

Low-level mechanisms do not explain paradoxical motion percepts

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Classic psychophysical studies have shown that increasing the size of low-contrast moving stimuli increases their discriminability, indicating spatial summation mechanisms. More recently, a number of studies have reported that for moderate and high contrasts, size increases yield substantial deteriorations of motion perception—a result described as psychophysical spatial suppression. While this result resembles known characteristics of suppressive center-surround neural mechanisms, a recent study (C. R. Aaen-Stockdale, B. Thompson, P. C. Huang, & R. F. Hess, 2009) argued that observed size-dependent changes in motion perception might be explained by differences in contrast sensitivity for stimuli of different sizes. Here, we tested this hypothesis using duration threshold measurements—an experimental approach used in several spatial suppression studies. The results replicated previous reports by demonstrating spatial suppression at a fixed, high contrast. Importantly, we observed strong spatial suppression even when stimuli were normalized relative to their contrast thresholds. While the exact mechanisms underlying spatial suppression still need to be adequately characterized, this study demonstrates that a low-level explanation proposed by Aaen-Stockdale et al. (2009) cannot account for spatial suppression results.

Keywords: spatial suppression, contrast sensitivity, motion, motion—2D

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Introduction

A number of classic psychophysical studies have shown that increases in stimulus size yield improvements in motion discrimination—a result described as *spatial summation* (Anderson & Burr, 1991; Lappin & Bell, 1976; Watson & Turano, 1995). A common feature of these studies has been the measurement of contrast or coherence thresholds, and thus, reliance on low-visibility motion stimuli. To investigate motion perception across a broad range of visibilities, we previously examined effects of stimulus size using methods that allow independent manipulation of size and contrast (e.g., Tadin, Lappin, Gilroy, & Blake, 2003). The key finding of these studies is that as the size of a high-contrast stimulus increases, discriminability of its motion sharply decreases—an effect described as psychophysical *spatial suppression*. This is in contrast with the spatial summation observed for low-contrast stimuli, manifested as decreasing thresholds with increasing size. We, as well as others, have described this contrast-dependent integration of motion signals using direction discriminations (Betts, Sekuler, & Bennett, 2009; Betts, Taylor, Sekuler, & Bennett, 2005; Golomb et al., 2009; Lappin, Tadin, Nyquist, & Corn, 2009; Seitz,

Pilly, & Pack, 2008; Tadin, Kim et al., 2006; Tadin & Lappin, 2005a; Tadin et al., 2003), motion after-effect (MAE; Falkenberg & Bex, 2007; Tadin et al., 2003; Tadin, Paffen, Blake, & Lappin, 2008), reverse correlation (Neri & Levi, 2009; Tadin, Lappin, & Blake, 2006), binocular rivalry (Paffen, Alais, & Verstraten, 2005; Paffen, Tadin, te Pas, Blake, & Verstraten, 2006; Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004), and reaction times (Tadin, Grdinovac, Hubert-Wallander, & Blake, 2007). Special population studies revealed that spatial suppression is abnormally weakened in schizophrenia (Tadin, Kim et al., 2006), old age (Betts et al., 2009, 2005), and in patients with a history of major depression (Golomb et al., 2009). These deficits are characterized by enhanced motion perception of large, high-contrast moving stimuli and are possibly related to the impairments in the GABA-ergic system in these populations (Kalueff & Nutt, 2007; Leventhal, Wang, Pu, Zhou, & Ma, 2003; Wassef, Baker, & Kochan, 2003). It is important to point out that a majority of these studies utilized brief motion stimuli, usually measuring duration thresholds—the method used in the present paper.

These counterintuitive psychophysical results have been linked to suppressive center-surround receptive fields, such as those found in cortical area MT (Tadin & Lappin,

2005b), although earlier mechanisms cannot be fully excluded (Tadin & Lappin, 2005a; Paffen, van der Smagt, te Pas, & Verstraten, 2005). Center-surround neurons in MT decrease their firing rate as the size of a stimulus is increased beyond the boundaries of the classical receptive field—a response property described as surround suppression (Allman, Miezin, & McGuinness, 1985a; Born, 2000; Born & Tootell, 1992). Recent work has demonstrated that as stimulus contrast decreases, surround suppression weakens or even reverses to spatial summation. This often results in stronger responses to large low-contrast motions than to higher contrast stimuli of the same size (Pack, Hunter, & Born, 2005).

However, in addition to surround-suppressed cells, area MT contains neurons that prefer large, moving fields (“wide-field” neurons; Allman, Miezin, & McGuinness, 1985b; Born & Tootell, 1992). These two types of neurons are clustered anatomically (Born & Tootell, 1992) and make different efferent connections (Berezovskii & Born, 2000). Their functional roles are likely different, with center-surround neurons coding object motion and wide-field neurons signaling background motion (Born, Groh, Zhao, & Lukasewycz, 2000). A recent study found that while surround-suppressed MT neurons exhibit good directional selectivity for brief stimuli, wide-field MT neurons have poor directional selectivity for brief stimuli of any size (Churan, Khawaja, Tsui, & Pack, 2008). Thus, as a population, MT neurons exhibit strong directional selectivity for brief stimuli only when the stimulus size is small enough to evade the inhibitory surround response. As mentioned above, most psychophysical studies of spatial suppression relied on briefly presented motion stimuli, which, as it is now known, might be a good strategy to better isolate surround suppressive mechanisms (Churan et al., 2008).

All aforementioned studies measured spatial suppression by manipulating stimulus size at a constant *absolute* stimulus contrast. Given that contrast thresholds for motion discriminations decrease with increasing stimulus size (Aen-Stockdale, Thompson, Huang, & Hess, 2009; Anderson & Burr, 1991; Watson & Turano, 1995), the *relative* stimulus contrast in these studies increased with increasing size. In other words, a large stimulus has higher relative-to-threshold contrast than a small stimulus presented at a same absolute contrast. Recently, Aen-Stockdale et al. (2009) argued that this increase in relative stimulus contrast might provide a low-level explanation of seemingly paradoxical spatial suppression results. For stimuli of varying size and contrast, the authors measured the amount of contrast imbalance needed to transform a counterphasing grating into a stimulus that was perceived as predominantly moving in one direction. At a fixed high contrast, the authors found that as the stimulus size increased, a larger contrast imbalance was required to disrupt observers’ perception of a directionally balanced counterphasing grating—a size-dependent effect similar to

that observed in spatial suppression studies (e.g., Tadin et al., 2003). This size-dependent effect, however, disappeared when the contrast of different size stimuli was normalized relative to their contrast thresholds. From these results, Aen-Stockdale et al. (2009) concluded that previously observed psychophysical spatial suppression findings (e.g., Tadin et al., 2003) might be entirely explained by size-dependent changes in relative stimulus contrast. While it might not be straightforward to relate these results to spatial suppression studies that relied on unidirectional motion stimuli, the general issue of relative vs. absolute contrast is potentially relevant to all studies that vary stimulus size. Here, we examine this issue in the context of duration threshold measurements—the most common approach used to study spatial suppression.

As psychophysical spatial suppression strongly depends on stimulus contrast, ensuring that all stimuli have the same *relative* contrast will affect the results. However, the important question is whether controlling for relative contrast will actually abolish detrimental effects of size on motion discrimination (Tadin et al., 2003). To answer this question in the context of duration threshold estimates, we cannot employ a staircase design as is typically used in such studies. As Aen-Stockdale et al. (2009) point out, it is practically impossible to control for relative contrast and at the same time measure duration thresholds using a staircase procedure like QUEST because contrast integration over time yields different contrast thresholds at different durations (Burr, 1981). However, the method of constant stimuli can be straightforwardly applied to circumvent this practical problem.

Here, we employ the method of constant stimuli to both (1) replicate the findings of earlier studies that relied on staircase designs (cf., Betts et al., 2009, 2005; Golomb et al., 2009; Lappin et al., 2009; Tadin & Lappin, 2005a; Tadin et al., 2003) and (2) measure the effects of increasing stimulus size when the relative contrast for small and large stimuli is equalized. Further, we seek to differentiate between the contributions of psychophysical spatial suppression and the relative contrast hypothesis proposed by Aen-Stockdale et al. (2009). If spatial suppression can be explained by differences in contrast relative to discrimination threshold, then size-dependent worsening of motion discrimination will be eliminated once contrast of large stimuli is adjusted to equal relative-to-threshold contrast of small moving stimuli. Conversely, if a large difference between discriminability of small and large stimuli exists even after controlling for the relative stimulus contrast, then size-dependent differences in relative stimulus contrast are insufficient to explain spatial suppression findings.

We found that at a fixed high absolute contrast, all observers were considerably better at discriminating motion direction for small than large stimuli. As expected from previous work, decreasing contrast of large stimuli to equalize relative contrast of small and large stimuli

yielded improvements in direction discriminations of large motions. Nonetheless, all observers were still considerably better at direction discrimination of small moving stimuli—a result indicating spatial suppression.

Experimental procedures

Stimuli were created in MATLAB with the Psychophysics Toolbox (Brainard, 1997) and Video Toolbox (Pelli, 1997) and shown on a linearized CRT monitor (24" Sony GDM-FW900 driven by an NVIDIA GeForce 7300 graphics card at 1024×640 resolution and 120 Hz). Viewing was binocular at 77 cm. The ambient illumination was 0.8 cd/m^2 and the background gray-level luminance was 60.5 cd/m^2 . Grayscale resolution was expanded from 256 to 768 levels by a bit-stealing technique (Tyler, 1997).

Stimulus size was defined as the radius of the raised cosine. Contrast was defined as the peak contrast of the spatial envelope. All temporal envelopes were square-wave. All experiments complied with institutionally reviewed procedures for human observers.

Experiment 1

In Experiments 1 and 2, the stimuli were dense random pixel motion patterns made up of light and dark pixels (each 6×6 arcmin) with a velocity of $4^\circ/\text{s}$, presented in a raised cosine spatial envelope. Four naive but experienced psychophysical observers participated in the study.

Two stimulus sizes were used: 0.67° radius and 10° radius. The small stimulus size was chosen based on the results of pilot experiments designed to estimate the optimal stimulus size at 99% contrast (cf., Tadin & Lappin, 2005a).

The aim of this experiment was to replicate earlier measurements of psychophysical surround suppression, using the method of constant stimuli. For each condition, we selected between 4 and 9 stimulus durations guided by pilot experiments using a staircase method (and constrained by the 120-Hz monitor refresh rate). Each observer completed 4 blocks of trials, with a total of 160 trials per stimulus level. On each trial, a moving stimulus was presented foveally and the observer indicated the perceived direction (left or right) by a key press. Feedback was provided. In separate blocks, observers viewed foveally presented motion stimuli of two different sizes (0.67° and 10° radii), both presented at 99% contrast. These data were fitted with a Weibull function to estimate 82% thresholds and analyzed using a bootstrap procedure (Wichmann & Hill, 2001a, 2001b) to estimate associated confidence intervals.

Experiment 2

The aim of this experiment was to measure the effect of stimulus size while controlling for relative contrast. Specifically, for each observer in Experiment 1, we identified three stimulus durations where there was a large difference in proportion correct between results for small and large stimuli. Next, for each selected stimulus duration, we measured contrast thresholds for motion direction discriminations for both 0.67° and 10° stimuli. Thresholds (82%) were estimated by interleaved QUEST staircases (Watson & Pelli, 1983). For each size and duration, observers participated in three blocks, with two interleaved staircases in each block. For each observer, and at each stimulus duration, the resultant contrast thresholds were used to calculate a contrast change for a large stimulus required to equalize its relative contrast with a small, 99% contrast stimulus. As large stimuli yielded lower contrast thresholds, this always resulted in a contrast reduction of large stimuli. Specifically, large stimulus contrast was set by first expressing small stimulus contrast in terms of multiples of its contrast threshold and then multiplying contrast threshold for large stimuli with the resulting number. Finally, motion direction discrimination measurements for large stimuli were then repeated at this reduced contrast (see Experiment 1 for details) and compared to the results for small stimuli. Note that possible effects of practice would benefit the relative contrast condition, thus ensuring that any practice effects would go against our hypothesis (Experiment 3 is designed to control for possible practice effects).

Experiment 3

While the use of texture patterns is advantageous because it allowed us to set the small stimulus size to be near optimal (Tadin & Lappin, 2005a), their broadband nature raises an issue worth addressing. Specifically, for a broadband stimulus at contrast threshold, performance will be determined only by the most sensitive spatial channel(s). As the contrast increases, however, additional channels may contribute to performance, possibly complicating an interpretation of our results. To control for this possible issue and to establish the generality of our results, we measured the effect of stimulus size while controlling for relative contrast using narrowband sinusoidal gratings ($\text{SF} = 1 \text{ c}/^\circ$, $4^\circ/\text{s}$). Stimulus sizes were 1° and 10° . Additionally, it is useful to replicate Experiments 1 and 2 using gratings as such stimuli are often used in spatial suppression studies (e.g., Betts et al., 2009, 2005; Tadin, Kim et al., 2006; Tadin et al., 2003). Three naive subjects, none of whom participated in Experiment 1 or 2, took part in this experiment.

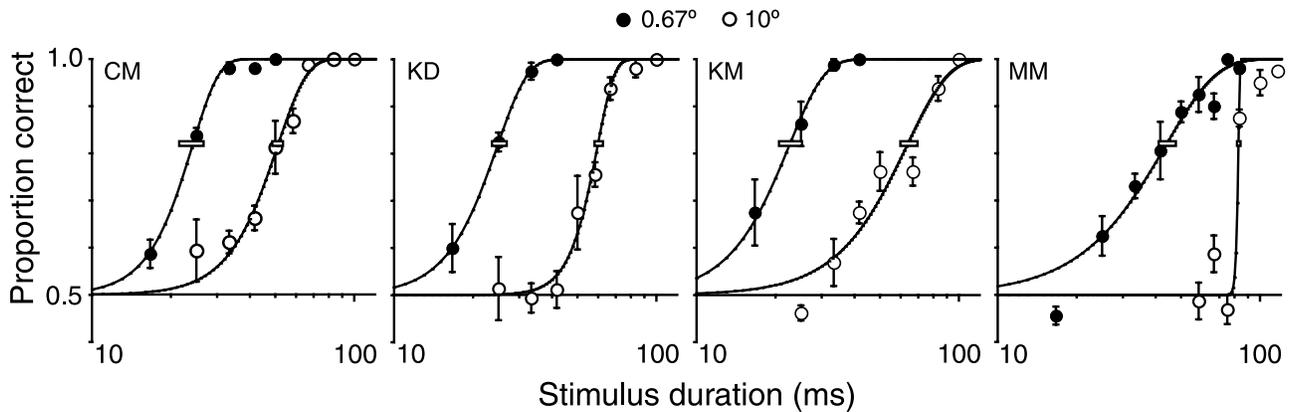


Figure 1. Psychometric functions for motion direction discriminations for small (0.67° , filled circles) and large (10° , open circles) stimuli for individual observers. Error bars are *SEM*. Solid lines show Weibull fits. Open bars show 95% confidence intervals (CI) around 82% threshold estimate.

First, we used the method of limits to quickly estimate stimulus durations where there was a large difference in proportion correct results for small and large stimuli (note that this effectively accomplished the same purpose as the constant stimuli method in Experiment 1). Specifically, the method of limits was used to estimate the minimum duration required for each subject to perfectly discriminate small (1°) high-contrast (99%) sinusoidal gratings ($SF = 1\text{ c}^\circ$, $4^\circ/\text{s}$). For each observer, a small grating stimulus was first presented at a long duration where direction discriminations were trivially easy (approximately 100 ms). Then, each time the observer correctly indicated stimulus motion direction, stimulus duration was reduced by one frame. This was repeated until the observer responded incorrectly. This process was repeated ten times, and the result was the minimum duration for which the observer responded correctly in all ten presentations. For the main experiment, we then selected the result of the method of limits along with two adjacent frame durations (i.e., one frame longer and one frame shorter) as stimulus durations. Figure 4B shows that this approach successfully identified appropriate stimulus durations for each observer (note the large difference in proportion correct results for small and large stimuli).

Experiment 2 was then repeated for the selected durations, using sinusoidal gratings instead of broadband noise. All three stimulus conditions (1° size at 99% contrast; 10° size at 99% contrast; 10° size at relative contrast) were interleaved to preclude any differential practice effects.

Results

Experiment 1

The results obtained at 99% contrast are shown in Figures 1 and 2. Figure 1 shows fitted psychometric functions for each observer for 0.67° and 10° stimuli.

Threshold estimates (Figure 2) were considerably lower for 0.67° stimuli than for 10° stimuli—a result replicating previous findings (e.g., Tadin et al., 2003).

Experiment 2

From each observer in Figure 1, we selected 3 stimulus durations where there was a large difference in discriminability of large and small stimuli. At these durations, contrast thresholds for small stimuli were on average 3.5 times higher than those measured with large stimuli (Figure 3B). To equalize relative contrast for two stimulus sizes used here, it was necessary to decrease the contrast of large stimuli to an average of 28.3%.

The results obtained with these relative contrast-matched stimuli are shown in Figure 3A. The thick black lines and white bars are replotted from Experiment 1 and

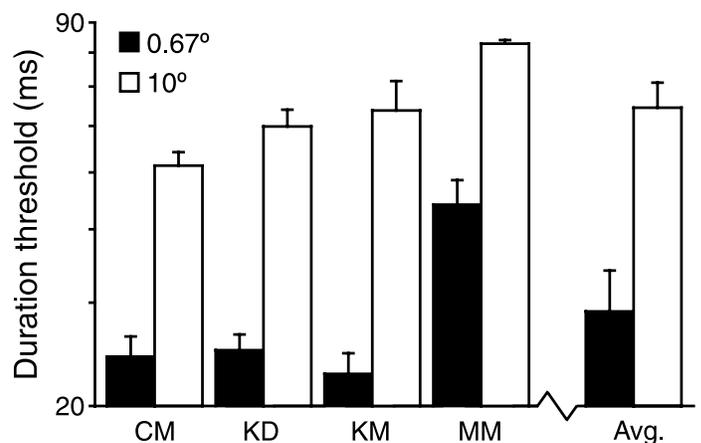


Figure 2. Duration threshold estimates (82%) for direction discriminations of small (0.67° , black bars) and large (10° , white bars) moving stimuli. Error bars represent 95% CI for individual observers and *SEM* for the group average.

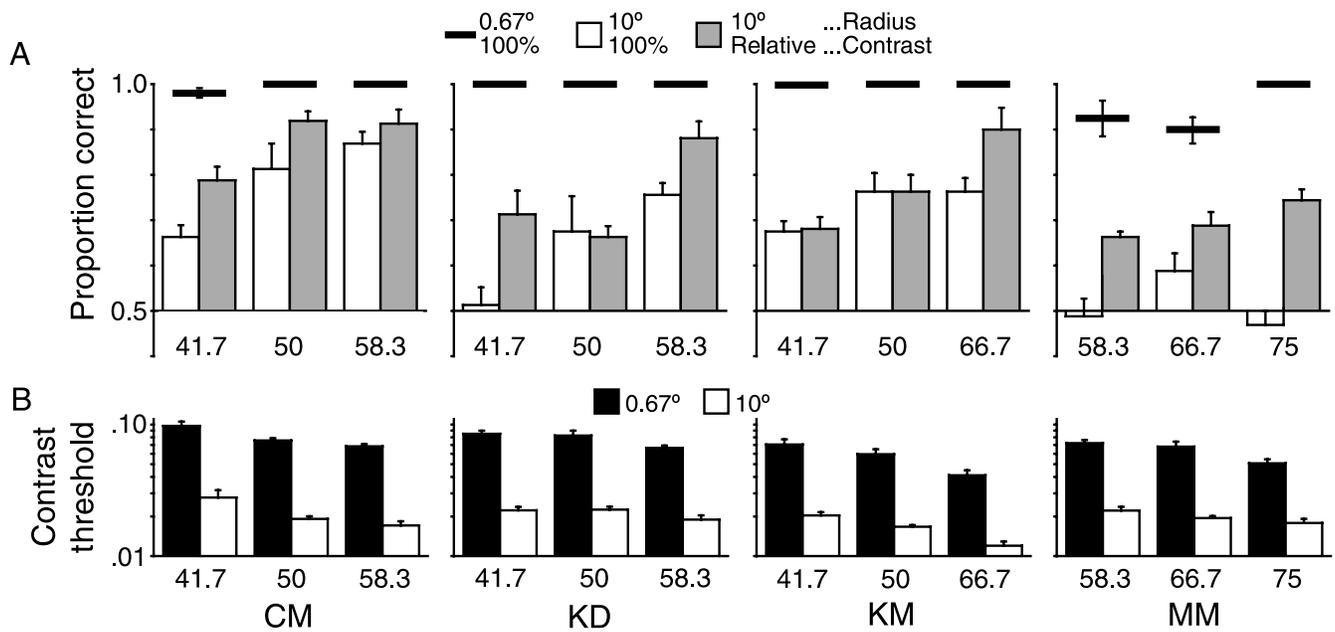


Figure 3. (A) Comparison of motion discriminations for small and large stimuli at 99% contrast (black lines and white bars, respectively; redrawn from Figure 1) and large stimuli whose contrast was reduced to match the relative contrast of corresponding small stimuli (gray bars). (B) Contrast thresholds for each subject for small (black bars) and large (white bars) stimuli. All error bars are SEM.

represent performance for 0.67° and 10° stimuli at 99% contrast. The gray bars show percent correct for 10° stimuli whose contrast was decreased (see above) to match relative contrast of small stimuli at each presentation duration. As expected, this decrease in contrast improved performance in nearly every case. Nevertheless, for all observers, performance in the relative contrast condition was still considerably worse for large stimuli than for small stimuli of equivalent relative contrast.

Experiment 3

The contrast thresholds measured for each observer, at each size, are shown in Figure 4A. The thick bars represent the average contrast threshold for small (1°) stimuli, and the thin bars represent the average contrast threshold for large (10°) stimuli. In each case, as expected, contrast thresholds were considerably lower for the large stimuli than the small stimuli. As in Experiment 2, these

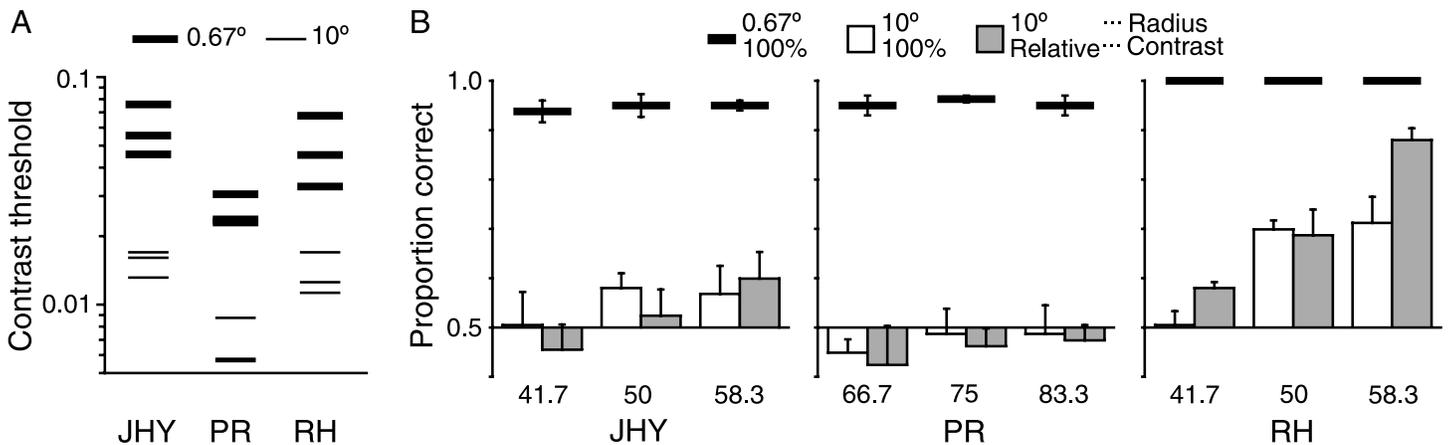


Figure 4. (A) Small (thick lines) and large (thin lines) contrast thresholds for the three tested durations for each subject. Average SEM for JHY = 0.0057, PR = 0.0012, and RH = 0.0036. (B) Comparison of motion discriminations for small and large gratings at 99% contrast (black lines and white bars, respectively) and large stimuli whose contrast was reduced to match the relative contrast of corresponding small stimuli (gray bars). Error bars are SEM.

results were used to equalize the relative contrast for two stimulus sizes tested here.

The results obtained with relative contrast-matched grating stimuli are shown in [Figure 4B](#). As we selected stimulus durations corresponding to the shortest durations where observers started to exhibit ceiling performance with small stimuli, we expected poor performance with large, high-contrast stimuli (Tadin et al., 2003; also see [Figure 1](#)). Indeed, all observers performed considerably worse for large stimuli than for small stimuli. Importantly, this result was observed regardless of whether the contrast was “equalized” in absolute or relative terms. These findings show that the results from Experiment 2 obtained with broadband textures generalize to narrowband grating stimuli.

Discussion

Here, we show that spatial suppression of motion signals—a substantial deterioration of motion discriminations with increasing stimulus size at suprathreshold contrasts—is observed even when the effective stimulus contrast is carefully matched across stimulus sizes. This finding differs from a recent result by Aaen-Stockdale et al. (2009) who described a motion task, which, at an absolute high contrast, is also characterized by a size-dependent increase in thresholds. The authors measured the amount of contrast imbalance required to bias observers’ motion perception of a counterphasing grating into one direction. In their task, however, equalizing effective stimulus contrast eliminated the threshold increases with increasing stimulus size. There are several factors that may have contributed to this discrepancy.

Aaen-Stockdale et al. (2009) measured the amount of contrast imbalance needed to transform a counterphasing grating into a stimulus that was perceived as predominantly moving in one direction. Neural responses to such opposing motion stimuli, however, tend to differ from those to unidirectional motion (Garcia & Grossman, 2009; Heeger, Boynton, Demb, Seidemann, & Newsome, 1999; Kohn & Movshon, 2003; Krekelberg & Albright, 2005; Qian & Andersen, 1994; Snowden, Treue, Erickson, & Andersen, 1991; Thiele, Dobkins, & Albright, 2000). Importantly, provided that the stimulus contrast is sufficiently high (Kohn & Movshon, 2003), suppressive interactions between overlapping motion directions are observed even if the contrasts of two components are different (as in the stimuli of Aaen-Stockdale et al., 2009). Additionally, both psychophysical and neurophysiological results indicate that the inhibitory interactions between superimposed opposing motions are absent at low contrasts and only emerge at medium and high contrasts (Kohn & Movshon, 2003; Levinson & Sekuler, 1975; Stromeyer, Kronauer, Madsen, & Klein, 1984; Thiele et al., 2000;

Watson, Thompson, Murphy, & Nachmias, 1980). In sum, the neural responses to superimposed opposing motions differ from those to unidirectional motion. Moreover, the observed differences are most pronounced at high contrasts, which are particularly relevant to the present discussion. These results might possibly account for the discrepancy between our findings and those of Aaen-Stockdale et al. (2009), with the two studies, at least in part, reflecting different mechanisms. What is more, there is currently no research showing how the responses to superimposed opposing motions change with increasing stimulus size—a question also highly relevant to this discussion. Specifically, it is unknown whether the presence of an opposing motion affects surround suppression in addition to modulating the response within the classical receptive field.

Another difference worth considering is stimulus duration. The stimuli used by Aaen-Stockdale et al. (2009) were almost an order of magnitude longer than those used here. One consequence of using brief motions is that such stimuli, by virtue of their broad temporal frequency spectrum, contain motion energy in both directions. However, duration-dependent change in motion energy occurs independently of stimulus size and cannot account for the present results. Additionally, while the broad temporal frequency spectrum of brief stimulus might also be considered a form of motion opponency, there is no evidence that such stimuli weaken directional selectivity of MT neurons, so long as the stimulus is confined to the classical receptive field (Churan et al., 2008).

Given that a contribution of surround-suppressed MT neurons to motion direction discriminations is larger at very brief durations (Churan et al., 2008; see [Introduction](#) section for more details), it is possible that the duration threshold method used in the present study is better suited to reveal psychophysical consequences of spatially suppressive neural mechanisms. That said, it is unlikely that correction for relative stimulus contrast would explain other spatial suppression findings observed at longer durations. For example, using binocular rivalry to explore center-surround interactions in motion perception, we found evidence for strong spatial suppression (Paffen et al., 2006). Notably, suppression was observed at all contrasts above about 2–4% (unpublished observation). It is highly unlikely that size-dependent differences in relative contrast would be large enough to require reducing large stimulus contrast to 4% to match the small stimulus at 100%.

Our initial use of duration threshold measurements (Tadin et al., 2003) was based on the assumption that if the neural response to a stimulus is weak or noisy, then longer stimulus exposure will be required for correct perception. More specifically, deciding whether an object is moving in one of two possible directions can be conceptualized as a process involving the accumulation of sensory evidence over time (Kiani, Hanks, & Shadlen, 2008; Roitman & Shadlen, 2002). When neuronal

responses are noisy or attenuated, as with a highly suppressed motion stimulus, sensory evidence accumulates more slowly and a correct decision may require longer exposure duration (Roitman & Shadlen, 2002).

Duration threshold measurements, however, typically necessitate the use of transient stimuli. Using a task where motion-step thresholds were measured (i.e., phase shift), Churan, Richard, and Pack (2009) found that spatial suppression was eliminated when a stationary stimulus preceded target motion (presumably eliminating onset transients). Aaen-Stockdale et al. (2009) identified this possible confounding role of onset transients as a motivation to focus on longer duration stimuli. However, there are several reasons arguing against the onset transient confound. First, the addition of the stationary stimulus in Churan, Richard et al.'s (2009) study also decreased task difficulty, yielding phase-shift thresholds of only 2 arcmin. Such small displacements correspond to very slow speeds that are likely lower than the speed limits of MT neurons (Lagae, Raiguel, & Orban, 1993; Priebe, Lisberger, & Movshon, 2006) and first-order motion perception (Tsujimura & Zaidi, 2002). In agreement with the results of Churan, Richard et al. (2009), we recently reported that spatial suppression disappears at very slow speeds (Lappin et al., 2009). Second, the same authors (Churan, Khawaja, Tsui, & Pack, 2009) showed that elimination of onset transients does not improve directional selectivity of surround-suppressed MT neurons to brief motions. Finally, using reaction time measurements, we found that the strength of spatial suppression did not depend on whether a moving stimulus abruptly appeared or if the stimulus was first stationary and then abruptly moved (Tadin et al., 2007).

Conclusion

Here, we showed that spatial suppression could be observed at both relative and fixed stimulus contrasts, as long as stimulus contrast is relatively high. While the exact mechanisms underlying psychophysical spatial suppression still need to be adequately characterized, this study demonstrates that the simple low-level explanation proposed by Aaen-Stockdale et al. (2009) cannot account for spatial suppression results.

Finally, it is important to consider which way of equalizing stimulus contrast—absolute or threshold relative—is more appropriate when studying contrast-dependent integration of motion signals over space. Relative stimulus contrast is potentially relevant because contrast thresholds decrease with increasing stimulus size (Anderson & Burr, 1991; Lappin & Bell, 1976; Watson & Turano, 1995)—a result indicating spatial summation. Thus, as the stimulus size increases, the visual system is able to pool stimulus information to improve motion

discriminations. Our previous and present results indicate that at high contrasts the nature of motion integration over space is rather different, as evidenced by findings of spatial suppression. If the nature of motion integration radically changes with increasing contrast, is it appropriate to normalize high-contrast stimuli by the results obtained at contrast threshold, ignoring evidence that different processes might operate at different contrast levels?

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