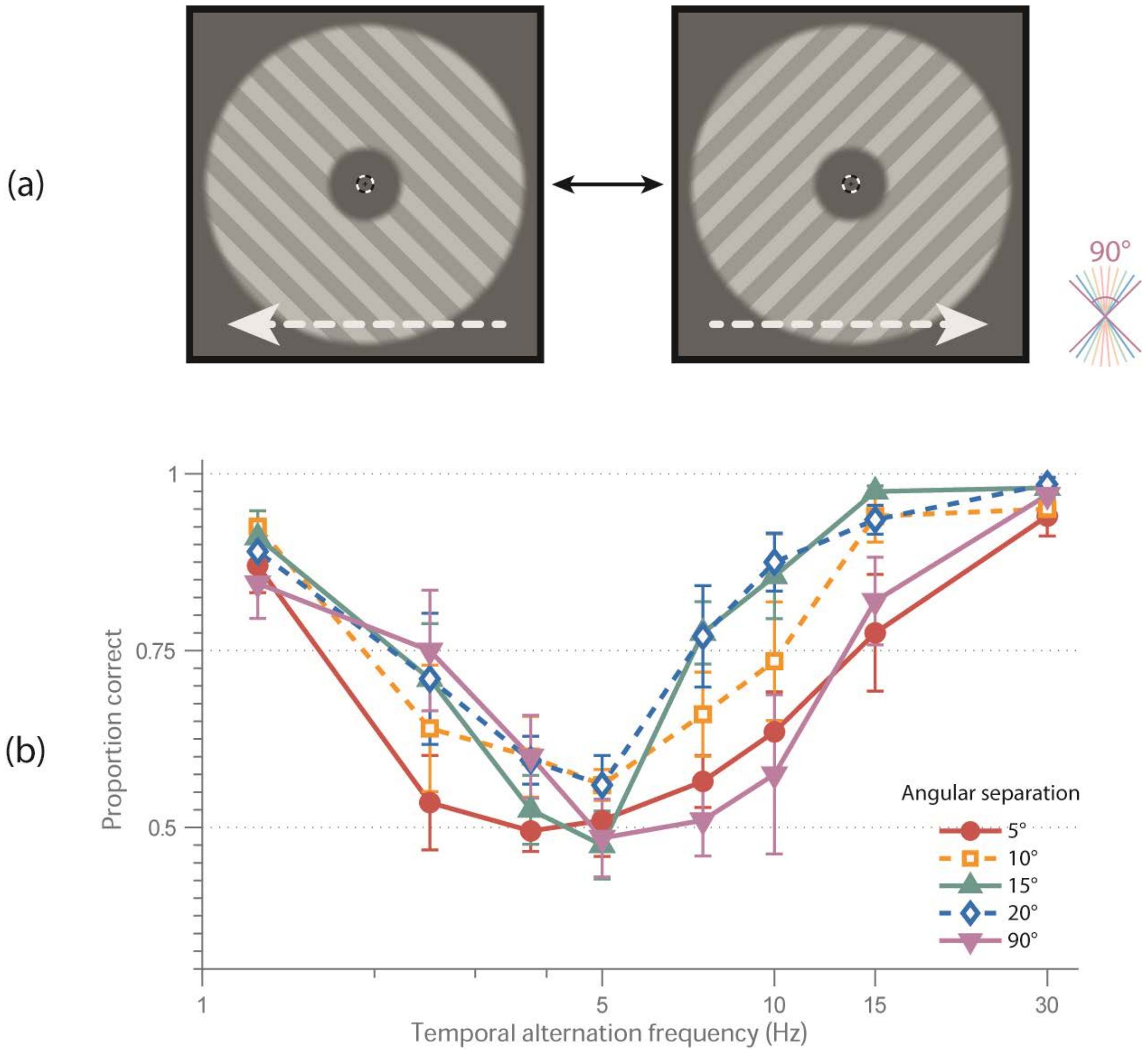

Figure 3.7. Stimulus design and results of Experiment 6B. (a) Alternations between two tilted monochrome gratings assigned opposite directions of motion were presented. Variations in temporal alternation and angular separation were assessed. **(b)** Mean motion-orientation conjunction discrimination across subjects (*n*=5) as a function of both the angular separation and the temporal alteration frequency. Error bars denote ±1 SEM.

3.8.3. Results and discussion

The aim of this experiment was to investigate the effects of angular separation on motion-orientation conjunction discrimination (Figure 3.7b), and draw a comparison to the ways that angular separation affects colour-orientation feature binding. While there was a main effect of angular separation ($F_{4,16} = 6.31$, $p = 0.003$), a systematic increase in angular separation was not associated with a corresponding increase in conjunction discrimination (linear trend: $F_{1,4} = 0.70$, $p = 0.45$). Similarly, while a significant interaction between angular separation and alternation frequency was present ($F_{28,112} = 2.40$, $p = 0.001$), there was no evidence that angular separation systematically affected conjunction discrimination (linear interaction: $F_{1,4} = 0.436$, $p = 0.55$).

Across angular separation, the main effect of temporal alternation frequency ($F_{7,28} = 30.07$, $p < 0.001$) exhibited a significant quadratic trend ($F_{1,4} = 139.95$, $p < 0.001$). In contrast to the pattern of results in Experiment 1B (Figure 3.2c), this set of data more closely resembled the data observed in the colour-motion experiments of Chapter 2 . That is, conjunction discrimination across all angular separations was close to ceiling at the lowest (1.25 Hz) and highest (30 Hz) frequencies tested. However, approaching 5 Hz, conjunction discrimination dropped to chance.

Overall, the results of this experiment suggest that an orthogonal set of gratings is not sufficient to generate surface segregation, and thus accurate conjunction discrimination, at 5 Hz. However, the reasons behind this are speculative. One can speculate that the removal of colour may be a factor, although its weak effect on surface segregation cannot completely account for these results (Experiment 9A, Edwards & Badcock, 1996; Mitchell et al., 2003; Stoner & Blanc, 2010; Valdes-Sosa et al., 2000). More likely is that the addition of motion into this display adversely affected perceptual segregation of each grating. A primary source of task difficulty in the previous experiments of this chapter was the lack of surface segregation at 5 Hz when combined with a low angular separation. The apparent motion of rapidly alternating, gratings at a low angular separation may have generated the impression of a single surface rotating and changing colour (Green, 1986). In this experiment, however, the physical motion of each grating provides a potentially stronger source of confusion at all angular separations in a similar manner. That is, in a manner similar to the colour-motion displays in Chapter 2, displaying a pair of gratings alternating in motion here may generate the impression of a single surface alternating in both motion and orientation.

3.9. Experiment 7B: Discrimination of spatially segregated colour-orientation conjunctions

3.9.1. Rationale

Conjunction discrimination appears to operate in a serial manner at low frequencies (Nakayama & Silverman, 1986; Poisson & Wilkinson, 1992; Treisman & Gelade, 1980; Treisman & Sato, 1990). It follows then, that surface segregation would provide a negligible perceptual advantage when identifying feature pairs at these low frequencies. Nevertheless, as the experiments in Chapter 2 (1A, 2A, 4A, 5A, 7A, 8A) and 3 (1B, 5B, 6B) have demonstrated, surface segregation most likely provides an advantage to accurate discrimination at higher frequencies. Therefore, to study the underlying feature binding process, it must first be isolated from any effects of surface segregation. Here, Experiment 7B used a stimulus where the colour and orientation features were segregated spatially (e.g. Fujisaki & Nishida, 2010; Holcombe & Cavanagh, 2001; Karlsen et al., 2010), as features that are not co-located cannot produce the impression of a single surface. In such an arrangement, the temporal coincidence of the colour and orientation pairings remains unchanged from Experiments 1B and 2B, but now accurate conjunction discrimination can no longer be supported by the formation of transparent surface representations.

3.9.2. Experimental methods

3.9.2.1. Subjects

A subset of five of the same six subjects who participated in Experiment 1B also took part in Experiment 7B (4 male; age range 22-29).

3.9.2.2. Visual stimuli

The annulus in this experiment was divided along the horizontal meridian (Figure 3.8a). In one half, a grey square-wave grating was displayed, while in the other, a solid block of colour was displayed. Gratings had identical physical properties to those in Experiment 1B (luminance, spatial frequency, and angular separation), but here they were grey. The block of colour was either orange (CIE: x = 0.33, y = 0.36) or blue (CIE: x = 0.24, y = 0.28) with a luminance of 26

Cd m^{-2}. Both halves of the display alternated simultaneously at one of several temporal alternation frequencies. Each half was separated vertically by a 1.5° gap, plus a raised cosine contrast ramp of 0.84°. The grating always alternated between left and right tilted, and the block of colour always alternated between blue and orange. Each condition was counterbalanced for orientation and colour location: that is, each feature would be assigned to the upper or lower portion of the annulus on each trial.

3.9.2.3. Design and procedure

As in Experiment 1B, subjects performed a colour-orientation ‘binding’ task where they reported the tilt of the grey grating that was paired with the orange block of colour. A 5 ‘angular separation’ (5°, 10°, 15°, 20°, and 90°) × 8 ‘temporal alternation frequency’ (1.25, 2.5, 3.75, 5, 7.5, 10, 15, and 30 Hz) within-subjects factorial design was also employed. Subjects performed 5 repeat runs for a total of 40 trials per condition. In addition to onset frame and colour-orientation pairing, location (upper or lower) of orientation and colour were also counterbalanced.

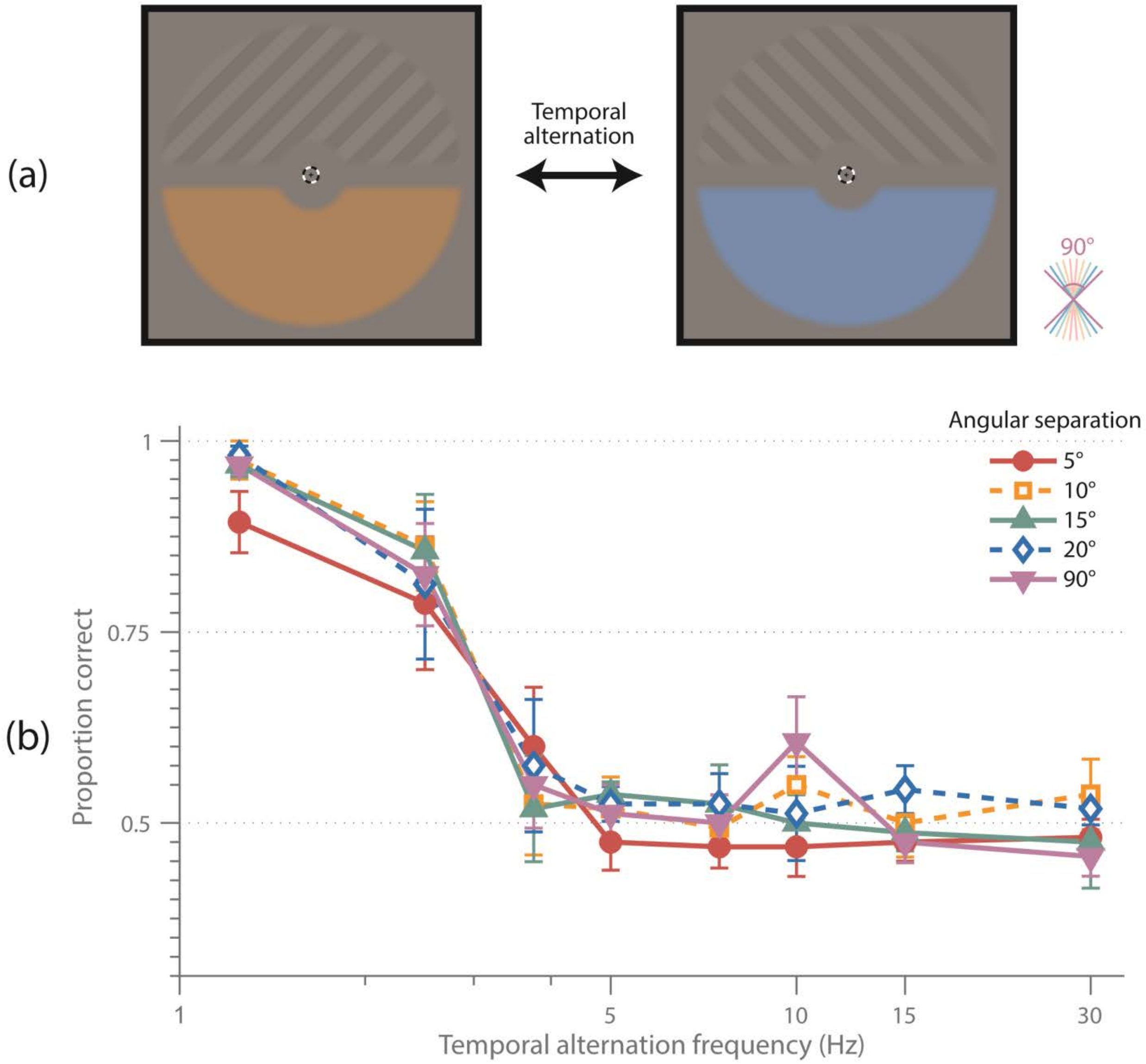

Figure 3.8. Stimulus design and results of Experiment 7B. (a) A grey square-wave grating and a solid block of colour temporally alternated in orientation and colour, respectively. Subjects reported the colour-orientation pairing. Gratings were again presented at one of 5 angular separations (90° in this example; shown in purple). **(b)** Mean colour-orientation conjunction discrimination across subjects (*n*=5) as a function of both the angular separation and the temporal alteration frequency. Error bars denote ±1 SEM.

3.9.3. Results and discussion

The results of separating colour and orientation are displayed in Figure 3.8b. Using a two-way repeated measures ANOVA, accurate conjunction discrimination was possible for temporal frequencies below 5 Hz (main effect of alternation frequency: $F_{7,32} = 25.31$, $p < 0.001$), qualitatively matching the results of Experiment 1B at lower alternation frequencies (Figure 3.2c). However, from 5 Hz and beyond, conjunction discrimination remained at chance for all angular separations and did not systematically increase within the 7.5-15 Hz range. Furthermore, there was no significant main effect of angular separation ($F_{4,12} = 1.83$, $p = 0.24$) or angular separation by alternation frequency interaction ($F_{28,84} = 0.79$, $p = 0.52$). The non-significant main effect of angular separation indicates that the discrimination of a left from a right-tilted grating was not a factor influencing task difficulty in Experiment 1B.

The spatially segregated stimulus used here provides results in line with traditional thinking on feature binding. That is, the identification of features and assuring their temporal coincidence is a process with a relatively low temporal resolution (Holcombe, 2009; Treisman, 1998; Treisman & Gelade, 1980). Despite a high temporal alternation frequency, surface segregation was not possible here as colour and orientation attributes were not spatially co-located (Holcombe, 2001), and thus accurate conjunction discrimination was not supported at intermediate alternation frequencies as it was in Experiment 1B. However, it is demonstrated in Experiment 8B that this low resolution can be overcome if the gratings are perceived as separate, transparent surfaces.

3.10. Experiment 8B: Discrimination of temporally-distributed colour-orientation conjunctions

3.10.1. Rationale

Experiment 7B examined colour-orientation binding processes in a stimulus where the two features were not conjoined at overlapping spatial locations, but were present at the same point in time. In Experiment 8B, a stimulus is introduced where the colour-orientation conjunction information is distributed over two check patterns. Here, colour and orientation features are not paired either spatially or temporally, but rather distributed equally in a chequered manner. Upon an extended inspection of a single check pattern, subjects would identify that the orange and blue squares are arranged such that there is no left- or rightward tilt bias, producing chance-level discrimination (Figure 3.9b). Instead of relying on spatial and temporal coincidence as was the case in Experiments 1 and 3, the colour and orientation pairing here can only be found through grouping by colour over time across check patterns. Grouping the same colour across both check patterns in this way produces gratings identical to those previously used, thus revealing the associated orientation.

The logic of this display is similar to that used in Holcombe (2001), who used a display separated into two halves with differing luminances in each half. When each half varied in luminance simultaneously at a high alternation frequency (14 Hz), subjects tended to group gratings by luminance, rather than by their physical, temporal coincidence. J. Watanabe and

Nishida (2007) used a stimulus with temporally and spatially alternating red and green patches. Given an equal distance between colours, as is the case in this experiment, subjects tend to integrate across the same colour. In this way, the effect of transparent surface segregation on conjunction discrimination can be isolated from the low-resolution feature binding processes measured in Experiment 7B. In addition, another prediction from Holcombe and Cavanagh (2001) can be tested. If feature pairs are coded in conjunction at an early stage, accurate conjunction discrimination should not be supported in this type of display. Thus, the existence of a high-resolution feature binding mechanism that detects spatially co-located pairs of features should result in low conjunction discrimination across all alternation frequencies.

3.10.2. Experimental methods

3.10.2.1. Subjects

Five experienced psychophysical subjects (3 male; age range 22–46), including the author, two other experimenters, and two naïve subjects participated in this experiment.

3.10.2.2. Visual stimuli

Two types of stimuli were used here. The grating display was identical to the 90° condition in Experiment 1B (Figure 3.9a). The check display contained the same colour-orientation conjunction information as the grating display, but was distributed temporally over two blue-orange checked stimuli (Figure 3.9b). Both displays and both colour-orientation pairings summed to an identical grey plaid (Figure 3.9c).

Unlike the grating display, the colour-orientation conjunction in the check display was not available within a single half-cycle of the stimulus. However, colour information can be extracted and grouped together temporally across a full stimulus cycle. If colours are grouped in this way, subjects would be left with the perception of coherent, oriented strips as per the grating condition. In this way, although the time-averaged information in the grating and check displays was the same (e.g. Figure 3.9c), the check stimulus required temporal transparency in order for the conjunction information to be extracted.

3.10.2.3. Design and procedure

This experiment employed a 2 ‘display type’ (grating, check) × 8 ‘temporal alternation frequency’ (1.25, 2.5, 3.75, 5, 7.5, 10, 15, and 30 Hz) within-subjects factorial design was employed. As in Experiments 1 and 3, subjects performed a colour-orientation ‘binding’ task for both grating and check displays. However, subjects’ conjunction discrimination for the check display was a measure of how temporal integration interacted with the check stimulus to produce the perception of a conjunction. An accurately perceived check display would reveal no left or right tilt for each colour by design, which was predicted to be the case at low alternation frequencies. However, rapid alternations between check displays may instead bias subjects’ perception of the stimulus, but only if similar colours tended to be perceptually grouped over time as per surface segregation. Thus, for the check display, the measured ‘proportion of correct conjunction discrimination responses’ was in fact measure of how well subjects identified the spatial and temporal relationships between individual check patterns.

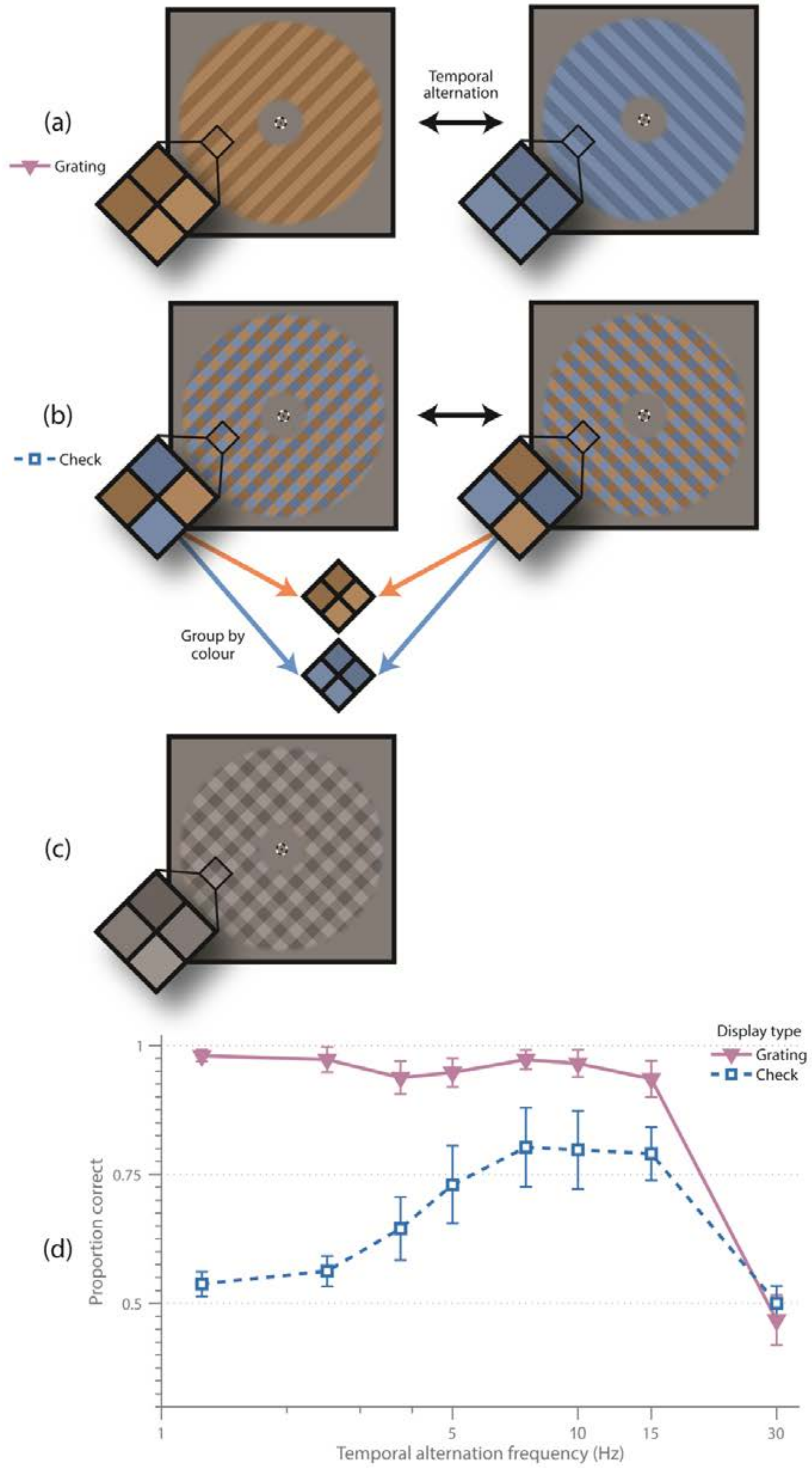
(a)
Grating
Temporal alternation
(b)
Check
Group by colour
(c)
(d)
Display type
Grating
Check
Proportion correct
1
0.75
0.5
1
5
10
15
30
Temporal alternation frequency (Hz)

Figure 3.9. Stimulus design and results of Experiment 8B. (a) Grating stimuli were identical to those used in Experiment 1B. In this experiment however, only angular separations of 90° were used. **(b)** Check stimuli were designed such that only grouping by colour across time revealed the colour-orientation pairing, as demonstrated in the micro-pattern portion. For both **a** and **b**, subjects reported the tilt of the orientation (left or right) associated with orange. **(c)** As in Experiment 1B, both grating and check stimuli summed physically to an achromatic plaid wherein the display type was masked, and the colour-orientation pairing information lost. **(d)** Mean colour-orientation conjunction discrimination across subjects (*n*=5) for both grating and check displays at each temporal alteration frequency. Error bars denote ±1 SEM.

3.10.3. Results and discussion

In Experiment 7B the temporal coincidence of colour and orientation features in the check stimulus was removed such that the conjunction information was not available within a single half-cycle of the stimulus (Figure 3.8b). Extraction of the feature conjunction necessitated the temporal integration of feature information. Thus the isolated, temporal profile of the feature binding process acting on segregated, transparent surface representations was observed.

Figure 3.9d shows two conditions: the novel check display (blue squares) and a condition identical to the orthogonal grating condition in Experiment 1B (purple triangles in both experiments). A two-way repeated measures ANOVA indicated a significant linear interaction between the stimulus display type (perpendicular grating vs. check) and the temporal frequency ($F_{1,4} = 182.31$, $p < 0.001$), in addition to main effects of both stimulus display type ($F_{1,4} = 53.23$, $p = 0.002$) and temporal frequency ($F_{1,4} = 28.23$, $p < 0.001$). Similar to the results of Experiment 1B, at the highest frequency tested (30 Hz), the checks were indistinguishable from a plaid (Figure 1c) and conjunction discrimination fell to chance for both display types. Apart from this, reliable discrimination of the colour-orientation conjunctions was possible in both the perpendicular grating and check displays, but only within an intermediate range of temporal frequencies for the checks (around 7.5-15 Hz). Similar to Experiment 1B, at the highest frequency tested (30 Hz), the checks were indistinguishable from a plaid (Figure 3.2c) and conjunction discrimination fell to chance for both display types. At the lowest frequencies tested (1.25-2.5 Hz), the conjunction could still be reliably discriminated in the grating display, but not the check display. The lower alternation frequency here was not sufficient to facilitate temporal integration. Given that Clifford et al. (2003) found evidence for a small asynchrony between colour and orientation processing, the results observed here reflect the time required by the visual system to identify and process both features individually.

Here the check display was compared to an orthogonal set of gratings (e.g. the 90° angular separation in Experiment 1). The linear interaction reported here is not likely due to an artefact of the ceiling performance observed in the grating display type in this experiment. A repeated measures ANOVA between the check display and any of the angular separations from Experiment 1 also produced statistically significant linear interactions (e.g. 15° and checks: $F_{1,4} = 43.20$, $p = 0.003$). The comparisons between Experiments 1A and 4A, where performance was not always at ceiling, and the comparison between display types within Experiment 4A both provide statistically significant linear interaction effects. These indicate that the reduction in discrimination differences between grating and check display types is better accounted for by a similarity in the way that alternation frequency affected the perception of each display type.

The check display viewed at an intermediate range of frequencies (7.5-15 Hz) enabled accurate reporting of conjunctions on average over 80% of the time. That the conjunction discrimination did not reach ceiling here potentially suggests the spatial coincidence of colour and orientation (within one half-cycle) provides additional cues for accurate discrimination. Nevertheless, the check display demonstrated that conjunction discrimination was only possible within the specific range of temporal frequencies supporting temporal transparency: too slow an alternation would impede the integration of the feature information over time while too rapid an alternation would cause the checks to fuse perceptually into a static plaid in the same way as the gratings (Figure 3.9c). Accurate conjunction discrimination within this range also indicated that the temporal transparency percept was one where check displays were grouped by colour, instead of them being perceived as two individual check patterns – a tendency associated with surface segregation (Watt & Phillips, 2000). That the grating and check data tended to converge as the alternation frequency increased suggests that similar strategies were being used in both displays. That is, a higher alternation frequency facilitated temporal integration, resulting in an extended window in which colour-orientation pairs could be ascertained. The way in which this process may occur is addressed in both the Chapter Discussion (Section 3.12) and General Discussion (Chapter 4).

3.11. Experiment 9B: Decoding colour-orientation conjunctions in human early visual areas

3.11.1. Rationale

In Experiment 8B, a unique stimulus and ‘binding’ task was developed in order to isolate the effect of temporal integration on feature binding. Furthermore, although the colour-orientation conjunction was present in the stimulus, it was imperceptible at slower alternation frequencies.

Thus, having established the conditions under which bound features could and could not be perceived accurately (while still keeping the conjunction present in all conditions), the stimulus was next adapted to an fMRI paradigm. Through multivariate analysis, neural activity could be assessed in two ways. Firstly, patterns of neural activity were tested to identify if the combination of orange-left and blue-right feature pairs could be distinguished from orange-right and blue-left. Second, the coding of one feature pair was tested to see if it generalised across conditions. Using these approaches, it can be determined if decoding of neural activity requires perceptual awareness of the conjunction in early visual areas: fMRI results were compared from conditions in which conjunctions are perceptually visible (2.5 and 7.5 Hz gratings, 7.5 Hz checks) to the one where the conjunction was invisible (2.5 Hz checks), based on the findings of Experiment 8B.

3.11.2. Experimental methods

3.11.2.1. Subjects

The same 5 experienced psychophysical subjects (3 male, age range: 25-46) as in Experiment 8B took part in this experiment. All subjects have had previous experienced being scanned in this manner. Visual correction in the MRI scanner took the form of prescription squash goggles. The experimental protocol was approved by the University of Sydney Human Research Ethics Committee.

3.11.2.2. Apparatus

Data were collected using a Philips Achieva 3T TX scanner (Philips, Amsterdam) with a whole head coil. A field-echo echo-planar imaging (FEEPI) pulse sequence was used to acquire T_2*-weighted functional MR images of blood oxygenation level-dependent (BOLD) contrast. The FEEPI protocol was defined according to the following parameters: time to echo (TE) = 32 ms, time to repetition (TR) = 3000 ms, flip angle = 90°, field of view = 69 × 192 × 192 mm, matrix = 128 × 128, voxel size = 1.5 mm (isotropic). The images were acquired in 46 interleaved ascending slices (1.5 mm thickness) in a tilted coronal plane that covered the entire occipital cortex as well as a portion of the posterior parietal and temporal lobes. In addition to the functional scans, a whole-head structural MR image (voxel size = 1 mm isotropic) was obtained for each subject within each experimental scanning session for co-registration purposes, using a turbo field echo protocol for optimal grey and white matter contrast.

Stimuli were generated on a Dell Precision M4400 laptop with an nVidia Quadro FX 1700M display adapter and displayed on an MR-compatible “BOLDscreen” liquid crystal display (Cambridge Research Systems) via a fibre optic DVI cable. The BOLDscreen had a resolution of 1920 × 1200 pixels, a refresh rate of 60 Hz and a mean luminance of 147.9 Cd/m^2 and was calibrated with measurements obtained via a PR-670 SpectraScan spectrophotometer (Photo Research Inc.). Images were viewed at a total distance of 121.5 cm through a rear-facing first surface mirror mounted upon the head coil, giving a viewing angle of 15.2° (0.013° per pixel). The subjects’ behavioural responses during scanning were collected via an MR-compatible LU400-PAIR Lumina response pad (Cedrus, San Pedro, CA).

3.11.2.3. Visual stimuli

Stimuli were identical to Experiment 8B.

3.11.2.4. Design and procedure

This experiment was a 2 ‘stimulus display type’ (gratings/checks) × 2 ‘temporal alternation frequency’ (2.5 and 7.5 Hz) within-subjects block design. In Experiment 8B, it was observed that there was a large conjunction discrimination difference when viewing temporally alternating checks at 2.5 and 7.5 Hz. These values were chosen to maximise the perceptual differences of the stimulus. Further, as temporal alternation frequency itself could be a confounding factor, the same two frequencies were paired with the orthogonal grating display used in the previous experiments, for a total of 4 different conditions.

Stimuli were presented in counterbalanced blocks of 15 seconds, aligned with 5 volume acquisitions (3000 ms each). Stimuli were continuously presented during each block with a 500 ms raised cosine contrast ramp over their onset and offset. Block order was counterbalanced both between and within runs. Stimulus blocks were presented in groups of four, separated by 15 second fixation-only blocks. Each condition was presented 4 times per run, for a total of 21 blocks per run. Runs lasted for 315 seconds, and subjects viewed 12 runs in total.

To control for attention and fixation, subjects performed an attentionally-demanding dimming task throughout each run (Figure 3.10). In order to confirm that subjects were fixating and keeping their spatial attention directed at the fixation spot, mutual information analysis was performed in order to determine the correlation between stimulus and response. In the centre of the display, the fixation cross alternated between black and grey on average every 1500 ms, jittered randomly by ± 500 ms. Subjects indicated (by holding down one of the two buttons on the response pad) the current state of the fixation cross (dimmed or not dimmed). Button press data was used to quantify participants' ability to maintain fixation during their time in the scanner.

Button-press data for the attention task at fixation were assessed using a mutual information (MI) analysis, given in Equation 6:

$$MI = \sum_{r,s} p(s)\, p(r \mid s) \log_2 \frac{p(r \mid s)}{p(s)} \tag{6}$$

where $p(r)$ is the probability of a response, $p(r|s)$ is the probability of a response given the stimulus, and MI is expressed in bits of information. Response data were time-shifted with respect to the time course of the fixation cross luminance change in order to find the lag (approximating reaction time) at which the maximal amount of mutual information was provided. Mutual information was then converted to efficiency, given in Equation 7:

$$Efficiency = \frac{100 \times MI}{H(s)} \tag{7}$$

where $H(s)$ is the entropy of the stimulus display train, defined in Equation 8 as:

$$H(s) = -\sum_{s} p(s) \log_2 p(s) \tag{8}$$

Efficiency denotes the degree to which the stimulus predicts the response, with a higher efficiency indicating a better correspondence between stimulus and response time courses, reflecting appropriate fixation and spatial attention directed towards the fixation spot.

Measured at a resolution of 60 Hz, the minimum efficiency in a single run averaged across subjects was 33.4% (*SD* = 10.1%), and the maximum was 61.6% (*SD* = 3.4%) (Figure 3.10). Minimum efficiencies were well above chance, suggesting subjects were fixating and attending to the fixation task across all runs of the study. If subjects were responding at random in the fixation task, efficiency close to 0% would be expected.

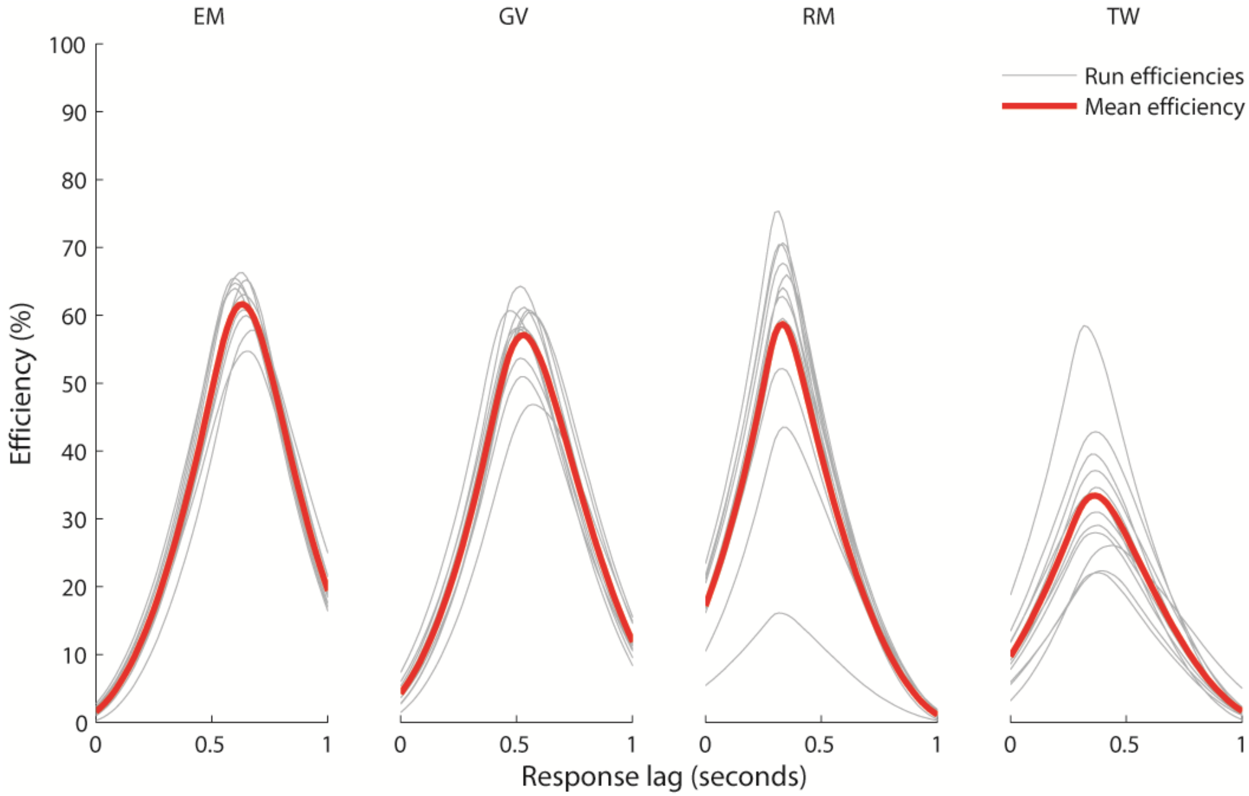

Figure 3.10. Individual run and mean efficiencies on the fixation task. Fixation task performance (*n*=4) is presented on a per-subject basis. Thin grey lines indicate the efficiency score for one subject on one run. Red lines indicate the mean efficiency for one subject averaged over 12 runs. The locations of the peak mean efficiency on the x-axis represent subjects' mean reaction times. Subject CC's data is not displayed as an error prevented recording of button-press data.

3.11.2.5. Retinotopic mapping/definition of ROIs

In prior scanning sessions, both functional and high-resolution anatomical scans were acquired for each subject. An average anatomical image was prepared consisting of whole-head sagittal and transverse images (voxel size = 1 mm isotropic) and a higher-resolution partial coronal image (voxel size = 0.75 mm isotropic) of the caudal brain to maximize anatomical detail in the occipital lobes. Before averaging, the images were aligned using normalized mutual information-based coregistration, inhomogeneity corrected (Manjon et al., 2007), and normalized according to their peak white matter intensities and resampled (where necessary) to a voxel size of 0.75 mm (isotropic). The average anatomical image of each subject was then segmented using the automatic algorithms of ITK-SNAP (www.itksnap.org; Yushkevich et al., 2006) and mrGray (Teo et al., 1997), supplemented with careful manual editing.

Functional scans were obtained of subjects viewing clockwise/counter clockwise rotating wedges and expanding/contracting ring stimuli as described in Wandell et al. (2007). Data were coregistered through SPM5 (www.fil.ion.ucl.ac.uk/spm/software/spm5/; K J Friston et al., 2007) and organized into ROIs. The maximal activations of each voxel to the wedge stimuli was then used to generate a polar angle map of the visual cortex using the best-fitting sinusoid for the time course of each voxel (Larsson & Heeger, 2006). From this map, visual areas were manually defined in mrVista (white.stanford.edu/software).

Functionally defined early visual cortex was delineated for each subject using the nomenclature and criteria of Wandell et al. (2007) and Larsson and Heeger (2006), in the same manner as previous studies from this laboratory (e.g. Supplementary Figure 1 in Mannion et al., 2010). According to this scheme, areas V1-V3 and hV4 share a foveal representation at the occipital pole, whereas V3A and V3B (which were not separated in this analysis) share a dorsal foveal representation and border the dorsal portion of V3. Area hV4 was defined as a hemifield representation of the contralateral visual field bordering the ventral portion of V3 (Goddard et al., 2011). In separate localizer scans, area V5/MT+ was localized as a region of lateral visual cortex in the ascending limb of the inferior temporal sulcus responding to coherently moving versus static random dot stimuli presented at low contrast (Dumoulin et al., 2000).

3.11.2.6. Analysis

Neural activity was measured in retinotopically-defined striate (V1) and extrastriate visual cortex (V2, V3, V3AB, and hV4). Multivariate pattern analysis (MVPA) techniques were used to decode different combinations of colour and orientation within each perpendicular grating and check display. This allowed us to probe the representation of feature conjunctions under conditions where the conjunction could be reliably discriminated and hence “bound” (as measured in the binding task of Experiment 8B), compared to those where it could not. To determine whether the classifier could decode feature conjunctions from a given visual area reliably above chance, 1-sample *t*-tests were performed on the mean decoding performance across the four stimulus conditions for the five subjects.

A generalized linear model (GLM) contrast of fixation vs. all stimulus blocks was first performed, using SPM5 (http://www.fil.ion.ucl.ac.uk/spm/software/spm5/). Only those voxels within each ROI that gave a significant response ($p < 0.05$, 1-tailed, uncorrected) to the stimulus over baseline in the t-map of activations were selected for further multivariate analyses (see below). Note that this contrast is orthogonal to those between the stimulus conditions of interest. The mean number of voxels in each ROI before and after masking are given in Figure 3.11. After masking ROIs in this way, the striate ROI contained a mean of 492 voxels (across subjects; *s.d.* = 259 voxels) that responded significantly more to the stimulus compared to fixation. The extrastriate ROI contained 676 significant voxels (*s.d.* = 355 voxels).

The multivariate analysis grouped BOLD responses in each stimulus condition by colour-orientation conjunction. For each voxel, the time series of responses to each conjunction in a stimulus block within each run was z-scored (fixation blocks were not used in the analysis) and a response to each conjunction computed as the mean of the z-scores from the 5 corresponding TRs within a single block. A linear support vector machine (SVM) as implemented in SVMLight (Joachims, 1999; C parameter set to 1.0) compared the difference in the patterns of activation for each visual area between orange-left/blue-right and orange-right/blue-left within a single condition. 11 runs were used as training data, and the 12th was used as a test. For each visual area and each subject, this process was repeated 12 times such that all permutations of test and training assignments were run.

Reported classifier performance accuracies for each subject were the average decoding performance across the 12 permutations, and these were compared against chance performance (50%) using one-sample *t*-tests to establish significance. A baseline decoding rate was calculated by shuffling conjunction labels within each condition, and performing the analysis. This procedure was repeated 200 times, after which, median decoding values were calculated for each subject and averaged together (Dotted lines in Figures 7 and 8). One sample *t*-tests confirmed these values did not differ significantly from chance (50%). The bootstrapped distributions of the means of these shuffled labels were obtained, and the 95% confidence limit (one-tailed) was calculated for each condition. For the data presented in Figures 3.11, 3.12, and 3.13, the 99th percentile of the null distribution was used to allow for Bonferroni correction over n=5 regions of interest for each subject. All results found to be significant using one-sample *t*-tests were confirmed to be significant at $p < 0.05$ using this method.

3.11.3. Results and discussion

Figure 3.11 displays the performance of a multivariate classifier. Discrimination of colour-orientation feature pairs from patterns of neural activity was calculated for each condition, and averaged together. Only visual areas V1 and V2 performed at a level significantly above chance following Bonferroni correction over the five visual areas (V1 mean performance: 64.3%, t_4 = 15.18, $p < 0.001$; V2 mean performance: 62.7%, t_4 = 6.78, $p = 0.012$). Subsequent follow-up analyses were thus restricted to areas V1 and V2 (Figures 3.12 and 3.13). A three-way repeated measures ANOVA revealed no significant effects of stimulus display type (perpendicular grating vs. check), temporal frequency (2.5 or 7.5 Hz), or visual area (V1 or V2) on classifier performance (Figure 3.12). There were also no significant two- or three-way interactions. However, decoding performance in the crucial 2.5 Hz check condition (Figure 3.12, 2.5 Hz Checks) was significantly better than chance in V1 (mean performance: 63.3%, $t_4 = 4.69$, $p = 0.009$) while failing to reach significance in V2 (mean performance: 59.2%, $t_4 = 2.00$, $p = 0.12$).

To increase our power to detect whether information about the imperceptible conjunctions in the 2.5 Hz check condition was in fact available beyond striate cortex, the voxels from V2 were combined with those from V3, V3A/B and hV4 to create a single 'extrastriate' visual area (Figure 3.12, purple bars). Decoding performance from the extrastriate area on the 2.5 Hz check condition was significantly better than chance (mean performance: 62.9% $t_4 = 3.56$, $p = 0.024$). Thus, although decoding performance on the 2.5 Hz check condition from V2 in isolation failed to reach significance, positive evidence is available that conjunction information is available not only within V1 but also reaches extrastriate cortex even when those conjunctions are inaccessible to subjects' perceptual awareness.

Following up on this, a multivariate classifier was trained to discriminate conjunctions across display types (Figure 3.13). This was done in order to assess if conjunctions were coded in the same general form across display types and temporal alternation frequencies. The classifier trained on patterns of activity in V1 and V2 associated with each colour-orientation conjunction in one stimulus display (e.g. checks at both alternation frequencies) and was then tested on the other (e.g. gratings at both frequencies). Classifier performance was significantly greater than chance (using one-sample *t*-tests) across both display types and across temporal alternation frequency for both V1 and V2. These results demonstrate that learned patterns of neural activity could be generalised across different conditions. This suggests that colour-orientation conjunctions may be coded in a form more general than the base physical stimulus characteristics. That is, coding for a specific colour-orientation conjunction appears to be independent of irrelevant stimulus attributes such as display type and frequency.

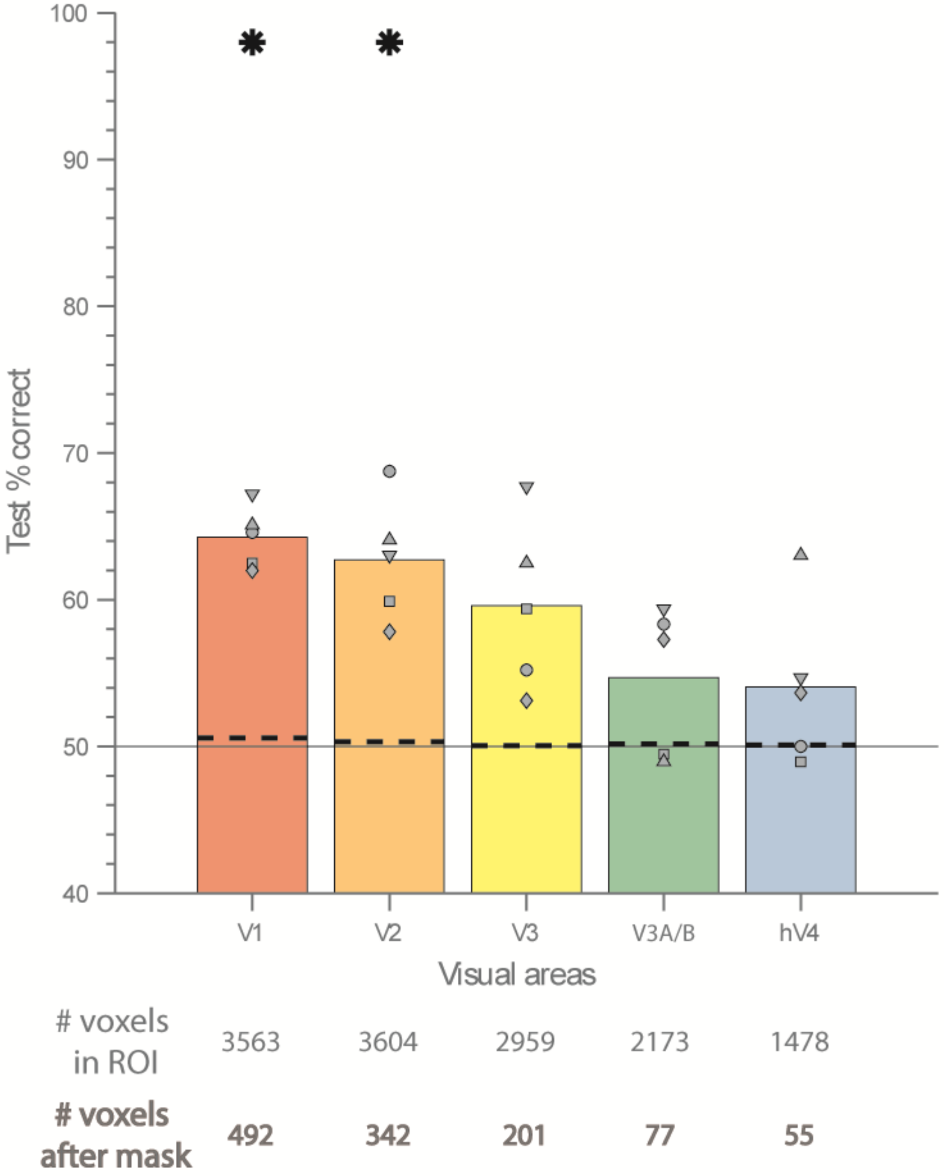

Figure 3.11. Averaged fMRI multivariate classifier performance. Average performance (*n*=5) of a multivariate classifier discriminating colour-orientation conjunctions. Average decoding performance from a multivariate classifier was obtained for each combination of display type (grating, checks) and temporal alternation frequencies (2.5, 7.5 Hz). Decoding performance for each subject was averaged over each condition (small grey shapes). Coloured bars represent the average decoding performance across subjects for each visual area. For these areas,

asterisks denote significantly greater classification performance than chance (50%, as indicated by the solid black horizontal line), following Bonferroni correction for the number of visual areas ($p < 0.01$). Dotted black lines indicate average classifier performance over 200 repeats where conjunction labels were randomly shuffled within each stimulus condition. Note that fMRI data shown here are from the same 5 subjects who participated in Experiment 8B.

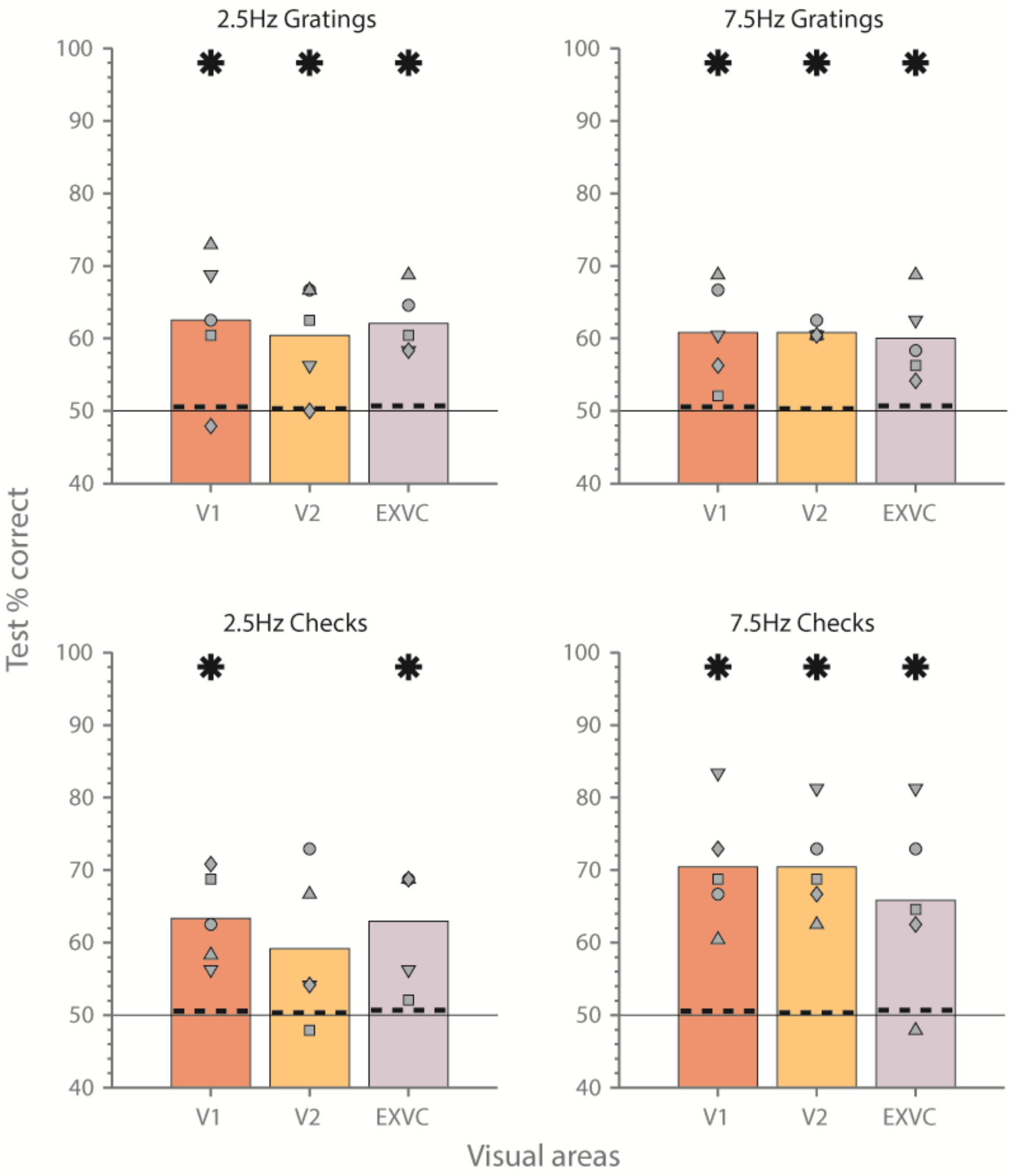

Figure 3.12. Functional MRI multivariate classifier performance. Average performance (*n*=5) of a multivariate classifier discriminating colour-orientation conjunctions within the same stimulus conditions as those highlighted in Figure 3.2b, for striate (V1), V2, and extrastriate visual cortex (EXVC). Coloured bars indicate average performance across subjects in decoding conjunctions by the classifier. Small grey icons indicate classifier performance for individual subjects. Asterisks denote significantly greater classification ($p < 0.05$) than chance (50%, as indicated by

the black horizontal line). Dotted black lines indicate average classifier performance over 200 repeats where conjunction labels were randomly shuffled within each stimulus condition.

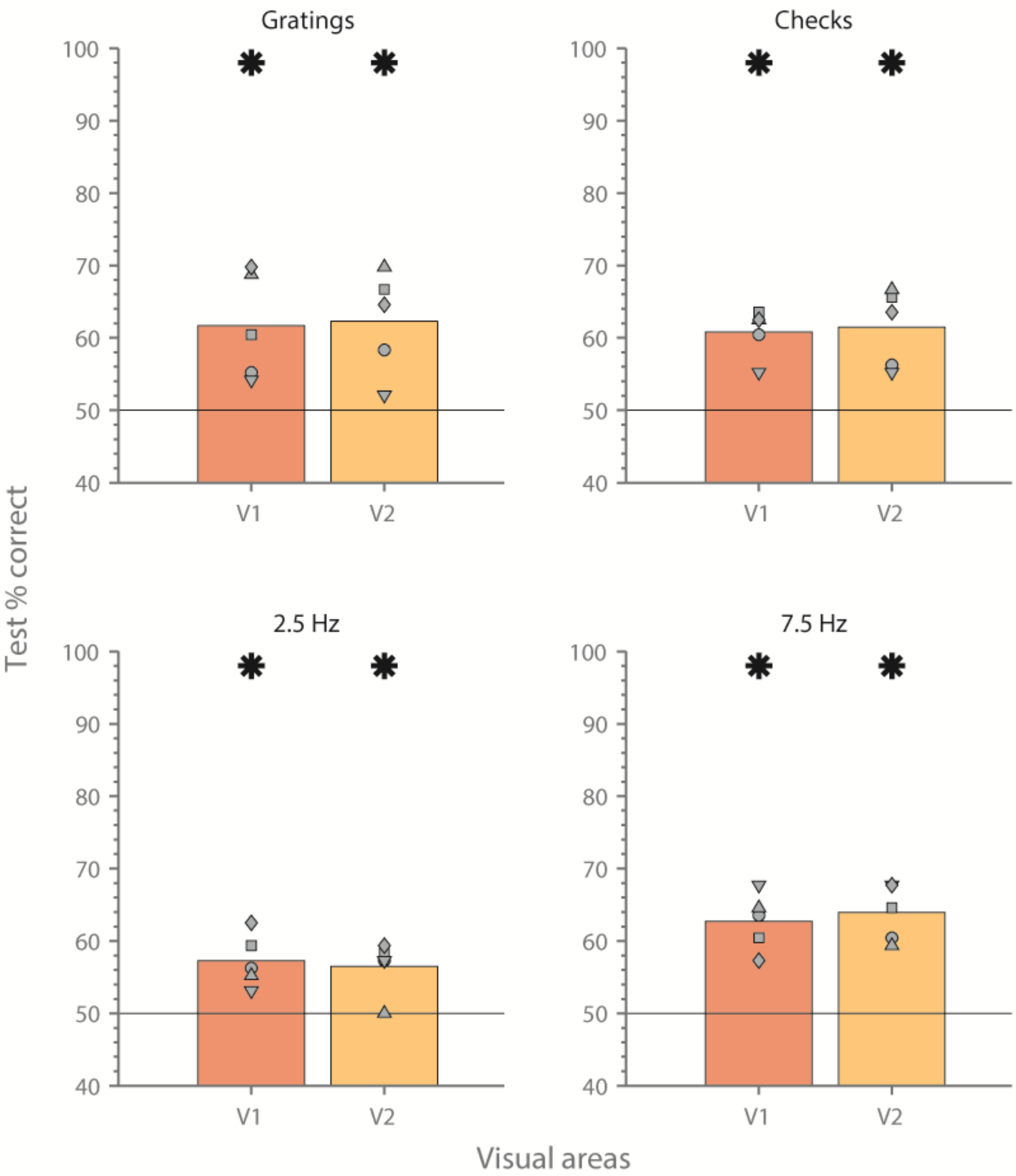

Figure 3.13. Classifier generalization performance. Average generalization performance (*n*=5) of a multivariate classifier trained on one type of stimulus display to discriminate colour-orientation conjunctions, and tested on the other type of display, for visual areas V1 and V2. Each figure shows the mean of the two combinations of training/testing within the four stimulus conditions. For example, the top left panel ('Gratings') shows the mean generalization performance after the classifier was trained on the 2.5 Hz grating condition and then tested on the 7.5

Hz grating, and the opposite: training on the 7.5 Hz grating and testing on the 2.5 Hz grating. The bottom two panels show testing and training generalisation across stimulus display type (gratings and checks) at 2.5 and 7.5 Hz temporal frequencies, respectively.

3.12. Chapter discussion

This series of experiments explored the spatial and temporal dynamics of colour-orientation binding and temporal transparency, with respect to the known properties of surface segregation (Clifford, Spehar, et al., 2004; Moradi & Shimojo, 2004; Suzuki & Grabowecky, 2002). In turn, these stimulus designs were adapted for use in an fMRI study in order to explore the neural representation of perceived and imperceptible conjunctions. In summary, a series of experiments were designed in order to investigate the seemingly paradoxical findings of Holcombe and Cavanagh (2001). They found a high temporal resolution for feature binding, a result contrary to a majority of studies that concluded otherwise (e.g. Bodelón et al., 2007; Holcombe, 2009; Seymour, McDonald, et al., 2009; Treisman, 1996). To resolve this discrepancy, the hypothesis put forward by Moradi and Shimojo (2004) with respect to colour and motion, as supported by the experiments presented in Chapter 2, were applied to colour-orientation stimuli. They suggest that accurate conjunction discrimination at high alternation frequencies was supported by surface segregation. In effect, the ability to segregate a display into multiple surfaces aided in the process of identifying temporally coincident feature pairs, normally a difficult and slow task due to the low temporal resolution of feature binding. This investigation into the properties of colour-orientation binding and its relationship to surface segregation revealed several spatial and temporal factors influencing the feature binding process.

3.12.1. Temporal integration is required for accurate conjunction discrimination

In Experiment 1B, a reduction in angular separation resulted in a corresponding conjunction discrimination decrease in the 1.25-5 Hz temporal alternation frequency range. Beyond 5 Hz however, conjunction discrimination increased: a pattern of results that would not be observed if angular separation alone influenced the discriminability of grating tilts. Instead, the non-monotonic conjunction discrimination was a result of both angular separation (Nothdurft, 1991) and temporal alternation frequency (Moradi & Shimojo, 2004) acting as surface segregation cues. The perceptual effects of angular separation and temporal alternation frequency were tested in Experiment 2B. Observers reported their subjective impression of stimulus ‘transparency’. Within the 5-15 Hz frequency range, perceptual reports of perceiving multiple surfaces correlated well with increases in conjunction discrimination and were indicative of a transitional frequency range in how the stimulus was perceived.

To confirm that these manipulations were having the desired effect on surface segregation, Experiment 3A was devised. Prior evidence suggests that a small perceptual asynchrony of colour and orientation exists (Moutoussis & Zeki, 1997b) (Clifford et al., 2003), which may be contributing to overall task difficulty. Furthermore, as both variations in temporal alternation frequency (Nishida & Johnston, 2002) and differences in angular motion (Arnold & Clifford, 2002) can also affect perceived asynchrony, it is important to determine if the manipulations here of angular separation and alternation frequency were affecting perception in an unintended way. These factors were therefore tested in Experiment 3B where the relative phase of the change in colour and orientation was varied. However, even at the 5 Hz alternation frequency, where conjunction discrimination was most affected, there was little evidence for a perceptual colour-orientation asynchrony.

Convergent support for the effects of surface segregation on conjunction discrimination was provided by Experiments 4B and 5B, which examined the role of temporal integration on feature binding. A reduced number of stimulus cycles significantly reduced conjunction discrimination at all angular separations. However, an increase in the number of stimulus cycles resulted in significantly increased conjunction discrimination only when coupled with an alternation frequency that supported surface segregation. A similar result occurred with Experiment 6B. That is, high conjunction discrimination was associated with a high alternation frequency. However, unlike previous experiments, here it was demonstrated that a large angular separation is not always sufficient for surface segregation. Even orthogonal gratings can fail to produce accurate conjunction discrimination in some circumstances, such as when horizontally translating in opposite directions.

3.12.2. Feature binding can occur in two different ways

This transitional range in conjunction discrimination evident from Experiments 1B and 2B was further clarified by the distinct and mostly separate ranges of alternation frequency supporting accurate conjunction discrimination in Experiments 7B and 8B. In Experiment 7B, surface segregation was prevented through the spatial segregation of colour and orientation (Holcombe & Cavanagh, 2001). Through this method, accurate feature binding requires a pair of features to be bound within a single presentation. As discrimination was only high at the lower frequencies, where feature pairs are presented for longer, it was demonstrated that the binding process has a low temporal resolution. This is a result representative of the majority of the feature binding literature, as it is often not possible for surface segregation to occur in these experiments. However, this low resolution can be overcome if feature conjunctions can be temporally integrated across successive presentation invertvals. Experiment 8B necessitated temporal integration in order to perceive the correct feature conjunction in the check stimuli, as it could not be determined within a stimulus half cycle unlike previous experiments. It was demonstrated that the temporal integration was essential to extract colour-orientation information at higher temporal frequencies. Furthermore, a high resolution binding mechanism could not account for this result as the ability to resolve individual check patterns did not reveal the colour-orientation pairing.

3.12.3. A half-wave rectification mechanism for parsing colour-orientation stimuli

Taking into account what is known of the underlying physiology (Schiller, 1992; M. A. Smith, Bair, & Movshon, 2002) supported by perceptual studies (e.g. Badcock, Clifford, & Khuu, 2005; Chubb & Nam, 2000), a simple rectification mechanism can serve to make the colour-orientation pairing explicit. Half-wave rectification occurring early in the visual system (M. A. Smith et al., 2002) would yield oriented structure (Figure 3.14) if the light and dark colour portions of the stimulus are processed by separate On- and Off-channels (Schiller, 1992). It has been noted that these on- and off- channels may play a role in the perception of transparency (Bartley, 1939;

Holcombe, 2001), although Holcombe (2001) points out that some equiluminant displays (i.e. those that cannot be separated by on- and off- processing channels) can also lead to the perception of transparency. The aforementioned role of targeted feedback may be a means by which equiluminant stimuli can be discriminated, as here only orientation and colour information are needed to discriminate a conjunction, rather than luminance-defined strips.

Temporal integration within either (or both) of these pathways could then provide a coherent colour signal from which the associated orientation could be extracted. For the stimuli in Experiment 8B, both check and grating displays can be parsed by luminance in the same manner, yielding separate light and dark coloured bars (Figure 3.14). Temporal integration within either (or both) of these pathways could then provide a coherent colour signal from which the associated orientation could be extracted. However, this process is dependent on the temporal alternation frequency at which the stimulus is presented. If the temporal alternation frequency is too low, the resultant percept would simply be a representation of the half-wave rectified stimulus, which would support conjunction discrimination for the grating stimuli, but not for the checks. If the alternation rate is too high, then any temporal integration prior to the half-wave rectification results in the static gray plaid that is perceived at frequencies greater than 15 Hz. Furthermore, if the orientations are too close (i.e. angular separations of 15° or less), lateral inhibition between mechanisms selective for nearby orientations would interfere with temporal integration processes (Blakemore, Carpenter, & Georgeson, 1970; Blakemore & Tobin, 1972). This is a result consistent with studies that report adaptation to invisible conjunctions (Blaser et al., 2005; Houck & Hoffman, 1986; G. K. Humphrey & Goodale, 1998; Vul & MacLeod, 2006).

In these studies, fused colour information cannot be segregated into separate surfaces, resulting in colour-contingent after-effects from feature conjunctions that were not perceived.

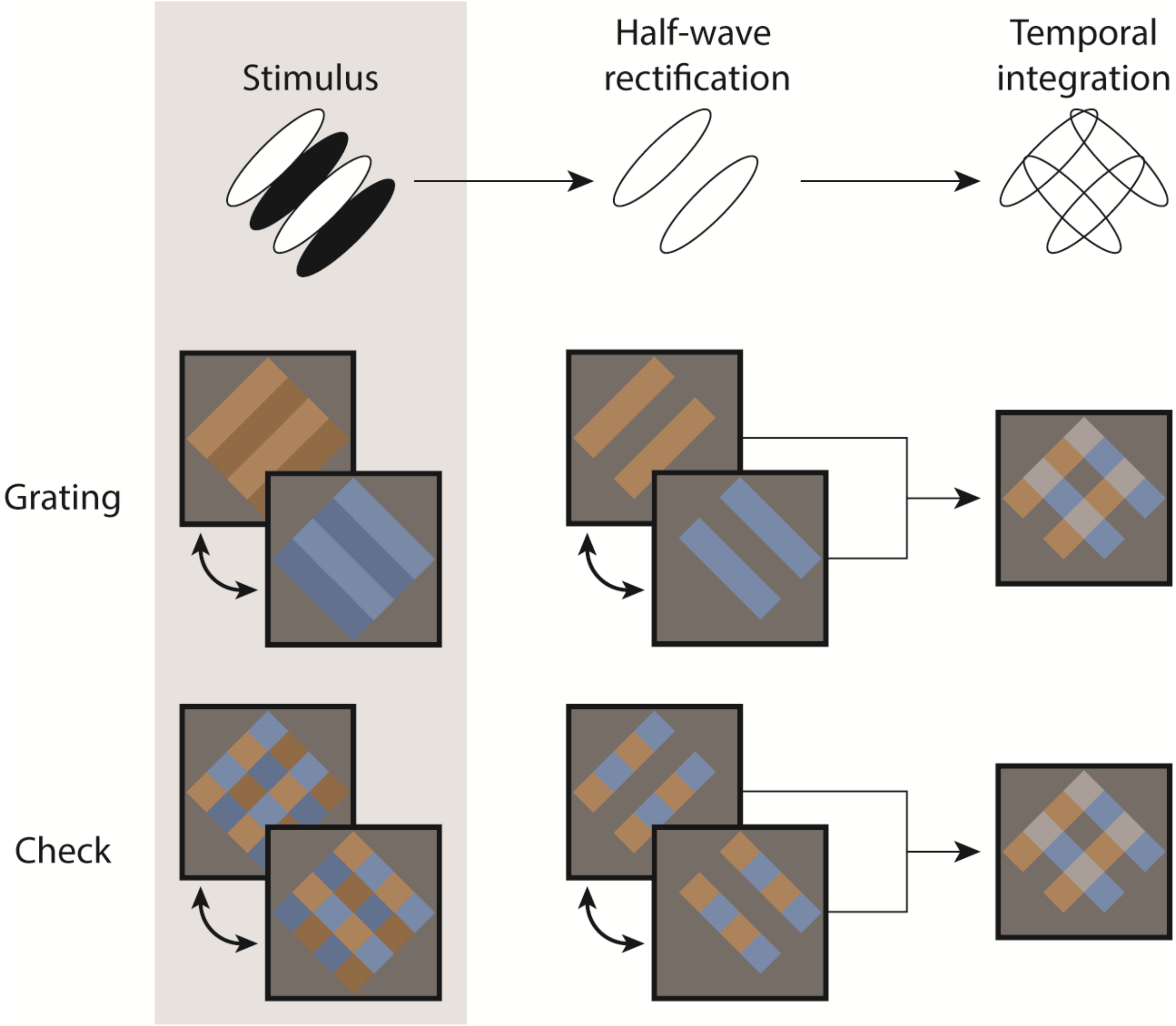

Figure 3.14. Half-wave rectification of grating and check stimuli. Representation of how an early half-wave rectification mechanism may parse the experimental stimuli. In order to discriminate the colour-orientation pairing in both types of stimuli, gratings and checks are first separated by on- and off- luminance channels. Note that in this

Figure, only the light strips are represented for clarity. Once separated, and if the stimulus facilitates temporal integration, the combination of strips are used to arrive at the correct feature combination.

3.12.4. Colour-orientation conjunctions are represented in human early visual cortex

The results of the aforementioned psychophysical experiments were well complimented by the fMRI study, Experiment 9B. From the results of Experiment 8B, two temporal alternation frequencies were chosen with which to display both grating and check display types. At 2.5 Hz, conjunction discrimination was only poor in the check condition. However, at 7.5 Hz, accurate conjunction discrimination occurred in both check and grating conditions. Therefore, confidence in the observed neural activity obtained in Experiment 9B regarding perceived and non-perceived feature conjunctions could be achieved, while still controlling for temporal alternation frequency. Previously, studies have indicated that early visual cortex responds to invisible features such as orientation (Haynes & Rees, 2005; He et al., 1996), motion (Moutoussis & Zeki, 2006), and flicker (Gur & Snodderly, 1997; Jiang et al., 2007). Here, the results of the study indicated that both striate and extrastriate cortex code for feature conjunctions - even those contained in the imperceptible 2.5 Hz check display.

In line with the results of this experiment, single-cell studies in non-human primates have found that many colour selective neurons in V1 and V2 are also selective for orientation (Burkhalter & Van Essen, 1986; Gegenfurtner et al., 1996; Johnson et al., 2008; Leventhal et al., 1995). Using multivariate fMRI techniques, previous studies have also demonstrated that human early visual cortex can code for conjunctions of several visual features including colour-motion (Seymour, McDonald, et al., 2009; Zhang et al., 2014), colour-orientation (Sumner et al., 2008), colour-form (Seymour et al., 2010), and motion-stereoscopic depth (Seymour & Clifford, 2012).

Expanding on these studies, it was demonstrated that significant multivariate classification could also generalise across display types and frequencies. These results are consistent with psychophysical evidence for orientation-contingent chromatic adaptation at stimulus alternation rates beyond conscious perception (Vul & MacLeod, 2006).

3.12.5. Conclusions

The results presented here reflect the complex temporal dynamics of surface segregation and feature binding processes. Across this chapter’s experiments, it was demonstrated that feature binding can extract the information contained in rapidly formed surface representations. In effect, the information used by surface segregation can bypass the low temporal resolution of feature binding by generating persistent representations. However, the binding process itself has a low temporal resolution, as when surface segregation does not occur, conjunction discrimination falls to chance at intermediate and high alternation frequencies. However, even when conjunctions are not perceived, they appear to be coded in some form in striate and extrastriate cortex. This suggests that the binding process is initiated, but not fully resolved, by early visual processes. While information about feature conjunctions is encoded in the activity of populations of neurons as early as primary visual cortex, decoding of this information into an explicit form available to conscious perceptual awareness requires temporally extended processes involving areas within, and possibly beyond, extrastriate visual cortex (He et al., 1996; Shipp et al., 2009; Zhang et al., 2014).

General discussion

The experiments detailed in this thesis examined the spatial and temporal relationships between stimuli that affected visual feature binding. Specifically, the dynamics of binding colour with motion (Chapter 2) and colour with orientation (Chapter 3) were explored. It was determined that perceptual surface segregation, through the temporal integration of similar visual attributes, accounted for both the successes and failures of feature binding that were observed at intermediate and high temporal alternation frequencies. These results provide evidence clarifying the suggestion that feature binding is an early or otherwise rapid process (Bodelón et al., 2007; Holcombe, 2009; Holcombe & Cavanagh, 2001; Maloney et al., 2013; Rousselet et al., 2002). Previously, the dissociation within the feature binding literature has implicated two feature binding mechanisms with different temporal resolutions. However, the results here appear to provide evidence for a single binding mechanism with a low temporal resolution. That is, conjunction discrimination is high when feature binding mechanisms can extract information from rapidly formed surface representations. Importantly, when surface segregation is disrupted, the observed patterns of results closely matches theories which predict a low temporal resolution for feature binding (Quinlan, 2003; Treisman, 1996; Treisman & Schmidt, 1982). In essence, the pattern of conjunction discrimination at both intermediate and high frequencies can be accounted for by surface segregation. Perceptual segregation of the stimulus effectively circumvents the relatively slow resolution of feature binding. Surface segregation allows the visual system to parse and extract feature pairs in cases where such surface representations are available (Moradi & Shimojo, 2004). When they are not, accurate conjunction identification is instead reliant on binding features during a single presentation of a feature pair. Importantly, this account of feature binding can account for otherwise discrepant findings consistent with both past and more recent research.

The reasoning behind the proposed relationship between surface segregation and feature binding is discussed here in a more general form. Some broad conclusions are drawn about the nature of feature binding in general by observing both the similarities and differences of the results obtained in Chapters 2 and 3.

4.1. Differentiated visual attributes allow for more accurate feature binding

The first experiments of Chapters 2 (1A-3A) and 3 (1B-2B) demonstrated that several cues to surface segregation exist, and these can influence feature binding at both intermediate and high frequencies. At intermediate frequencies (around 5 Hz) where colour-motion binding was typically poor, Experiments 1A-3A demonstrated that additional dots enhanced binding when they shared the same colour, dot configuration and motion direction of the preceding target RDK (Adelson & Movshon, 1982; Masson et al., 1999; Snowden & Verstraten, 1999; Stoner & Blanc, 2010; Treisman & Kanwisher, 1998; Valdes-Sosa et al., 2000). However, an arguably stronger segregation cue at the same intermediate frequencies is the orientation difference that was manipulated in Experiments 1B and 2B. While the colour-motion displays in Experiments 1A-3A required a second set of additional dots in order to facilitate the surface segregation process, likely due to a combination of temporal integration and motion contrast (Heeger et al., 1999;

Shulman et al., 1998; Tynan & Sekuler, 1984), the only surface segregation cues that were manipulated in Experiments 1B and 2B were angular separation and alternation frequency. A 90° separation was sufficient for ceiling conjunction discrimination at 5 Hz. That angular separation alone was able to support feature binding at intermediate frequencies without a hypothetical set of ‘additional’ gratings to facilitate temporal integration suggests an advantage for orientation. This may be due to the half-wave rectification mechanism (Schiller, 1992; M. A. Smith et al., 2002) discussed in Chapter 3, giving the colour-orientation displays a processing advantage over the colour-motion ones.

Nevertheless, a large angular separation cannot always ensure the occurrence of surface segregation. This was demonstrated by Experiment 6B, which used a motion-orientation display that alternated between two grey gratings with opposite orientations and motions. Unlike the angular separation manipulation in Experiment 1B that generated a graded distribution of conjunction discrimination by angular separation, motion-orientation discrimination appeared to be on the whole unaffected by modifying angular separation. The results generated were more similar to the control conditions of Experiments 1A and 2A. That is, conjunction discrimination was at ceiling at both the lowest and highest alternation frequencies tested, but this was reduced to chance as the alternation frequency approached 5 Hz, suggesting the same binding mechanisms are involved across these experiments.

While a thorough investigation into the stimulus characteristics that can facilitate motion-orientation binding is beyond the scope of this thesis, this experiment in isolation demonstrated that a large angular separation was not sufficient to promote accurate binding across all temporal alternation frequencies. Both the different dot configurations between additional RDKs in the colour-motion experiments and a small difference in angular separation in the colour-orientation experiments resulted in disrupted feature binding at intermediate frequencies. Upon observation of the common visual feature between the colour-motion and orientation-motion experiments (that is, motion), one may speculate that the constant reversals of motion facilitate temporal integration across both gratings into a single surface containing both orientation and motion attributes, in turn impairing the discrimination of the correct motion and orientation. This would be akin to the colour-motion experiments where, despite different dot configurations between RDKs, conjunction discrimination was still poor at intermediate alternation frequencies (also Moradi & Shimojo, 2004).

Apart from this interesting observation, it appears that when colour is paired with orientation or motion, the perceptual differentiation between each RDK or grating is able to enhance surface segregation and allow accurate feature binding when it would otherwise fail. The role of a high temporal alternation frequency as another segregation cue is the focus of the following section for a similar reason. That is, a higher alternation frequency allows for better and more rapid comparisons, making the differences between the two feature pairs more apparent (Clifford, Spehar, et al., 2004; Moradi & Shimojo, 2004; Nothdurft, 1991; T. Watanabe & Cavanagh, 1996). This in turn facilitates surface segregation, resulting in a clearly segregated percept from which feature pairs can be extracted.

4.2. Feature binding is enhanced by temporal integration of stimuli

In Experiments 5A and 6A, two factors affected accurate conjunction discrimination: a high alternation frequency enhanced the temporal integration across successive stimulus presentations (Brockmole et al., 2002; Di Lollo, 1980; Eriksen & Collins, 1967), and this was combined with the consistent motion trajectory of individual RDKs. Perceptual segregation was also facilitated when RDKs were sufficiently differentiated in their trajectories and dot configurations (Adelson & Movshon, 1982; Baylis & Driver, 1992; Bergen & Landy, 1991; Masson et al., 1999; Snowden & Verstraten, 1999; Treisman & Kanwisher, 1998). When RDKs had incoherent motion paths, temporal integration was instead disrupted, reducing conjunction discrimination (Lankheet & Palmen, 1998; Snowden & Verstraten, 1999; Watamaniuk et al., 2003). In these display types, motion was not an effective cue for the differentiation of RDKs when averaged over a full stimulus cycle, causing them to appear less distinct. A similar parallel can be drawn through the angular separation manipulations of the colour-orientation experiments in Chapter 3. Experiments 1B and 2B demonstrated that a lower angular separation reduces the distinctiveness of the two gratings, disrupting temporal integration in a similar manner to the colour-motion stimuli (Nothdurft, 1991; T. Watanabe & Cavanagh, 1996). The check stimulus in Experiment 8B also demonstrated that even without temporal or spatial coincidence, temporal integration was sufficient to extract and identify the correct colour-orientation pairing. However, what may be the most significant evidence comes from Experiments 4B and 5B, where the interaction between stimulus similarity, alternation frequency and temporal integration were investigated.

The effects of presentation duration and angular separation were the main focus of Experiments 4B and 5B. Specifically in Experiment 4B, a single cycle of the grating stimulus was presented at various frequencies, preventing the temporal integration of colour-orientation information over multiple presentations. As alternation frequency approached 30 Hz, all angular separations tended towards chance conjunction discrimination. This confirmed that no matter the magnitude of angular difference between gratings, stimuli at the higher alternation frequencies tested still required temporal integration to be accurately perceived. Furthermore, as stimulus presentation duration decreased, displays with a lower angular separation displayed a more rapid decrease in conjunction discrimination. This indicated that lower angular separations affected the temporal integration across the display, a trend that was confirmed in Experiment 5B.

In Experiment 5B, presentation duration of the stimulus was again varied, while the alternation frequency of the stimuli was kept constant at either 5 or 7.5 Hz. In order to demonstrate a relationship between conjunction discrimination and temporal integration, the presentation duration of the stimulus was varied. At 5 Hz, conjunction discrimination remained relatively stable despite an increase in presentation duration. However at 7.5 Hz, the frequency at which conjunction discrimination began to improve in Experiment 1B, an increase in presentation duration was associated with higher conjunction discrimination. Considering this pattern of results was evident throughout the colour-motion experiments, Experiment 5B may indicate that at 7.5 Hz and onwards, temporal integration is facilitated across stimulus presentations in colour-orientation stimuli (Clifford, Holcombe, et al., 2004; Moradi & Shimojo, 2004). The decision making model in Chapter 2 explored this process further, modelling temporal integration over the stimulus duration to come to a correct decision.

However, at high alternation frequencies, temporal integration is not the only factor that must be considered. This is evident from both the stimulus manipulations at very high alternation frequencies and the differences between colour-motion and colour-orientation discrimination. At frequencies higher than 15 Hz, colour-motion conjunction discrimination remained close to ceiling while colour-orientation discrimination is reduced to chance. Experiment 7A demonstrated that increasing the alternation frequency of a display resulted in a larger effect of visual persistence (Di Lollo, 1980; Di Lollo & Wilson, 1978; Georgeson, 1987; Snowden & Braddick, 1991; Watamaniuk & Sekuler, 1992), effectively masking the present feature conjunction. Similar to the function of temporal integration, persistence is thought to enhance perception of the display by providing an extended temporal window in which the stimulus can be perceived (Dixon & Di Lollo, 1994). However, Experiment 7A and all of the experiments of Chapter 3 were designed such that visible persistence masked colour and consequently prevented accurate conjunction discrimination (Holcombe & Cavanagh, 2001).

In this way, a variety of complex stimulus characteristics allow both the colour-motion and colour-orientation stimuli to be perceived at high alternation frequencies. A single RDK or grating must remain constant across presentations, or act in a consistent and predictable manner to facilitate temporal integration. Total stimulus duration is also a concern, as an overall shorter presentation duration did not allow for sufficient temporal integration over successive stimulus presentations. RDKs or gratings must also be significantly differentiated in order for segregation, rather than integration, to take place. And finally, stimuli must be presented in a way such that at high alternation frequencies, colour addition does not mask the correct conjunction.

4.3. Simultaneously presented features enhance feature binding

The previous two sections have focused on the visual interpretation of alternating stimuli. However, an interesting duality is apparent upon comparison of an alternating display to one where both feature pairs are presented simultaneously (Moradi & Shimojo, 2004). This is revealed when comparing the results of the same motion type between Experiments 5A to 6A, and also between sequential and segregated display types in Experiment 8A. Despite being a display that is inherently more complex (two pairs of features to disentangle at a single point in time rather than one), a simultaneous display generates ceiling conjunction discrimination across a range of alternation frequencies, when compared to a sequential display.

In a similar manner, a ‘piecemeal’ colour-orientation display whereby features were presented simultaneously was piloted by the author (Figure 4.1). This display was constructed by applying a checkerboard mask over blue and orange gratings, a set of squares from one grating with the other. This resulted in a display where each square in the checkerboard pattern still alternated, but overall, both conjunction pairs were on-screen at all times. A full-length pilot experiment (*n*=1) produced ceiling performance across a set of alternation frequencies (1.25, 2.5, 3.75, 5, 7.5, 10, and 15 Hz) for all angular separations (5°, 10°, 15°, 20°, 90°). Producing a set of results that were now independent of angular separation was promising, although there were some issues with the display which prevented further experimentation. There are several options to consider when creating a colour-orientation display in which both feature pairs are presented simultaneously, such as the pilot display or a physical overlay of each grating. However, it was also important that the display appeared transparent in a way that was similar to the percept generated by gratings presented at high frequencies. This was achieved using colour-motion stimuli, as confirmed by the subjective judgement task in Experiment 9A, but could not be replicated using coloured, oriented gratings. Furthermore, a smaller, denser checkerboard pattern resulted in the perception of a grey plaid, and for a larger pattern like that in Figure 4.1, individual squares could clearly be distinguished independent of alternation frequency. Similarly, to adapt this stimulus for use in an fMRI experiment, alternating and piecemeal gratings that yielded similar percepts would be required in order to disentangle the neural representation of physically different stimuli that are nevertheless perceptually indistinguishable.

The question remains as to why simultaneous presentation of colour-motion or colour-orientation feature pairs produced better, or at least equal, conjunction discrimination when compared to an alternating counterpart. From the overall conclusions of all these experiments, the answer may again be linked to surface segregation. A high temporal alternation frequency provides more opportunities to make a comparison between feature pairs, leading to better segregation, and ultimately better conjunction discrimination. In a similar manner, the physical presentation of both feature pairs may also allow for a clearer and more direct comparison between feature pairs, potentially involving both motion opponency (H. Jones et al., 2001; Lindsey & Todd, 1998), an imbalance of local motion cues (Qian et al., 1994). As both feature pairs are present simultaneously, given sufficiently differentiated features (e.g. angular separation), the result should be the perceptual segregation of each pair.

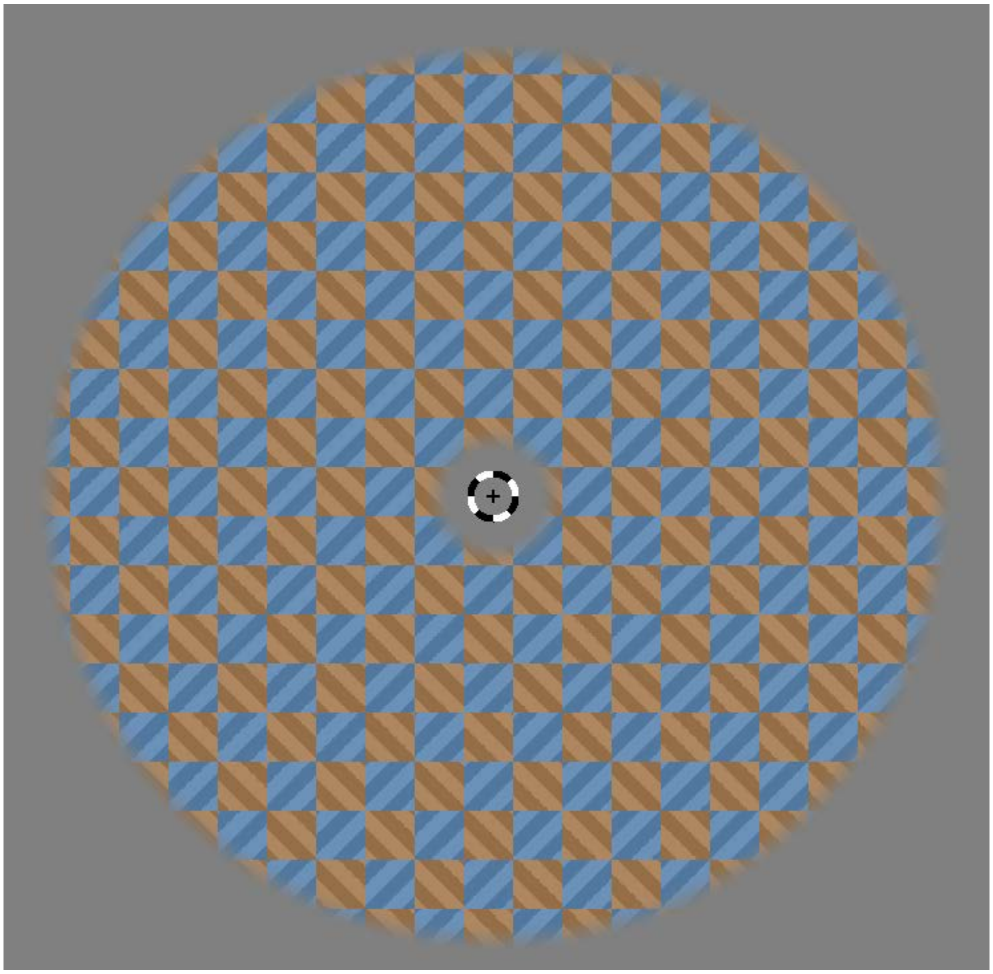

Figure 4.1. Piloted colour-orientation ‘piecemeal’ stimulus. Each square alternated between orange tilted right and blue tilted left at one of several alternation frequencies. For all squares, the colour-orientation pairing changed simultaneously.

4.4. Overlapping neural activity generated by colour-motion and colour-orientation stimuli

Two fMRI experiments were reported across Chapters 2 and 3 (Experiment 10A and 9B respectively), where the neural correlates of surface segregation and feature binding were investigated. In observing the neural responses of early visual areas to certain displays, Experiment 10A investigated the perception of multiple surfaces in sequential and simultaneously presented grey RDKs while Experiment 9B examined perceived colour-orientation conjunctions in grating and check displays. In the accompanying psychophysical experiments (8A and 8B respectively), all display types supported accurate conjunction discrimination at high alternation frequencies, but only the simultaneous RDK and grating display type continued to support high discrimination at intermediate alternation frequencies. In Experiment 10A, univariate responses in early visual areas (V1, V2, V3, V3AB, and hV4) mirrored this tendency, with responses from each display type converging when presented at the higher of the two alternation frequencies (15 Hz). Responses in each area diverged at the lower frequency, 5 Hz, overall producing significant interaction effects in most of the early visual areas that were tested.

Using a multivariate classifier, significantly above chance decoding was observed in Experiments 10A and 9B. In Experiment 10A, these observations matched the univariate results as decoding of display type was significantly above chance only when stimuli were presented at the lower of the two alternation frequencies. At 5 Hz, decoding could be achieved based on the overall differences in response magnitudes observed in the univariate results. However, decoding at 15 Hz was not significantly above chance, which indicates that the patterns of activity produced by both sequential and simultaneous display types were similar. This result matched the subjective measure of the stimulus (Experiment 9A) where these stimuli tended to appear less similar at lower frequencies. Experiment 9B demonstrated that features were coded in conjunction in early visual cortex. The results from both striate and extrastriate cortex indicated that feature conjunctions were coded in a way that was independent of the display type and alternation frequency. Overall, comparisons between the results of both fMRI experiments indicate that correlates of both surface segregation and feature binding mechanisms are apparent in the activity of early visual cortex.

Surface segregation appears to be a rapid and early process, and this was reflected in the selective modulation of early visual areas in these experiments. The experiments of Chapters 2 and 3 have strongly suggested that the process of feature binding is linked to surface segregation. Despite the stimulus differences between Experiments 10A (grey RDKs) and 9B (coloured gratings), the similarity of the results across both colour-motion and colour-orientation psychophysical experiments results suggest a comparison can also be made between fMRI results. Here, in both fMRI experiments there were significant multivariate effects in early visual areas, aligning well with research that indicating that both surface segregation (Garcia & Grossman, 2009; Heeger et al., 1999; Muckli et al., 2002; Treue et al., 2000) and feature binding (Seymour & Clifford, 2012; Seymour et al., 2010; Seymour, McDonald, et al., 2009; Zhang et al., 2014) are both linked and are processed in some form in early visual cortex.

4.5. Targeted feedback

Based on the experiments presented here, a targeted feedback model is now introduced which provides a solution to the binding problem in a way that can account for the patterns of data that have been observed. While colour and orientation are shown here, orientation can be easily interchanged with motion direction. Figure 4.2a demonstrates the binding problem from a neural perspective. Previous work has demonstrated the modulatory role of feedback signals in early visual cortex (Andolina, Jones, Wang, & Sillito, 2007; Juan & Walsh, 2003; Lamme et al., 1998; Shipp et al., 2009). In this model (Figure 4.2), feedback from higher areas target ‘double-duty’ neurons that code conjointly for orientation and colour (Burkhalter & Van Essen, 1986; Johnson et al., 2008; Leventhal et al., 1995). Feedback selectively targets and thus enhances the responses of those double-duty neurons responsive to one of the two orientations present in the display, resulting in a corresponding increase in the response to the associated colour. In this way, targeted feedback allows the correct pairing of colour and orientation that can be decoded from the response profile of the population of double-duty neurons.

In this model, feedback from higher areas targets one of the two orientations present in the display (Figure 4.2b). Consistent with previous research, feedback in this way can enhance the responses of neurons responsive to the targeted orientation (Andolina et al., 2007; Juan & Walsh, 2003; Lamme et al., 1998; Shipp et al., 2009). Included are the neurons that code for both orientation and colour (Burkhalter & Van Essen, 1986; Gegenfurtner & Kiper, 2003; Johnson et al., 2008; Leventhal et al., 1995), resulting in an overall increase in the response to the correct feature conjunction. In this way, coincident colour and orientation features can be decoded by an enhancement in response from the respective populations of neurons.

Effects of angular separation on conjunction discrimination in Chapter 3 could be explained through a combination of both apparent motion and mutual inhibition (Blakemore et al., 1970; Blakemore & Tobin, 1972; Green, 1986). A lower angular separation would cause gratings to appear more similar (Holcombe & Cavanagh, 2001; Kawabe & Miura, 2004; Nothdurft, 1991; T. Watanabe & Cavanagh, 1996), facilitating integration between, rather than within, gratings. At a low angular frequency, the perception of a single, moving grating would be equivalent to viewing Chapter 2’s colour-motion displays at intermediate frequencies, where conjunction discrimination is poor (Moradi & Shimojo, 2004). However, mutual inhibition could also play a role here, based upon the introduced framework whereby targeted feedback enhances processing of individual features. Lower angular differences are more likely to activate populations of neurons with overlapping tuning curves (e.g. Bredfeldt & Ringach, 2002; Ringach, Shapley, & Hawken, 2002). If the orientations are too close (i.e. angular separations of 15° or less), lateral inhibition between mechanisms selective for nearby orientations would interfere with both selection from feedback and temporal integration processes (Blakemore et al., 1970; Blakemore & Tobin, 1972), consequently reducing conjunction discrimination.

A detailed account of the conjunction discrimination process can be identified by combining the various models throughout this thesis. As described here, targeted feedback would first be responsible for decoding conjunctions from several populations of feature and conjunction detecting neurons. However, the noise inherent at the neuronal level (Zeki, 1993) must be spatially and temporally averaged in order for confident perception of a stimulus to take place. To this end, the responses of these neuronal populations can be assessed by higher areas in a manner similar to the accumulator model previously discussed in Chapter 2. That is, a consistent pattern of neuronal responses over time could eventually signal the presence of a particular feature pair. Importantly, the process of evidence accumulation is acutely dependent on the underlying neural responses, in that an incoherent signal would prevent any evidence towards a feature pair from being accumulated.

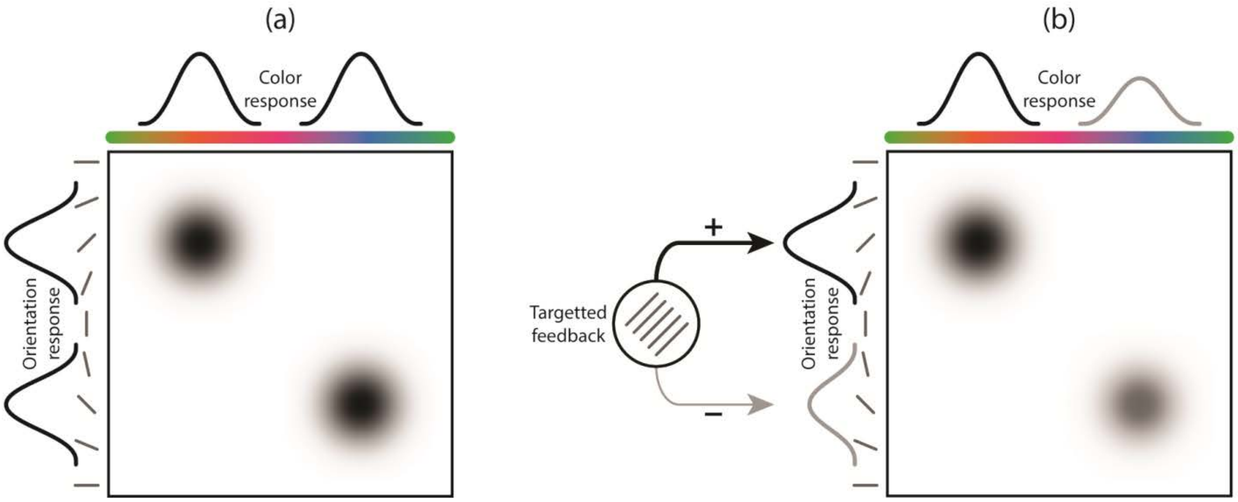

Figure 4.2. Schematic of a proposed conjunction identification mechanism. **(a)-(b)** The x- and y-axes represent the preferred colour and orientation (or motion), respectively, of a population of neurons selective to both stimulus attributes. Population response profiles for each visual feature are centred on the colours (orange and blue) and orientations (±45° tilted from vertical) that are physically present in the stimulus. Each Gaussian blob represents the combined response to a presented feature pairing. **(a)** The neural response creates a binding problem when viewing any display in this thesis that alternated between two pairs of features, as the same populations of neurons would be active regardless of the current colour-orientation (or colour-motion) conjunction. Thus, the correct colour-orientation combination (here, orange grating tilted rightward with a blue grating tilted leftward) is unable to be distinguished from the opposite combination from just the low level neural response. **(b)** To resolve this, feedback from higher areas enables the selection of a particular orientation (in this example, right tilted gratings). This in turn boosts the signal of the neurons that jointly code for the preferred orientation and colour, resulting in an asymmetrical neural response that reveals the correct colour-orientation pair.

4.6. Study limitations

While due care was taken in designing and conducting these experiments, a couple of factors may have affected the observed conjunction discrimination results in unintended ways. For example, the use of similar subjects across experiments may have produced higher conjunction discrimination due to practice effects. This was a concern driving the investigation in Experiment 4A of the significant difference between the control conditions of Experiments 1A and 2A. As effects of both dot speed and off-screen behaviour did not reach significance for the most part, it was concluded that effects of practice may account for the observed differences. However, while the addition of more naïve subjects should remedy this, the signal to noise ratio of the experiments should also be considered. That is, experienced psychophysical subjects are typically expected to produce less variable data and responses. This is especially important for the fMRI experiments, as the BOLD response is inherently a noisy measure of neural activity.

Another point to consider is the sample size of these experiments. Most experiments in this thesis included between 5-7 subjects, although a large number of data points were gathered per subject to make up for this. While a larger sample size is generally always desired, it is also important that p-values are not inflated due to large sample sizes (Lindley & Scott, 1995; Royall, 1986). The number of subjects used here was chosen to be roughly equal to other visual psychophysical experiments of a similar nature after taking number of trials into consideration (e.g. Holcombe & Cavanagh, 2001; Moradi & Shimojo, 2004; Stoner & Blanc, 2010) , and small-*n* designs have a well-established history when investigating low-level visual psychophysics. Here, significant results for all experiments were obtained without an excessive number of subjects. This being the case, I feel that the number of subjects used across these experiments was satisfactory.

4.7. Future directions

Upon reading this thesis, and especially this chapter, the reader may have noticed several asymmetries between the colour-motion and colour-orientation experiments that were conducted. As is the case in all areas of science, there is no limit to the number of experiments that can be conducted on a particular topic of interest, especially one as broad as visual feature binding. Detailed here are what may be considered the most logical follow-up experiments to those presented in the previous chapters. First, a theoretical series of experiments is presented that takes the stimulus manipulations from one feature binding task (e.g. angular separation for colour-orientation binding) which are then applied to the other (varying the direction of motion for colour-motion binding). Secondly, a set of experiments that may be considered another step forward are removed from the experimental designs of this thesis, but may nevertheless prove beneficial in further understanding the underlying mechanisms of feature binding.

While a number of colour-motion asynchrony experiments have been conducted (Arnold, 2005; Arnold & Clifford, 2002; Arnold et al., 2001; Aymoz & Viviani, 2004; Barbur et al., 1998; Clifford, Spehar, et al., 2004; Johnston & Nishida, 2001; Linares & López-Moliner, 2006; Moutoussis & Zeki, 1997a, 1997b), it would be nevertheless be interesting to observe if that asynchrony remains after applying the additional dots used in Experiments 1A and 2A. This would parallel the logic of the asynchronous colour-orientation presentation used in Experiment 3B, where it was hypothesised that a reduced angular separation may also affect the perceived colour-orientation asynchrony. Considering that accurate colour-motion binding occurred when any additional dots were present, this may correlate with the reduction of any perceived asynchrony. If colour-motion asynchrony could be modulated with the same surface segregation cues that were used here, it would corroborate the finding from Clifford, Spehar, et al. (2004) that indicated perceptual segregation of a stimulus resulted in synchronous perception of visual features. This result may also be similar to Holcombe and Cavanagh (2008), who found that exogenous attention cues remove the perceived colour-motion asynchrony.

The manipulations of presentation duration in Experiments 4B and 5B revealed that temporal integration was required at higher alternation frequencies in order to perceive the correct colour-orientation conjunction. A similar manipulation could be applied, but using colour and motion attributes. A particularly interesting manipulation might be to present a single cycle of the colour-motion stimulus both with and without the additional dots used in Experiments 1A and 2A. The additional dots, along with the shortened presentation duration may reveal a shift in the binding strategy that is used with regards to temporal integration.

Experiment 8B’s check condition had colour and orientation features distributed over time such that only temporal integration could resolve the correct feature pair. In a variation of this using Experiment 2A’s design, colour and motion features could be distributed over time by employing RDKs that turn grey while rotating, and only gain a colour while stationary. Both orange and blue RDKs would be present on-screen simultaneously, but only one would be rotating (without colour) while the other remained stationary, but coloured. Manipulations of dot configuration could also be applied here. Extending this to an fMRI experiment, the levels and patterns of activity generated by the aforementioned display may be compared to a control where RDKs were coloured while rotating and grey while stationary. Considering the results of Experiment 9B, where different display types generated similar patterns of activity when the colour-orientation conjunctions were matched, a similar result might be expected for this hypothetical experiment.

Experiments 5A and 6A used off-screen changes in motion in order to disrupt the surface segregation present at high alternation frequencies. A similar manipulation may be applied to colour-orientation stimuli. Of course, this change would have to occur along either the colour or orientation dimensions, as these displays contained no motion component. Perhaps a colour/orientation jitter or spatial phase randomisation of the grating during the interval in which the grating is off-screen may disrupt temporal integration in a similar way to the change in off-screen motion of the colour-motion stimuli. Perhaps applying either these manipulations or those detailed in Section 4.3 and Figure 4.1 may result in an experiment that can be used to investigate the perception of surfaces in early visual cortex. This would be an equivalent experiment to 10A, where the neural correlates of surface segregation and its relationship with feature binding were investigated.

Finally, I present some experiments that take the knowledge and concepts gained from these experiments, and apply them in unique and interesting ways. The majority of these experimental designs have been suggested by other researchers and colleagues, which in turn piqued my own interest. For example, while half-wave rectification was proposed as a mechanism by which a feature conjunction could be extracted from an alternating grating display (Chapter 3), a pair of alternating, equiluminant gratings can also appear transparent in some cases. It would be interesting to investigate the cases where an absence of luminance-defined bars can still lead to a transparent percept, and any differences in conjunction discrimination between it and a grating containing both colour and luminance defined strips. Another suggestion has been adding an attentional or cognitive load to the binding task. For example, the use of a concurrent "greeble" identification task (Gauthier & Tarr, 1997) or a linguistic task (Rees, Frith, & Lavie, 1997) may assist in determining if certain methods of feature binding (e.g. in a single presentation or over time) are in some part reliant on attention or working memory. A concurrent cognitive load could also disrupt or break down low-level visual binding processes, helping to reveal their temporal and/or spatial limits.

In order to determine the extent to which transparent surface segregation can enable accurate perception of a stimulus, an experiment could be conducted using three separate RDKs, each with a unique colour and motion combination. For example, a display may cycle through a 3 different RDKs moving in directions separated by 120°: one red RDK moving diagonally up and to the right, another blue RDK moving up-left, and a yellow RDK moving directly downward. Each RDK would need to be displayed for a minimum of two frames in order for motion to be present within a single presentation. Even at a monitor refresh rate of 60 Hz, the highest alternation frequency at which this stimulus can be displayed is 10 Hz, which is still within the range that can facilitate temporal transparency (Holcombe, 2001). Another similarly complex display that could be employed is a triple conjunction task using colour, orientation and motion (for example, an orange grating tilted left, but moving right with a blue grating tilted right, moving left). Experiment 6B could easily be modified to use coloured gratings to this end. Triple conjunctions have been studied to an extent (e.g. Baluch & Itti, 2010; Eckstein, Thomas, Palmer, & Shimozaki, 2000; D. G. Humphrey & Kramer, 1997; Williams & Reingold, 2001), but may further advance the study of feature binding when tested with a stimulus supporting visual transparency.

4.8. Concluding remarks

The experiments presented here have demonstrated that feature binding is a complex and dynamic process. The interdependence of the overall binding process with feature perception, temporal integration, surface segregation, and visual persistence has been explored. In order to account for the dispute in the feature binding literature surrounding a fast or slow binding mechanism, this thesis has presented a set of feature binding experiments. From the results obtained, it appears that binding is indeed a process with a comparatively low temporal resolution. Critically, the apparently high temporal resolution that feature binding can appear to exhibit stems from a dependence on surface segregation. Perceptual segregation of a stimulus into component surfaces enables a surface's constituent features to be extracted and subsequently processed. Without this perceptual transparency, however, binding is reduced to chance at intermediate and high alternation frequencies. This explanation can parsimoniously account for both past and present results in the feature binding literature, while remaining simple and intuitive.

Contrasting the conclusions of these experiments with the typically seamless way in which we perceive our environment, the efficiency of the visual system is further emphasised. By pushing the boundaries of feature binding research and the study of perception in general, we can further our understanding of visual perception in general and, ultimately, the workings of the human brain.

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Appendix A. Author contributions to experimental work

The following experiments presented in the thesis have been submitted for publication or published in scientific journals.

Experiments 1A, 5A and section 2.13.5

Vigano, G. J., Maloney, R. T., & Clifford, C. W. G. (Accepted 2015). Transparent surface segregation enables visual feature binding in rapidly alternating displays. *Journal of Vision*.

Experiments 8A, 9A, and 10A

Vigano, G. J., Maloney, R. T., & Clifford, C. W. G. (2014). Motion-defined surface segregation in human visual cortex. *Journal of Cognitive Neuroscience, 26*(11), 2479-2489.

Appendix B. Stimulus movie legends

Chapter 2

MovieS1.mov

Demonstration of the control display from Experiment 2A (identical to the ‘stopping’ display type in Experiment 5A) displayed at 3 temporal alternation frequencies: 1.67, 5 and 15 Hz. Here, each random dot kinematogram (RDK) stopped rotating while off-screen. In this and subsequent movies for Chapter 2, the colour-motion stimulus conjunction is orange paired with a clockwise rotation and blue with an anticlockwise rotation. For illustrative purposes, the movies shown here are extended in duration compared to the actual experimental stimuli. Mean discrimination in the binding task for these conditions was approximately 80, 55 and 95% correct for the alternation frequencies 1.67, 5 and 15 Hz, respectively.

MovieS2.mov

Demonstration of the ‘Grey, different configuration’ display type from Experiment 2A at the same 3 temporal alternation frequencies as MovieS1: 1.67, 5 and 15 Hz. In this stimulus, two stationary, grey RDKs were added to the control stimulus (MovieS1) alternating at the same frequency as the target RDKs. Mean accuracy in the binding task for these conditions was approximately 90, 70 and 85% correct for the alternation frequencies 1.67, 5 and 15 Hz, respectively. As with MovieS1, for illustrative purposes stimuli are shown extended in duration here compared with the actual experimental stimuli.

MovieS3.mov

Demonstration of the ‘Resetting and unpaired’ display type from Experiment 5A. Here, RDKs reset to their initial position while off-screen. The same 3 temporal alternation frequencies as MovieS1 and MovieS2 are shown: 1.67, 5 and 15 Hz. Mean accuracy in the binding task for these conditions was approximately 85, 55 and 55% correct for the alternation frequencies 1.67, 5 and 15 Hz, respectively. For illustrative purposes stimuli are shown extended in duration here compared with the actual experimental stimuli.

Chapter 3

MovieS4.mov

Demonstration of the perpendicular grating stimulus (90° angular separation) from almost all Experiments in Chapter 3, shown at 3 temporal alternation frequencies: 2.5, 5 and 7.5 Hz. Each demonstration has a 250ms raised cosine contrast ramp on and off. In this and subsequent movies, the colour-orientation stimulus conjunction is orange paired with a rightward tilted orientation and blue with a leftward tilted orientation. For each subject, stimuli were calibrated for colour saturation and luminance prior to the experiment. For illustrative purposes, the movies shown here are extended in duration compared to the actual experimental stimuli. Mean accuracy in the binding task for these conditions was approximately 90, 90 and 95% correct for the alternation frequencies 2.5, 5 and 7.5 Hz, respectively.

MovieS5.mov

Demonstration of the grating stimulus used in most experiments in Chapter 3 with an 15° angular separation between gratings of 15° (±7.5° from vertical). The same 3 temporal alternation frequencies as MovieS5 is shown: 2.5, 5 and 7.5 Hz. Mean accuracy in the binding task for these conditions was approximately 80, 55 and 85% correct for the alternation frequencies 2.5, 5 and 7.5 Hz, respectively. As with MovieS5, for illustrative purposes stimuli are shown extended in duration here compared with the actual experimental stimuli.

MovieS6.mov

Demonstration of the check display type from Experiment 8B and 9B at the same 3 temporal alternation frequencies as MovieS5 and MovieS6: 2.5, 5 and 7.5 Hz. Mean accuracy in the binding task for these conditions was approximately 55, 75 and 80% correct for the alternation frequencies 2.5, 5 and 7.5 Hz, respectively. As with MovieS5 and MovieS6, for illustrative purposes stimuli are shown extended in duration here compared with the actual experimental stimuli.