Suprathreshold contrast summation over area using drifting gratings

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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° × 3.33° for some observers. Previous studies in which the spatial structure of the pedestal and target covaried were unable to demonstrate spatial summation, potentially due to increasing amounts of suppression from gain-control mechanisms 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 inoperable 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

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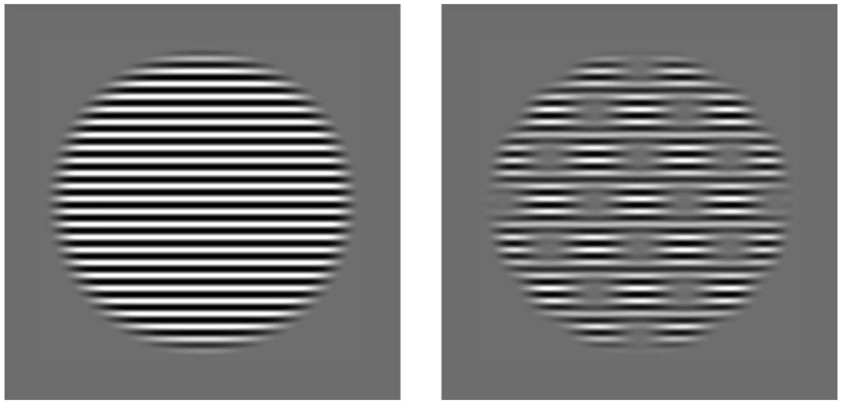

Figure 1. An example of the Swiss Cheese stimulus (right) and full stimulus (left) used in Meese and Summers (2007).

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, for example, 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 covaried) 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 is to determine whether the visual system is indeed capable of suprathreshold summation of contrast over area for drifting grating stimuli.

Method

Apparatus

The stimuli were computer generated using MATLAB 8.2.0.701 (MathWorks, Natick, MA) on a PC and presented on a Sony Trinitron Multiscan G520 Monitor (screen resolution: 1,024 pixels wide × 768 high; refresh rate: 100 Hz) from the frame store (256 MB) of a Cambridge Research Systems ViSaGe graphics system. The observers used a chin-rest to maintain a viewing distance of 65.5 cm. 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 <1 cd/m^2). The screen space-averaged luminance was 45 cd/m^2, 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;

$$C_M\% = \left(\frac{L_{max} - L_{min}}{L_{max} + L_{min}}\right) \times 100 \quad (1)$$

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

$$C_{dB} = 20\log_{10}(C_M\%) \quad (2)$$

Observers

Data were collected from four participants (two male, two female); 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/deg 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.

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 interstimulus interval. The observers used a button box to indicate which interval

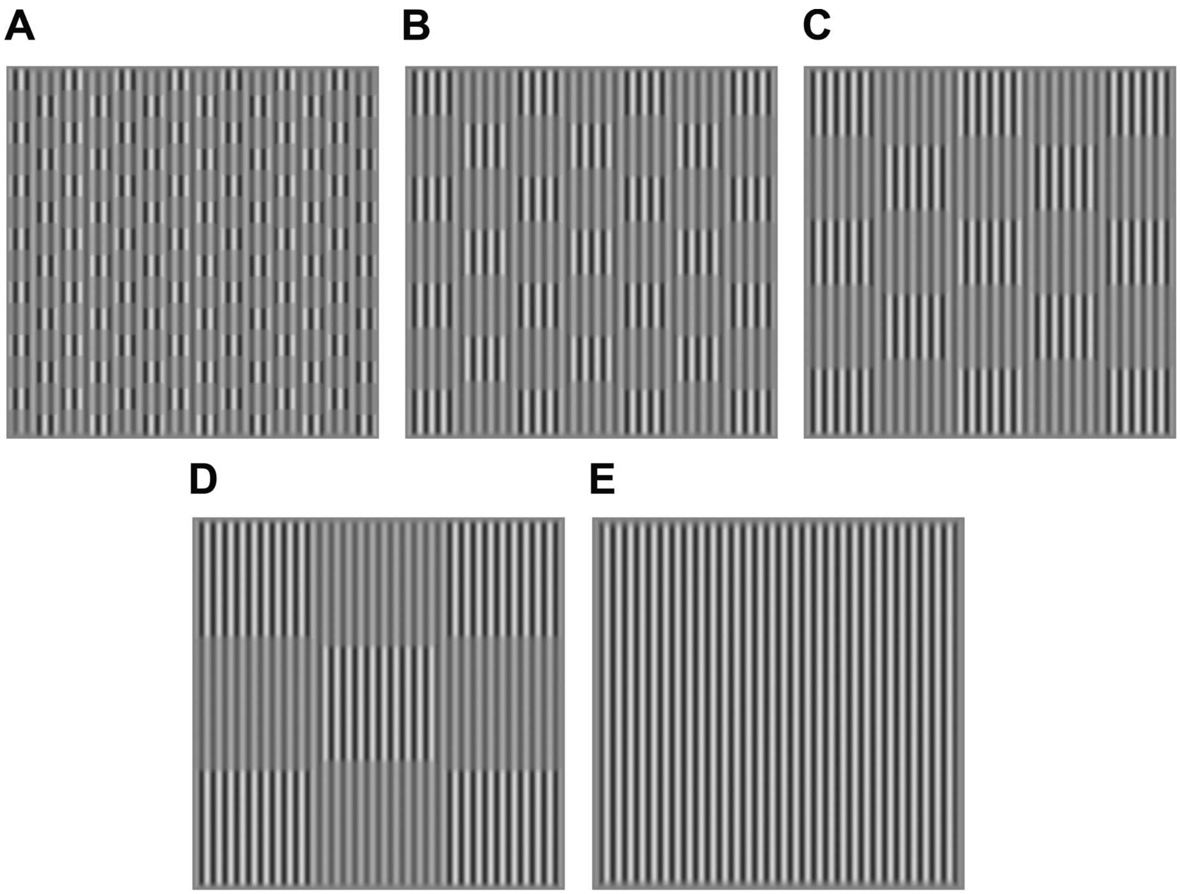

Figure 2. Examples of the stimuli used as the target stimulus in this experiment. Battenberg patterns which had check sizes of 0.71°, 1.43°, 2.00°, or 3.33° (A–D, respectively) were added to a full grating contrast pedestal (10° side length). Panel E shows the target used in the full stimulus condition which was a full grating contrast increment added to a full grating pedestal.

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 (1.5 cd/m^2) square fixation point ($4' \times 4'$ visual angle) was presented in the center of the screen at the beginning of each trial to guide the observer.

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 analyzed using repeated measures one-way ANOVA which showed a significant effect of check size on threshold, $F(4, 12) = 10.129$, $p = 0.001$, $\eta^2 = 0.771$. 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, $F(1, 3) = 108.277$, $p = 0.002$, $\eta^2 = 0.973$, the 1.43° condition, $F(1, 3) = 16.070$, $p = 0.028$, $\eta^2 = 0.843$ and also the 2.00° condition $F(1, 3) = 10.371$, $p = 0.49$, $\eta^2 = 0.776$. The results for the 3.33° condition were not significantly different from the full condition, $F(1, 3) = 0.881$, $p = 0.416$, $\eta^2 = 0.227$. The full stimulus contrast

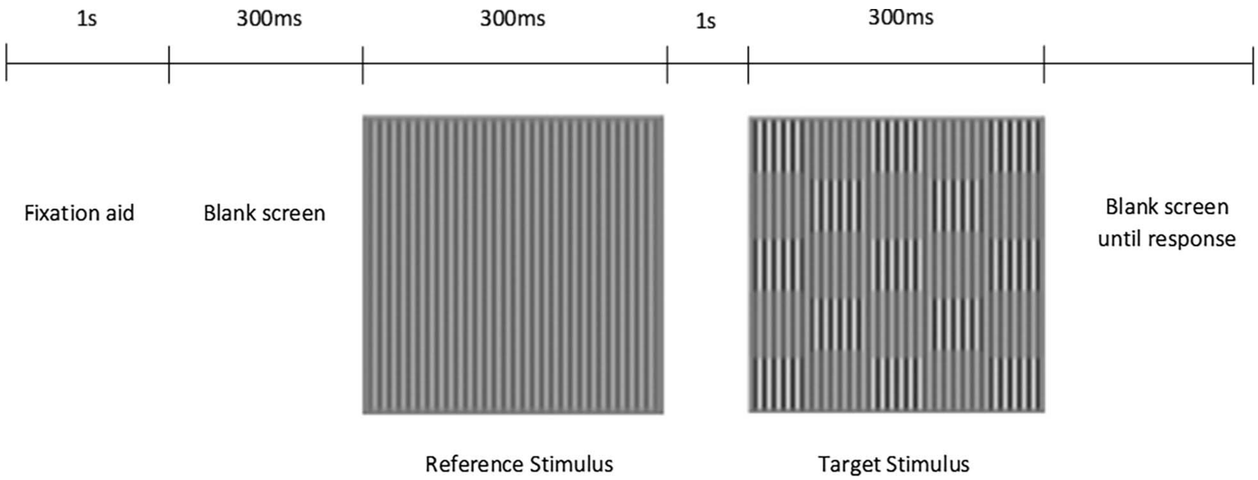

Figure 3. A schematic representation of a single trial. The trial began with a fixation point (1 s) followed by a blank screen set at mean luminance (300 ms). The stimulus intervals containing either the pedestal alone (reference) or the pedestal plus the contrast increment (target) were presented in a randomly selected order for 300 ms each, separated by a 1 s interstimulus 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.

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.

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) and 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.

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°. 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° × 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 the pedestal and the target increment regions covaried, 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

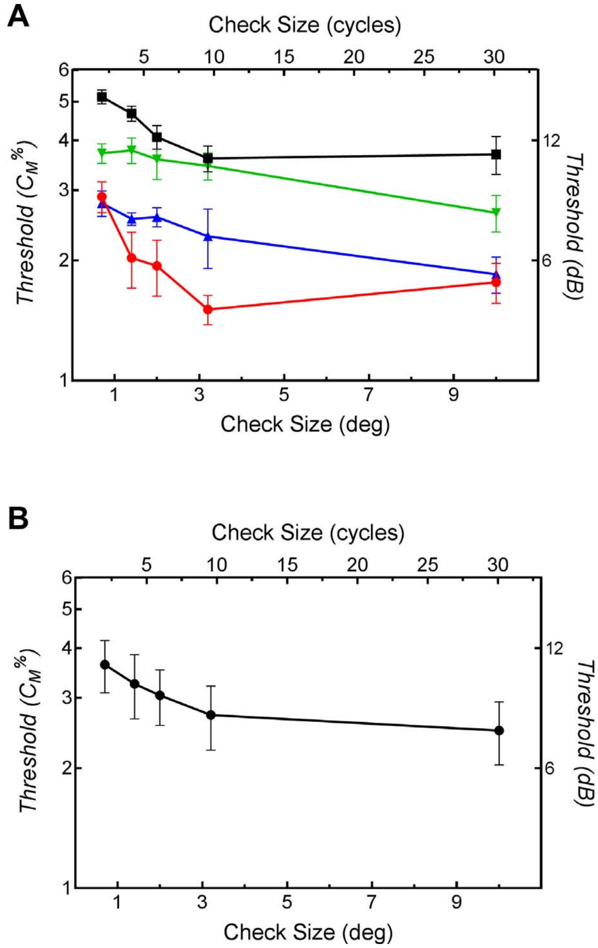

Figure 4. Contrast increment thresholds for each of the checked Battenberg stimuli and the full stimulus condition are shown for each observer (A) and the average of all four observers (B). The size of the check is represented as a function of degrees on the lower *x* axis, and number of cycles on the upper *x* axis. All error bars represent 1 *SEM*.

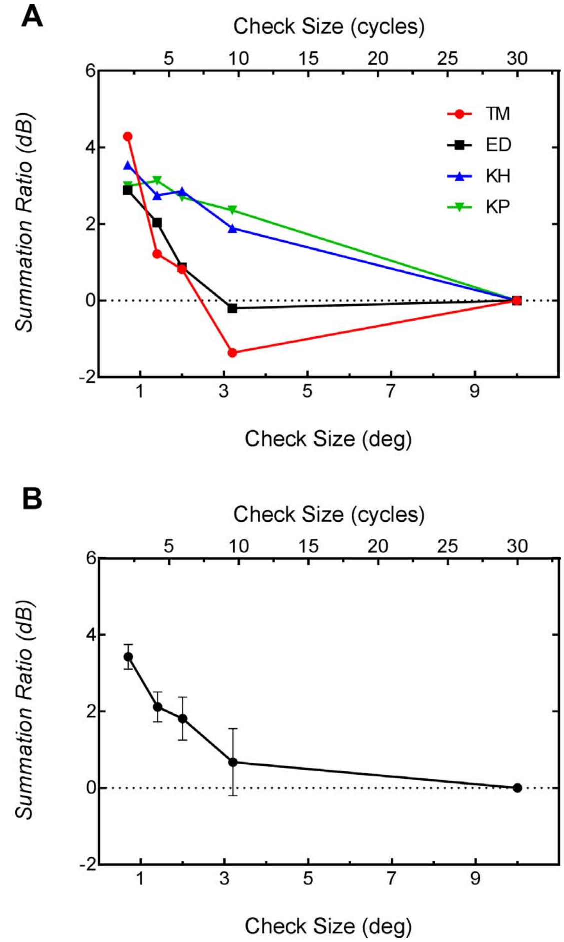

Figure 5. Raw thresholds are converted into summation ratios (Battenberg/Full) which represent the level of summation for each Battenberg stimulus. Ratios for the individual observers are shown in Panel A, and the group average is shown in Panel B. The size of the check is represented as a function of degrees on the lower *x* axis, and number of cycles on the upper *x* axis. Error bars represent 1 *SEM*.

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 covaried in size. This provides confirmation that the benefit of areal summation above threshold can be offset by increasing amounts of countersuppression 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° × 1.43°. However, KH and KP showed evidence of summation process that can take place over a square area of at least 3.33° × 3.33°. 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° (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° to 1.5° (defined as 2 *SD* 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° to 5.0°, consistent with 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° × 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) favored 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 the 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), and 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 investigate 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.

Keywords: contrast, motion, summation, suprathreshold, suppression

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