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

Thomas J. McDougall
School of Psychology, The University of Western Australia, Crawley, West Australia, Australia

J. Edwin Dickinson
School of Psychology, The University of Western Australia, Crawley, West Australia, Australia

David R. Badcock
School of Psychology, The University of Western Australia, Crawley, West Australia, Australia

This study reevaluated the 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 that 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 with 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.

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 one to two 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 covaried 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 reevaluate 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 (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. For this study, we have chosen to use gratings with a spatial frequency of 3 c/° 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 3 c/° grating was approximately 0.5°. These summation estimates could have been obfuscated by increases in noise as the stimulus size increased because 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 behavior 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, whereas 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. In addition, dots are considered to be two-dimensional (2D) signals, and this may yield different summation behavior 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 that 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 medial superior temporal (MST) area 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 whereas 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 behavioral 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 center-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 behavior can be studied with a Battenberg stimulus containing opposing motion, a stimulus that will also affect motion segregation mechanisms. Meese (2010) found that for Battenbergs containing opposing motion, a stimulus integration over larger areas.

Experiment 1A: Single-motion experiment

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 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 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

\[ L(x, t) = L_m[1 + c \cdot \cos(2\pi f_s \cdot x + 2\pi f_t \cdot t + \phi)] \quad (3) \]

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 center to the nearest edge of the square check. The blurring in the corners was therefore \( \sqrt{2} \) wider.

**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 interstimulus 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 45 cd/m². 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 his or her 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

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**Figure 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.
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 center of the stimulus. A fixation point was presented at the beginning of each run.

Results

The top row of Figure 2 shows raw contrast detection thresholds for the stimulus layouts depicted in Figure 1. Results are presented for four observers individually on the left (Figure 2A), and the average of all four observers is shown on the right (Figure 2B). In the bottom row of Figure 2, the thresholds have been transformed in the manner consistent with Meese (2010, figure 4) to indicate summation ratios; the difference in threshold between the full stimulus and each of the checked Battenberg stimuli (Full/Battenberg) 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 2C, and the averaged ratios across the four observers are shown in Figure 2D. These ratios closely parallel those reported for static patterns by Meese (2010, 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 3. Average summation ratios are replotted as a function of signal area, on a log axis, and fitted by a power function.

Figure 2 indicate that there is still a significant improvement for the full stimulus compared with the 3.33° check pattern, as the ratio is significantly larger than 0 (one-sample t test: \( t(3) = 6.350, p = 0.008, 95\% \) confidence interval [CI] [1.311 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 \( 3.33^\circ \times 3.33^\circ \) (11.09°²). 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 used 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 replotted using a logarithmic x-axis showing stimulus area, rather than side length (see Figure 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 limits of summation over the entire range of sizes we have employed.

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 \( 3.33^\circ \times 3.33^\circ \). Conventional studies that 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 \( 1.0^\circ \) (width) for detection of a \( 3.0^\circ \) moving grating (Anderson & Burr, 1991). However, results here show that performance did not asymptote at this \( 1.0^\circ \) limit and instead continued to improve over the full range of sizes tested. The summation ratio is reduced for the largest check size \( (3.33^\circ) \) but is still considered more potent than a process of probability summation \( (<1.5 \text{ dB}) \) across multiple independent mechanisms. Because 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 technique 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 with 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, & Hendrickson, 1990; Smith et al., 2001; Virsu, Rovamo, Laurinen, & Näsinen, 1982). 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 3 shows integration at the same rate across the full 10°. These results suggest the involvement of a system separate from 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 that are more contrast sensitive than earlier stages because of 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 used 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.

### Experiment 1B: Opposing-motion experiment

#### Introduction

The previous experiment examined summation for stimuli containing motion in a single direction and provided behavioral 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 that is functionally and anatomically distinct from the system that collects signals over wider areas (Layton, Mingolla, & Browning, 2012; Tanaka et al., 1993). This property could be a general feature of the motion system that 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 moving stimuli 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.

#### Observers

Data were collected from the same psychophysical observers (K. T., M. T., S. C., T. M.) who were used in the previous experiment.
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 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.

Results

The top rows of Figure 5 show raw contrast detection thresholds for the each of the opposing-motion stimuli with a check size of 3.33°. The stimulus is the same as the previous experiment (see Figure 1) except the blank checks have been replaced with checks containing motion in the opposite direction.

Figure 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 (full/Battenberg) 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).
motion Battenberg stimuli and the full stimulus (reused from the single-motion experiment). Results are shown for four observers individually on the left (5A), and the average of all four observers is shown on the right (5B). The data for the single motion experiment (2B) is also replotted on this graph for comparison. In the bottom row of Figure 5 the thresholds have been transformed to indicate summation ratios, the difference between the full stimulus and each of the checked Battenberg stimuli (full/Battenberg) 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 5C, and the averaged ratios across the four observers are shown in Figure 5D. The data for the single motion experiment (2D) is also replotted on this graph for comparison.

Contrast detection thresholds for the opposing-motion Battenberg stimuli show a decrease as check size increases, indicating spatial summation. The summation ratios in Figure 5 indicate that there is still a significant improvement of the full stimulus compared with 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 = 0.025, 95% CI (0.5767 to 4.2122)), indicating that increases in size still produce improvements in performance, implying that summation can extend over areas at least as large as 3.33° × 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 replotted using a logarithmic x-axis showing stimulus area, rather than side length (see Figure 6), the data conform to a straight line with a steep slope of −0.80, indicating that there is no apparent change in summation behavior 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, $F(4, 12) = 22.043, p < 0.001$. 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 with the 0.71° check condition, $F(1, 3) = 59.717, p = 0.005, r^2 = 0.95$; the 1.43° check condition, $F(1, 3) = 19.676, p = 0.021, r^2 = 0.86$; the 2.0° check condition, $F(1, 3) = 21.230, p = 0.019, r^2 = 0.88$; and the 3.33° check condition, $F(1, 3) = 50.597, p = 0.006, r^2 = 0.94$. This suggests that long-range summation is not occurring indiscriminately over area and motion direction; if it were, we would expect there to be no difference in thresholds because in all cases, the full 10° × 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 modeling, 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.
Discussion

This experiment found that for the range of sizes examined in this study, there is no gross difference in the range of behaviorally 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; Kaplan, Westheimer, & Gilbert, 1999; Kasamatsu, Miller, Zhu, Chang, & Ishida, 2010; Levitt & Lund, 1997; Sceniak, Ringe, Hawken, & Shapley, 1999), and this area is also found in MT neurons (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 over area MT/V5 in human participants (Tadin, Silvanto, Pasqual-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.

Experiment 2: High-contrast summation

Introduction

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 with 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 center-surround mechanisms in MT/V5 are theorized 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 & Lappin, 2005a). Allman and colleagues (1985a) were the first to provide evidence that the characteristics of center-surround mechanisms are well suited to figure-ground discrimination. By recording from MT in owl monkeys, they discovered center-surround neurons responded poorly to large, uniform “background
motion” covering both the center 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 that prefers to integrate over smaller areas to subserve segregation and one that prefers to integrate over larger areas. They suggested that both mechanisms contribute to motion processing, but the one that 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 center-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 behavior 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 center-surround receptive fields that are thought to subserve motion segmentation mechanisms (Allman et al., 1985a, 1985b; Born, Groh, Zhao, & Lukasewycz, 2000; Nakayama & Loomis, 1974). Second, it is of interest to determine whether the summation results for the single-motion Battenberg in the detection experiment generalize 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.

**Observers**

Data were collected from the same psychophysical observers (K. T., M. T., S. C., T. M.) who were used in the previous experiments. Observers gave their informed consent before participating in this experiment.

**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 7A). The Battenberg in the target interval contained the 20% contrast pedestal plus a contrast increment (Figure 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.

Results

Figure 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 (Figure 8A), and the opposing-motion experiment, on the right (Figure 8B). The average threshold of all four observers for both conditions is shown in the bottom panel (Figure 8C).

Raw contrast discrimination thresholds show no dependence on check size and 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 contained motion in only 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 $F(4, 12) = 4.159$, $p = 0.013$. 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 with the 0.71 check condition, $F(1, 3) = 184.841$, $p = 0.001$, $r^2 = 0.99$; the 1.43 check condition, $F(1, 3) = 12.634$, $p = 0.038$, $r^2 = 0.81$; the 2.0 check condition, $F(1, 3) = 9.672$, $p = 0.050$, $r^2 = 0.76$; and the 3.33 check condition, $F(1, 3) = 16.557$, $p = 0.027$, $r^2 = 0.85$.

In the previous experiment, the full stimulus had a significantly lower threshold than all the opposing-motion check conditions, because of summation of a single direction occurring over a larger area (potentially up to $10^\circ$, depending on receptive field size of a
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 behaviorally 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 that 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 that 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 because of 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 center-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 with 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 center-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 center-surround mechanisms in area MT, which are functionally distinct from the mechanisms that 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 countersuppression 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 while keeping the size of the pedestal constant across all conditions. If summation can be found, then reevaluation of the underlying cause of diminished summation in this study and other behavioral 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 two identical sinusoidal gratings drifting in opposite directions and measured the contrast imbalance required until motion was perceived consistently in a single direction. They found evidence for weakening of spatial summation at higher contrasts, consistent with previous studies, but demonstrated 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 behavioral spatial suppression. Glasser and Tadin (2010) reexamined contrast-dependent motion suppression by measuring duration thresholds, as they had previously, while 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 to 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 because of 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.

Keywords: motion, summation, segmentation, contrast, center-surround antagonism

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Corresponding authors: Thomas J. McDougall and David R. Badcock.
Email: thomas.mcdougall@research.uwa.edu.au; david.badcock@uwa.edu.au.
Address: School of Psychology, The University of Western Australia, Crawley, WA, Australia.

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