Spatial summation of motion: Considering the effects of psychophysical method and healthy ageing

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B.A. (Hons.)

This thesis is presented for the degree of Doctor of Philosophy of The University of Western Australia
School of Psychological Science
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Thesis declaration

I, Thomas McDougall, certify that:

This thesis has been substantially accomplished during enrolment in the degree.

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Written patient consent has been received and archived for the research involving patient data reported in this thesis.

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This thesis contains published work and/or work prepared for publication, some of which has been co-authored.

Signature

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Thesis abstract

Perceiving motion plays an important role in our ability to identify and interact with the world around us. Motion signals arising from one moving object or surface must be spatially integrated, and segmented from other moving object or surfaces. This thesis uses psychophysical experiments to re-investigate the visual system’s capacity to integrate motion signals over area, and how this is balanced with the need for segmentation. To measure summation, the experiments in this thesis employ the use of Battenberg stimuli. These stimuli allow for summation to be measured within a fixed overall area. The advantage of this, over studies that vary the overall area, is that the level of internal noise does not co-vary with stimulus size so performance changes a more likely to reflect changes in signal only. In Chapter 2 this methodology was successful in revealing larger summation areas for the detection of motion at contrast threshold, compared to the conventional studies. This result persisted even when the stimulus contained motion in opposing directions, suggesting that for low contrast motion stimuli, summation dominates regardless of other stimulus properties that might otherwise drive segmentation. Chapter 3 also showed extensive summation over area when the observer is required to discriminate motion direction, consistent with research suggesting that detection and discrimination are underpinned, at least in part, by the same summation mechanisms. Chapter 2 showed that for high contrast Battenberg stimuli, summation was absent, i.e. there was no improvement with increasing signal area when the task was to discriminate which one of two patterns was higher in contrast. This was consistent with previous research showing that summation is reduced at high contrast, in favour of enhancing segmentation. However, in that experiment the contrast increment to be discriminated was added to a pedestal with the same spatial arrangement. Previous studies suggest that when the contrast pedestal and the
target increment co-vary in this way, the pedestal can suppress any area benefit of the target increment due to increases in suppressive gain control mechanisms from the concomitant increase in pedestal area. Therefore, in Chapter 4, the spatial structure of the pedestal was fixed across all conditions, so as to keep the contribution of suppressive gain control constant, and only the area of the target increment was varied, similar to the methodology used by Meese and Summers (2007) for examining suprathreshold summation of static grating patterns. With this method, the detectability of small contrast increments was found to increase with area, providing evidence of extensive summation at high contrast. For some observers, the amount of summation was over a smaller area than seen previously in the experiments employing low contrast stimuli. This is consistent with the notion that at high contrast summation may not be as strong (potentially to assist with segmentation), but this balance seems to show some variability across observers which is consistent with previous findings.

One of the potential sources of variability controlling the balance between summation and suppression is age. This is based on previous research showing decreased spatial suppression for large high contrast motion in older observers relative to younger observers. This is hypothesized to be underpinned by reduced neural inhibition in the ageing visual cortex. Reduced inhibition predicts increased excitation which may result in a general expansion of the size of excitatory receptive field allowing perceptual summation to be measurable over a larger area, even at low contrast. This suggestion was tested using the Battenberg stimuli. Compared to younger observers, older observers show poorer direction discrimination thresholds overall, but they also show smaller improvements in threshold for the full field Battenberg compared to the Battenberg with small checks.
(smaller signal area). This may be underpinned by larger summation areas for the perception of small moving stimuli.

Overall this thesis shows that the motion system can integrate contrast over larger areas than previously suggested for both low contrast and high contrast stimulus conditions, and provides new evidence that ageing can affect spatial summation of motion at low contrast levels.
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Finally, thanks to my mother, Lee, for your love, support and understanding during all my many years of education. Your selflessness is what made it possible for me to get here in the first place and I will be forever grateful.
## Statement of Candidate’s Contribution

All work reported in this thesis was designed and implemented by the author. This thesis contains work that has been published (Chapter 2, 4 and 5) The contributions of each author have been outlined in the following pages.

### Details of the work:

The work in Chapter 2 looked at integration of motion signals over area at low contrast and high contrast levels using a novel stimulus design called the “Battenberg”. This work has been published in *Journal of Vision*.


### Location in thesis: Chapter 2

### Student contribution to work:

As primary author of this publication, I was primarily responsible for design, implementation, data analysis and manuscript production in collaboration with the co-authors (J. Edwin Dickinson and David R. Badcock). I was primarily responsible for programming the experimental procedures and received some assistance from both J. Edwin Dickinson and David R. Badcock. All data was collected and analysed by myself with guidance from both J. Edwin Dickinson and David R. Badcock. I prepared the manuscript with assistance from both J. Edwin Dickinson and David R. Badcock.

### Co-author signatures and dates:

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Details of the work:
The work in Chapter 4 looked at integration of motion signals at high contrast using a slightly different methodology than the previously used. This work will be submitted for publication prior to submission of the thesis.

Location in thesis: Chapter 4

Student contribution to work:
As primary author of this publication, I was primarily responsible for design, implementation, data analysis and manuscript production in collaboration with the co-authors (J. Edwin Dickinson and David R. Badcock). I was primarily responsible for programming the experimental procedures and received some assistance from both J. Edwin Dickinson and David R. Badcock. All data was collected and analysed by myself with guidance from both J. Edwin Dickinson and David R. Badcock. I prepared the manuscript with assistance from both J. Edwin Dickinson and David R. Badcock.

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Details of the work:
The work in Chapter 5 looked at how summation of motion signals is affected by normal health aging. It has been published in Vision Research.


Location in thesis: Chapter 5

Student contribution to work:
As primary author of this publication I was primarily responsible for design, implementation, analysis and manuscript production, in collaboration with the co-authors (Bao N. Nguyen, Allison M. McKendrick, and David R. Badcock). I was primarily responsible for programming the experimental procedures and received some assistance from all co-authors. Bao N. Nguyen performed all optometric screening. Testing of participants was conducted with the assistance of Bao N. Nguyen. All data was analysed by myself with guidance from all co-authors. I prepared the manuscript with assistance from all co-authors.

All co-authors have individually provided approval for these publications to be included in this thesis. Bao N. Nguyen and Allison M. McKendrick were unable to provide signatures.

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I, David Badcock, certify that the student statements regarding their contribution to each of the works listed above are correct

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Date: 13.12.2017
Publications Arising from this Thesis


Chapter 1: General Introduction
A kangaroo is seen bounding across the plain in the distance. The light reflecting from the kangaroo is projected onto the retina, activating photoreceptors that are sensitive to changes in luminance. The kangaroo’s movement causes a change in the pattern of activation of these cells across the retina. Changes in relative activation over time are then processed by higher visual areas that are responsible for estimating motion in the visual environment. At these later processing stages, all the motion signals belonging to one object, such as the kangaroo, are pooled together and segregated from other objects such as trees or other animals. This seemingly effortless ability of the visual system provides crucial information for us to be able interpret, and interact with, the environment around us.

Extensive pooling of motion signals may not always be beneficial and, for example, could potentially lead to erroneously pooling together the motion signals arising from the kangaroo with the motion signals arising from a mob of emus moving in the background. This can also occur with physically stationary objects in the background (such as trees) as our own eye and head movements causes the images of them to move on our retinas. Therefore, the demands of segmentation mechanisms may operate to adaptively limit the extent of motion integration in some circumstances. However, the balance of these two processes may not depend solely on the presence of typical cues that elicit integration and segmentation, e.g. direction, speed, or depth of motion (Regan, 2000). The general quality or salience of sensory signals is also thought to mediate the balance of integration and segmentation. For example, spatial summation is increased and surround suppression, a receptive field property that enables motion segmentation, is reduced when stimulus visibility (contrast) is decreased (Tadin, Lappin, Gilroy, & Blake, 2003), potentially reflecting an adaptive property of the visual system to increase neuronal
sensitivity to, and detection of, low signal-to-noise ratio stimuli (Marr, 1982). The overall aim of this thesis is to re-examine the extent of motion summation and segmentation, and how the strength of these two processes changes when moving from low to high contrast conditions.

The magnitude of spatial summation has also been reported to vary with the age of the individual observer. Elderly observers have been shown to have decreased perceptual surround suppression of motion (Betts, Taylor, Sekuler, & Bennett, 2005). Potential differences between these groups are proposed to be underpinned by imbalances in excitation and inhibition in areas of visual cortex that are thought to be involved in summation and segregation of motion (Betts, Sekuler, & Bennett, 2012; Betts et al., 2005). It is therefore interesting and important to assess performance for different age groups to ensure the conclusions can generalise. Using the methods developed in the earlier chapters, these groups will be used to distinguish between changes in overall sensitivity from changes in the areas over which signals can be summed.

Motion signals generated by the visual scene need to be transmitted from the retina, to primary visual cortex, to higher-tier visual areas capable specialised for motion processing. The nature of these pathways will be reviewed first so that potential bases for summation and segmentation of signals can be appropriately considered.

1.1 Motion processing pathway: Retina to Primary Visual Cortex

Information is carried from the retina to the lateral geniculate nucleus (LGN) by three anatomically separate pathways made up of different types of retinal ganglion cells (RGCs). Midget RGCs are relatively small with axons that convey signals along the optic nerve and optic tract eventually synapsing with Parvocellular-cells, or P-cells, located in the upper layers of the LGN; making the processing pathway called the Parvocellular
pathway. Parasol RGCs have relatively large receptive fields and their axons project to Magnocellular, or M-cells, which are located in the lower layers of the LGN; making up the pathway called the Magnocellular pathway. The cells in the Magnocellular pathway have, on average, greater sensitivity to higher temporal frequencies and therefore respond more preferentially to moving and flickering stimuli (Merigan & Maunsell, 1993; Schiller, Logothetis, & Charles, 1990) whereas the cells in the Parvocellular pathway have, on average, greater sensitivity to higher spatial frequencies (and lower temporal frequencies) and respond more preferentially to form and texture information, with minimal response to motion information in stimuli (Livingstone & Hubel, 1988; Merigan, Byrne, & Maunsell, 1991). Despite difference in peak sensitivity, the spatial and temporal tuning functions of Magnocellular and Parvocellular cells show substantial overlap (Merigan & Maunsell, 1993).

The Magnocellular and Parvocellular pathways remain anatomically divided as they project to layers 4Cα and 4Cβ, respectively, within primary visual cortex (V1, Hendrickson, Wilson, & Ogren, 1978). A more recently discovered pathway between the retina and the brain is the Koniocellular pathway which includes the small Koniocellular cells located between each of the M and P layers of the LGN and which receive input from small bistratified, large sparse, and broad thorny RGCs (Hendry & Reid, 2000; Szmajda, Grünert, & Martin, 2008). Koniocellular cells project to layers 1-3 of V1 carrying blue/yellow (S cones – (L cones + M cones)) colour signals (Chatterjee & Callaway, 2003; Hendry & Reid, 2000). There is also evidence for a direct Koniocellular projection from LGN to motion sensitive middle temporal (MT) area which bypasses V1, implying that the Koniocellular pathway may also have a role in the detection of moving objects (Sincich, Park, Wohlgemuth, & Horton, 2004). A disynaptic projection has been found between the
Parvocellular layers of the LGN and area MT (Nassi & Callaway, 2006), taken together this further suggests that motion processing may not be exclusive to the Magnocellular pathway. This and other research, such as the discovery of Magnocellular-projecting smooth cells which may serve a different function from the Magnocellular-projecting parasol cells (Crook et al., 2008), suggests that there are additional (functionally and anatomically distinct) sub-streams; challenging the classical 3-stream paradigm (Kaplan, 2008, 2014). Instead it can be argued that our ability to perceive motion is achieved by multiple processing streams. However, it is important to note that deficits in motion perception were only found to occur after Magnocellular lesions, and did not occur after Parvocellular lesions (Schiller & Logothetis, 1990), although at high contrasts and low temporal frequencies the deficits caused by Magnocellular lesions are small, suggesting there may be some contribution of the Parvocellular system to the perception of motion information. In support of this, Parvocellular lesions have been shown to produce small, but significant response reductions in MT (Maunsell, Nealey, & DePriest, 1990) further implying that motion processing may not be exclusive to the Magnocellular stream. Moreover, human psychophysical studies have also shown that pattern information with properties closely matched to the tuning of Parvocellular system can provide input to motion processing (Apthorp et al., 2013; Badcock & Dickinson, 2009; Ross, Badcock, & Hayes, 2000; Tang, Dickinson, Visser, & Badcock, 2015).

As mentioned previously, the Magnocellular and Parvocellular pathways project to different layers in V1. From V1 these layers project separately to dorsal and ventral areas of the extrastriate cortex, forming the ventral and dorsal streams, respectively. The ventral stream transmits information through V2 and V4 and then to areas of the temporal lobe. The dorsal stream projects to dorsal extrastriate areas such as middle temporal (MT) area
and medial superior temporal (MST) area, and then to areas in the parietal lobe (ventral intraparietal (VIP), lateral intraparietal (LIP), medial dorsal parietal (MDP), medial intraparietal (MIP), area 7a and area 7b). The dorsal pathway is critical to processing information about self-motion relative to the environment (Duffy & Wurtz, 1991; Smith, Wall, & Thilo, 2012), recognizing an object’s spatial location and motion (Ungerleider & Haxby, 1994), and has a role in the guidance of actions such as grasping and reaching (Culham et al., 2003; Goodale & Milner, 1992).

### 1.2 Primary Visual Cortex

Further visual processing, including motion processing, takes place in primary visual cortex (V1) and is performed by neurons which each receive information from the retina about a small region of visual space. Hubel and Wiesel established that V1 neurons in cat (Hubel & Wiesel, 1959, 1962) and monkey (Hubel & Wiesel, 1968) respond best to oriented lines appearing in their receptive field. In addition to this, approximately 30% of V1 neurons, particularly those of layers 4A, 4B, 4ca, and 6, are also selective for the direction in which a luminance-defined stimulus is moved across the receptive field (Hawken, Parker, & Lund, 1988; Hubel & Wiesel, 1968; Livingstone & Hubel, 1984). Unlike the temporal frequency tuned neurons in pre-cortical areas, these V1 neurons are considered to be “direction tuned”, meaning they respond maximally to motion in their preferred direction and minimally to motion in the opposite (null) direction. Because of the orientation selectivity, the direction preferred tuning of each neuron is in the direction orthogonal to its preferred spatial orientation (Born & Bradley, 2005; Maunsell & Newsome, 1987; Movshon, Adelson, Gizzi, & Newsome, 1985), with the full 360° range of motions being represented by the system of neurons. Therefore, the neural properties necessary for extracting motion direction signals are present at least as early as V1.
Due to the relatively small size of V1 receptive fields (Hubel & Wiesel, 1968), they usually respond to a restricted, localized, portion of a moving bar or edge, and signal the motion vector in the cell’s preferred direction (Adelson & Movshon, 1982). This local motion response is proportional to the motion vector perpendicular to the cell’s preferred orientation and may not directly reflect the overall motion direction of the object or surface from which it was derived. This results in directionally-ambiguous responses for all moving lines or edges that extend beyond the range of the receptive field. An ambiguity that is known as the “aperture problem” (Adelson & Movshon, 1982). To resolve this problem and for the human visual system to be able to perceive the motion of objects and surfaces accurately, the local motion estimates must be integrated and combined at a later stage in the visual processing pathway.

1.3 Middle temporal area (MT/V5)

The next stage of motion processing in the visual pathway occurs in middle temporal (MT) area or area V5 (Born & Bradley, 2005; Maunsell & Newsome, 1987). The significance of area MT/V5 for motion perception was first revealed when Allman and Kaas (1971) recorded from the entire cortex of New World (owl) monkeys and found an area of dense myelination that responded more strongly to drifting bars than to flashing spots, delineating it as a specific cortical area which they named MT. Dubner and Zeki (1971) concurrently examined the corresponding area in Old World (rhesus macaque) monkeys and discovered it also had dense myelination, with high concentrations of directionally-selective cells, establishing it as a functionally separate visual cortical area, which they subsequently referred to as area V5. The two alternative names are agreed to refer to the same area and hence are frequently referred to as MT/V5, as seen in this chapter. Further neurophysiological recordings from MT/V5 in New world monkeys and
Old world monkeys have since established that nearly all of the neurons in area MT/V5 show direction selective responses and are organised in a retinotopic fashion covering the upper and lower visual fields (Albright, 1984; Albright, Desimone, & Gross, 1984; Desimone & Ungerleider, 1986; Felleman & Kaas, 1984; Maunsell & van Essen, 1983b). Within this retinotopic map the direction selective neurons show a strong columnar organization with smooth changes in direction preference (Albright et al., 1984). Single cell activity in macaque MT/V5 has been causally linked to motion perception (Britten, Newsome, Shadlen, Celebrini, & Movshon, 1996). For example, Salzman, Britten, and Newsome (1990) showed that electrical micro-stimulation of clusters of direction selective MT/V5 cells in macaque monkeys biased the monkey’s perceptual decisions toward the directional preference of the cells that were being stimulated. Lesions to this area also caused elevations in motion direction discrimination thresholds but caused no changes in spatial orientation discrimination performance (Newsome & Pare, 1988). In humans, transcranial magnetic stimulation (TMS) over area the human homologue of area MT/V5 affected performance on motion perception tasks requiring direction discrimination (Beckers & Zeki, 1995; Tadin, Silvanto, Pascual-Leone, & Battelli, 2011). Therefore, activity of MT/V5 cells is considered to have a critical link with motion processing.

In order to further appreciate the contribution of MT/V5 to motion processing, and specifically the role it has in motion integration, it is important to consider the properties of inputs to MT/V5 from earlier motion sensitive cortical pathways that contribute to this process.

MT/V5 receives signals from many visual areas, see Figure 1.1, including V2, V3, V3A and LGNd (Felleman & van Essen, 1991; Maunsell & van Essen, 1983a; Sincich et al., 2004), but the main input comes from V1 (Born & Bradley, 2005; Maunsell & van
Essen, 1983a), receiving approximately 6% of fibres projecting from V1 (Lennie, 1998).

There is evidence that MT/V5 cells receive direct and exclusive input from direction-selective cells located in layer 4B and 4C of V1 (Movshon & Newsome, 1996; Nassi & Callaway, 2006; Shipp & Zeki, 1989a). Some V1 cells project indirectly to MT/V5 via V2 (Ponce, Lomber, & Born, 2008; Shipp & Zeki, 1989b) and V3 (Maunsell & van Essen, 1983a), and are thought to carry information on binocular disparity and contribute to processing of fast moving stimuli (Ponce, Hunter, Pack, Lomber, & Born, 2011). MT/V5 also receives input from V3A (Tootell et al., 1997; Zeki, 1980) and V6 (Galletti et al., 2001) which carry vestibular signals and information about head-centred flow motion rather than retinal motion, with a bias for the peripheral visual field (Cardin & Smith, 2011; Fischer, Bülthoff, Logothetis, & Bartels, 2012; Pitzalis et al., 2013a; Pitzalis, Fattori, & Galletti, 2013b; Zeki, 1980), and for this reason they are considered by some to be part of separate, functionally distinct, parallel motion pathways to MT/V5 (see Gilalae-Dotan, 2016). There is also evidence that the LGN and the inferior pulvinar have direct “V1-bypassing” inputs into MT/V5 which are reported to be involved in detection of fast motion (Ajina, Kennard, Rees, & Bridge, 2015; Berman & Wurtz, 2010, 2011; Ffytche, Guy, & Zeki, 1995; Maunsell & van Essen, 1983a; Schmid et al., 2010; Sincich et al., 2004).

The outputs of motion analysers with spatially localized receptive fields in V1 feed into, and activate a second-stage of analysis in area MT/V5 that is capable of integrating motion signals over more extended areas of visual space (Adelson & Movshon, 1982; Movshon et al., 1985). Given that receptive fields of MT/V5 neurons are approximately ten times larger than V1 receptive fields they will collect information relevant to a much larger area of the visual field (Albright & Desimone, 1987; Kolster, Peeters, & Orban,
2010; Movshon & Newsome, 1996), many V1 units provide convergent input into an individual MT/V5 unit, thus endowing MT/V5 cells with signals that cover a larger receptive field. This convergent property is consistent with the implication that there is a stage of processing in MT/V5 that integrates local motion information over larger areas of visual space (Amano, Edwards, Badcock, & Nishida, 2009; Movshon et al., 1985).

Figure 1.1 A schematic representation of some of the main inputs into MT/V5 discussed above. Dashed borders indicate structures within the thalamus rather than the cerebral cortex.
1.4 Motion integration and area MT/V5

Several psychophysical studies have attempted to determine the spatial limit over which motion signals are integrated in order to characterize the receptive field properties of the underlying neural mechanisms in MT/V5 (Anderson & Burr, 1987, 1991; Anderson, Burr, & Morrone, 1991; Watson & Turano, 1995). These studies typically measure improvements in detection or direction discrimination performance as the size of a moving stimulus increases. An initial steep slope of approximately 1 for the function describing threshold sensitivity against area; known as Riccò’s law (Riccò, 1877) is indicative of a process of linear summation within receptive fields of detectors (Barlow, Fitzhugh, & Kuffler, 1957), while a shallower slope of approximately 0.25 is argued to be more consistent with probability summation across space or between independent detectors (Robson & Graham, 1981). The stimulus size at which improvements in sensitivity are no greater than that predicted by probability summation, or become constant, is used to derive an estimate of the receptive field size of a motion detector (Anderson & Burr, 1991). These behavioural estimates reflect the signal processing properties of psychophysically defined motion units, rather than neurophysiological properties of individual neurons, and are likely to reflect the processing stage in the neural pathway which has the highest spatial resolution in terms of discrete receptive fields for the particular stimulus employed.

Anderson and Burr (1987) measured contrast thresholds for observers to be able to discriminate the motion direction of a drifting sinewave grating. To measure changes in sensitivity as stimulus area increases (summation), the drifting sinewave grating was modulated by a stationary, two-dimensional, Gaussian function of variable width. Spatial frequency was also manipulated by varying the viewing distance. The results showed that the extent of summation (defined as 2 standard deviations of the Gaussian envelope
applied to the sinewave stimulus) varied as a function of spatial frequency of the grating used, reflecting a progressive decrease in receptive field size with increasing spatial frequency (Figure 1.2). For high frequency gratings (10 c/°) summation occurred over only 0.1° of visual angle, whereas for low frequency gratings (0.5 c/°) the summation limit was approximately 1° of visual angle. The motion receptive field size for very low frequency gratings of 0.01 c/° was estimated to be much larger; approximately 7-8° of visual angle. Anderson and Burr (1991) also investigated motion summation by measuring contrast thresholds for detection of motion in addition to thresholds for motion direction discrimination, as a function of stimulus length and width to determine if detection and discrimination abilities are subserved by the same underlying mechanisms. The contrast required for detection of gratings was the same as that required for discrimination of the direction of drift, consistent with previous research suggesting direction can be discriminated at threshold for detection (Derrington & Henning, 1993; Levinson & Sekuler, 1975; Watson, Thompson, Murphy, & Nachmias, 1980). This was consistent across all stimulus lengths and widths, indicating that performance on the two tasks is affected by changes in signal area in the same way as might be anticipated if the same receptive fields were supporting both tasks. The summation data permitted a single model of receptive field size to be accurately fitted to both the detection and discrimination thresholds. Similar to the results of Anderson and Burr (1987), the estimated limit of summation (length and width) of the receptive fields varied as a function of their spatial-frequency preference from approximately 1.2° at low spatial frequencies (0.1 c/°) to approximately 0.05° at high spatial frequencies (10 c/°). The receptive fields were approximately as tall as they were wide (an aspect ratio of 1) across all spatial frequencies (Anderson & Burr, 1991). These findings were supported in a follow-up study that
combined psychophysical masking techniques and summation techniques to produce very similar estimates of receptive field length and width for motion units, for both high and low frequency stimuli, concluding that receptive fields of motion detectors are circular in shape across all spatial scales, and not elongated in the direction of motion (Anderson et al., 1991). Watson and Turano (1995) investigated the summation properties of the motion stimulus that was most easily detected by the visual system, i.e. had the lowest contrast threshold. They found that the drifting grating stimulus that produced the lowest contrast threshold had a spatial frequency of 3c/° and a width and height of 0.44°. This finding in combination with the existing summation data has provided convergent evidence that many spatial frequency tuned motion detectors, including those which are the most sensitive to contrast, are capable of integrating over relatively limited spatial areas to reach that contrast threshold.
Further psychophysical studies using drifting sparse random dot patterns and spatial summation techniques have found that the proportion of dots needed to move in a common direction to detect the presence of coherent flow (coherence thresholds) decreases with increasing signal area (Barlow & Tripathy, 1997; Lappin & Bell, 1976; Watamaniuk & Sekuler, 1992). These dot patterns consist of “signal” dots moving in a given direction which are intermingled with “noise” dots moving in random directions. When the proportion of signal dots is high enough, they appear to move coherently in the global direction of the signal dots. Threshold is defined as the minimum proportion of signal dots required to reliably discriminate the global motion direction (Edwards & Badcock, 1994).
translational motion signals; up to 9° in diameter for a circular summation area when presented in the peripheral visual field (Watamaniuk & Sekuler, 1992) and up to 4° when presented in the central visual field (Ledgeway, McGraw, & Simmers, 2011). The integration of distributed signal elements for translational global motion detection is thought to rely on mechanisms in MT/V5 due to relatively large receptive field sizes of this area (Britten, Shadlen, Newsome, & Movshon, 1992) and studies which have shown that task performance is significantly impaired by lesions to MT/V5 in macaque monkeys (Newsome & Pare, 1988).

The visual motion system is also thought to have distinct mechanisms that are capable of integrating local motion signals that conform to more complex, optic flow, trajectories (Morrone, Burr, & Vaina, 1995). Burr, Morrone, and Vaina (1998) investigated the spatial summation properties of patterns composed of drifting dots representing complex motions such as rotation, expansion and contraction (Figure 1.3).

![Figure 1.3. Schematic examples of complex flow motion stimuli](image)

They found evidence of strong summation for large image sizes of at least 36° and extending up to 72°. This occurred regardless of whether the dots were confined to
separate, oppositely positioned, sectors within the stimulus. The extent of summation for simple unidirectional (translational) dot patterns was not as large as that for the complex motion. The encoding of complex motion is therefore thought to be governed, at least in part, by MST, an area with larger receptive fields, beyond MT/V5 along the motion processing pathway (Desimone & Ungerleider, 1986; Raiguel et al., 1997) that preferentially responds to rotation, expansion and spiral motion (Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Orban et al., 1992; Tanaka et al., 1986; Tanaka & Saito, 1989). This selectivity of the visual motion system is thought to be responsible for analysing and integrating optic flow signals produced by self-motion through the environment (Warren, 2004). The results of these studies taken together provide evidence consistent with larger receptive fields in higher motion areas for the integration of local motion signals. Morrone et al. (1995) also investigated summation for dot-patterns containing complex motion, but in addition to coherence thresholds they also measured contrast thresholds for pattern detection and motion direction discrimination. The coherence thresholds showed evidence consistent with extensive summation over area by large detectors integrating over the entire display which in this case was 10° in diameter. The contrast threshold results, on the other hand, exhibited different summation trends. Morrone et al. (1995) suggest that integration of contrast over area for motion perception is limited by contrast sensitive mechanisms in V1, or smaller sub-units in MT/V5, that have limited spatial summation capacities. This is consistent with the findings of relatively small receptive field sizes of the motion mechanisms most sensitive to luminance contrast (Watson & Turano, 1995). Therefore, different experimental tasks will reflect the operation of motion units in different cortical levels, with different receptive field geometry, to best code for the particular stimulus employed. This thesis focusses on re-
examining receptive field size of the motion mechanisms tuned to luminance contrast and therefore employs contrast detection and contrast discrimination tasks to tap these motion units.

1.5 Surround suppression of motion

The receptive field of a neuron is conventionally defined as the retinal region within which a neuron’s response is altered when a stimulus is presented. Within this area is a primary centre region known as the classical receptive field (CRF) which can encompass both ON and OFF subregions of the receptive field. Neurophysiological motion summation studies have revealed that cells in MT/V5 possess a surround region, conventionally known as the non-classical receptive field (nCRF), which when stimulated can weaken or enhance motion summation by altering neural firing rate to an appropriate stimulus presented simultaneously within the CRF, but has no effect when stimulated alone (Allman, Miezin, & McGuinness, 1985a, 1985b). Given that the surrounds have no effect when there is no stimulus in the CRF, the centre and surround mechanisms are described as having non-linear relationship (Allman et al., 1985a; Born, 2000; Raiguel, Hulle, Xiao, Marcar, & Orban, 1995; Tanaka et al., 1986). Allman et al. (1985a) recorded responses of MT/V5 neurons in macaque monkey to moving dot-arrays presented concurrently to the CRF and the nCRF. The dots presented to the CRF always moved in the neuron’s preferred direction. The direction of the background dot-array presented to the nCRF was one of twelve possible directions. For the majority of cells tested, the firing rate of the neurone, when presented with their preferred motion direction in the CRF was maximally suppressed when the dots within the nCRF moved in the same direction (Figure 1.4). Therefore, these surround receptive fields are directionally selective, suppressing most actively for stimuli moving in the cell’s preferred direction, and least for motion opposite
to the cell’s preferred direction (Allman et al., 1985a). The surrounds in MT/V5 are estimated to be 3-5 times larger than the CRF (Raiguel et al., 1995; Tanaka et al., 1986) and are often reported to be irregular in shape, sometimes only encompassing a small fraction of the perimeter of the CRF (Xiao, Raiguel, Marcar, Koenderink, & Orban, 1995; Xiao, Raiguel, Marcar, & Orban, 1997), contrary to initial reports that described surround as encircling the CRF (Tanaka et al., 1986).

Figure 1.4. Responses recorded from a directional selective centre-surround MT/V5 neuron in owl monkey. The graph on the left shows the response of the cell when an array of dots moving in one of twelve directions is presented to the area corresponding to the CRF, surrounded by a background of stationary dots. Responses are normalized to the average levels of spontaneous activity (0%), therefore 100% is equal to the cells optimal direction. The graph on the right shows the response of a cell when an array of dots moving in the cells preferred direction is presented to the area corresponding to the CRF,
surrounded by an array of dots moving in one of twelve directions. The stimulus conditions are presented schematically above each graph. Adapted from Allman et al. (1985a)

The predominant nature of these centre-surround interactions reported thus far is inhibitory. In contrast to these antagonistic inhibitory surrounds, facilitatory surrounds, which prefer motion in the same direction as the centre have also been reported, but they are found in smaller proportions (Allman et al., 1985a; Pack, Hunter, & Born, 2005; Tanaka et al., 1986). In the case of these neurons, the firing rate to centre motion increases when the motion is concurrently presented to the surround. Depending on where the cells are located within MT/V5, some surrounds show inhibition, others facilitation (Born & Tootell, 1992). The different types of neural centre-surround interactions (inhibitory vs facilitatory), and their separate cortical locations, may help MT/V5 to participate in different behavioural functions. For example, antagonistic MT/V5 surrounds help facilitate the detection of direction discontinuities in the visual scene, thus are thought to have a critical role in segmenting moving objects from their background and from other surrounding objects (Allman et al., 1985a; Born, 2000; Braddick, 1993; Gautama & Van Hulle, 2001; Lamme, 1995; Nakayama & Loomis, 1974) whereas integrative surrounds are thought to have a role in encoding the wide-field background motion, and separating wide-field motion signals from those generated by self-motion during eye-movements (Born, Groh, Zhao, & Lukasewycz, 2000; Braddick, 1993; Huang, Albright, & Stoner, 2007). For surround suppressed neurons, an estimate of the size of the CRF can be garnered based on the measured onset of surround suppression, which can be determined neurophysiologically or inferred from behavioural performance. However, there is converging evidence that the strength of surround suppression in centre-surround MT/V5
neurons is modulated under certain conditions, and in turn, the measurable summation area of the CRF of a centre-surround neuron may vary depending on the nature of the stimulus used. For example, neurophysiological and behavioural research has shown that suppression increases as stimulus contrast increases; this contrast-dependency of summation/suppression is a key concern of this thesis and will be further discussed in the following section.

### 1.6 Contrast-dependent centre-surround interactions

Previous studies have suggested that the size and shape of the CRF and the nCRF of centre-surround neurons are dependent on stimulus conditions. For example, reducing retinal illumination caused the diameter of the summation region of retinal ganglion cell receptive fields to increase while surround regions became relatively ineffective (Enroth-Cugell & Robson, 1966). More recent studies have reported that the extent of spatial summation and suppression of V1 neurons depends on stimulus conditions such as contrast. Neurophysiological recordings from macaque monkeys have found that the extent of summation in centre-surround V1 neurons increases as contrast decreases and the relative extent/strength of the suppressive surround region becomes diminished (Cavanaugh, Bair, & Movshon, 2002; Kapadia, Westheimer, & Gilbert, 1999; Kasamatsu, Miller, Zhu, Chang, & Ishida, 2010; Levitt & Lund, 1997; Sceniak, Ringach, Hawken, & Shapley, 1999; Schwabe, Ichida, Shushruth, Mangapathy, & Angelucci, 2010). Chen, Song, and Li (2012) found, in cat V1 neurons, the CRF expanded under low contrast conditions and the strength of surround suppression became significantly reduced. Neurophysiological studies on motion selective centre-surround MT/V5 neurons in macaque monkey have shown that surround suppression is reduced under low contrast conditions, just as in V1, (Pack et al., 2005; Tsui & Pack, 2011). Pack et al. (2005)
recorded responses from 110 MT/V5 neurons in macaque monkeys to high contrast (root mean square (RMS) contrast, of 9.8cd/m²) and low contrast (0.7cd/m² RMS contrast) dot-stimuli of varying diameters. Under high contrast conditions the neurons responded strongly to the smallest dot-motion stimuli used (approximately 5-10° diameter) but as the size was increased beyond 10° in diameter the response of the neuron was suppressed. Under low contrast conditions, the response of those same neurons increased as the stimulus diameter increased, across the whole range of sizes tested (up to 35° in diameter) consistent with strong area summation with increasing size. As shown in Figure 1.5, the response of the neuron to the largest stimulus diameter, which would normally stimulate the suppressive surround, was stronger under low contrast conditions than in high contrast conditions. To relate the findings to differences in surround suppression, a “suppression index” was calculated. For some cells, the suppression index was calculated as 86% for high contrast and 0% for low contrast. In other words, some MT/V5 cells lost their surround suppression entirely under low contrast conditions. Across the population of 110 MT/V5 cells, the median surround suppression index was 35% for the high contrast stimuli, and 12% for the low contrast stimuli.
Figure 1.5. Contrast-dependent centre-surround interactions in area MT/V5. Panel A shows the response of one MT/V5 neuron to high contrast and low contrast dot-motion stimuli of increasing size. Panel B shows the suppression index for all 110 MT/V5 neurons that were tested, as a function of stimulus contrast. Image from Pack et al. (2005).

In humans, behavioural correlates of contrast-dependent centre-surround interactions in cortical area MT/V5 have been found using psychophysical techniques. A well-known example is the motion task employed by Tadin et al. (2003) which measured duration thresholds for observers to be able to correctly identify motion direction (left or right) of a drifting Gabor patch presented at varying contrast levels. For low contrast stimuli, observers motion direction sensitivity increased as the size increased, consistent with psychophysical spatial summation over area, as reported previously for tasks in which minimum contrast thresholds were measured and therefore also employed low contrast stimuli (Anderson & Burr, 1991; Watson & Turano, 1995). For high contrast stimuli observers required longer presentation times to correctly discriminate the direction of
motion as the size of the Gabor increased from 0.7° to 5°, to the point where observers showed far worse performance for the large high contrast stimuli, than for the same sized stimuli shown at low contrast (Figure 1.6).

Figure 1.6. Results for Tadin et al. (2003) psychophysical spatial suppression task. Mean duration thresholds for motion direction discrimination are shown as function of stimulus size at different contrast levels. Stimulus sizes depicted schematically above the graph. For low contrast stimuli, performance improves with increasing Gabor size; spatial summation. For high contrast stimuli, performance deteriorates with increasing Gabor size; spatial suppression. Adapted from Tadin (2015).

Contrast-dependent summation/suppression has been corroborated by further motion studies using direction discrimination (Tadin et al., 2006; Tadin & Lappin, 2005), motion aftereffect (Tadin et al., 2003; Tadin, Paffen, Blake, & Lappin, 2008), binocular
rivalry (Paffen, Tadin, Te Pas, Blake, & Verstraten, 2006; Paffen, Te Pas, Kanai, Van Der Smagt, & Verstraten, 2004; Paffen, van der Smagt, te Pas, & Verstraten, 2005) and also speed discrimination (Verghese & Stone, 1996). In general, these studies report poorer motion perception performance for large high contrast stimuli. Decreased motion sensitivity for large high contrast stimuli is considered to be a major perceptual consequence of the surround inhibition from centre-surround antagonistic properties of motion-sensitive neurons in area MT/V5, whereas increased summation at low contrast is thought to reflect either enhancement from the surround and/or expansion of the CRF of MT/V5 neurons due to reduced surround effectiveness (Figure 1.7). Converging evidence has further supported this link between behavioural measures of spatial summation/suppression and cortical summation/suppression in area MT/V5. For example, the “critical size” where suppression is first observed corresponds to the size of foveal MT/V5 receptive fields in macaque monkey (Raiguel et al., 1995). A further study which used transcranial magnetic stimulation (TMS) to disrupt normal functioning of area MT/V5 in human participants found that spatial suppression was reduced resulting in better-than-normal perception of large high contrast motion stimuli (Tadin et al., 2011) but did not cause a change in perception of small gratings, and the effects were not seen when stimulating occipitally located visual areas, suggesting that the impairments produced were specific to surround inhibition in MT/V5. This added some causal support for the hypothesis that behaviourally observed spatial suppression is a perceptual correlate of centre-surround antagonism in area MT/V5. A recent fMRI study by Schallmo et al. (2017) showed that activity in MT/V5 increased with stimulus size at low contrast (summation), and decreased with stimulus size at high contrast (suppression). This neural firing showed better agreement with psychophysically observed summation and suppression than the
pattern of activity observed in early visual cortex, leading to the conclusion that both motion summation and suppression are underpinned, at least in part, by neural activity in MT/V5 (Schallmo et al., 2017).

Figure 1.7. Conventional assumptions regarding contrast-dependent receptive field properties adapted from Schallmo et al. (2017). A; As the size of a high contrast grating is increased it activates the inhibitory surround region (red arrows) which suppresses firing rate of the neuron. B; An equally large low contrast stimulus causes an increase in firing rate (summation), potentially due to concurrent excitation from the surround (blue arrows) or activation of an expanded CRF.

Aaen-Stockdale, Thompson, Huang, and Hess (2009) have argued that increased suppression and the concomitant loss of summation at high contrast can be explained by low level mechanisms. They presented observers with a fixed duration stimulus
comprising of two identical sinusoidal gratings drifting in opposite directions and measured the contrast imbalance required for motion to be perceived consistently in a single direction. At a fixed high contrast, they found evidence for increasing suppression as stimulus size increased, consistent with previous studies. However they note “a large stimulus with contrast of 5.5% could be many times higher in contrast than the contrast threshold for detection, while the smallest stimulus with the same contrast (5.5%) may be just above contrast threshold” (Aaen-Stockdale et al., 2009, p. 2). They went on to demonstrate that suppressive effects with increasing size were eliminated once the contrast of different sized stimuli were normalised to a multiple of the observer’s individual contrast threshold, favouring a low-level explanation of these suppressive effects.

However this explanation has been dismissed in a follow up study by Glasser and Tadin (2010) which re-examined contrast-dependent motion suppression by measuring duration thresholds, as they had previously, whilst setting the contrast of all the stimuli to be a fixed multiple of the stimulus’ contrast threshold in order to equalize differences in relative contrast sensitivity for stimuli of different sizes. This produced an increase in sensitivity to the large high contrast stimuli, however direction discrimination for large high contrast stimuli was still worse than that for the small high contrast stimuli, consistent with suppression. Tadin (2015) and Glasser and Tadin (2010) also argue that it may not be appropriate to normalize high contrast stimuli based on measurements obtained at contrast threshold given that research suggests there are different processes occurring under different stimulus conditions, e.g. contrast (Braddick, 1993; Marr, 1982; Pack et al., 2005; Tadin et al., 2003).

Contrast is also integrated over time (Burr, 1981; Legge, 1978), so it is important to draw attention to the fact the Tadin studies (and other related ones) use stimuli of different
presentation durations (in order to find duration threshold). As such, performance
differences may reflect, in part, changes in temporal integration capacities and therefore
the “duration threshold” method is perhaps not the most direct performance measure for
studying contrast-dependent integration of motion signals over area. Despite the
implications of these suppression studies that motion summation is enhanced at low
contrast and decreased at high contrast, no studies have directly estimated the measurable
area of psychophysical summation at high and low contrast using performance measures
that, presumably, will correspond closely with the neural mechanics of the visual function
in question. The studies in this thesis therefore utilize contrast detection and contrast
discrimination threshold measurements with fixed duration stimuli, to explore integration
of luminance contrast over area for motion detection and direction discrimination. We will
look at this at high and low contrast levels without normalizing the high contrast stimuli to
the observer’s contrast threshold, as we are interested in the different spatial processes that
may be occurring at different contrast levels. Furthermore, unlike any of the previous
studies, we will also control for changes in area-dependent noise by keeping overall
stimulus dimensions constant across conditions, this will be explained in more detail in
section 1.8.

1.7 Surround suppression and ageing

As described previously, the study by Tadin et al. (2003) found evidence for
increased perceptual spatial suppression of large stimuli at high contrast and increased
expanse of spatial summation at low contrast for motion direction discriminations when
measuring duration thresholds in normal healthy observers. The Tadin et al. (2003) task
has also been used in the investigation of motion perception in clinical populations that are
thought to have impairments in the functioning of the inhibitory cortical processes that
govern perceptual surround suppression. Betts et al. (2005) examined spatial suppression in older adults using the same task used by Tadin et al. (2003). The results showed that older adults had shorter duration thresholds for perceiving the motion direction of large high contrast drifting Gabor stimuli than the younger observers, implying that only the younger adults exhibit significant spatial suppression (Figure 1.8), a behavioural effect that has been replicated in further studies (Aaen-Stockdale et al., 2009; Betts, Sekuler, & Bennett, 2009; Karas & McKendrick, 2012; Yazdani, Serrano-Pedraza, Whittaker, Trevelyan, & Read, 2015).

![Figure 1.8](image.png)

*Figure 1.8.* Data from Betts et al. (2005) for the spatial suppression task. Mean duration thresholds are plotted as a function of stimulus size for low contrast stimuli (left panel) and high contrast stimuli (right panel) for older and younger observers. For low contrast stimuli both older and younger observers show decreasing thresholds with increasing stimulus size; spatial summation. For high contrast stimuli only the younger observers show evidence of spatial suppression; performance gets significantly worse as stimulus size is increased. Image adapted from Betts et al. (2005).
This age related reduction in surround suppression (and improvement in perception of large high contrast patterns) has been hypothesised to be due to a reduction in efficacy of cortical inhibition, specifically GABA-mediated inhibition. Evidence for altered cortical inhibition in the ageing brain has been gathered from neurophysiological studies on senescent animals which have shown altered functioning of processes known to be subserved, at least in part, by cortical inhibition. For example, orientation and direction tuning of V1 cells, which depends on properly functioning inhibitory circuits (Carandini & Ferster, 2000; Isaacson & Scanziani, 2011; Rose & Blakemore, 1974) is significantly reduced in the brains of aged macaque monkeys (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000; Yu, Wang, Li, Zhou, & Leventhal, 2006) and aged cats (Hua et al., 2006). These declines are accompanied by increased spontaneous, and visually evoked, neural activity (Leventhal et al., 2003; Schmolesky et al., 2000; Yu et al., 2006). Fu et al. (2010), more recently, found that V1 neurons of older animals that were less orientation and direction selective also exhibited reduced surround suppression, consistent with an underlying decrease in inhibition. Liang et al. (2010) recorded from single cells in both V1 and MT/V5 of aged macaque monkeys and found that both areas exhibited decreased direction selectivity, increased spontaneous activity and decreased signal-to-noise ratios. Moreover, direction selectivity was significantly more reduced in motion sensitive area MT/V5 than in V1 (Liang et al., 2010). There is some evidence that these degraded response characteristics in V1 and MT/V5 are a consequence of reduced GABA-mediated inhibition. Administration of GABA and GABA agonists to individual V1 cells was found to decrease visual responsiveness, decrease spontaneous activity, and improve orientation and direction selectivity in aged brains, but had no effect on response properties of V1 cells in younger brains (Leventhal et al., 2003). A recent study found that
gene expression of glutamic acid decarboxylase (GAD65) enzymes, which are thought to have a critical role in GABA synthesis, were significantly reduced in primary visual cortex of aged macaques (Liao, Han, Ma, & Su, 2016). Taken together with reports that GABAergic interneurons are widely distributed in macaque MT/V5 (Thiele, Distler, Korbmacher, & Hoffmann, 2004) the suggestion can be made that functional declines in both V1 and MT/V5 during senescence may be due, at least in part, to decreased GABAergic inhibition in aged visual cortex. Reduced inhibition with ageing would be assumed to result in an increase in the spatial area of excitation in older observers, as weaker inhibition would allow the influence of the excitatory receptive field to be measureable over larger areas. Therefore, when assessing summation areas, it is of interest to include groups of older observers as this, together with the information on how excitation/inhibition changes with age, may help further our understanding of how the underlying neural mechanisms operate in normal vision and in normal healthy ageing. Therefore, this thesis will investigate the summation of motion signals in the normal visual system, as well as in normal healthy ageing. This will be carried out with the assistance of a newly developed psychophysical approach known as the “Battenberg” summation method (Meese, 2010).

1.8 Battenberg summation

In nearly all the studies of motion summation described in the preceding sections, the general method involved increasing the overall size of the stimulus to measure potential improvements in performance with increasing signal area. For example, Anderson and Burr (1991) increased the overall size of a drifting grating to measure improvements in contrast threshold for direction discrimination. Contrast sensitivity improved with increasing area, implying a process of spatial summation within receptive
fields of detectors. For larger areas the rate of improvement tapered off significantly, suggesting relatively small receptive field sizes – no more than 1-2 cycles of periodicity of the sinusoidal stimuli. Above these maximum receptive field sizes, the slight improvements in contrast sensitivity have been attributed to probability summation across independent detecting mechanisms (Anderson & Burr, 1991; Robson & Graham, 1981).

A limitation of the approach used in these summation studies is that the number of excited detectors increases as the overall retinal size of a stimulus increases, with each detector contributing its own intrinsic amount of internal noise to the integration process. This would also be the case for large, overlapping, receptive fields as larger stimuli would stimulate more of them even if the stimulus was not large enough to extend beyond the edges of the receptive field the stimulus was centred on. The detrimental effects of additional noise with increasing physical size may limit the performance benefit (signal-to-noise ratio) of the extra signal of increasingly larger stimuli. This may lead to the potency of areal summation mechanisms being underestimated when signal area is manipulated in this way.

A novel set of stimuli have been designed by Meese and colleagues to try and overcome the limitations of previous studies concerning the summation of luminance contrast over area. “Battenberg” stimuli (Meese, 2010), and the closely related “Swiss cheese” stimuli (Meese & Baker, 2011; Meese & Summers, 2007) have a fixed diameter and contain interdigitated signal regions (set a particular contrast level) and blank regions (set at zero contrast, see Figure 1.9). The signal regions in the Battenberg are square shaped checks (resembling a Battenberg cake) and are created from arrays of “micro-patterns” where each micro-pattern is a single square cycle of a sine-wave carrier grating multiplied by an orthogonal cosine half-cycle at half the spatial frequency of the carrier.
The checks making up the Swiss cheese stimulus have much smoother edges and therefore resemble circles as they are produced by multiplication of a sinewave carrier with a higher spatial frequency and a raised sinusoidal plaid modulator with a lower spatial frequency (see Figure 1.9).

![Figure 1.9. The top row shows the stimuli used by Meese (2010). The first panel in the sequence shows the full stimulus. The subsequent panels show Battenberg stimuli with increasing check sizes to measure summation. The numerical insets indicate the total number of “micro-patterns” and demonstrate that the full stimulus has approximately double the amount of signal as each Battenberg pattern. The bottom row shows the stimuli used by Baker and Meese (2011). The first panel in the sequence shows the full stimulus and the subsequent panels show the Swiss cheese stimuli with increasingly larger sized “cheese” and “hole” regions.](image)

Improvements in sensitivity (summation) can be measured by varying the spatial arrangement of the signal regions (e.g. varying the number and position of micro-patterns in the Battenberg), without changing the overall stimulus dimensions and with minimal
changes in the overall signal area present. This method revealed that the summation of luminance contrast for the detection of static grating-like patterns can extend over much larger areas than originally proposed by conventional summation studies in which the level of noise co-varied with stimulus size (Robson & Graham, 1981). The psychophysical data, in conjunction with computational modelling, revealed an initial stage of short-range contrast summation occurring within linear filter elements (i.e. individual receptive fields), followed by a nonlinear contrast transducer, and then a stage of long-range contrast summation across filter elements. The final stage of spatial summation occurs across separate filter groups and most likely involves a probability summation process (Figure 1.10), however Meese (2010) showed that the cross-group pooling can be stronger than that predicted by probability summation for orthogonally oriented textures. The long-range contrast summation stage was estimated to pool over as much as 16 grating cycles for Battenberg stimuli with a spatial frequency of 2.5c/° (Meese, 2010). The extent of summation of contrast for Swiss Cheese patterns was estimated to be up to 8-12 cycles (or up to 5.75° in diameter), and this was consistent across a wide range of stimulus spatial frequencies that were tested (Baker & Meese, 2011). The summation effects were always too large to be attributed to models of probability summation across independent detecting mechanisms. This summation method has been applied to other domains to reveal larger areal summation for textural signals (Baldwin, Husk, Meese, & Hess, 2014) and second-order (contrast-modulated) stimuli (Summers, Baker, & Meese, 2015).

It should be noted that the models used in above studies use a fourth-root summation rule to approximate probability summation. This interpretation has been called into question recently with the suggestion that fourth-root summation does not necessarily represent probability summation. Baldwin and Meese (2015), Kingdom, Baldwin, and
Schmidtmann (2015), and Meese and Summers (2012) instead argue that the summation values obtained in the original Swiss Cheese and Battenberg studies thought to be consistent with probability summation could actually be interpreted as additive summation. This is based on recent predictions of probability summation based on Signal Detection Theory. However there is still debate about the appropriateness of such predictions given that probability summation estimates based on Signal Detection Theory are highly contingent on assumptions such as the number of channels being monitored (Green, Dickinson, & Badcock, 2017). The experiments in this thesis will estimate probability summation based on the original Swiss Cheese and Battenberg papers as this is the most conservative and stringent approach and is less likely to lead to false rejection of probability summation in favour of additive summation.

Figure 1.10. Schematic of the three stages of spatial summation proposed by (Baker & Meese, 2011; Meese, 2010). Stage 1 involves short-range summation within linear filter
elements. Non-linear contrast transduction is followed by Stage 2 in which long-range contrast summation is performed across filter elements. Stage 3 employs probability summation to pool across separate filter groups.

The Battenberg or Swiss Cheese summation paradigm has not yet been applied to the motion domain. Given that previous experiments concerning motion summation varied the overall size of the stimulus which confounds signal summation with summation of internal noise, it is conceivable that they may have also underestimated the potency of the underlying summation mechanisms. This thesis will therefore use the Battenberg approach to re-examine summation behaviour for luminance defined motion signals. The following section outlines the experimental work in this thesis.

1.9 Thesis overview

In Chapter 2 we will re-examine the ability of the human visual system to integrate motion signals over area by using the Battenberg summation method (Meese, 2010). The Battenberg resembles a checkerboard pattern and the size of the checks (luminance-modulated drifting gratings) is varied to measure summation, but overall dimensions are fixed to keep the stimulus area that is being monitored constant and therefore help to keep noise levels approximately equal across all conditions. We measure contrast detection thresholds for our motion Battenberg patterns to determine if summation is possible over larger areas than previously asserted once the contribution of area-dependent noise is controlled for. We will also do this for a Battenberg pattern containing opposing directions of motion with the aim of revealing if there are any differences in summation when
segmentation is necessitated, as previous research has suggested that extensive summation is not as beneficial when motion signals need to be segregated (Braddick, 1993).

Previous research has suggested that spatial summation is weakened at high contrast levels, potentially due to the dominance of segmentation mechanisms that limit the spatial extent to which motion signals are combined, presumably in favour of detecting motion discontinuities in highly visible visual scenes. Therefore, in Chapter 2 we will also examine summation for both pattern types (single motion and opposing motion) at suprathreshold contrast levels to determine if there are any gross changes in summation at high contrast levels.

Assuming that the Battenberg will be capable of revealing more extensive summation process for motion detection in Chapter 2, we expect the motion direction discrimination will also show extensive summation areas given that previous results suggest both processes are underpinned by the same mechanism. To investigate this, in Chapter 3, we will measure direction discrimination thresholds for Battenberg patterns with the aim of confirming that motion detection and discrimination are mediated by mechanisms with the same summation properties, and therefore direction discrimination of motion also shows extensive summation.

As mentioned, Chapter 2 will examine summation of motion at suprathreshold contrast levels. In the design of that study, the spatial arrangement of the contrast pedestal will match that of the target Battenberg increment. Previous research using suprathreshold static patterns has suggested that when the spatial arrangement of the target and pedestal co-vary, improvements generated from increasingly larger target increment regions may be obfuscated by a concomitant increase in suppression from the pedestal of matched size (Meese & Summers, 2007). This leads us to examine, in Chapter 4, whether more
extensive contrast summation for motion signals can be demonstrated when the spatial arrangement of the Battenberg target increment is varied, and applied to a full fixed-sized grating pedestal such that any suppression from the pedestal will be kept constant across conditions.

In Chapter 5 we will investigate whether spatial summation of motion changes with age. Previous research has found weakened cortical surround inhibition in the ageing visual cortex (Fu et al., 2010) and reduced perceptual spatial suppression for large high contrast motion stimuli (Betts et al., 2005). Taken together, these findings lead to the prediction that perceptual summation may be measurable over a larger area in older observers. However no studies have closely examined summation of motion in older adults, as distinct from surround suppression, by measuring contrast thresholds for motion direction discrimination. We did so with the assistance of the Battenberg stimuli (the control of the amount of noise is of extra benefit when studying older visual systems) to better characterise whether older observers have larger psychophysical summation areas for the perception of low contrast stimuli.

Finally in Chapter 6 an overall summary of the four experimental chapters will be provided describing what our findings contribute to our understanding of the mechanisms underlying spatial summation of luminance contrast for motion detection and discrimination. We will also discuss directions for future research and how the Battenberg summation method could be of benefit to future studies examining spatial summation of motion.
References


Chapter 2: Larger receptive fields revealed using Battenberg stimuli to assess contrast summation with moving patterns


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*Keywords: Motion, summation, segmentation, contrast, centre-surround antagonism*
Abstract

This study re-evaluated summation extent for moving stimuli using the Battenberg summation paradigm (Meese, 2010) which aims to circumvent internal noise changes with increasing stimulus size by holding display size constant. In the checkerboard stimulus, the size of the checks (luminance-modulated drifting gratings) was varied to measure dependence on signal area. Experiment 1 was a contrast detection task which used either, signal checks alternating with uniform, mean luminance, checks (single-motion), or alternate checks containing gratings moving in opposite directions (opposing-motion). The latter was designed to test whether summation extent changes when segregating regions based on motion direction. Results showed summation over a square summation area with a side length of 3.33°, much larger than previous estimates of less than 1° for similar stimuli (Anderson & Burr, 1991). This was found for both motion combinations, providing no evidence that summation extent differs when segregating patterns based on direction, at contrast detection threshold. These results are in close agreement to those obtained for static patterns (Meese, 2010) and support the same underlying summation model. Experiment 2 was a contrast increment detection task conducted to determine whether differences in summation extent arise under suprathreshold contrast conditions. There was no dependence on check size for either condition, across the range of sizes tested. This supports the suggestion that segmentation mechanisms dominate perception under high contrast conditions, a potential adaptive strategy employed by the visual system.
2.1. Introduction

It is well established that human sensitivity to motion signals is greater when stimuli cover a larger area (Anderson & Burr, 1987; Burr, Morrone, & Vaina, 1998; Watson & Turano, 1995). There have been several attempts to determine the area over which motion signals are integrated. Classic area summation studies increase the overall size of the stimulus to increase signal area and measure sensitivity (Anderson & Burr, 1991; Robson & Graham, 1981). Studies have shown that contrast sensitivity for direction discrimination and simple detection of moving targets increases as stimulus size increases, implying a process of spatial summation within the receptive fields of detectors. These studies show that for larger areas the rate of improvement in sensitivity tapers off significantly. This very slight dependence on area has been attributed to probability summation across independent detecting mechanisms (Anderson & Burr, 1991; Robson & Graham, 1981) suggesting very limited regions over which signal can be integrated, estimated at no more than 1-2 cycles of periodicity of the stimulus.

A limitation of the approach used in these classic summation studies is that as stimulus area increases, so does the population of stimulated and monitored detectors, with each detector contributing an independent amount of internal, noise to the system. Increases in signal are therefore accompanied by increases in noise which can potentially confound estimates of spatial summation of the signal. As a result, the potency of summation mechanisms may be underestimated when taking this approach and the spatial properties of receptive fields described based on these psychophysical observations may be inaccurate. Meese (2010) introduced ‘Battenberg’ stimuli to circumvent this problem for the summation of luminance contrast over area. Battenberg stimuli allow the manipulation of contrast signal area within a stimulus of fixed display size and eccentricity. This design
encourages observers to monitor a fixed retinal area across all conditions, but still allows
the experimenter to vary the area of the region covered by the target and measure
improvements in contrast detection threshold as the target area increases. The purpose of
this approach is to clamp the level of internal noise that may be acting to degrade
sensitivity and therefore help to obtain a cleaner measure of summation of the contrast
signal. Using the Battenberg method to assess the spatial summation of stationary grating
stimuli, Meese (2010) was able to demonstrate that summation of luminance contrast, for
pattern detection, extends over a much larger area than indicated by estimates from
conventional studies in which the amount of internal noise co-varied with stimulus size
(Robson & Graham, 1981). The current study used this novel approach to examine spatial
summation of contrast signal in drifting motion patterns, and specifically, to re-evaluate
the size of the area over which the human visual system can sum motion signals carried by
sinusoidal grating patterns.

Studies that have measured the increase in contrast sensitivity as a function of the
size of a luminance modulated drifting grating increases show that the extent of summation
varies with the spatial frequency of the grating used (Anderson & Burr, 1987). For high
frequency gratings (10c/°) summation occurred over only 0.1° of visual angle, whereas for
low frequency gratings (0.5c/°) the summation limit was approximately 1° of visual angle.
For this study we have chosen to utilise gratings with a spatial frequency of 3c/° to explore
the effects of using the Battenberg summation method for motion. Anderson and Burr
(1987) reported that the summation limit of a motion detector for a 3c/° grating was
approximately 0.5°. These summation estimates could have been obfuscated by increases
in noise as the stimulus size increased since that could reduce sensitivity and the
summation area estimate. Therefore, experiments using Battenberg patterns, which
mitigate the problem of changes in noise, have the capacity to reveal more extensive summation, potentially providing more accurate insight into summation behaviour of psychophysically defined motion receptive fields.

Other motion summation studies, using relatively sparse fields of moving dots, have suggested that only motion coherence thresholds benefit from summation, while contrast thresholds for motion detection and motion direction discrimination show little to no benefit of spatial summation with increasing signal area (Chakraborty et al., 2015; Morrone, Burr, & Vaina, 1995). Although these studies had the advantage of fixed stimulus area, the dots are composed of a broad spectrum of spatial frequencies and it is not clear which ones will be most informative in a particular condition. Given that summation varies with spatial frequency (Anderson & Burr, 1987), this could have confounded the results. Additionally, dots are considered to be 2D signals and this may yield different summation behaviour relative to gratings (Amano, Edwards, Badcock, & Nishida, 2009). We were particularly interested to use grating stimuli for comparability with Anderson and Burr (1991) and Meese (2010).

Using the Battenberg method we can also study the relationship between stimulus conditions and changes in the size of the summation area. This will help determine whether the motion system can modulate the extent of summation as a strategy to process different types of visual scenes; such as when focusing on a moving object against a background or viewing multiple objects moving in different directions.

Summation and segregation constitute two fundamental types of motion processing (Braddick, 1993; Burr & Thompson, 2011) and how the motion system implements their opposing requirements is not yet fully understood. Braddick (1993) suggests that it could involve motion analysis at multiple spatial scales. Signals may be combined or
differentiated within receptive fields that vary in size depending on the task at hand. Large motion receptive fields could derive summation over extended areas to subserve perception of large uniform regions. Smaller receptive fields could generate strong signals at motion discontinuities and lead to the perception of segmented regions to assist with the detection of moving objects. Alternatively, the motion system may employ adaptive strategies to prevent summation over large, fixed, areas so that the motion from two disparate objects does not inappropriately pool together. The motion system may adaptively switch between a mode that extensively pools motion signals, and one that establishes segmentation, depending on the task (Allman, Miezin, & McGuinness, 1985a; Braddick, 1993; Maunsell & van Essen, 1983; Movshon & Newsome, 1996; Raiguel, Hulle, Xiao, Marcar, & Orban, 1995; Smith, Singh, Williams, & Greenlee, 2001). Warren (2004) suggested that the units in the visual system which are responsible for detection of optic flow motion (self-motion relative to the environment) are not involved in the segregation of moving objects because they fail to differentiate local object motion and optic flow, thus indicating a task specific cortical mechanism that is responsible for the analysis and summation of large field motion. Indeed there is evidence to suggest that area MST possesses distinct functional regions. The dorsal part of MST in macaque is responsible for analysis of wide-field motion whereas the ventral part is implicated in the analysis of small-field motion (Tanaka et al., 1986; Tanaka, Sugita, Moriya, & Saito, 1993). This property may underlie how the visual system copes with summation and segregation, consistent with Braddick’s (1993) proposals. The spatial properties of the two regions support this idea as MSTd cells have relatively large receptive fields while MSTv cells have smaller receptive fields (Nelissen, Vanduffel, & Orban, 2006) and possess antagonistic surrounds (Tanaka et al., 1986) which are thought to facilitate motion segregation (Allman et al., 1985a), possibly by adaptively
modulating the area of summation. There is also neurophysiological (Churan, Khawaja, Tsui, & Pack, 2008; Hunter & Born, 2011; Pack, Hunter, & Born, 2005) and behavioural evidence (Tadin, Lappin, Gilroy, & Blake, 2003) that the summation area of MT neurons is not fixed and can vary depending on stimulus conditions. Further, many neurons in area MT exhibit centre-surround antagonism (Allman et al., 1985a) suggesting that processing within MT also involves distinct mechanisms equipped for segregation, similar to those found in MST. More recently, Lui, Dobiecki, Bourne, and Rosa (2012) have provided evidence consistent with separate systems in MT of marmoset monkeys, one which restricts summation over small areas and one which can extend integration over larger areas.

Summation behaviour can be studied with a Battenberg stimulus containing opposing motion; a stimulus which will also affect motion segregation mechanisms. Meese (2010) found that for Battenbergs containing interdigitated patches of orthogonally oriented elements, summation persisted over extensive areas independently for the two orientations. This was followed by a further stage of summation across independent summation mechanisms. For motion, when the task demands segregation of opposing directions it may be more efficient to adaptively reduce “wide-field” spatial summation, or perhaps employ a system of neurons with smaller summation areas that can segment patterns more effectively (Braddick, 1993). This study will therefore help to explore how motion segregation is implemented and how it may impact large area summation at both absolute threshold (detection of pattern presence), and at suprathreshold contrast levels (pattern discrimination). It will also provide insight into whether there is any pooling across motion directions following summation over area by independently tuned
mechanisms, assuming that the opposing directions will be independently processed at early cortical stages (Levinson & Sekuler, 1975).
2.2. General Methods

2.2.1 Apparatus

The stimuli were generated using MATLAB 7.0.4 (Mathworks, Natick, Ma, USA) on a Pentium 4 PC (3.0GHz) and presented on a Sony Trinitron Multiscan G520 Monitor (screen resolution: 1024 × 768 [34° 08’ × 25° 36’], refresh rate: 100Hz) from the frame store (256MB) of a Cambridge Research Systems ViSaGe graphics system. The observers viewed the monitor from a distance of 65.5cm which was maintained using a chin-rest. At this viewing distance each pixel subtended 2’ of visual angle. Testing took place in a darkened room (ambient luminance of < 1cd/m²). The background screen luminance was set at 45cd/m², calibrated using an Optical OP 200-E photometer (Head model #265) and associated software (Cambridge Research Systems, Kent, UK). A CRS CB6 button box was used to record observer responses. Contrast is defined as Michelson contrast in percent;

\[ C_M\% = \left( \frac{L_{max} - L_{min}}{L_{max} + L_{min}} \right) \times 100 \]  

(2.1)

where L is luminance. Following Meese (2010) this will be expressed in dB units (Baker & Meese, 2011; Meese, 2010) which are defined as;

\[ C_{dB} = 20\log_{10}(C_M\%) \]  

(2.2)

2.2.2. Observers

Data were collected from four experienced psychophysical observers; KT, MT, SC and TM, all of which were recruited from the Human Vision Laboratory of the University of Western Australia. Observer TM was an author of the study, the other observers were
naïve to experimental aims of the study. All observers had normal or corrected-to-normal visual acuity. All experiments were performed binocularly with natural pupils. Observers gave their informed consent before participating in the study. The treatment of participants in this study complied with the guidelines set by the Human Research Ethics committee of the University of Western Australia and therefore was in accordance with the tenets of the Declaration of Helsinki.

2.3. Experiment 1A: Single Motion Experiment

2.3.1. Stimuli

Battenberg stimuli are checkerboard patterns containing signal checks alternating with uniform (blank) checks. Signal regions contain luminance-modulated, drifting (1°/s) sine wave gratings with a spatial frequency of 3c/°. Uniform checks are set at 0% contrast and have the same mean luminance as the background of the display. The size of the check regions within the Battenberg containing signal can be varied to measure dependence on signal area without adjusting the overall extent of the stimulus across conditions. Four different square check sizes were used (see Figure 2.1): 0.71°, 1.43°, 2.0°, 3.33° in side length, as well as the ‘full’ stimulus which was a 10° grating with no blank regions (Figure 2.1E). The overall size of the checked Battenberg stimuli was 10° which is equal to the extent of the ‘full’ stimulus.

The equation for a sine wave grating is:

\[ L[x, t] = L_m[1 + c \cdot \cos(2\pi f_s \cdot x + 2\pi f_t \cdot t + \phi)] \]  

(3)

where \( L_m \) is the mean luminance of the display, \( c \) is amplitude (contrast of the grating), \( f_s \) is the spatial frequency, \( f_t \) is the temporal frequency and \( \phi \) adjusts the phase of the grating.

The checks were smoothed at the edge using a raised sine envelope that occupied a
uniform width strip equal to 10% of the distance from the centre to the nearest edge of the square check. The blurring in the corners was therefore $\sqrt{2}$ wider.

Figure 2.1. Examples of the “Battenberg” stimuli used in this experiment. The full stimulus (10°) is shown (E) as well as the four Battenberg patterns used which had check sizes of 0.71°, 1.43°, 2.0° and 3.33° (A-D, respectively). In the experiment all checks drifted in the same direction with drift being randomly either left or right, on an individual trial.

2.3.2. Procedure

Contrast detection thresholds for Battenberg stimuli were measured using a two-interval forced-choice (2IFC) procedure. Target stimuli were presented for 300 ms in one
of two randomly-selected temporal intervals, at a particular contrast level. Each interval was marked by an auditory beep and separated by a 1 s inter-stimulus interval. In the interval that did not contain the stimulus, the reference interval, contrast was set to 0 and the display remained at a constant mean luminance of 45cd/m\(^2\). The observer was required to indicate which interval they believed contained the target stimulus using a button box. The observer received auditory feedback to indicate whether their response was correct or incorrect. There was a 1 s pause before the commencement of the next trial. On each run, a three-down, one-up staircase procedure was used to converge upon contrast detection threshold; the 79.4% correct contrast threshold (Wetherill, 1963; Wetherill & Levitt, 1965). The procedure terminated after eight reversals and threshold was calculated as the mean of the contrast level for the last four reversals. Each check size condition was repeated five times by each observer and these were averaged to give a single threshold estimate per condition per observer. Observers fixated in the centre of the stimulus. A fixation point was presented at the beginning of each run.

2.3.3. Results

The top row of Figure 2.2 shows raw contrast detection thresholds for the stimulus layouts depicted in Figure 2.1. Results are presented for four observers individually on the left (2.2A), and the average of all four observers is shown on the right (2.2B). In the bottom row of Figure 2.2 the thresholds have been transformed in the manner consistent with Meese (2010) to indicate summation ratios; the difference in threshold between the full stimulus and each of the checked Battenberg stimuli (Battenberg/Full) in dB units. This illustrates the reduction of spatial summation for each of the Battenberg stimuli relative to the full stimulus (the summation ratio) and also adjusts for overall differences in individual sensitivity. Summation ratios are shown for each individual observer in Figure
2.2C and the averaged ratios across the four observers are shown in Figure 2.2D. These ratios closely parallel those reported for static patterns by Meese (2010, Figure 4, note that the ratios for the full stimulus are represented on the far right, whereas in Meese (2010) they appear on the far left).

Contrast detection thresholds are highest for the Battenberg stimulus with the smallest check size (0.71°) and show a decrease as check size increases; evidence of spatial summation occurring to produce improvements in threshold. The summation ratios in Figure 2.2 indicate that there is still a significant improvement for the full stimulus compared to the 3.33° check pattern, as the ratio is significantly larger than 0 (one-sample t-test: \( t(3) = 6.350, p = .008, 95\% \text{ CI } [1.311 \text{ to } 3.9437] \)), indicating that increases in size still produce significant improvements in performance and therefore suggest that the area of summation is larger than 3.33° x 3.33° (11.09 deg²). To simplify presentation we will refer to this area by the side length of a square summation area in the following. For the largest check size, a relatively high summation ratio of 3 dB was maintained (in the range of 4-6 dB for all other sizes), consistent with substantial summation of contrast signal over area. The maximum (6 dB) and minimum (3 dB) values closely approximate those reported by Meese (2010), and following his reasoning, this summation level is also too large to be attributed to a process of probability summation. Previous studies that have utilised Battenbergs and the closely related “Swiss Cheese” stimuli argue that summation ratios of 1.5 dB or less are equivalent to a fourth-root summation rule, consistent with probability summation across independent noisy mechanisms for detection of the patterns (Baker & Meese, 2011; Meese, 2010). This interpretation has been challenged recently with the suggestion that fourth-root summation does not necessarily represent probability summation (Baldwin & Meese, 2015; Kingdom, Baldwin, & Schmidtmann, 2015; Meese
& Summers, 2012). These studies argue that this rate of improvement could be interpreted as additive summation or probability summation, or even a combination of the two. If this is the case, the relatively high ratio of 3 dB for the largest check size is even more likely to be rejected as probability summation. To be consistent with the original Meese (2010) study we will continue to use 1.5 dB as the approximation of probability summation.

Furthermore, when the results are re-plotted using a logarithmic x-axis showing stimulus area, rather than side length (see Figure 2.3), all the data points conform to a straight line. The fitted power function has a steep slope of -1.19 suggesting that there is no apparent deviation from the strong levels of summation, over the entire range of sizes we have employed.
Figure 2.2. Contrast detection thresholds for the ‘full’ stimulus and each of the checked Battenberg stimuli for each observer (A) and the average of all four observers (B) are presented as a function of check size in degrees (lower axis) and number of cycles (upper axis). In the bottom row thresholds are transformed into summation ratios (Battenberg/Full) to indicate the level of summation for each Battenberg stimulus. Error bars represent one standard error of the mean. Error bars around the individual ratios were calculated using conventional error propagation techniques (Meyer, 1975).
2.3.4. Discussion

This study used modified Battenberg stimuli (Meese, 2010) to estimate the extent of the area over which the human visual system can sum contrast signals in the motion system. Using appropriate stimuli we have shown that the motion system can achieve significant spatial summation over an area larger than 3.33 x 3.33°. Conventional studies which vary the overall size of the motion stimulus and are therefore also limited by increases in internal noise have suggested that the spatial summation area is no larger than 1.0° (width) for detection of a 3.0c/ moving grating (Anderson & Burr, 1991). However, results here show that performance did not asymptote at this 1.0° limit and instead continued to improve over the full range of sizes tested. The summation ratio is reduced for the largest check size (3.33°), but is still considered more potent than a process of probability summation (<1.5 dB) across multiple independent mechanisms. Since our results closely resemble those of Meese (2010) it is also reasonable to consider the model he developed to explain them as it
may provide a sensible starting point for understanding summation with moving stimuli. The first stage of the model involves short-range summation with a predicted peak of approximately 6 dB. The second stage includes segmentation for separate sets of independently tuned filters, and long-range spatial summation within those filters. Finally, Meese (2010) proposed a cross group summation stage, to account for both pools of filters contributing to thresholds for mixed stimuli.

The long-range summation for motion reported here is in agreement with neurophysiological evidence that neurons in motion processing areas have relatively large receptive fields (Maunsell & van Essen, 1983; Raiguel et al., 1995; Smith et al., 2001), suited to sum signals over large areas. Psychophysical studies using techniques that vary the relative proportions of dots moving in signal and noise directions have revealed extensive spatial summation for the discrimination of global motion direction when measuring coherence thresholds, a task specifically involving the role of neurones in MT (Britten, Shadlen, Newsome, & Movshon, 1992; Morrone et al., 1995; Movshon & Newsome, 1996; Newsome & Pare, 1988; Vaina, Cowey, Eskew, LeMay, & Kemper, 2001). Watamaniuk and Sekuler (1992) measured motion coherence thresholds for random-dot stimuli in the peripheral visual field and estimated that the visual system can sum motion direction over areas as large as 9° in diameter of a circular summation area. For central vision the summation limit has been estimated to be 4° in diameter in terms of a circular summation area (Ledgeway, McGraw, & Simmers, 2011). This difference in size for central vision compared to measurements in the periphery is consistent with reports that the area of spatial summation increases with retinal eccentricity (Khuu & Kalloniatis, 2015), which can be attributed to the larger receptive fields of the cells at the more peripheral locations (Curcio, Sloan, Kalina, &
Furthermore, Morrone et al. (1995) also measured summation of contrast signals for radial, circular and translational global dot motion patterns but found they did not exhibit the same summation trends as the motion coherence threshold data, which they interpreted as a limit to the integration of contrast sensitivity being set by earlier contrast sensitive mechanisms. However, our study suggests that extensive motion summation may not be limited to motion coherence and can also apply to summation of contrast sensitivity for the detection of motion stimuli. Furthermore, a 6 dB difference is obtained between the smallest sized check and the full condition, consistent with linear summation taking place within linear filter elements, implying a basic receptive field with at least four positive and four negative lobes (to cover all the cycles in the signal check, and the blank check); bigger than what Meese (2010) reported in the spatial domain. Indeed, Figure 2.3 shows integration at the same rate across the full 10°. These results suggest the involvement of a system separate to that responsible for basic contrast detection of spatial patterns, and is not spatially limited by encoding of contrast by V1 units as Morrone et al. (1995) suggests. A likely alternative candidate is area MT which is thought to contain cells which are more contrast sensitive than earlier stages due to effective summation over larger receptive fields (Sclar, Maunsell, & Lennie, 1990). Although Morrone et al. (1995) had the benefit of a fixed signal area like our Battenberg approach, they utilised dot stimuli which provide 2D motion signals and contain a broad range of spatial frequencies. Amano et al. (2009) have shown that 2D stimuli are integrated differently from 1D gratings when determining motion direction and this could underlie the differences between the studies seen here.
2.4. Experiment 1B: Opposing Motion Experiment

The previous experiment examined summation for stimuli containing motion in a single direction and provided behavioural evidence that the visual system can sum the contrast of motion signals over large spatial regions. There is psychophysical evidence for motion-sensitive systems that can integrate signal over large areas for coherence discrimination in optic flow stimuli (Burr et al., 1998; Morrone et al., 1995) and global motion stimuli (Watamaniuk & Sekuler, 1992). The previous experiment shows there are also large receptive fields for detection of the contrast of motion signals. In addition to summation, the motion system is also able to segment a moving object against a stationary background, or segment oppositely moving objects or regions from each other (Allman et al., 1985a; Allman, Miezin, & McGuinness, 1985b; Braddick, 1993; Levinson & Sekuler, 1975). Spatially extensive summation may not be useful when the system is also required to segregate motion. For the perception of optic flow motion, studies have suggested that there is a separate system for the perception of small segmented regions which is functionally and anatomically distinct from the system which collects signals over wider areas (Layton, Mingolla, & Browning, 2012; Tanaka et al., 1993). This property could be a general feature of the motion system which underlies the balance between the demands of segmentation and summation. To explore this, we evaluated the impact on the contrast thresholds for the detection of a Battenberg containing opposing motion signals. These signals should be detected by independent direction-selective filters at early stages of processing much like the orthogonal orientation patterns were in Meese’s (2010) spatial experiments. We keep orientation constant here to ensure that only motion-direction dissociates the regions. The aim was to determine whether the spatial extent of summation differs for a stimulus that also
evokes the involvement of the characteristic segregation mechanisms in the motion processing system.

2.4.1. Observers

Data was collected from the same psychophysical observers (KT, MT, SC, TM) that were used in the previous experiment.

2.4.2. Stimuli and Procedure

The stimuli were identical to the previous experiment with the exception that the blank checks were replaced with signal checks. The added signal checks were gratings drifting in the opposite direction to the existing checks to create an opposing motion Battenberg (see Figure 2.4). This type of stimulus is designed to evoke the involvement of summation and segregation mechanisms in the motion processing system. The procedural task used to measure contrast detection thresholds for the presence of these opposing motion stimuli was identical to the previous experiment.
Figure 2.4. Example of the opposing motion Battenberg stimulus with a check size of 3.33°. The stimulus is the same as the previous experiment (see Figure 2.1) except the blank checks have been replaced with checks containing motion in the opposite direction.

2.4.3. Results

The top rows of Figure 2.5 show raw contrast detection thresholds for the each of the opposing motion Battenberg stimuli and the full stimulus (re-used from the single motion experiment). Results are shown for four observers individually on the left (2.5A), and the average of all four observers is shown on the right (2.5B). The data for the single motion experiment (2.2B) is also replotted on this graph for comparison. In the bottom row of Figure 2.5 the thresholds have been transformed to indicate summation ratios; the difference between the full stimulus and each of the checked Battenberg stimuli (Battenberg/Full) in dB units. This illustrates the level of spatial summation for each of the Battenberg stimuli. Summation ratios are shown for each individual observer in Figure 2.5C and the averaged ratios across the four observers are shown in Figure 2.5D. The data for the single motion experiment (2.2D) is also replotted on this graph for comparison.
Figure 2.5. Contrast detection thresholds for the ‘full’ stimulus and each of the opposing motion Battenberg stimuli for each observer (A) and the average of all four observers (B). The green line in (B) indicates a 1.88 dB difference in threshold that Meese (2010) obtained for summation across orientation in static patterns. In the bottom row thresholds are transformed into summation ratios (Battenberg/Full) to indicate the level of summation for each Battenberg stimulus. Error bars represent standard error of the means, for the individual ratios these were calculated using standard error propagation techniques (Meyer, 1975).
**Figure 2.6.** Average summation ratios are replotted as a function of signal area, on a log axis, and fitted by a power function.

Contrast detection thresholds for the opposing motion Battenberg stimuli show a decrease as check size increases; indicating spatial summation. The summation ratios in Figure 2.5 indicate that there is still a significant improvement of the full stimulus compared to the 3.33° check size as the ratio is still significantly larger than that of the full condition (one-sample t-test: \( t(3) = 4.192, p = .025, 95\% \text{ CI} \left[0.5767 \text{ to } 4.2122\right] \)), indicating that increases in size still produce improvements in performance, implying that summation can extend over areas at least as large as 3.33° x 3.33°. Increased sensitivity for the opposing motion Battenberg is due to the additional signal in the stimulus which is processed by independent detectors tuned to the opposite direction. This results in summation ratios that are lower than when there is only a single motion direction present. This outcome is analogous to the results Meese (2010) obtained when adding orthogonally oriented spatial signal. Similar to the single motion data they still maintain a relatively high
summation ratio consistent with summation over extensive areas, and have not dropped to
the low levels that would reflect probability summation across multiple mechanisms.
Indeed, when the results are re-plotted using a logarithmic x-axis showing stimulus area,
rather than side length (see Figure 2.6), the data conforms to a straight line with a steep
slope of -0.80, indicating that there is no apparent change in summation behaviour over the
entire range of areas we have employed. These results suggest that the segmentation
evoked by the opposing motion stimuli does not affect the strength of long-range
summation that occurs for the sizes tested here. In fact the lower ratios would indicate that
at this stage, long-range summation seems to occur over extensive areas selectively for the
two different directions, as Meese (2010) found for static stimuli composed of orthogonal
orientation checks.

The differences in contrast thresholds between the full stimulus and the opposing
motion stimuli provide another line of support for direction selectivity in the motion
summation process. A one-way repeated-measures analysis of variance on the thresholds
for the opposing motion check patterns and the full pattern revealed a significant effect of
condition $F(4, 12) = 22.043, p < .001$. Planned contrasts between the full condition and
each of the four opposing check conditions revealed that the sensitivity was significantly
better for the full stimulus compared to the 0.71° check condition ($F(1,3) = 59.717, p =
.005, r^2 = 0.95$), the 1.43° check condition ($F(1,3) = 19.676, p = .021, r^2 = 0.86$), the 2.0°
check condition ($F(1,3) = 21.230, p = .019, r^2 = .88$) and the 3.33° check condition ($F(1,3)
= 50.597, p = .006, r^2 = 0.94$). This suggests that long-range summation is not occurring
indiscriminately over area and motion direction, if it were then we would expect there to
be no difference in thresholds because in all cases the full 10° x 10° area contains moving
signal. Rather it is consistent with long-range summation occurring within direction-selective channels.

The average difference in thresholds between the single and opposing motion Battenbergs was 1.86 dB which represents the magnitude of summation across directional features. This relatively high level of summation is very similar to what Meese (2010) found for summation across orthogonal texture signals (1.88 dB). Based on computational modelling which included an additional square-law transducer, Meese (2010) suggests a ratio as low as 0.75 dB to be consistent with probability summation across filters tuned to different features. Therefore, the performance benefit of adding gratings with different motion directions does not seem to be consistent with a process of probability summation thus implying that for motion, there is also a final stage of pooling for contrast threshold which sums across detectors tuned for different motion directions.

2.4.4. Discussion

This experiment found that for the range of sizes examined in this study, there is no gross difference in the range of behaviourally measured spatial summation between the two different types of motion stimuli at detection threshold, implying that summation remains strong even when the visual system is expected to segment regions of the stimulus moving in opposite directions. At contrast threshold, increased summation may be an adaptive mechanism that operates to enhance sensitivity when the signal is weak (low contrast). This is consistent with studies reporting that summation area is dependent on stimulus contrast. Neurophysiological recordings from V1 in macaque have shown that this area increases as contrast decreases (Cavanaugh, Bair, & Movshon, 2002; Kapadia, Westheimer, & Gilbert, 1999; Kasamatsu, Miller, Zhu, Chang, & Ishida, 2010; Levitt & Lund, 1997; Sceniak, Ringach, Hawken, & Shapley, 1999) and this is also found in MT
neurones (Pack et al., 2005). Increased spatial summation under low contrast conditions has also been observed in psychophysical studies on human observers that measured duration thresholds for the discrimination of motion direction (Betts, Taylor, Sekuler, & Bennett, 2005; Tadin et al., 2003). Performance on the Tadin et al. (2003) task is thought to be governed, at least in part, by motion sensitive neurons in area MT and this link has been supported by a study using transcranial magnetic stimulation (TMS) over area MT/V5 in human participants (Tadin, Silvanto, Pascual-Leone, & Battelli, 2011). These findings suggest that the same relationship between contrast and summation area exists for motion detectors. This provides a potential explanation for failing to find any gross difference in the size of the summation area for the opposing motion Battenberg relative to the single motion Battenberg. MT neurons tuned for a particular direction may be predisposed to selectively sum over large areas when the contrast signal from moving stimuli is weak, such as for the low contrast stimuli used here. This large area summation occurs irrespective of whether the stimulus contains opposing motion or not, because the two motion directions are subserved by independent detectors with large long-range summation areas and perception depends on whichever one is most sensitive in each instance. A similar result was obtained in research using counterphase gratings which demonstrated the existence of direction selective channels that function as independent contrast summation mechanisms, near threshold (Levinson & Sekuler, 1975). Directional selectivity is therefore an important feature for motion integration, arising before the stage at which pooling of contrast signal takes place within extensive area summation mechanisms at low contrast. We have further proposed that this is followed by a stage of pooling (not simply probability summation) across the output of these directionally selective mechanisms.
2.5. Experiment 2: High contrast summation

As previously outlined, psychophysical estimates of spatial summation have been found to be dependent on stimulus contrast. Spatial summation is pronounced at low contrast; evidenced as a decrease in duration threshold for discrimination of motion direction as stimulus size increases. For higher contrast stimuli, summation is gradually reduced and surround suppression begins to appear and dominate the process for larger stimuli, evidenced by an increase in duration threshold for motion discrimination as the size of a high contrast stimulus increases (Tadin et al., 2003). This effect, which yields poorer direction discrimination for large high contrast stimuli than low contrast stimuli of the same size, is thought to be a consequence of suppressive surrounds that are selectively activated by high contrast stimuli (Tadin & Blake, 2005; Tadin & Lappin, 2005b; Tadin et al., 2003). Neurophysiological studies have also shown that summation and suppression are dependent on stimulus contrast. They found that inhibitory surround receptive fields of macaque MT cells were less active for the perception of low contrast stimuli compared to high contrast stimuli (Pack et al., 2005; Tsui & Pack, 2011). For low contrast stimuli, increases in size yielded stronger neural activity in MT - consistent with spatial summation within receptive fields, whereas a decrease in neuronal firing was recorded as the size of a high contrast stimulus was increased, consistent with suppression (Churan et al., 2008; Hunter & Born, 2011; Pack et al., 2005). Given that the experiments in the current study were conducted at contrast threshold we can assume that there was minimal or no inhibitory effect of the surround receptive field.

The operation of inhibitory centre-surround mechanisms in MT/V5 are theorised to be very important for the segmentation of moving spatial patterns (Allman et al., 1985a, 1985b; Born, 2000; Born & Tootell, 1992; Nakayama & Loomis, 1974; Tadin, 2015; Tadin
Allman and colleagues (1985a) were the first to provide evidence that the characteristics of centre-surround mechanisms are well suited to figure-ground discrimination. By recording from MT in owl monkeys they discovered centre-surround neurons responded poorly to large, uniform “background motion” covering both the centre and surround, but were highly sensitive to a stimulus containing discontinuities such as differences in direction of motion across space. This led to the suggestion that one of the primary roles of this population of neurons is to help segment smaller, moving objects from a background flow field.

Lui et al. (2012) also demonstrated the contribution of two distinct neural populations, in marmoset MT, that have different functional roles; one which prefers to integrate over smaller areas to subserve segregation and one which prefers to integrate over larger areas. They suggested that both mechanisms contribute to motion processing, but the one which dominates may depend on which is more sensitive, which may depend on stimulus conditions such as contrast. The outputs could also be selectively monitored by attentional processes reflecting task requirements. Lui et al. (2012) found that less visible camouflaged bars exhibited more extensive length summation than highly visible solid bar stimuli; possibly a consequence of the same mechanisms underlying increased summation for low contrast stimuli found in other experiments, most likely attributable to reduced suppression.

The lack of contribution of these centre-surround suppression effects, due to the low contrast signals used in the previous experiments, could explain why there was no difference in summation extent for a Battenberg stimulus filled in with opposing motion signals.
Following this reasoning we next inquire whether filling in the Battenberg stimulus with opposing motion will produce a difference in summation behaviour when the task is performed well above the contrast threshold required for pattern detection. At these higher contrast levels the motion signal is stronger requiring observers to discriminate suprathreshold contrast signals. This will more likely trigger the centre-surround receptive fields that are thought to subserve motion segmentation mechanisms (Allman et al., 1985a, 1985b; Born, Groh, Zhao, & Lukasewycz, 2000; Nakayama & Loomis, 1974). Secondly it is of interest to determine whether the summation results for the single motion Battenberg in the detection experiment generalise to conditions with suprathreshold base contrast levels. These kinds of suprathreshold contrast discriminations are typical tasks the visual system would encounter in the natural environment.

2.5.1. Observers

Data were collected from the same psychophysical observers (KT, MT, SC, TM) that were used in the previous experiments. Observers gave their informed consent before participating in this experiment.

2.5.2. Stimuli and procedure

The stimuli and procedure were similar to that used in the previous experiments. The 2IFC procedure was the same except that in this experiment a visible Battenberg stimulus was presented in both intervals. A suprathreshold, 20% contrast, pedestal was present in the signal checks of the Battenberg in the reference interval (Figure 2.7A). The Battenberg in the target interval contained the 20% contrast pedestal plus a contrast increment (Figure 2.7B). Participants were instructed to choose the interval with the highest contrast stimulus. The same three-down, one-up staircase procedure was used to converge upon the contrast discrimination threshold. Contrast discrimination thresholds
were obtained for both the single motion Battenberg and the opposing motion Battenberg. Each check size condition was repeated five times by each observer and these were averaged to give a single threshold estimate per condition per observer.

Figure 2.7. Example of the Battenberg stimuli used in the contrast discrimination experiment. (A) shows an example of the stimulus used in the reference interval - a Battenberg pattern containing a 20% contrast pedestal in the signal checks. (B) shows an example of the stimulus used in the target interval – a Battenberg pattern containing a 20% contrast pedestal plus a contrast increment.

2.5.3. Results

Figure 2.8 shows raw contrast discrimination thresholds for the single motion condition and the opposing motion condition. Results are shown for four observers individually for the single motion experiment, on the left (2.8A), and the opposing motion experiment, on the right (2.8B). The average threshold of all four observers for both conditions is shown in the bottom panel (2.8C).
Figure 2.8. Contrast discrimination thresholds for the ‘full’ stimulus and each of the single motion (A) and opposing motion Battenberg stimuli (B) for each observer, and the averaged data for single motion and the opposing motion conditions (C). The green line in (C) indicates a 1.88 dB difference in threshold that Meese (2010) obtained for summation across orientation in static patterns. Error bars represent standard error of the means.

Raw contrast discrimination thresholds show no dependence on check size, thus no evidence of long-range summation of contrast signal over area for the single motion or opposing motion Battenberg stimuli. Furthermore, the contrast discrimination threshold for the full stimulus which only contained motion in a single direction was higher than that for
all of the opposing motion Battenberg patterns which had the same amount of contrast
signal as the full stimulus. A one-way repeated-measures analysis of variance on the
thresholds for the opposing motion check patterns and the full pattern revealed a
significant effect of condition $F(4, 12) = 4.159, p = .013$. Planned contrasts between the
full condition and each of the four opposing check conditions revealed that the sensitivity
was significantly poorer for the full stimulus compared to the 0.71° check condition
($F(1,3) = 184.841, p = .001, r^2 = .99$), the 1.43° check condition ($F(1,3) = 12.634, p =
0.038, r^2 = .81$), the 2.0° check condition ($F(1,3) = 9.672, p = .050, r^2 = .76$) and the 3.33°
check condition ($F(1,3) = 16.557, p = .027, r^2 = .85$).

In the previous experiment the full stimulus had a significantly lower threshold
than all the opposing motion check conditions, due to summation of a single direction
occurring over a larger area (potentially up to 10°, depending on receptive field size of a
directionally tuned neuron). However, the data here suggests no summation with high
contrast discrimination as there is no improvement in sensitivity with increasing check size
and no benefit offered by the full stimulus in comparison to the checked stimuli, consistent
with diminished long-range area summation. The average difference in thresholds between
the single and opposing motion Battenbergs was 1.99 dB. It is difficult to make firm
conclusions about this value given that the parameters of the underlying model may differ
at suprathreshold levels to incorporate stages of contrast gain control (Meese & Baker,
2011). Nonetheless, the relatively high ratio suggests that summation across direction
filters is not consistent with a process of probability summation, and implies that
summation occurs across the output of directionally tuned filters at preceding stages –
similar to what we found in the previous experiment at motion detection threshold and to
the results of Meese (2010) for summation across orthogonal spatial filters at contrast threshold with static stimuli.

2.5.4. Discussion

Increases in the signal area of a motion stimulus typically results in improvements in threshold sensitivity, consistent with spatial summation. In our previous set of experiments we found evidence of summation over large areas for a stimulus that could evoke motion segmentation. This was potentially due to the input of direction selective mechanisms that are predisposed to sum over larger areas when visibility is decreased. The current experiment set out to study whether the extent of behaviourally measured spatial summation for a motion stimulus containing opposite directions of movement differs from that for a stimulus containing motion in a single direction when the contrast signals are stronger, more visible and more likely to evoke suppressive surround effects (i.e., high contrast).

The results showed that there was no dependence on check size across the range of sizes tested, and this was found for both the single motion and opposing motion conditions. Thus, spatial summation was diminished when the task was performed at high contrast. This finding is analogous to previous studies that have found reduced summation for discrimination of motion direction under high contrast conditions, (Betts et al., 2005; Tadin et al., 2003). It is also in agreement with neurophysiological recordings that suggest receptive field size “shrinks” as stimulus contrast increases for cells in MT (Churan et al., 2008; Hunter & Born, 2011; Pack et al., 2005). Our findings further suggest that summation of motion over area also plays a minor role in the discrimination of suprathreshold, high contrast patterns. It suggests that the mechanism governing segregation, with its limited integration capacities, is always more sensitive under high
contrast conditions, regardless of the actual need for segregation. Conversely, the influence of a mechanism which sums over large regions becomes attenuated. These findings converge with the neurophysiological summation results from marmoset MT which also varied in response to stimulus contrast and visibility (Lui et al., 2012). Despite the differences in long-range summation for high contrast stimuli, the results still showed evidence of a stage which pools across different motion directions as the difference in thresholds was too high to be attributed to probability summation. This outcome is the same as Meese (2010) suggested was consistent with summation across filter groups in his static-mixed orientation patterns.

The results for the single motion condition are more consistent with segmentation than summation. This segmentation mechanism potentially became more informative due to the highly visible differences between the signal checks and the blank checks. The visual motion system can then base decisions on the relative contributions of summation and segregation processes using the most information in the stimulus conditions experienced.

It is noteworthy that the thresholds for the full stimulus were equivalent to, or slightly worse than, the thresholds for the single motion Battenbergs which had half the amount of contrast signal of the full pattern. Perceptual insensitivity to high contrast, large-field, uniform stimuli is consistent with previous motion summation studies and is considered to be a property of spatial suppression (Tadin et al., 2003; Tadin et al., 2011). These studies posit the involvement of antagonistic centre-surround neurons in V5/MT. Verghese and Stone (1996) also found that speed discriminations for suprathreshold gratings were poorer for a single large contiguous patch compared to the same stimulus segmented into smaller patches, and the authors suggest this may be a consequence of
surround suppression. It is therefore possible that the suprathreshold stimuli used in our experiment were indeed effective in stimulating these centre-surround antagonistic neurons in MT, producing limited summation over area. Thus providing support for the suggestion that the link between high contrast conditions and the capacity to segregate motion is underpinned, at least in part, by the activity of centre-surround mechanisms in area MT which are functionally distinct from the mechanisms which are responsible for summation of large moving fields.

Another potential explanation for the lack of summation of contrast over area at suprathreshold contrast levels is due to the experimental design. Meese and Summers (2007) found that spatial summation of contrast operates at all contrast levels when the target area increases but the pedestal area is fixed, suggesting that for static patterns, the suprathreshold loss of area advantage shown in previous studies (Legge & Foley, 1980) is due to a concomitant increase in suppression from the contrast pedestal. This counter suppression has also been found to extend to the integration of orientation and temporal signals (Meese & Baker, 2013), as well as to the integration of signals across the eyes (Meese & Baker, 2011; Meese, Georgeson, & Baker, 2006). This effect may also extend to motion summation and explain why no benefit arises from an increase in signal area at high contrast. Therefore, an important avenue for future research would be to test for evidence of summation by increasing the size of the target whilst keeping the size of the pedestal constant across all conditions. If summation can be found then re-evaluation of the underlying cause of diminished summation in this study and other behavioural motion studies would be required. However, the current evidence that contrast threshold does not vary with stimulus area is still an important finding in itself given that this may be how
summation operates when performing many natural visual tasks that involve the integration of suprathreshold visual signals.

The issue surrounding loss of motion summation has also been raised by Aaen-Stockdale, Thompson, Huang, and Hess (2009). They presented observers with a stimulus comprising of two identical sinusoidal gratings drifting in opposite directions and measured the contrast imbalance required until motion was perceived consistently in a single direction. They find evidence for weakening of spatial summation at higher contrasts, consistent with previous studies, but demonstrate that these suppressive effects are predictable from the observers threshold for each size relative to the absolute contrast of the stimulus, and therefore support a low-level explanation of behavioural spatial suppression. Glasser and Tadin (2010) re-examined contrast-dependent motion suppression by measuring duration thresholds, as they had previously, whilst setting the contrast of all the stimuli to be a fixed multiple of the stimulus’ contrast threshold in order to equalize differences in effective contrast. This produced an increase in sensitivity to the large stimuli, however direction discrimination for large stimuli was still worse than that for the small stimuli, consistent with suppression. This particular debate reinforces the need for future research to understand how motion summation operates at high contrast.

In summary, the Battenberg paradigm allows us demonstrate more extensive contrast summation for drifting grating patterns at threshold, presumably because noise levels are controlled. We also corroborated previous evidence that summation dominates at low contrast, but at high contrast segmentation is more likely, and this is potentially due to the contribution of adaptive spatial suppression mechanisms that operate only when sensory inputs are strong enough to guarantee visibility. However, further research is needed to rule out other explanations for diminished summation at high contrast.
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Chapter 3: Battenberg summation reveals larger psychophysical receptive fields for the discrimination of motion direction at contrast threshold.
Abstract

This study used the Battenberg paradigm (Meese, 2010) to examine summation behaviour for the discrimination of motion direction at contrast detection threshold. The Battenberg summation method aims to control the influence of locally generated internal noise changes by holding overall display size constant, producing more accurate estimates of summation area than conventional methods which vary the diameter of the whole stimulus. In this checkerboard stimulus, check size (luminance-modulated drifting gratings alternating with mean luminance areas), but not display size, is varied to measure dependence on signal area. This method has previously revealed larger summation regions when measuring the contrast threshold for the detection of moving patterns (McDougall, Dickinson & Badcock, 2016). In this experiment, observers were required to discriminate the direction of motion contained in Battenberg patterns, ensuring that the motion processing system must be engaged. The results showed contrast summation operable over a large square area with side length of 3.33° which was inconsistent with a process of probability summation. Summation behaviour closely resembled that of the motion detection data, confirming that detection and discrimination are mediated by mechanisms that have the same summation properties. This has been proposed to include a stage of short-range summation within linear filters, followed by a spatially extensive long-range summation process.
3.1. Introduction

In the previous chapter (McDougall, Dickinson, & Badcock, 2016) it was demonstrated that receptive fields of motion detectors can sum over larger areas than previously estimated. We measured contrast sensitivity for detection of direction of drift for a 3c/° grating and found evidence of long-range summation over a square shaped area with side length of at least 3.33°. In comparison, previous studies estimate the length of summation to be no more than 1° for a detector tuned to a drifting 3c/° grating (Anderson & Burr, 1987). Anderson and Burr (1991) measured both direction discrimination and detection thresholds to compare the spatial properties of the mechanisms which subserve detection and discrimination. They showed that the contrast required for the detection of gratings was the same as that required for discrimination of the direction of drift, consistent with previous research suggesting direction can be discriminated at threshold for detection (Derrington & Henning, 1993; Watson, Thompson, Murphy, & Nachmias, 1980). They found this was consistent across all stimulus lengths and widths, indicating that performance on the two tasks is affected by changes in signal area in the same way. The summation data permitted a single model of receptive field size to be accurately fitted to both the detection and discrimination thresholds, further suggesting that the two processes are mediated by mechanisms that have the same summation properties, and therefore the predicted estimates of the size of psychophysical summation is the same regardless of whether the task is to detect or discriminate. Based on their model, the estimated size of summation (length and width) is less than 1° for a drifting grating with spatial frequency of 3c/°.

Morrone, Burr, and Vaina (1995) have suggested that more extensive spatial summation occurs for motion coherence thresholds for discriminating direction of radial,
circular and translational motion in random dot patterns, but contrast thresholds for
detection and discrimination with those same patterns shows very limited summation over
area, i.e. the sensitivity improvements were consistent with probability summation across
independent detectors once the area became larger than about 1° (diameter of a spatially
curtailed circle) consistent with previous estimates using drifting gratings (Anderson &
Burr, 1987, 1991) described above. Morrone et al. (1995) suggested this is the
consequence of a limit to the integration for contrast sensitivity which is enforced by
preceding contrast sensitive mechanisms in V1, or small sub-units in MT/V5.

In the previous study we used Battenberg stimuli to explore summation of motion
at contrast threshold. Battenberg stimuli were introduced by Meese (2010) as a way of
dissociating changes in signal area from changes in internal noise, by keeping overall
display size constant. The originally proposed benefit of this approach was that changes in
detection threshold would only reflect changes in signal, since noise was proportional to
the area monitored and that doesn’t change, allowing more accurate estimates of
summation area to be obtained. In McDougall et al. (2016) it was demonstrated that the
area of summation for contrast detection of motion is more extensive than classical
summation studies postulate, therefore it is natural to ask whether this result also extends
to motion direction discrimination. Assuming that contrast detection of motion and
discrimination are tapping the same underlying mechanisms, sharing the same spatial
properties, then we would expect to find the same larger area of summation for direction
discrimination. This will be investigated by employing the direction discrimination
criterion for Battenberg patterns.
3.2. Method: Motion direction discrimination

3.2.1. Apparatus

The stimuli were generated using MATLAB 7.0.4 (Mathworks, Natick, Ma, USA) on a Pentium 4 PC (3.0GHz) and presented on a Sony Trinitron Multiscan G520 Monitor (screen resolution: 1024 × 768 [34° 08’ × 25° 36’], refresh rate: 100Hz) from the frame store (256MB) of a Cambridge Research Systems ViSaGe graphics system. The observers viewed the monitor from a distance of 65.5cm which was maintained using a chin-rest. At this viewing distance each pixel subtended 2’ of visual angle. Testing took place in a darkened room (ambient luminance of < 1cd/m²). The background screen luminance was set at 45cd/m², calibrated using an Optical OP 200-E photometer (Head model #265) and associated software (Cambridge Research Systems, Kent, UK). Contrast is defined as Michelson contrast in percent;

\[
C_M \% = \left( \frac{L_{\text{max}} - L_{\text{min}}}{L_{\text{max}} + L_{\text{min}}} \right) \times 100
\]  

where \( L \) is luminance. Conventionally, this is often expressed in dB units where;

\[
C_{dB} = 20\log_{10}(C_M \%)
\]  

3.2.2. Observers

Data were collected from three experienced psychophysical observers; KT, MT, and TM, all of whom were recruited from the Human Vision Laboratory of the University of Western Australia and were observers in the previous Battenberg summation study. Observer TM was an author of the study, the other observers were naïve to experimental aims of the study. All observers had normal or corrected-to-normal visual acuity. All
experiments were performed binocularly with natural pupils. Observers gave their informed consent before participating in the study. The treatment of participants in this study complied with the guidelines set by the Human Research Ethics committee of the University of Western Australia and therefore in accordance with the tenets of the Declaration of Helsinki.

3.2.3. Stimuli

Battenberg stimuli have a checkerboard arrangement, consisting of signal checks alternating with uniform luminance checks. Signal regions contain luminance-modulated, drifting (1°/s) sine wave gratings with a spatial frequency of 3c/°, consistent with McDougall et al. (2016). Uniform regions are set at 0% contrast and have the same luminance as the background of the display and the mean luminance of the grating patches. The size of the check regions within the Battenberg can be varied to measure dependence on signal area without adjusting the overall extent of the stimulus across conditions. Four different check sizes were used (see Figure 3.1): 0.71°, 1.43°, 2.0°, 3.33° in width and height, as well as the ‘full’ stimulus which was a 10° square grating with no blank regions (Figure 3.1E). The overall size of the checked Battenberg stimuli was 10° which is equal to the extent of the ‘full’ stimulus.

The one-dimensional sine wave grating is a function of space (x) and time (t) and is described by:

\[ L[x,t] = L_m[1 + c \cdot \cos(2\pi f_s \cdot x + 2\pi f_t \cdot t + \phi)] \]  

where \( L_m \) is the mean luminance of the display, \( c \) is amplitude (contrast of the grating), \( f_s \) is the spatial frequency (cycles per degree, c/deg), \( f_t \) is the temporal frequency and \( \phi \) adjusts the phase of the grating. The checks were smoothed at the edge using a raised sine
envelope that occupied a uniform width strip equal to 10% of the distance from the centre to the nearest edge of the square check. The blurring in the corners was therefore $\sqrt{2}$ wider.

*Figure 3.1.* Examples of the “Battenberg” stimuli used in this experiment. The full stimulus is shown (E) as well as the four Battenberg patterns used which had check side lengths of 0.71°, 1.43°, 2.0° and 3.33° (A-D respectively). In the experiment all checks drifted in the same direction with drift being randomly either left or right, on an individual trial. This figure is reproduced from McDougall et al. (2016)

3.2.4. Procedure

Contrast detection thresholds were measured for direction discrimination judgements (left or right) of Battenberg stimuli to ensure direction-selective processing
was required. Battenberg patterns were presented for 300 ms in a single temporal interval, at a particular contrast level. A central fixation point was presented at the beginning of each run. Presentation of the stimulus was demarcated by an auditory beep. Motion direction (left or right) was selected randomly at the start of each trial. The observer was required to indicate which direction they believed the pattern to be moving and made their response using a button box. The observer received auditory feedback to indicate whether their response was correct or incorrect. There was a 1 s pause before the commencement of the next trial. On each run, a three-down, one-up staircase procedure was used to converge upon contrast detection threshold; the 79.4% correct performance level (Wetherill, 1963; Wetherill & Levitt, 1965). The procedure terminated after eight reversals and threshold was calculated as the mean of the contrast levels for the last four reversals. Each check size condition was repeated five times by each observer and these were averaged to give a single threshold per condition per observer. Observers were instructed to fixate in the centre of the stimulus. For all participants, practice runs were conducted until they were comfortable with the task. Data was collected over multiple sessions of 1-2 hours duration. Rest breaks were permitted as required.

3.3. Method: Contrast detection of motion

The contrast detection data were collected in a previous study, refer to McDougall et al. (2016), the previous chapter, for the method used. All experimental variables were identical to this study except that in McDougall et al. (2016) there were two intervals, one containing a Battenberg (drifting left or right, chosen randomly) and the other blank (mean luminance displayed) and they were required to detect which of the two intervals contained the Battenberg target. Staircase and threshold procedures in McDougall et al. (2016) were identical to this study. The detection data collected from three of the participants (TM, MT,
KT) in McDougall et al. (2016) who also completed this discrimination study, was re-used for comparison. Discrimination data were collected after (6 months maximum) detection data so any potential improvements in overall performance may reflect practice, but changes across check size within a task should not as the effects would be equal across all conditions and the relative differences would remain.

3.4. Results

Figure 3.2 shows raw contrast direction discrimination thresholds and contrast detection thresholds for each observer individually (replotted from previous study) and averaged across observers for the stimuli shown in Figure 3.1. In Figure 3.3 the thresholds have been transformed to indicate summation ratios; the difference between the contrast threshold for the full stimulus and each of the checked Battenberg stimuli (Battenberg/Full) in dB units, consistent with Meese (2010). This indicates the reduction in the level of summation for each of the Battenberg check sizes relative to the full stimulus and also adjusts for differences in overall sensitivity to the full stimulus.
Figure 3.2. Individual contrast thresholds for the “full” stimulus and each of the checked Battenberg stimuli for the direction discrimination experiment are shown for each individual observer (A-C) along with contrast detection thresholds collected in the previous study (McDougall et al., 2016). The averaged data from the same three observers for both the contrast detection and the direction discrimination task are shown in panel D. Error bars represent 95% confidence intervals.

3.4.1. Contrast threshold analysis

Contrast thresholds show improvement as check size increases, as seen in Figure 3.2, consistent with a process of spatial summation. The detection and discrimination threshold data were compared using a two (task: detection or discrimination) by five (check size) repeated measures analysis of variance (ANOVA) with contrast threshold as
the dependent variable. The analysis revealed a significant main effect of check size $F(4,8) = 52.27, p < .0001$, partial $\eta^2 = .97$, indicating that increases in check size produced significant improvements in performance (spatial summation) and this was present for both the discrimination and detection data as there was no significant interaction effect $F(4,8) = .308, p = .865$, partial $\eta^2 = .133$. There was no main effect of task condition $F(1,2) = 3.395, p = .207$, partial $\eta^2 = .578$, meaning motion direction discrimination thresholds were not significantly different from motion detection thresholds. This is consistent with previous research suggesting that motion direction can be discriminated at threshold for contrast detection of motion (Derrington & Henning, 1993; Watson & Robson, 1981). Given that we have used two different procedures for the two tasks, and a 1AFC task yields a different threshold to a 2AFC task, producing differences in proportion correct for the same stimulus magnitudes, it would be plausible to expect a difference in thresholds of approximately $\sqrt{2}$ according to Kingdom and Prins (2010). The difference in thresholds for our data do not reach $\sqrt{2}$, but do show a slight difference in the expected direction i.e. the discrimination thresholds (1AFC) are slightly higher than the detection thresholds (2AFC) by a factor of 1.13. Observers completed the detection task before the discrimination task and were presumably more practiced for discrimination and this could have produced lower discrimination thresholds, possibly accounting for the less than $\sqrt{2}$ difference in our data. Any overall practice effects arising from the order of the tasks should be normalised out in the following summation ratio analysis.
Figure 3.3. Summation ratios (the difference between the contrast direction discrimination thresholds for the full stimulus and each of the checked Battenberg stimuli in dB units; Battenberg/Full) indicating the level of summation for each Battenberg stimulus are shown for individuals (A). The averaged data are plotted on panel B along with the summation ratios for contrast detection of motion collected in the previous study. Error bars represent 95% confidence intervals.

3.4.2. Summation ratio analysis

The summation ratio data for contrast detection and direction discrimination, presented in Figure 3.3, was also compared by conducting a 2 (task: detection or discrimination) x 5 (check size) repeated measures ANOVA. The analysis revealed there was no main effect of task condition $F(1, 2) = .8629, p = .451$, partial $\eta^2 = .357$, indicating that summation ratios for the contrast detection of motion task were comparable to the motion direction discrimination task. A significant main effect of check size was found $F(4, 8) = 634, p < .001$, partial $\eta^2 = .973$. Post-hoc tests, with Bonferroni corrections to control for familywise error rate, were performed to follow up this effect and found significant differences between the full pattern and every check size for the motion detection condition ($p < .001, p < .001, p = .0016, p = .0341$ for 0.71°, 1.43°, 2.0°, 3.33°,
respectively) and also for the motion direction discrimination condition \((p < .001, p < .001, p = .002, p = .0049\) for \(0.71°, 1.43°, 2.0°, 3.33°\), respectively). This indicates that there is still strong summation in place for the largest size tested for the direction discrimination task, and for the contrast detection of motion task as previously reported in McDougall et al. (2016). Furthermore a relatively high summation ratio of approximately 2 dB was maintained for the largest check for both the contrast detection and direction discrimination tasks. This level is consistent with a process of long-range summation of contrast signal over area and is too high to be attributed to probability summation over space; 1.5 dB or less being the fiducial value used to approximate a fourth-root summation rule in previous Battenberg summation studies (McDougall et al., 2016; Meese, 2010).

3.5. Discussion

In this experiment we assessed spatial summation using a direction discrimination task and the Battenberg summation paradigm. The results for motion direction discrimination show the same summation behaviour as that for contrast detection (McDougall et al., 2016) and other studies that have utilised Battenberg patterns (Baker & Meese, 2011; Baldwin, Husk, Meese, & Hess, 2014; Meese, 2010). Meese and colleagues (2010) argue that the initial peak in summation for the smallest check size (again approximately 6 dB in this study) is consistent with short-range summation within linear filters (stage one). The level of summation drops as check size increases but remains more potent than a process of probability summation (1.5 dB or less) for the range of sizes tested here, which Meese (2010) argued suggested a subsequent stage of long-range summation (stage two). The results of this study show that this long-range summation extends over an area with dimensions larger than \(3.33° \times 3.33°\) for discrimination of motion direction at contrast threshold. The fact that the same underlying model accounts both the contrast
detection of motion and direction discrimination data is consistent with the previous research by Anderson and Burr (1991) which found that a single model of receptive field size could be fitted to both the discrimination and detection thresholds, confirming that detection and discrimination are mediated by mechanisms that have the same summation properties. However we suggest that, when noise levels are held constant, the size of the summation area revealed is much larger than conventional contrast summation estimates of less than 1° for the detection and discrimination of 3c/° gratings.

This is an important step toward the generality of the conclusions set out in the previous study that argued motion summation can occur over larger areas than previously implied. Morrone et al. (1995) found that contrast thresholds for both motion detection and motion direction discrimination, for dot patterns, show little to no benefit of spatial summation with increasing signal area, which they interpreted as a limit to the integration of contrast sensitivity imposed by earlier contrast sensitive mechanisms. The slight improvement with area they find was attributed to probability summation among these earlier independent mechanisms, responding locally to the direction of motion. Although their study also had the benefit of a fixed stimulus area across conditions, a potential cause for the lack of summation could have been the use of dot-stimuli which represent a broad range of spatial frequencies, and it is uncertain which ones would be driving summation. Summation behaviour is thought to vary with spatial frequency (Anderson & Burr, 1991) and this could have obscured mechanisms underpinning the findings. Furthermore, research has shown that 2D stimuli (such as dot patterns) are integrated differently from 1D gratings when determining motion direction (Amano, Edwards, Badcock, & Nishida, 2009) and this could also contribute to the difference seen in the two studies.
Taken together with the results of the previous study, summation can be achieved over large areas and this generalises to both contrast detection of motion and motion direction discrimination, and does not seem to be limited by a process of probability summation among local motion detectors. This is at least the case for drifting gratings when the overall stimulus area is fixed across conditions. Future research that aims to investigate summation, for either motion detection or motion direction discrimination, should consider utilising this approach to achieve a cleaner measure of the integration process.
References


Chapter 4: Suprathreshold contrast summation over area using drifting gratings.


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*Keywords: contrast, motion, summation, suprathreshold, inhibition*
Abstract

This study investigated contrast summation over area for moving targets applied to a fixed-size contrast pedestal - a technique originally developed by Meese and Summers (2007) to demonstrate strong spatial summation of contrast for static patterns at suprathreshold contrast levels. Target contrast increments (drifting gratings) were applied to either the entire 20% contrast pedestal (a full fixed-size drifting grating), or in the configuration of a checkerboard pattern in which the target increment was applied to every alternate check region. These checked stimuli are known as “Battenberg patterns” and the sizes of the checks were varied (within a fixed overall area), across conditions, to measure summation behavior. Results showed that sensitivity to an increment covering the full pedestal was significantly higher than that for the Battenberg patterns (areal summation). Two observers showed strong summation across all check sizes (0.71°-3.33°), and for two other observers the summation ratio dropped to levels consistent with probability summation once check size reached 2.00°. Therefore, areal summation with moving targets does operate at high contrast, and is subserved by relatively large receptive fields covering a square area extending up to at least 3.33° x 3.33° for some observers. Previous studies in which the spatial structure of the pedestal and target co-vary were unable to demonstrate spatial summation, potentially due to increasing amounts of suppression from gain-control mechanism which increases as pedestal size increases. This study shows that when this is controlled, by keeping the pedestal the same across all conditions, extensive summation can be demonstrated.
Introduction

Many psychophysical studies have explored the way in which the human visual system constructs representations of large scale surfaces and objects by using stimuli presented at or near threshold for detection or discrimination. It is also important to understand how vision achieves this task for suprathreshold stimuli, which are more representative of the contrast levels in the natural visual environment. Legge and Foley (1980) conducted a psychophysical investigation of spatial summation of luminance contrast by comparing contrast discrimination thresholds for small and large grating areas but found this produced no differences in performance when the pedestal contrast was well above threshold. They suggested that the benefit of larger signal area is lost above detection threshold because the noise among the detecting mechanisms becomes correlated, nullifying the advantage of having multiple detection mechanisms such that not even probability summation can improve performance. However, Legge and Foley (1980) measured thresholds for targets of varying size presented on pedestals of matched extent, leaving open the possibility that the process of areal summation remains operative for the target increment but is nullified by extra suppression from the pedestal as it concomitantly increases in size. Despite this potential limitation in the study, the finding led to the orthodox view that there is minimal or no areal summation of signal contrast well above detection threshold.

Recent studies have corrected for the potential limitations of the original Legge and Foley (1980) study that suggested spatial summation is inoperative at suprathreshold contrast levels. Meese and Summers (2007) measured contrast discrimination functions for a wide range of pedestal contrasts. The targets were increments applied to either the entire stimulus (referred to as the “full” target stimulus), or in multiple patches across the
pedestal. These patchy targets were referred to as “Swiss Cheese” stimuli and were created by multiplying a sinewave carrier and a checkerboard plaid modulator to produce interdigitated check regions sinusoidally varying between high contrast and zero contrast, e.g. Figure 1 (Baker & Meese, 2011; Meese & Summers, 2007). In this experimental design the pedestal area is fixed across conditions and changes in performance reflect changes in only the area of the target increment region. Meese and Summers (2007) found that observers performed better for the full target increment (see Figure 1) than with the Swiss Cheese target increment (which had approximately half the amount of signal over area compared to the full target) across a large range of pedestal contrasts (up to 32% contrast). They interpreted this as evidence for a strong spatial summation process for luminance contrast occurring well above detection threshold, inconsistent with the orthodox view that spatial summation is abolished at suprathreshold levels. Meese and Summers (2007) posited that for more conventional suprathreshold stimulus arrangements, such as when the diameter of a grating is varied across conditions (Legge & Foley, 1980), there is no sensitivity benefit with increasing grating area because of suppression from contrast gain control mechanisms, which have an increasingly stronger input as the size of the pedestal increases (Meese, 2004; Meese, Hess, & Williams, 2005).

This suggestion that benefits of increasing target size are obfuscated by detrimental effects of increasing pedestal size also has support from a study by Bonneh and Sagi (1999) which measured contrast discrimination thresholds for Gabor patches of different sizes added to a 30% contrast pedestal of matched extent, or one fixed at maximal size. When the size of the target and pedestal increased together, contrast discrimination thresholds were constant; no evidence of summation. When the target Gabor size was increased but the pedestal was fixed at maximum size, contrast discrimination thresholds
improved, owing to spatial summation of contrast across space. They also attribute the difference between these two conditions to inhibition arising from gain control mechanisms which increases and cancels out summation when the pedestal area increased concomitantly with the target.

Summation of contrast over area for motion direction discrimination is also suggested to be reduced or lost above detection threshold. Tadin, Lappin, Gilroy, and Blake (2003) found that for high contrast motion stimuli, duration thresholds for direction discrimination did not improve when stimulus area was increased, a finding that has since been replicated several times (Battista, Badcock, & McKendrick, 2010; Betts, Taylor, Sekuler, & Bennett, 2005; Glasser & Tadin, 2010; Golomb et al., 2009; Melnick, Harrison, Park, Bennetto, & Tadin, 2013; Read et al., 2015; Tadin et al., 2006; Yazdani, Serrano-Pedraza, Whittaker, Trevelyan, & Read, 2015). This counterintuitive result was suggested to be a consequence of surround suppression, underpinned by antagonistic center-surround properties of motion sensitive neurons, which are more active under high contrast conditions (see Tadin, 2015 for review). In our previous study we found that contrast discrimination thresholds for high contrast moving Battenberg patterns (similar to Swiss Cheese stimuli except the ‘checks’ are square rather than circular) showed no dependence on target size (McDougall, Dickinson, & Badcock, 2016). There was a slight trend toward an increase in threshold for the largest size in some observers, consistent with the suggestion of reduced summation at high contrast for moving gratings, potentially due to the operation of center-surround inhibition becoming more influential under high contrast conditions. However in that study the spatial arrangement of the contrast pedestal matched that of the target Battenberg increment (i.e. area of pedestal and target co-varied) and this could have obscured the results in the same way it did for the Legge and Foley (1980)
study, if we assume the same problem is applicable to the motion domain. Whether contrast summation for drifting grating stimuli can be demonstrated at suprathreshold contrast levels when the target arrangement is manipulated independently of the pedestal remains an unanswered question. We can address this here using a method similar to that used by Meese and Summers (2007) for the summation of luminance contrast over area for stationary stimuli. By keeping the structure of the contrast pedestal constant across conditions (a full fixed size grating) and varying only the spatial arrangement of the contrast increment applied to the pedestal (by manipulating the size of the Battenberg checks, within the same fixed overall size) we can control the amount of suppression from contrast gain control because the total amount of active mechanisms will be approximately constant across conditions, ensuring that changes in performance reflect changes in the signal alone. The aim being to determine whether the visual system is indeed capable of suprathreshold summation of contrast over area for drifting grating stimuli.

Figure 1. An example of the Swiss Cheese stimulus (right) and full stimulus (left) used in Meese and Summers (2007).
Method

Apparatus

The stimuli were computer generated using MATLAB 8.2.0.701 (Mathworks, Natick, Ma, USA) on a PC and presented on a Sony Trinitron Multiscan G520 Monitor (screen resolution: 1024 pixels wide × 768 high, refresh rate: 100Hz) from the frame store (256MB) of a Cambridge Research Systems ViSaGe graphics system. The observers used a chin-rest to maintain a viewing distance of 65.5cm. At this distance each pixel subtended 2’ of visual angle and the display area 34° 08’ × 25° 36’. Testing took place in a darkened room (ambient luminance of < 1cd/m²). The screen space-averaged luminance was 45cd/m², calibrated using a ColorCAL MKII Colorimeter and associated software (Cambridge Research Systems, Kent, UK). A CRS CB6 button box was used to record observer responses. Contrast is defined as Michelson contrast in percent;

\[ C_M\% = \left( \frac{L_{max} - L_{min}}{L_{max} + L_{min}} \right) \times 100 \]  

(1)

where \( L \) is luminance. Following Meese (2010) this will be expressed in dB units (Baker & Meese, 2011; Meese, 2010) where

\[ C_{dB} = 20\log_{10}(C_M\%) \]  

(2)

Observers

Data were collected from four participants (2 male); TM, ED, KH and KP, all of whom were recruited locally from the University of Western Australia. Observers TM and ED were authors of the study, however ED was largely naïve to experimental aims. KP and KH were fully naïve to experimental aims of the study. All observers had normal or corrected-to-normal visual acuity. All participants used binocular viewing, except ED who
has a divergent squint (both eyes supporting normal visual acuity) and was therefore tested monocularly by covering one eye with a black, opaque, eyepatch. Observers gave their informed consent before participating in the study. The treatment of participants in this study complied with the guidelines set by the Human Research Ethics committee of the University of Western Australia and therefore was in accordance with the tenets of the Declaration of Helsinki.

**Stimuli**

Battenberg stimuli have a checkerboard arrangement of signal checks alternating with 0% contrast (blank) checks. Signal regions contained luminance-modulated, drifting (1°/s) sine wave gratings with a spatial frequency of 3 c/° to be consistent with McDougall et al. (2016). The size and arrangement of the check regions containing signal can be varied to measure dependence on signal area without adjusting the overall extent of the stimulus across conditions. Four different square check sizes were used; 0.71°, 1.43°, 2.00°, 3.33° in side length (see Figure 2), as well as the ‘full’ stimulus grating which had a side length of 10° and contained no blank regions (Figure 2E). The pedestal stimulus (reference) used in the experiment was identical to the full stimulus but had a fixed contrast of 20%. The target stimulus was created by adding one of the four Battenberg patterns, or the full grating pattern, to the contrast pedestal. Summation can be quantified by comparing contrast increment thresholds for the Battenberg stimuli with that for the full grating stimulus which has approximately double the amount of signal over area.
Figure 2. Examples of the stimuli used as the target stimulus in this experiment.

Battenberg patterns which had check sizes of 0.71°, 1.43°, 2.00° or 3.33° (A-D, respectively) were added to a full grating contrast pedestal (10° side length). Panel E shows the target used in the full stimulus condition which was a full grating contrast increment added to a full grating pedestal.

Procedure

Contrast increment detection thresholds were measured using a two-interval forced-choice (2IFC) procedure, see Figure 3. One interval contained only the pedestal (reference) and the other interval contained the pedestal plus the Battenberg or full stimulus contrast increment (target). Both stimuli were presented for 300 ms, in a rectangular temporal
window, in a randomly selected order, and were separated by a 1 s inter-stimulus interval. The observers used a button box to indicate which interval they believed contained the additional contrast increment target. The direction of drift was the same for both intervals and was randomly selected (left or right) before commencement of each trial. The observer received auditory feedback to indicate whether their response was correct or incorrect. There was a 1 s pause before the commencement of the next trial. On each run, a three-down, one-up staircase procedure was used to converge upon the 79.4% correct performance level for detecting the contrast increment (Wetherill, 1963; Wetherill & Levitt, 1965). The procedure terminated after eight staircase reversals and threshold was calculated as the mean of the contrast increment level for the last four reversals, and an error estimate. Each check size condition was repeated five times (the order of conditions was randomized within each of the repeats) and were averaged to give a single threshold estimate per condition. Observers were instructed to fixate in the center of the stimulus. A black (1.5cd/m²) square fixation point (4’ x 4’ visual angle) was presented in the center of the screen at the beginning of each trial to guide the observer.
Figure 3. A schematic representation of a single trial. The trial began with a fixation point (1 s) followed by a blank screen set at mean luminance (300 ms). The stimulus intervals containing either the pedestal alone (reference) or the pedestal plus the contrast increment (target) were presented in a randomly selected order for 300 ms each, separated by a 1 s inter-stimulus interval set at mean luminance. A blank screen set at mean luminance was displayed until the observer made a response and remained for 1 s until the start of the next trial.

Results

Raw contrast increment thresholds are shown in Figure 4 for the individuals (4A) and the group-averaged data (4B). Contrast increment detection thresholds improved as check size increased for each observer, consistent with a spatial summation process. Importantly, observers performed better for the full stimulus increment compared to most of the Battenberg increments, which had half the amount of contrast increment signal. Raw thresholds were analysed using repeated measures one-way ANOVA which showed a significant effect of check size on threshold, $F(4, 12) = 10.129, p = .001, \eta^2 = .771$. Planned contrasts were conducted between the full condition and each of the Battenberg
check conditions. There was a significant difference between the full condition and the 0.71° condition, $F(1,3) = 108.277, p = .002, \eta^2 = .973$, the 1.43° condition, $F(1,3) = 16.070, p = .028, \eta^2 = .843$ and also the 2.00° condition $F(1,3) = 10.371, p = .49, \eta^2 = .776$. The results for the 3.33° condition were not significantly different from the full condition, $F(1,3) = .881, p = .416, \eta^2 = .227$. The full stimulus contrast increment yielded improvements in threshold compared to the Battenberg check increments, suggesting that there are indeed mechanisms in the visual system capable of performing summation of luminance contrast over area for suprathreshold (high contrast) drifting gratings. However, given that the full stimulus increment offered no further benefit relative to the 3.33° check condition, a limit to spatial summation may have been reached, at least for some observers. Individual differences were explored by interpreting the summation ratios to help assess whether the summation magnitude was inconsistent with probability summation across independent detectors.
Figure 4. Contrast increment thresholds for each of the checked Battenberg stimuli and the full stimulus condition are shown for each observer (A) and the average of all four observers (B). The size of the check is represented as a function of degrees on the lower x-axis, and number of cycles on the upper x-axis. All error bars represent one standard error of the mean.
In Figure 5, thresholds were transformed to indicate summation ratios; the difference between the full stimulus and each of the checked Battenberg stimuli (Battenberg/Full) in dB units, following (McDougall et al., 2016; Meese, 2010). This transformation indicates the benefit of the full stimulus compared to each checked Battenberg stimulus, providing a measure of the magnitude of summation for each check size and also adjusting for overall differences in individual sensitivity to the full stimulus.
Figure 5. Raw thresholds are converted into summation ratios (Battenberg/Full) which represent the level of summation for each Battenberg stimulus. Ratios for the individual observers are shown in Panel A and the group average is shown in Panel B. The size of the check is represented as a function of degrees on the lower x-axis, and number of cycles on the upper x-axis. Error bars represent one standard error of the mean.
For observers KP and KH a relatively high summation ratio is maintained (2-3 dB) across all check sizes, consistent with strong summation. Importantly, it has not dropped to 1.5 dB or below which is the fiducial value used to approximate probability summation (fourth root summation rule) in previous Battenberg studies (Meese, 2010). However, for observers TM and ED, the summation ratio drops to below 1.5 dB once check size reaches 2.00°. Therefore, with high contrast Battenberg stimuli, strong summation appears to operate with moving stimuli with relatively large receptive fields that cover a square area of at least 1.43° x 1.43°. For some observers this seems to extend up to and possibly beyond 3.33°. Regardless of this difference between observers this result still provides evidence of a contrast summation process for motion stimuli at high contrast levels.

**Discussion**

In our previous study using high contrast Battenberg patterns we found that sensitivity did not improve across any of the check sizes, or even for the full stimulus which had double the amount of signal (McDougall et al., 2016). However in our previous Battenberg summation study, the spatial arrangement of pedestal and the target increment regions co-varied and it is possible that the excitatory area summation processes for the increasing target size are counteracted by suppressive contrast gain control mechanisms that are expected to accompany increases in the size of the high contrast pedestal (Meese, 2004; Meese et al., 2005). Here we used a different approach to our previous Battenberg summation study, maintaining the original advantages of the Battenberg paradigm (fixed display size to keep internal noise levels constant across all conditions), but in this experiment the pedestal was a fixed full grating across all conditions and hence the overall level of suppression from the pedestal is approximately equal across conditions. As recognized elsewhere, in studies using static patterns, it is important that this is done so
that the target region is not confounded with different levels of pedestal suppression, for example Meese and Summers (2007) showed that when pedestal structure is kept constant, spatial summation of luminance contrast is robust. By adopting a similar approach to Meese and Summers (2007) we have revealed stronger summation of luminance contrast over area for suprathreshold (high contrast) drifting gratings, compared to our previous study when the target region and pedestal structure co-varied in size. This provides confirmation that the benefit of areal summation above threshold can be offset by increasing amounts of counter-suppression from the pedestal. More specifically, for observers ED and TM we found that summation of high contrast drifting gratings takes place over a square area of at least $1.43^\circ \times 1.43^\circ$. However, KH and KP showed evidence of summation process that can take place over a square area of at least $3.33^\circ \times 3.33^\circ$. For these two observers this estimate is consistent with that found for Battenberg summation of drifting gratings at contrast threshold which remained inconsistent with probability summation up to (and potentially beyond) $3.33^\circ$ (McDougall et al., 2016).

Tadin and Lappin (2005) used psychophysical data to model optimal size for perceiving direction of dense random-pixel motion patterns at a range of contrast levels and found that optimal size decreased with contrast. Specifically, for a 20% contrast stimulus the optimal size was reported to be approximately $0.8^\circ$-$1.5^\circ$ (defined as 2 standard deviations of a spatial Gaussian) suggesting that this is the limit of spatial summation by the excitatory center mechanisms for this contrast level. Furthermore, Tadin et al. (2003) measured direction discrimination performance for Gabor patches of increasing size for a range of contrast levels. Performance deteriorated (thresholds increased systematically) as the width of a 22% contrast Gabor increased from $0.7^\circ$ to $5.0^\circ$, consistent summation being abolished and replaced by suppression at high contrast. Our estimates of the extensiveness
of summation for a motion stimulus of corresponding contrast (20% contrast pedestal) are therefore larger than both of these studies. This is potentially attributable to the use of the Battenberg design which circumvents internal noise changes with increasing stimulus size by holding display size constant, as well as the additional feature of this study being that pedestal size is also held constant across conditions thus controlling for suppressive gain control. However, it is important to point out that Tadin et al. (2003) and Tadin and Lappin (2005) measured duration thresholds for observers to be able to reliably discriminate motion direction whereas here we have measured thresholds for detection of a contrast increment applied to a 20% contrast pedestal, without requiring observers to discriminate direction. It is therefore difficult to make comparisons between these studies since they may be underpinned by mechanisms with different spatial properties. Nonetheless, the Tadin studies suggest that spatial summation of motion weakens or disappears at high contrast. Our results find some support for this given that two observers, TM and ED, show weaker summation compared to that established for Battenberg stimuli at low contrast which was found to occur over a square area at least as large as 3.33° x 3.33° (McDougall et al., 2016). Tadin (2015) has suggested that weakening summation at high contrast is due to increased surround suppression arising from antagonistic center-surround mechanisms in MT/V5. This coincides with neurophysiological research showing suppressive MT/V5 surrounds become more active under high contrast conditions (Churan, Khawaja, Tsui, & Pack, 2008; Hunter & Born, 2011; Pack, Hunter, & Born, 2005; Tsui & Pack, 2011). Furthermore, research has suggested that the strength of surround suppression, and in turn, the degree to which summation becomes diminished at high contrast shows a large amount of variability across individuals, for both static and drifting stimuli (Betts, Sekuler, & Bennett, 2009; Betts et al., 2005; Golomb et al., 2009; Karas &
McKendrick, 2012; Meese et al., 2005; Melnick et al., 2013; Pitchaimuthu et al., 2017; Tadin et al., 2006). However it is possible that such variability could be driven by individual differences in the limit of areal summation that are unrelated to shifts in strength of motion surround suppression. For example, Betts et al. (2005) found that older observers’ performed better than younger observers for motion direction discrimination of large high contrast drifting grating stimuli. To explain this finding Betts, Sekuler, and Bennett (2012) favoured a model that involved an increase in the area of the excitatory receptive field, as opposed to an alternative model which implied that inhibition from the surround receptive field is reduced. As such, it remains uncertain whether the changes in motion summation with contrast across individuals are the result of a suppressive surround influence, or an independent change in limit of areal summation. Given that our experimental approach is likely to control for surround suppression, we are inclined to suggest that individual differences in summation are the result of differences in excitatory summation mechanisms exclusively, and not a byproduct of individual differences in suppression.

It can be argued that the checkerboard arrangement of the high contrast Battenberg stimuli may be tapping into second-order mechanisms comparing luminance contrast in adjacent checks. Our experiment does not allow us to distinguish whether performance is governed by first-order mechanisms detecting local increments in luminance contrast or contributions from second-order contrast modulation detectors that pool information from first-order mechanisms (Henning, Hertz, & Broadbent, 1975). While this issue regarding underlying mechanisms does need further research it does not undermine the result of the study which is that contrast summation for drifting gratings can occur over extensive areas at suprathreshold contrast levels. The role of second-order mechanisms for the detection of
static Battenberg patterns and Swiss cheese patterns at and above threshold has also been addressed previously, see Meese and Baker (2011), Meese and Summers (2007), Meese (2010), Baker and Meese (2011).

We have found that it is possible to test for, and observe, stronger levels of spatial summation for high contrast drifting gratings by controlling the impact of suppressive contrast gain control mechanisms. However this does not mean we should dismiss the previous results that do not find evidence of summation when pedestal size increases with target size (McDougall et al., 2016). The fact that the two different methodologies yield different outcomes suggests that different stimulus conditions drive the underlying mechanisms in different ways. Both are important findings as the natural environment would contain examples of both of these conditions for us to process.

Future studies aiming to investigating contrast summation for drifting grating stimuli at high contrast could benefit from the approach we have used here to elucidate how the mechanisms operate without the confounding effects of differential suppression from contrast gain control mechanisms across conditions.

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References


Chapter 5: Mismatched summation mechanisms in older adults for the perception of small moving stimuli.

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Abstract

Previous studies have found evidence for reduced cortical inhibition in ageing visual cortex. Reduced inhibition could plausibly increase the spatial area of excitation in receptive fields of older observers, as weaker inhibitory processes would allow the excitatory receptive field to dominate and be psychophysically measureable over larger areas. Here, we investigated ageing effects on spatial summation of motion direction using the Battenberg summation method, which aims to control the influence of locally generated internal noise changes by holding overall display size constant. This method produces more accurate estimates of summation area than conventional methods that simply increase overall stimulus dimensions. Battenberg stimuli have a checkerboard arrangement, where check size (luminance-modulated drifting gratings alternating with mean luminance areas), but not display size, is varied and compared with performance for a full field stimulus to provide a measure of summation. Motion direction discrimination thresholds, where contrast was the dependent variable, were measured in 14 younger (24-34 years) and 14 older (62-76 years) adults. Older observers were less sensitive for all check sizes, but the relative sensitivity across sizes, also differed between groups. In the older adults, the full field stimulus offered smaller performance improvements compared to that for younger adults, specifically for the small checked Battenberg stimuli. This suggests ageing impacts on short-range summation mechanisms, potentially underpinned by larger summation areas for the perception of small moving stimuli.
5.1. Introduction

Age-related declines in human visual motion processing cannot be entirely due to increased intraocular light scatter or increased optical aberrations that accompany ageing, as degrading visual acuity in younger observers does not impair direction discrimination (Ball & Sekuler, 1986; Owsley, 2011). Rather, motion processing deficits may be the consequence of dysfunctional inhibitory mechanisms in the ageing brain (Leventhal, Wang, Pu, Zhou, & Ma, 2003; Schmolesky, Wang, Pu, & Leventhal, 2000). Liang et al. (2010), using single cell recording techniques, found reduced direction selectivity, increased spontaneous activity and decreased signal-to-noise in visual cortical areas MT and V1 of older macaques, which were suggested to arise, at least in part, from reduced age-related efficacy of inhibition.

One potential effect of reduced inhibition with ageing is disrupted balance of the excitatory-inhibitory receptive field properties of centre-surround visual cortical neurons. These neurons increase their response, due to summation of neural responses, as increasingly larger stimuli moving in the cell’s preferred direction are presented inside the classical receptive field (CRF, Allman, Miezin, & McGuinness, 1985). Once the spatial extent of the stimulus spreads beyond the CRF boundary, concurrently stimulating the extra-classical surround region, the neuron’s response is suppressed. The suppressive strength of the inhibitory receptive field of V1 cells has been reported to be reduced in older primates (Fu et al., 2010), a finding often attributed to a global decrease in GABA-mediated inhibition in the ageing brain (Hua, Kao, Sun, Li, & Zhou, 2008; Hua et al., 2006; Leventhal et al., 2003). In humans, post-mortem V1 samples from older adults (2 samples over 55 years old) contained reduced amounts of pre- and post-synaptic GABAergic markers compared to younger adults (2 samples between 18 and 45 years old).
Conversely, there is also emerging evidence for increased GABA levels in visual cortex of aged macaques (Liao, Han, Ma, & Su, 2016) and a recent study of human subjects found that pharmacologically increasing GABA-mediated neural inhibition lead to weaker spatial suppression and increased summation (Schallmo et al., 2017). Therefore, despite neurophysiological evidence for changes in GABA circuitry with ageing, these changes are complex and only partially understood, and whether these changes are related to increases/decreases in suppression/summation remains speculative at present.

A visual perceptual task used to examine visual cortical centre-surround summation and suppression of motion in humans was introduced by Tadin, Lappin, Gilroy, and Blake (2003). For low contrast drifting stimuli (Gabor patches) of increasing size, observers need shorter presentation times to correctly discriminate motion direction, due to spatial summation (Anderson & Burr, 1987, 1991). However, for high contrast stimuli of increasing size, longer presentation times are required for correct motion direction discrimination, an outcome that is considered to be a perceptual consequence of surround inhibition of motion-selective neurons in visual cortical areas MT/V5 (Tadin et al., 2003). To investigate the excitatory-inhibitory balance in visual cortex with age, Betts, Taylor, Sekuler, and Bennett (2005) measured performance on the motion direction discrimination task of Tadin et al. (2003) in older and younger observers. Older observers had shorter duration thresholds than younger observers for large, high contrast drifting Gabor stimuli. Later, Betts, Sekuler, and Bennett (2012) were able to best account for the effects of ageing by increases in the model parameter that governed the size of the excitatory receptive field (the gain model), rather than changes in suppression strength, and speculated that changes in GABAergic functioning could allow for the excitatory receptive field to expand. Following this notion that age may be associated with a general increase in
excitatory receptive field size, which may produce an expansion of the area over which excitation can be measured, we aimed to directly investigate summation, as distinct from surround suppression (by using low contrast stimuli), to better characterise the motion summation mechanisms in older human observers.

Given previous reports of increased spontaneous activity in motion sensitive neurones of older macaques (Liang et al., 2010), it is important to control for internal noise differences with age when measuring summation. Thus, in this study, we employed the Battenberg summation method, originally introduced by Meese (2010) as a way of dissociating changes in signal area from changes in internal noise, by keeping overall display size constant. Battenberg stimuli have a checkerboard arrangement covering a fixed retinal area, where check size is manipulated to measure improvement in contrast detection threshold as the check size increases (spatial summation). For gratings that vary in diameter, the number of stimulated detectors is thought to increase as the overall retinal size of a stimulus increases, with each detector contributing its own intrinsic amount of internal noise. Importantly, internal noise levels remain constant using the Battenberg stimulus – i.e. if the number of monitored detectors depends primarily on the overall stimulus size, then threshold changes only reflect signal summation properties, providing a cleaner measure of signal summation behaviour. It is especially useful to control for overall stimulus size in light of recent work by Liu, Haefner, and Pack (2016) in alert behaving primates, which found that neuronal noise correlations were most closely aligned with signal correlations for responses to larger moving stimuli, thus limiting performance benefits with increasing size (spatial summation). A further advantage of the Battenberg paradigm is that it provides insight into the different stages of summation. That is, smaller sized checks are thought to tap short-range mechanisms, whereas larger check sizes
measure of the potency of long-range summation mechanisms (McDougall, Dickinson, & Badcock, 2016; Meese, 2010).

We hypothesised that if older adults have a more expansive excitatory receptive field, then spatial summation will be measurable over a larger area. Moreover, the Battenberg method allowed us to look at the functioning of short-range and long-range summation mechanisms, separably, to determine whether ageing affects the summation properties of one or both of these mechanisms.

5.2. Method

5.2.2. Apparatus

Stimuli were generated using MATLAB 7.6.0 (Mathworks, Natick, Ma, USA) and presented on a Sony Trinitron Multiscan G520 Monitor (screen resolution: 1024 × 768, refresh rate: 100Hz; Tokyo, Japan) from the frame store (256MB) of a Cambridge Research Systems ViSaGe graphics system. Observers viewed the monitor binocularly from a distance of 65.5cm, which was maintained using a chin-rest. Participants were optimally refracted for this viewing distance. Testing took place in a darkened room (ambient luminance < 1cd/m²). The background screen luminance was set at 50cd/m². In this study, contrast is defined as Michelson contrast in percent;

\[ C_{M\%} = \left( \frac{L_{max} - L_{min}}{L_{max} + L_{min}} \right) \times 100 \]  

(1)

where L is luminance. This will also be expressed in dB units (Baker & Meese, 2011; Meese, 2010) where;

\[ C_{dB} = 20\log_{10}(C_{M\%}) \]  

(2)
5.2.3. Participants

Participants were recruited from the University of Melbourne community and from a database of previous research participants. The study was approved by the University of Melbourne Human Research Ethics committee. Participants provided written informed consent before participating, and the study protocol was compliant with the tenets of the Declaration of Helsinki. Two groups participated: 14 younger adults aged 24 to 34 years (mean age: 27 years, standard deviation = 3 years, 7 males) and 14 older adults aged 62 to 76 years (mean age: 69 years, standard deviation = 5 years, 6 males). Best corrected visual acuity was required to be 6/7.5 or better with a refractive error between ±5.00D spherical and ±2D cylinder astigmatism. Slit lamp and ophthalmoscopy examinations were conducted to ensure normal posterior and anterior ocular health. All participants had clear ocular media, defined as Grade 1.5 or less on the Lens Capacities Classification System III scale (Chylack et al., 1993). Participants were excluded for systemic conditions (e.g., migraine, epilepsy and diabetes), or medications (e.g., anti-depressant medications), known to affect visual performance or cortical function.

5.2.4. Stimuli

Battenberg stimuli have a checkerboard arrangement, consisting of signal checks alternating with uniform luminance checks. In this study, the signal checks contained luminance-modulated, drifting sine wave gratings with a spatial frequency of 3c/°. Uniform checks were 0% contrast and had the same mean luminance as the display background. The size of the check regions within the Battenberg stimulus containing signal could be varied to measure dependence on local signal area without adjusting the overall stimulus size; 10° across all conditions. Four different check sizes were used (Figures
5.1A-D): 0.71°, 1.43°, 2.0°, 3.33° to test performance for the Battenberg stimuli, as well as the ‘full’ stimulus (square of 10° side length) with no blank regions (Figure 5.1E).

The luminance variation across space and time ($L[x, t]$) of a drifting sine wave grating is:

$$L[x, t] = L_m[1 + c \cdot \cos(2\pi f_s \cdot x + 2\pi f_t \cdot t + \phi)]$$

(3)

where $L_m$ is the mean luminance of the display, $c$ is amplitude, $f_s$ is the spatial frequency, $f_t$ is the temporal frequency and $\phi$ adjusts the phase of the grating. The checks were smoothed at the edge using a raised sine envelope that occupied a uniform width strip equal to 10% of the distance from the centre to the nearest edge of the square check. The blurring in the corners was therefore $\sqrt{2}$ wider.
Figure 5.1. Examples of the stimuli used. The four Battenberg patterns had check edge sizes of 0.71°, 1.43°, 2.0° and 3.33°, (A-D respectively). The full stimulus (E) had a side length of 10°. All checks drifted in the same direction, randomly selected as left or right at the start of each trial.

5.2.5. Procedure

To ensure direction selective processing, the minimum contrast required to discriminate motion direction (left or right) was measured. Stimuli were presented for 300 ms in a single temporal interval marked by an auditory beep, followed by a 1 s pause before the next presentation. Motion direction (left or right) was selected randomly at the start of each trial with equal probability. Observers were required to indicate by pressing a
button box which direction they believed the pattern to be moving. Auditory feedback was provided. Observers fixated on a cross at the centre of the screen which was present before each trial. On each run, a three-down, one-up staircase procedure was used to converge upon the 79.4% correct performance level (Wetherill, 1963; Wetherill & Levitt, 1965). The procedure terminated after six reversals and threshold was calculated as the mean of the contrast levels for the last two reversals. Each condition (four Battenberg conditions and one full condition) was repeated five times and these were averaged to give a single threshold (the minimum contrast required to discriminate motion direction) per condition.

5.3. Results

Figure 5.2 shows raw motion direction discrimination thresholds for the stimuli shown in Figure 5.1. The top panel shows individual results and the bottom panel shows the averaged group data. In Figure 5.3, thresholds have been transformed to indicate summation ratios (contrast threshold for Battenberg/contrast threshold for full stimulus) in dB units, following previous work (Baldwin, Husk, Meese, & Hess, 2014; McDougall et al., 2016; Meese, 2010) This transformation indicates the reduction in the level of summation for each of the Battenberg stimuli, relative to the full stimulus and also adjusts for the overall differences in individual sensitivity to the ‘full’ stimulus.
Figure 5.2. Contrast thresholds for the ‘full’ stimulus and each of the checked Battenberg stimuli for younger (A) and older observers (B) individually. The averaged data for the older and younger groups are plotted in panel C. Error bars represent 95% confidence intervals of the mean.
5.3.2. Raw Threshold Analysis

Motion direction discrimination thresholds for both younger and older observers were highest for the Battenberg stimulus with the smallest sized check (0.71°) and decreased as check size increased, indicating that spatial summation occurred to produce improvements in threshold in both groups. A mixed design, two-way, repeated-measures analysis of variance (ANOVA) was conducted with contrast threshold as the dependent variable, and check size (0.71°, 1.43°, 2.0°, 3.33°, and ‘full’) and group (younger vs older) as independent variables. The analysis revealed a significant main effect of group, $F(1,26) = 21.683, p < .001$, partial $\eta^2 = .455$, indicating that older observers had higher contrast thresholds for discrimination of motion direction (Figure 5.2C). Post-hoc tests, with Sidak corrections to control for familywise error rate, confirmed that the threshold increase in older observers was consistent across all stimulus configurations (all $p$’s < .0014). The analysis also revealed a significant effect of check size, $F(4, 104) = 107.913, p < .001$, partial $\eta^2 = .806$, as expected from spatial summation, in both groups. In addition, there was a significant interaction between age and check size ($F(4, 104) = 9.747, p < .001$, partial $\eta^2 = .267$), indicating that check size had different effects in the two age groups. Separate analyses of the older and younger group data revealed that performance was different between all check sizes for the younger group (main effect of group: $F(4,52) = 107.510, p < .001$, post-hoc tests with Sidak corrections: all $p$’s < .01). There was a similar overall effect of check size for the older group ($F(4,52) = 51.740, p < .001$), however, post-hoc tests with Sidak corrections showed no difference in thresholds for the 2.0° vs 3.33° Battenberg stimuli ($p = .078$), whereas all other comparisons were statistically significant (all $p$’s < .05).
Figure 5.3. Individual summation ratios (Battenberg/Full) for younger (A) and older observers (B). The averaged summation ratio data for the younger and older groups are plotted in Panel C. Error bars represent the 95% confidence intervals around the mean.

5.3.3. Summation Ratio Analysis

The magnitude of summation across check sizes can be examined by calculating summation ratios (Battenberg/Full-sized stimulus), consistent with previous work (McDougall et al., 2016; Meese, 2010). This also normalises the data for the overall differences in thresholds between the two groups (higher thresholds in older observers). A two-way, repeated measures ANOVA conducted on the summation ratio data (Figure 5.3) indicated a main effect of check size, $F(4, 104) = 200.700, p < .001$, partial $\eta^2 = .885$, a
main effect of group, $F(1, 26) = 7.418, p = .011$, partial $\eta^2 = .199$, and a significant interaction $F(4,104) = 6.460, p = .011$, partial $\eta^2 = .186$ (Figure 5.3C). Post-hoc t-tests, with Sidak corrections, were conducted on the main effect of group to further explore this interaction. A significant difference in summation ratio between the older and younger observers was found for the $0.71^\circ$ condition ($p < .0001$, Cohens $d = .246$) and $1.43^\circ$ condition ($p = 0.032$, Cohens $d = .745$), but the groups did not differ for the larger check sizes ($2.0^\circ$ and $3.33^\circ$, $p = 0.216$ and $p = 0.922$, respectively).

### 5.4. Discussion

This study used the Battenberg paradigm to examine the effects of ageing on contrast summation for motion direction discrimination. Older adults had higher motion direction discrimination thresholds overall, consistent with previous research (Owsley, 2011). Both groups showed the same trend of lower thresholds as stimulus size increased. To assess summation we calculated a summation ratio, which conveniently normalises for differences in overall contrast threshold for the largest stimulus. For the younger observers the results follow the typical summation behaviour seen in previous Battenberg stimulus studies (McDougall et al., 2016; Meese, 2010) and the closely related Swiss Cheese stimulus study (Baker & Meese, 2011). Using Meese’s (2010) interpretation, the initial peak in summation for the smallest check size is consistent with short-range summation within linear filters (stage one). The summation ratios drop as check size increases but a relatively high summation ratio of $2 \text{ dB}$ was maintained for the largest check size in both groups (Figure 5.3C) and did not drop to low levels typically associated with probability summation; i.e. when $1.5 \text{ dB}$ is used as the fiducial value equivalent to a fourth-root summation rule (McDougall et al., 2016; Meese, 2010). Therefore, summation is unlikely to be compatible with a process of probabilistic summation of responses across multiple,
independent, detectors and is more likely to be subserved by a stage of long-range signal summation (stage two) within receptive fields that, in this case, extends over an area at least as large as 3.33°. Given that this was evident for both groups, it suggests that normal long-range summation mechanisms are in place for these sizes, irrespective of age.

Inspecting the manner in which the magnitude of summation changes as check size reduces allows us to examine short-range summation mechanisms. The average summation ratio for the younger observers for the smallest check size suggests that the full stimulus (which contains twice the amount of contrast signal) offered more than a doubling in threshold improvement, whereas for the older observers the full stimulus offers slightly less than a doubling in threshold improvement. It is important to point out that the average summation ratio for the younger observers for the smaller check sizes was 7.1 dB which is 1 dB more than the expected linear summation (6 dB) within filter mechanisms, based on previous Battenberg summation studies. However, the majority of observers cluster around 6 dB to 6.5 dB (see Figure 5.3A), which would suggest normal linear within-receptive field summation (a halving in threshold with a doubling in total signal) in most of our young observers. The more systematic change is the reduction in summation ratio for smaller checks in the older adults. This suggests abnormal spatial summation properties of short-range mechanisms with ageing. This may be due to increased summation area of these short-range mechanisms that are responsible for processing the smaller check sizes, and as such there is less of a benefit when extra signal is added (the ‘full’ stimulus), producing a reduction in relative sensitivity between the small check stimuli and the larger full field stimulus.

Given that previous studies show minimal contribution of motion surround suppression at low contrast (Hunter & Born, 2011; Pack, Hunter, & Born, 2005; Tadin,
2015; Tadin et al., 2003), the results here are more likely to be a consequence of a
dissociative change in summation mechanisms in older observers. This would be
consistent with the gain model proposed by Betts et al. (2012) which predicts an increase
in the size of the excitatory CRF’s responsive to motion. This model is less likely to be
explained by changes in GABA mediated inhibition in the ageing brain, however it is
possible that changes in GABA can potentially allow for expansion of the excitatory
receptive field, and therefore this link cannot be ruled out entirely (Betts et al., 2012). This
has some support from a recent study by Schallmo et al. (2017) which examined human
MT complex (hMT+) using magnetic resonance spectroscopy and found that GABA
concentration was correlated with better motion perception in general, but was not
correlated with the strength of spatial suppression specifically.

Differences in motion summation and suppression have been reported in other
clinical populations. For example Foss-Feig, Tadin, Schauder, and Cascio (2013) found
increased spatial summation for low contrast motion stimuli in a group of individuals
diagnosed with autism spectrum disorder (ASD). A recent psychophysical study found
that the differences in spatial summation for motion direction discrimination in ASD were
specific to small stimuli (Schauder, Park, Tadin, & Bennetto, 2017), similar to what is seen
here in this study for older adult observers. Schauder et al. (2017) used computational
modelling to reveal larger excitatory receptive field sizes in ASD as the mechanism
responsible for summation differences for perception of smaller stimuli. Our data, for older
observers, also implicates larger receptive field sizes for the perception of small moving
stimuli. Both ageing and autism have been proposed to have imbalances in excitation and
inhibition (Leventhal et al., 2003; Rubenstein & Merzenich, 2003) and in both groups this
may manifest as larger measurable excitatory receptive fields.
5.4.2. Conclusions

We have used Battenberg stimuli to reveal that ageing is associated with an increase in psychophysical summation area for the perception of small moving stimuli at threshold for direction discrimination. This summation enhancement may result in erroneously pooling together signals from distinct, small moving objects, which may lead to spurious percepts for older adults and thus contribute additional motion noise. In the younger visual system, smaller summation areas may be beneficial to increase spatial resolution and better detect local motion differences to facilitate effective motion segmentation in situations where segmentation is more useful (Braddick, 1993; Tadin, 2015). The control over the influence of noise offered by the Battenberg method changes summation estimates and suggests the procedure should be considered whenever studying groups that are suspected to have imbalanced cortical inhibition and excitation so that resultant differences in summation behaviour can be more clearly ascertained.

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Chapter 6: General Discussion
The overall aim of this thesis was to investigate the ability of the human visual system to integrate motion signals. Previous studies have psychophysically measured motion summation properties by showing how performance improves as the overall stimulus area increases. This behavioural performance is used to characterize receptive field properties of the motion sensitive neurons tuned to the stimulus properties used. As overall stimulus size increases, the neuronal pool generating the perceptual response for that stimulus also increases, with each neuron contributing its own amount of neural noise. The contribution of additional noise with increasing physical size can limit the performance benefit of the extra signal of increasingly larger stimuli. Therefore, summation capacity of the mechanisms may be underestimated in experiments that increase signal area by increasing the overall area of the stimulus. Meese (2010) designed a stimulus that allows summation of signal to be measured without confounding effects of noise changes with increasing overall size. This has been utilized in experiments to study summation of static grating patterns and static texture patterns (Baker & Meese, 2011; Baldwin, Husk, Meese, & Hess, 2014; Meese, 2010) and has been successful in revealing more extensive psychophysical summation areas than described in conventional studies that rely on increasing overall stimulus dimensions. This difference owing, at least in part, to the noise being approximately constant across conditions. This thesis adapted Meese’s Battenberg stimuli to re-investigate motion summation to better characterize the human visual system’s capacity to sum motion signals over area. We were particularly interested in summation of luminance contrast, as previous studies have shown summation of contrast for the detection and discrimination of motion direction signals occurs over a relatively small area.
6.1 Summation and segregation of motion at low contrast

Chapter 2 (McDougall, Dickinson, & Badcock, 2016) conducted a basic investigation of summation of luminance contrast over area for drifting stimuli at detection threshold. We used the Battenberg summation method to control for the influence of area-dependent changes in noise as previous studies, which do not control for this, may have come to incorrect conclusions about the capacity of the motion system to integrate contrast over area. The Battenberg stimulus resembles a checkerboard pattern; the overall size was not varied but the size of the checks making up the pattern was varied to measure summation. Specifically, the performance for each Battenberg pattern is compared to that of the full stimulus to derive a summation ratio. The summation ratio data showed evidence of strong summation across all sizes (i.e. the full stimulus which has approximately twice the amount of signal offered a significant improvement in threshold compared to all checked Battenberg stimuli), inconsistent with probability summation. Perception of the Battenberg stimuli with smaller sized checks was consistent with a stage of short-range summation within linear filters, whereas the larger size checks revealed a stage of long-range summation capable of accumulating signal over a square area of at least 3.33° x 3.33° in size. Therefore motion summation can occur over larger areas than previously assumed based on conventional studies that vary the overall stimulus size. The modest extent of areal summation in those studies is presumably due to accompanying changes in noise acting to limit the benefit of increasing signal area. We do not have an exact estimate of the limit to summation, as unveiling the absolute limit of summation was not the central focus of this thesis, and the estimate would be likely to vary depending on the spatial frequency used (Anderson & Burr, 1987), therefore, further studies would need to be conducted to determine this.
Following this demonstration of more extensive contrast summation for detection of motion signals, the next aim of the study was to investigate the nature in which summation behaviour changes for stimuli that contained motion signals in opposing directions. The motion system is highly capable of segmenting a moving object against a stationary background, or segmenting oppositely moving objects or regions from each other (Allman, Miezin, & McGuinness, 1985a, 1985b; Braddick, 1993; Levinson & Sekuler, 1975). Braddick (1993) suggests that one way the visual motion system may achieve this is by employing a system of neurons with smaller summation areas that can segment patterns more effectively. Centre-surround neurons in MT have been implicated as the candidate neurons for this task. These neurons have strong surround inhibition and may not integrate over such large areas but can generate strong signals at motion discontinuities to assist with the detection of separately moving objects (Allman et al., 1985a; Braddick, 1993). To explore this, we evaluated the impact on the contrast thresholds for the detection of the presence of a Battenberg stimulus containing opposing motion signals to determine if the summation behaviour is different when segregation of motion direction is invoked by a stimulus containing obvious motion discontinuities. The results were the same as obtained for the single motion condition in that the opposing motion stimulus still showed evidence for an extensive long-range summation process (i.e. summation ratio did not drop below 1.5 dB) extending over a square area of at least 3.33° x 3.33° in size. This was inconsistent with the notion that there is a different process employed with different summation properties when the visual system is presented with a motion stimulus that would drive segmentation (Braddick, 1993), at least for the range of sizes tested in this experiment. This long-range summation presumably occurs within independent mechanisms that are selectively tuned for one of the two motion directions.
due to the direction selectivity which arises at early cortical stages (Levinson & Sekuler, 1975). This is reflected in the summation ratios for the opposite direction Battenberg which are generally lower than when there is only a single motion direction present. An outcome which is analogous to the results Meese (2010) obtained when adding orthogonally oriented spatial signal; suggested to reflect long-range summation occurring within orientation selective mechanisms. While our stimuli were composed of motion direction signals, one may question the contribution of the motion direction information in driving the threshold performance given that observers were not required to make an explicit direction judgement. Segmentation would not arise if there is no direction processing which may explain the lack of difference in summation range for the opposing motion stimulus if it were unable to drive segmentation. However, in Chapter 3 we provide further evidence that direction selective summation mechanisms are active at threshold for detection of motion.

In Chapter 3 we measured contrast thresholds for motion direction discrimination for the single motion Battenberg patterns – a task that is more certain to ensure the active participation of motion sensitive neurons in the visual system. The raw thresholds for the detection and discrimination data were similar, consistent with previous research that motion direction can be discriminated at contrast threshold for detection (Levinson & Sekuler, 1975). Summation behaviour resembled that of the motion detection data in Chapter 2, confirming that detection and discrimination are mediated by mechanisms that have the same summation properties, consistent with previous research (Anderson & Burr, 1991), but we added that these mechanisms are both capable of more extensive summation than previously described. This also supports the plausibility of the underlying summation
mechanisms proposed in McDougall et al. (2016), specifically that long-range summation occurs within directionally selective mechanisms.

### 6.2 Summation and segregation of motion at high contrast

Previous research has suggested that surround suppression is less pronounced at low luminance contrast. Surround suppression is thought to assist in the segregation of motion signals (Allman et al., 1985a). If these mechanisms were not able to be invoked by our low contrast stimuli, then this could potentially explain why a Battenberg containing opposing motion signals does not produce a difference in the summation behaviour. Therefore we wanted to compare summation for the single and opposing motion Battenberg when they were presented at a high contrast level, thus the task becomes a luminance contrast discrimination task, where the observer is required to nominate which one of two sequentially presented Battenberg stimuli (or full stimuli) was higher in contrast. However the results showed there was no dependence on signal area in the observers’ ability to detect increments in contrast for both the single motion Battenberg and opposing motion Battenberg. Most strikingly, for the full stimulus which contains twice the amount of contrast signal, observers performed no better at discriminating the higher contrast pattern from the reference pattern (identical pattern fixed at 20% contrast), and actually exhibited slightly poorer performance, consistent with inhibition. No change in performance across check sizes for both the single motion and opposing motion suggests that at high contrast summation is restrained, even for a stimulus that does not obviously require segmentation (i.e. the single motion Battenberg). It could be argued that at high contrast, the salient differences between alternating signal checks and blank (mean luminance) checks in the single motion Battenberg, and the alternating regions of leftward and rightward motion in the opposing motion Battenberg are equally segmentable. Some
evidence for this suggestion comes from previous studies which found that when spatially separate patches of drifting gratings were presented at high contrast, each patch was more likely to be parsed as a separate moving object (Alais, van der Smagt, Van den Berg, & Van de Grind, 1998; Takeuchi, 1998). Therefore restricted summation may be argued as being just as necessary and likely for our single motion stimulus. Nonetheless, poor performance for the full stimulus, which would not contain the same potential segmentation cues, still supports the claim that, at high contrast, summation is reduced and segmentation is enhanced.

This has been shown in other behavioural studies using different psychophysical measurements, such as in studies that measure duration thresholds for motion direction discrimination (Tadin, Lappin, Gilroy, & Blake, 2003). Marr (1982) proposed that when a signal is strong the visual system is more likely to favour segmentation, but for weak signals the visual system is more likely to integrate over space to improve signal-to-noise ratio and enhance sensitivity for the detection of signal. In line with this proposal, contrast dependency of motion integration has been conceptualized in terms of an adaptive strategy put in place by the visual system to balance the demands of summation and segmentation in response to fluctuating stimulus conditions. Specifically, at high contrast levels, decreased areal summation of motion acts to reduce redundancy and enhance detection of motion discontinuities whereas at low contrast the detection of the presence of a motion stimulus is more important and therefore summation is increased to assist with this.

Furthermore, Hunter and Born (2011) recorded from MT cells in macaques that fired in response to the presentation of dot-motion stimuli (all dots moved coherently in the preferred direction and speed of the neuron) and found that neuronal suppression decreased, or was completely lost, as stimulus contrast decreased. Consistent with the
notion of increased spatial integration to enhance sensitivity to weak stimuli (low contrast). Therefore, an increased extent of spatial integration at low contrast is observed for psychophysical duration thresholds, coherence thresholds, as well as in neuronal responses to low contrast dot-motion stimuli. We have added to the generality of this finding by showing in McDougall et al. (2016) that contrast thresholds for detection (and discrimination; Chapter 3) of motion direction show summation over area at low contrast, but this is not the case at higher contrasts where increasing the area of a grating does not help detect small increments in contrast.

As discussed in Tadin (2015), the adaptive adjustment of the balance between summation and segregation may not always be beneficial. For example, obligatory reductions in summation and increases in suppression at high contrast may lead to excessive segmentation, and a lack of integration over area when it would be helpful. This may have been the case for our high contrast full stimulus, which arguably does not require segmentation. However, reduced sensitivity to a large background-like motion (redundancy reduction) could be interpreted as the visual system’s way of freeing up resources to focus on inputs that correspond to object motion (Tadin, 2015), regardless of whether such inputs are actually present or not.

So far we have conceptualized the processing of these stimuli as being underpinned by a single flexible integration/summation mechanism which adapts to the stimulus conditions, and this can result in decreased sensitivity to large background motions at high contrast. However it is possible there may be multiple representations of motion in different regions of the brain. For example, it is possible that the representation of large background-like motion is retained by separate mechanisms in the brain. Indeed, there is evidence that there are “wide-field” neurons in MT that do not have suppression and a
therefore well suited for processing this type of stimuli (Born, 2000; Born, Groh, Zhao, & Lukasewycz, 2000; Born & Tootell, 1992; Liu, Haefner, & Pack, 2016). If these mechanisms exist then why did the visual system not utilize this information for the perception of large stimuli? Derrington and Goddard (1989) have suggested that such mechanisms may be less sensitive at high contrasts because their response saturates, reducing their ability to provide a differential response to stimuli in that high contrast range. Another potential explanation for this comes from a more recent study by Liu et al. (2016) which recorded from small populations of neurons in area MT, in macaque monkeys trained to report the direction of a high contrast moving stimulus. Behaviourally, the monkeys’ performance deteriorated as stimulus size was increased, even though, on average, the neural population response to large stimuli was strong. The magnitude of neuronal suppression of individual surround-suppressed neurons accounted for only a small fraction of this performance decline. They quantified the relationship between the noise correlations and the signal correlations in pairs of suppressed and non-suppressed neurons, the latter are likely to be the most informative neurons for coding large motion stimuli (analogous to wide-field neurons discussed above). Compared to suppressed neurons, the slope of the line relating the noise correlations and signal correlations was significantly steeper for non-suppressed neurons (Figure 6.1) They suggest that, individually, the non-suppressed neurons are more informative than suppressed neurons for large moving stimuli as they can sum signal over larger areas, however, due to the correlation structure across the non-suppressed neurons, the stimulus information carried by the population as a whole is limited. Based on this research it appears that there are indeed, distinct, non-suppressed mechanisms capable of representing large field motion,
but these mechanisms may suffer from information-limiting noise correlations which may
contribute, at least in part, to poor performance for large high contrast stimuli.

*Figure 6.1.* Taken from Figure 4 in Liu et al. (2016). Scatter plot showing the relationship
between noise correlation and signal correlation for three types of neuron pairs: both non-
suppressed (NS-NS), both suppressed (SS-SS), and mixed (SS-NS).

It is important to reiterate the differences in stimuli and psychophysical
measurements between our study and the conventional spatial suppression task (Tadin et
al., 2003). In our study we used the Battenberg approach that keeps overall size constant
across conditions. We did not measure direction discrimination for these high contrast
stimuli, rather we presented observers with two intervals of identical stimuli except one is
slightly higher contrast (contains the target increment) which the observer was required to
discriminate. Despite these differences in methodology we still found evidence of poorer
than expected performance for large, high contrast stimuli, consistent with the previous
research.
With this method we also have the capacity to keep the high contrast pedestal the same size and configuration across all conditions, and independently vary the spatial structure of the additional contrast increment to be detected to measure summation. An advantage of this is that it will keep any performance limiting factors of the high contrast stimulus approximately constant across conditions and this may allow us to reveal a summation process in the presence of high contrast stimuli. This was our aim in Chapter 4.

6.3 Summation of motion at high contrast using fixed pedestals

In the high contrast experiment in Chapter 2 (McDougall et al., 2016), the spatial arrangement of the contrast pedestal matched that of the target Battenberg increment that needed to be detected by the observer. Previous research using suprathreshold static patterns has suggested that when the spatial arrangement of the target and pedestal co-vary, improvements generated from increasingly larger target increment regions may be obfuscated by a concomitant increase in suppression from the high contrast pedestal which is matched in size (Meese & Summers, 2007). This suppression is suggested to be caused, at least in part, by increased contrast gain control as part of a (divisive) normalization mechanism for high contrast stimuli (Heeger, 1992; Meese & Baker, 2011; Meese & Summers, 2007). Given the ubiquity of such gain control mechanisms throughout the visual system it has been suggested that this normalization may explain suppressive effects seen in other brain areas such as MT/V5 (Carandini & Heeger, 2012). Indeed, a recent study has suggested that this normalization framework is sufficient to explain contrast-dependent psychophysical (and neural) suppression and summation of motion signals (Schallmo et al., 2017). This lead us to examine, in Chapter 4 (McDougall, Dickinson, & Badcock, 2018a), whether contrast summation for motion signals can be demonstrated when the spatial arrangement of the Battenberg target increment is varied, and applied to a
full fixed-sized grating pedestal such that suppressive effects (gain control) from the high contrast pedestal are now kept constant across conditions. Using this approach we found evidence for contrast summation of motion signals at suprathreshold contrast levels; occurring over a square area of at least $3.33^\circ \times 3.33^\circ$ in some observers, which was the largest check size we tested. Some observers showed slightly less summation than this (up to a square area of $2.00^\circ \times 2.00^\circ$), but was still much greater than that when the target increment and the pedestal structure co-varied in McDougall et al. (2016). Therefore summation for a target can be shown under high contrast conditions, if the target area is manipulated separately from the high contrast background pedestal. The suppressive inputs posited for restricting summation in previous studies for large high contrast stimuli (such as counter-suppression from gain control, and/or unfavourable noise correlations) may still be present in our design, but these do not have the same negative effects on detection of small increments in this study because we change the area of these contrast increments without changing overall stimulus dimensions or the pedestal structure across conditions.

We have shown summation with increasing area can occur at high contrast levels when the pedestal is fixed across conditions, but does not occur when the target and the pedestal co-vary in area. The raises the question of what the visual system does under normal viewing conditions. However it is plausible that the visual system would encounter examples of both types of visual signals in the real world, therefore it is important to know how different stimulus arrangements drive these processes in different ways because it can help us gain a better understanding of how the system copes with a range of different tasks in natural viewing. Further research looking at how different arrangements of high contrast signals do or do not show summation would be useful to help complete this picture. A first step would be to employ a range of pedestals with different contrasts to map out the full
dipper function and ensure that summation is not lost at much higher contrast pedestals (> 20%). Furthermore, although we showed summation in our study, there was still evidence of some suppression (or weaker summation) in some observers for the full field stimulus (see individual results for ED and TM in Figure 4.5). Given that we have now also controlled for suppression arising from contrast gain changes, this difference may be attributable to individual differences in the strength of contrast integration, potentially due to individual differences in surround suppression. These individual differences are consistent with the original study on static gratings using similar stimuli (Swiss Cheese) by Meese and Summers (2007) in which three out of the six observers showed weaker summation for high contrast pedestals than the other three observers. Furthermore, individual differences in summation for suprathreshold contrast discrimination (for stationary gratings that varied in overall area) was the focus of a paper by Meese, Hess, and Williams (2005), with some observers showing some form of improvement with stimulus area while others showed no improvement. These studies both suggest this may be linked to individual differences in the balance between excitatory and inhibitory mechanisms. There is a growing body of research suggesting that there are differences in this balance in certain clinical populations (Betts, Taylor, Sekuler, & Bennett, 2005; Foss-Feig, Tadin, Schauder, & Cascio, 2013; Golomb et al., 2009; Karas & McKendrick, 2012; Pitchaimuthu et al., 2017; Tadin et al., 2006), and more recently there is evidence that the relative strength of excitation and inhibition (as measured behaviourally) varies substantially across normal healthy individuals (Cook, Hammett, & Larsson, 2016; Melnick, Harrison, Park, Bennetto, & Tadin, 2013) or varies substantially within distinct groups, e.g. groups of older and younger subjects (Pitchaimuthu et al., 2017). These individual differences could help explain the variability in our data.
Most of these experiments looking at individual differences have focused on finding differences between groups/individuals for spatial suppression of high contrast stimuli. For example Betts et al. (2005) found decreased suppression (decreased duration threshold for direction discrimination) for high contrast moving stimuli in older observers. If this is underpinned, at least in part, by excitatory/inhibitory imbalance then we may also expect to see an increase in summation area at low contrast, but this has not yet been closely examined. This was our aim in Chapter 4.

6.4 The effect of normal healthy ageing on summation of motion over area

In Chapter 5 (McDougall, Nguyen, McKendrick, & Badcock, 2018b) we wanted to investigate whether spatial summation of motion changes with age. Previous research has found weakened cortical inhibition in the ageing visual cortex (Fu et al., 2010; Leventhal, Wang, Pu, Zhou, & Ma, 2003) and this is thought to produce reduced perceptual suppression for high contrast motion stimuli (Betts et al., 2005). Reduced inhibition predicts that there may be a general expansion of the measurable size of excitatory receptive field, even at low contrast, as animal research suggests inhibitory and excitatory influences operate in a push-pull manner across all stimulus contrast levels (Kapadia, Westheimer, & Gilbert, 1999; Sceniak, Ringach, Hawken, & Shapley, 1999). If so, perceptual summation for low contrast motion stimuli may occur over larger areas in older observers. We examine this with the assistance of the Battenberg summation paradigm; the control of the amount of noise is of extra benefit here because older visual systems are known to have increases in neuronal noise (Liang et al., 2010). Compared to younger observers, older observers showed poorer contrast thresholds for direction discrimination overall, consistent with previous research (Owsley, 2011), but also showed smaller improvements in threshold for the full field stimulus compared to the smaller checked
Battenberg stimuli. We suggested this may be underpinned by larger summation areas for
the perception of small moving stimuli. In the Chapter, which is now a published paper
(McDougall et al., 2018b), we propose that the difference for the smaller sized check may
be due to the short-range mechanisms having larger summation areas in the older
observers. However, a reviewer has pointed out that in the original Battenberg, when the
short-range mechanisms are made larger in a computation model it does not cause a
decrease or increase in the summation ratio (dB) of the short-range mechanisms –
potentially ruling out our tentative explanation of an increase in the summation area of
short-range mechanisms in older adults. However there are some alternative explanations
which are still consistent with our overall conclusion that older adults have increased
summation for smaller stimuli, which do not rely on an increase in the summation area of
the short-range mechanisms. The older visual system is inherently noisy, and the output of
individual filters (short-range mechanisms) are less reliable. This may be compensated for
by extra pooling across detectors (long-range summation) and this is what results in a
decline in the summation ratio. Indeed, the summation ratio for the smallest size check is
within the range described to be consistent with long-range summation. In the less noisy,
younger visual system, these filters operate more effectively and therefore extra pooling
across detectors offers no further benefit. Given that we have not carried out any
computation modelling we cannot be certain whether the differences we have revealed are
due to a change in the size of the area of short-range summation mechanisms or increased
reliance on long-range summation for smaller check sizes due to poorer efficiency of short-
range mechanisms, either way we believe the overall conclusions are still valid – larger
summation areas for smaller sized stimuli in older observers. Future research using
computational models will be able to clarify the precise cause of this.
More extensive summation is consistent with the framework of reduced cortical inhibition in older visual cortex resulting in a larger excitatory summation area. Research on non-human primates (Leventhal et al., 2003), and cats (Hua, Kao, Sun, Li, & Zhou, 2008), has proposed that reduced cortical inhibition (and related changes to visual perception) is caused by a reduction in GABA concentration in ageing visual cortex. Contrary to this, a recent study using magnetic resonance spectroscopy found increased visual cortical (V1) GABA levels in older human subjects compared to younger controls (Pitchaimuthu et al., 2017). When both older and younger subjects were combined and analysed as a single sample, GABA levels correlated significantly (Pearson r = −0.38), but negatively, with perceptual estimates of surround suppression with moving stimuli, i.e. increased GABA was associated with reduced perceptual suppression. These findings are at odds with current predictions about the underlying neurochemical changes contributing to reduced perceptual inhibition in older observers. The authors provide a plausible alternative hypothesis that increased GABAergic inhibition may decrease unfavourable noise correlations (Liu et al., 2016, described in section 6.3) leading to reduced spatial suppression of motion and better perception of large high contrast targets. In relation to our results it is not clear how increased GABAergic inhibition and its potential connection with noise correlations may contribute to increased summation at low contrast levels for small targets, but our results don’t need to be explained in terms of reduced/increased inhibition, and may reflect changes in summation that are not necessarily driven by changes in inhibition. This would be consistent with one of the proposed models of Betts, Sekuler, and Bennett (2012), the gain model, which supports an expansion of the excitatory receptive field, unconnected to changes in suppression strength. Further experimentation could examine whether there is a relationship between decreased suppression for large high
contrast and increased summation for small low contrast stimuli by correlating individual performance for the two different conditions in a group of older adults. This would help determine if the two different findings are underpinned by the functioning of a common mechanism.

6.5 Future directions

The experiments here have shown that the area over which motion summation occurs is larger than previously estimated, however some questions still remain. The first being whether there is a limit on the extent over which summation of motion signals can occur at contrast detection threshold, and whether this shows some variability across observers or across different clinical groups. This could be easily evaluated by scaling up the size of the Battenberg and the full stimulus to measure summation for a range of larger check sizes to probe for a limit to area summation. This could be easily achieved by performing the experiment at a closer viewing distance, and adjusting the spatial frequency to match the original distance.

Previous studies have revealed individual variability in spatial summation of contrast for static patterns at suprathreshold contrast levels (Meese et al., 2005; Meese & Summers, 2007). We also found individual variability for spatial summation of contrast for drifting stimuli at suprathreshold contrast levels (McDougall et al., 2018a). Future studies could employ a larger sample to further our understanding of the magnitude of individual variability for this task and to try and understand what is driving this individual difference. One potential candidate is surround suppression, so performance could be correlated with a task known to tap into surround suppression mechanisms. One potential option is the centre-surround contrast discrimination task used in Battista, Badcock, and McKendrick
in which the observer selects which one of two circular gratings (one of which is surrounded by a high contrast annulus) appears to be higher in contrast.

6.6 Conclusions

The findings presented in this thesis have expanded our understanding of the area over which motion summation occurs and how best to estimate that area at both low and high contrast levels. The Battenberg summation method was successful in revealing more extensive summation of luminance contrast for the detection and discrimination of motion direction signals. This is presumably attributed to, at least in part, the way in which the Battenberg keeps noise levels approximately constant across experimental conditions. Furthermore, we have shown that motion summation is dependent on contrast, consistent with past research. Specifically, at low contrast levels motion summation is favoured to enhance sensitivity to near-threshold stimuli, but at high contrast motion summation is reduced and segmentation is favoured to assist with the detection of motion discontinuities corresponding with moving objects. Some research argues that loss of summation at high contrast may be caused by suppressive gain mechanisms acting to normalize contrast. In Chapter 4 (McDougall et al., 2018a) we showed that when the influence of this type of suppression is controlled for, a more extensive summation process at high contrast levels can be revealed. However, some observers still showed some spatial suppression (Figure 4.5) suggesting that reduced summation at high contrast levels cannot be entirely explained by contrast gain control mechanisms, and that the strength of this remaining suppression shows some individual variability. The fact that the two stimulus designs, both of which could have real environmental equivalents, yield such different results adds further evidence that performance of the visual system is driven in different ways depending on
the stimulus conditions. Finally, we showed that older observers have larger summation regions for small low contrast moving stimuli, and therefore changes in neural excitation and/or inhibition are associated with changes in perceptual summation of low contrast motion stimuli, in addition to high contrast stimuli.

Overall, the experimental results in this thesis have revealed new information about the motion system that is dissimilar to commonly accepted wisdom but is similar to what has been shown for spatial vision using the same methodology (e.g. Baker & Meese, 2011; Baldwin et al., 2014; Meese, 2010). This suggests a common process across the different streams of perception capable of summation over extensive areas of the visual scene. Future studies that are interested in examining area summation in either the normal visual system or the ageing visual system, and want to do so without the influence of area-dependent noise changes and varying amounts of contrast gain control (if using high contrast stimuli), would be advised to use the Battenberg method.
References


