Increasing stimulus size impairs first- but not second-order motion perception

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As stimulus size increases, the direction of high-contrast moving stimuli becomes increasingly difficult to perceive. This counterintuitive effect, termed spatial suppression, is believed to reflect antagonistic center–surround interactions – mechanisms that play key roles in tasks requiring sensitivity to relative motion. It is unknown, however, whether second-order motion also exhibits spatial suppression. To test this hypothesis, we measured direction discrimination thresholds for first- and second-order stimuli of varying sizes. The results revealed increasing thresholds with increasing size for first-order stimuli but demonstrated no spatial suppression of second-order motion. This selective impairment of first-order motion predicts increasing predominance of second-order cues as stimulus size increases. We confirmed this prediction by utilizing compound stimuli that contain first- and second-order information moving in opposite directions. Specifically, we found that for large stimuli, motion perception becomes increasingly determined by the direction of second-order cues. Overall, our findings show a lack of spatial suppression for second-order stimuli, suggesting that the second-order system may have distinct functional roles, roles that do not require high sensitivity to relative motion.

Keywords: spatial suppression, first-order motion, second-order motion

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Introduction

The perception of motion is a fundamental process in the human visual system. Decades of investigation have demonstrated that observers perceive coherent motion in a wide variety of temporally varying displays (e.g., Anstis, 1980; Braddick, 1974; Cavanagh, 1992; Chubb & Sperling, 1988; for a review, see Burr & Thompson, 2011). An important distinction that has emerged from these studies is the dissociation between the perception of so-called first-order (luminance-modulated) and second-order (modulations of other features, like contrast, texture, or disparity) motion (Cavanagh & Mather, 1989).

A question of longstanding interest is whether first- and second-order motion are processed by the same neural mechanisms. While investigation of this question is still ongoing, converging evidence from psychophysics (Chubb & Sperling, 1989; Derrington & Badcock, 1985; Ledgeway & Smith, 1994; Nishida & Sato, 1995), neuroimaging (Ashida, Lingnau, Wall, & Smith, 2007), and neuropsychology (Vaina & Cowey, 1996; Vaina, Soloviev, Bienfang, & Cowey, 2000) indicates that motion perception is subserved by at least two, and perhaps more (Lu & Sperling, 1995, 2001), subsystems. Indeed, many differences in the perceptual properties of first- and second-order motion have already been described (e.g., Ledgeway & Hutchinson, 2005; Nishida, 1993; Schofield & Georgeson, 2003). For example, while first-order motion can generate both static and dynamic motion aftereffects (MAEs), second-order motion has only been shown to generate dynamic MAE (Derrington & Badcock, 1985; Ledgeway, 1994). Additionally, longer presentation durations are required to perceive direction of second-order motion, typically not less than 120 ms versus approximately 20 ms for first-order motion (Cropper & Derrington, 1994; Derrington, Badcock, & Henning, 1993; Ledgeway & Hess, 2002). More recent work has found that the spatial tuning of near-threshold first- and second- order motion stimuli, as measured by minimum and maximum windows for spatial summation, differs considerably (Hutchinson & Ledgeway, 2010). The aim of the present work is to provide further comparative investigation of spatial properties of first- and second-order motion processing.

Our past work revealed that spatial integration of first-order motion signals dramatically depends on stimulus visibility (Tadin, Lappin, Gilroy, & Blake, 2003). At low contrasts, motion perception is characterized by spatial summation (Anderson & Burr, 1991; Tadin et al., 2003; Watson & Turano, 1995), i.e., increasing sensitivity with increasing size. At high contrasts, however, motion direction becomes increasingly harder to perceive as the stimulus size increases—a result described as spatial suppression (Tadin & Lapin, 2005b; Tadin et al., 2003). This pattern of results has been linked to spatial interactions in cortical area MT (Tadin & Lappin, 2005a; Tadin, Silvanto, Pascual-Leone, & Battelli, 2011) and has been observed in the activity of single units in macaque MT (Churan, Khawaja, Tsui, & Pack, 2008; Pack, Hunter, & Born, 2005). Both psychophysical and neurophysiological results (Born, Groh, Zhao, & Lukasewycz, 2000; Tadin & Lappin, 2005a; Tadin, Paffen, Blake, & Lappin, 2008) suggest that spatial suppression may play a role in motion segregation processes (Braddick, 1993).

Turning to second-order motion, it is unknown whether motion perception of second-order stimuli exhibits analogous interactive dependence on stimulus size and visibility. Previous work showed that second-order motion is a poor cue for motion segregation (e.g., Derrington & Badcock, 1985; Dosher, Landy, & Sperling, 1989; Nishida, Edwards, & Sato, 1997). Given a presumed link between spatial suppression and motion segregation (Born et al., 2000; Tadin & Lappin, 2005a; Tadin et al., 2008), this led us to hypothesize that second-order processes might not exhibit strong spatial suppression found for first-order motion.

Specifically, we sought to compare the spatial properties of first- and second-order motion perception at above-threshold levels of visibility (i.e., high contrast). Our hypothesis is that spatial suppression will be absent for second-order stimuli, which will affect the relative visibility of first- and second-order motion as the stimulus size increases. This expected pattern of results makes a direct prediction: If increasing stimulus size selectively degrades first-order motion perception, observers should show an increased reliance on second-order cues as stimulus size increases. This prediction was tested in the second experiment.

We found that the spatial tuning of second-order motion perception differs greatly from the tuning of first-order motion perception. As the radius of a luminance-modulated grating was increased, it took longer for observers to discriminate its motion—a replication of previous spatial suppression results. However, as the size of a contrast-modulated grating increased over the same range, there was no corresponding increase in discrimination thresholds. In the second experiment, we show that for stimuli with first- and second-order cues moving in different directions, increasing stimulus size gradually shifted perceived motion direction from first-order to second-order direction. In other words, for large stimuli, motion perception was determined by second-order cues. Overall, we show that first- and second-order motion systems exhibit distinct dependencies on stimulus size—a difference that may be related to their different functional roles.

Experimental procedures

Stimuli were created in MATLAB with the Psychophysics Toolbox (Brainard, 1997) and VideoToolbox (Pelli, 1997) and shown on a DLP projector (DepthQ WXGA 360 driven by an NVIDIA Quadro FX 4800 at 1280 × 720 resolution). The projector's color wheel was removed by the manufacturer, allowing the presentation of three grayscale images per cycle at 120 Hz, yielding an effective frame rate of 360 Hz (2.67-ms frame duration). Frame timing and duration was carefully verified with an oscilloscope. DLP projectors are inherently linear, and this was verified with a Minolta LS-110 photometer. Procedures for verifying psychophysical equiluminance are detailed below. Viewing was binocular at 146 cm, with each pixel subtending 1.75 arcmin of visual angle. The ambient illumination was 1.8 cd/m^2 and a 0.6 neutral density filter (Kenko) was used to lower the background gray-level luminance to 113.7 cd/m^2.

Stimulus size was defined as the radius of the raised cosine spatial envelope. Contrast was defined as the peak contrast within the spatial envelope. One author and three naive, but experienced, psychophysical observers completed both experiments. All experiments complied with institutionally reviewed procedures for human observers.

Experiment 1

The aim of this experiment was to measure psychophysical spatial suppression of first- and second-order motion stimuli. The first-order stimuli were luminance-modulated sinusoidal gratings (SF = 1 c/deg, TF = 4 Hz) presented at 99% contrast (Figure 1A). The second-order stimuli were contrast-modulated dynamic (360 Hz) random noise (SF of the contrast modulation = 1 c/deg, TF = 4 Hz, 99% noise contrast, 99% modulation depth, each noise element subtended 3.5 × 3.5 arcmin; Figure 1B). The stimulus characteristics of the second-order stimuli were designed to be analogous to the first-order stimulus, i.e., to ensure high visibility of the stimulus elements. We confirmed this by measuring modulation depth thresholds for detection of moving second-order stimuli of fixed duration (two-interval forced choice, 250 ms; radius = 8°; other methods as in Experiment 1). For three subjects, detection thresholds were: 9.1%, 12.7%, and 17.6% modulation depth.

The stimulus duration was defined as the full-width at half-height of the temporal envelope. The procedure for determining the temporal envelope has been previously described (Tadin et al., 2011). Specifically, for very brief stimuli ($\sigma < 15$ ms), the temporal contrast envelope was Gaussian. Longer temporal envelopes were trapezoid-like, where flanks were half-Gaussians and the central portion was set to the maximum contrast. Fine temporal precision was obtained by adjusting the *SD* of half-Gaussian flanks

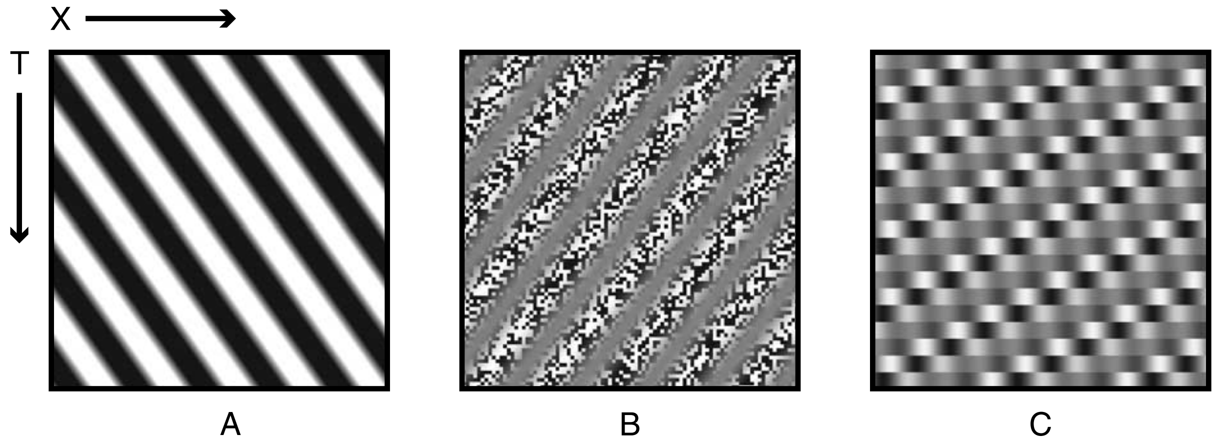

Figure 1. Schematic space–time plots of stimulus types used in Experiments 1 and 2. (A) Luminance-modulated sinusoidal grating moving to the right, used to measure first-order motion perception. (B) Contrast-modulated dynamic random noise moving to the left, used to measure second-order motion perception. (C) A 2f + 3f compound grating used in Experiment 2 to directly compare first- and second-order motion perception (Nishida & Sato, 1995). The first-order cues move to the right, which can be seen by noting the direction in which there is the shortest phase jump between successive stimulus frames (while ignoring amplitude changes between frames). In contrast, the second-order cues move to the left, which can be seen by tracking conspicuous stimulus features between successive frames. Note that contrast, spatial frequency, and noise element size have been altered for the purposes of illustration. Exact stimulus parameters can be found in the Experimental procedures section.

(with a constraint of $\sigma < 15$ ms) and transferring "excess" contrast to the flat central portion. This hybrid envelope allows fine temporal precision of brief stimuli and avoids protracted fade-in/out periods associated with prolonged temporal Gaussians.

Each block consisted of two interleaved QUEST staircases (Watson & Pelli, 1983), which were used to estimate duration thresholds for a direction discrimination task. We have previously shown that discrimination performance for near-threshold motion stimuli monotonically increases with increasing duration (Glasser & Tadin, 2010), making the use of these staircase procedures appropriate. Each observer completed four such blocks per stimulus size (1°, 1.6°, 3°, 5°, and 8°) and motion type (first and second order), yielding 10 stimulus conditions that were presented in random order.

The first block for each condition was thrown out as practice, and the final six staircases were averaged to give a duration threshold. 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.

A control experiment was conducted to ensure that there was no contamination of the second-order stimuli by psychophysical nonlinearities in the observers' visual systems. The procedure was similar to that used by several others (e.g., Ledgeway & Smith, 1994; Nishida et al., 1997). Specifically, observers were shown a four-frame stimulus interleaving two frames containing a luminance-modulated grating and two frames containing contrast-modulated random noise. There was a quarter phase (90°) shift in the grating pattern between each frame, which ensures that the stimulus can only be correctly discriminated if there is first-order contamination of the second-order frames. Each frame was presented for 33.3 ms, for a total stimulus duration of 133.3 ms. All other stimulus parameters were the same as described above. The largest stimulus size (8°) was used for this test, as any first-order contamination of the stimulus would have the strongest perceptual effect due to spatial summation of weak first-order signals (Anderson & Burr, 1991). None of the observers were able to discriminate the motion of this stimulus at better than chance levels (group mean (*SEM*) = 0.473(0.022)), indicating that no luminance artifacts were perceptible.

Experiment 2

The aim of this experiment was to compare the relative strengths of first- and second-order motion cues for compound grating stimuli of varying size. Here, we used 2f + 3f gratings, stimuli that contain first- and second-order cues drifting in different directions (Figure 1C; Nishida & Sato, 1995). They are formed by summing two sinusoidal gratings whose spatial frequency are two and three times a fundamental spatial frequency, respectively. These components interact, generating a periodic beat pattern, which causes a first-order signal to travel in one direction, while a second-order signal moves in the other (Figure 1C). Asking subjects to report which direction of motion seems stronger allows for direct comparison of the strength of the first- and second-order motion signals. The relative dominance of these cues can be altered by changing the interstimulus interval (ISI) between frames. It has been previously demonstrated that for short ISIs (i.e., at high temporal frequencies/velocities), subjects consistently report that the stimulus moves in the first-order direction, while increasing the ISI (i.e., at lower temporal frequencies/velocities) biases perception in the direction of the second-order motion (Nishida & Sato, 1995). However, it is unknown how changing stimulus size affects this balance between first- and second-order cues, as Nishida and Sato (1995) only tested one stimulus size (a 3° high by 9° wide rectangle).

Stimulus parameters were closely matched to those of Nishida and Sato (1995); the fundamental spatial frequency was 0.5 c/deg, and the contrast of each component grating was 30%. The fine temporal resolution of the projection system allowed the adjustment of the ISI in 2.7-ms steps. Seven ISIs were used, ranging from 11.1 to 50 ms. The total stimulus duration was 200 ms, and the temporal envelope was a square wave. In addition to seven ISIs, five stimulus sizes were tested (1°, 1.6°, 3°, 5°, and 8°), yielding 35 conditions that were presented in random order. Each observer completed 1750 trials (50 trials per each ISI–size combination). On each trial, a moving stimulus was presented foveally and the observer indicated the perceived direction (left or right) by a key press. No feedback was provided.

Results

Experiment 1

The results of Experiment 1 are shown in Figure 2. A two-way repeated measures ANOVA revealed significant main effects of motion type ($F(1,3) = 25.0$, $p = 0.015$) and

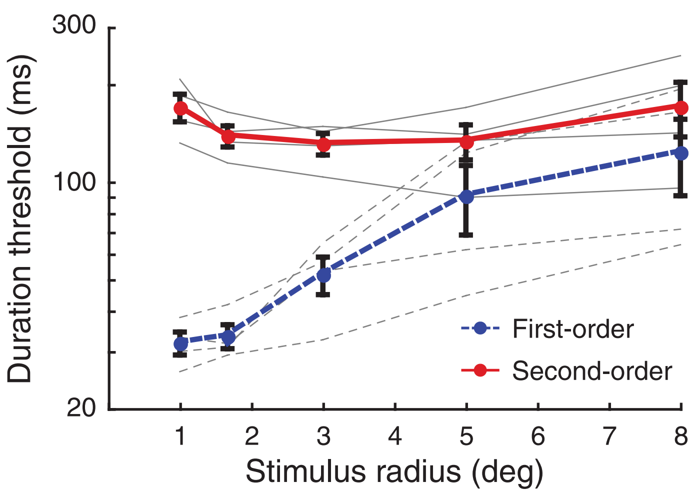

Figure 2. The effect of stimulus size on the perception of first-order (dashed blue) and second-order (solid red) motion (Experiment 1). Individual observers' data are plotted in gray. Threshold values are the full-width at half-height of the temporal envelope of the motion stimulus. Data points show the group mean ± *SEM* ($n = 4$).

stimulus size ($F(4,12) = 7.93$, $p = 0.002$), as well as a significant interaction between them ($F(4,12) = 3.79$, $p = 0.032$). As stimulus size increased, each observer showed a marked increase in discrimination thresholds for larger first-order motion stimuli ($F(4) = 4.91$, $p < 0.001$; Figure 2, blue), a result consistent with spatial suppression (Tadin et al., 2003). Conversely, there was no evidence of spatial suppression for second-order motion stimuli ($F(4) = 1.07$, $p = 0.41$; Figure 2, red); observers showed relatively flat sensitivity as the stimulus size was increased. As a result, as stimulus size increased, observers' first- and second-order thresholds converged, becoming statistically indistinguishable for the largest (8°) stimuli ($t(3) = 1.0$, $p = 0.39$).

Our duration thresholds for discriminating motion direction of second-order stimuli agree with previous estimates of exposure durations that are needed to perceive motion of such stimuli (Cropper & Derrington, 1994; Derrington et al., 1993; Ledgeway & Hess, 2002). Moreover, our results for small stimuli replicate the well-established superiority of first-order motion. However, our finding that first- and second-order discrimination thresholds are comparable at large sizes has no precedent that we are aware of.

Experiment 2

As spatial suppression seems to selectively affect processing of first-order motion information (Figure 2), observers should place more weight on first-order cues for small stimuli and place progressively more weight on second-order cues as the stimulus size increases. This straightforward prediction was tested in Experiment 2. Here, each observer judged the direction of 2f + 3f compound gratings, stimuli for which the first-order signal moves in the opposite direction from the second-order cues (Figure 1C; see Experimental procedures section). We recorded the proportion of responses consistent with second-order cues for each size and ISI. Previous work demonstrated that for short ISIs, subjects perceive stimulus motion that is consistent with the first-order direction. However, as the ISI increases, perceived stimulus motion changes to match the direction of the second-order cues (Nishida & Sato, 1995). Our aim was to investigate whether the relative dominance of first- and second-order cues in this compound stimulus is affected by stimulus size.

The data for each stimulus size was fit with a cumulative Gaussian function. The mean of the Gaussian was taken as a point of subjective equality (PSE), indicating a point where perception of first- and second-order direction was equally likely. For ISIs longer than the PSE, the perceived stimulus direction was predominantly in the direction of the second order. The results from a representative subject (Figure 3A) show that as the stimulus size increases, perceived direction shifts to the second-order direction at progressively shorter ISI. This

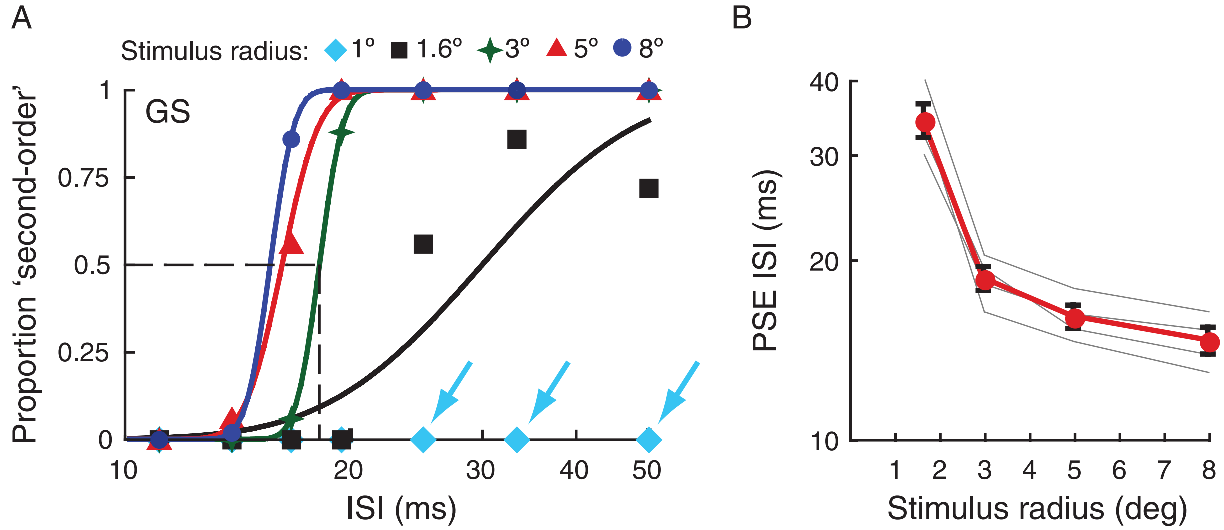

Figure 3. The effect of size on the relative perceptual strength of first- and second-order motion cues (Experiment 2). (A) Representative observer's data showing, for each stimulus size, the proportion of responses in the second-order direction as a function of ISI. (B) Dependency of the PSE on the stimulus size (n = 4). Data are the group mean ± *SEM* (red) and individual observers' data (gray). Note that there is no data point for the 1° size, as the second-order cues never dominated for any observer at any ISI (as seen in (A), cyan).

result is also evident in the average PSEs for the four largest stimulus sizes (Figure 3B). No PSEs could be computed for the smallest (1°) size, as the second-order cues never reached predominance, even at the longest ISI (see arrows in Figure 3A). As predicted, PSE decreased with increasing stimulus size ($F(3)$ = 48.5, p < 0.001). This indicates perceptual dominance of the second-order cues at progressively shorter ISIs as stimulus size increases.

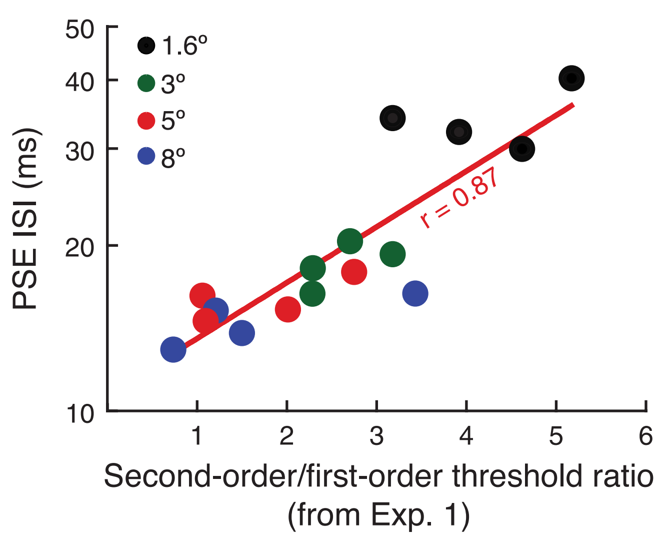

Figure 4. The ratio of each observer's first- and second-order motion discrimination thresholds (from Experiment 1) versus the PSE estimates from Experiment 2, for each stimulus size. The relationship is well captured by an exponential regression curve (red line). Note that there are no data points for the smallest (1°) size, as second-order cues never dominated for any observer at any ISI.

Next, we compared the outcomes of Experiments 1 and 2 to test whether differences in spatial suppression from Experiment 1 may predict outcomes of Experiment 2. For example, a condition where first-order direction discrimination thresholds are much lower than those for second-order stimuli (e.g., small stimuli in Figure 2) should also yield predominance of first-order direction over a broader range of ISI in Experiment 2. Moreover, individual differences in relative thresholds for first- and second-order stimuli in Experiment 1 should predict individual differences in Experiment 2. To test these predictions, we plotted the ratio of second-order to first-order thresholds from Experiment 1 against the PSE estimates in Experiment 2 for each stimulus size, for each subject. We found a strong relationship between these two sets of data (r = 0.87, p < 0.001; Figure 4), confirming these predictions.

Discussion

In two experiments, we found that second-order motion perception is not affected by changes in stimulus size in the same way as first-order motion perception. Thresholds for the discrimination of first-order motion increased almost fivefold as the stimulus size increased from 1° to 8°. In contrast, second-order motion discriminations remained largely flat over the same range of stimulus sizes. Interestingly, for the largest stimuli, observers' direction discrimination thresholds did not differ for the perception of first- and second-order motion. This asymmetric dependency of first- and second-order motion on stimulus size was also evident in observers' perception of compound grating stimuli. As the 2f + 3f gratings were enlarged, the second-order cue dominated at progressively shorter ISIs—those ISIs that normally favor first-order motion perception (Nishida & Sato, 1995).

These findings strongly suggest that first- and second-order motion information is processed by at least partially separate systems. While there is some literature that suggests that a common mechanism is possible (Hong, Tong, & Seiffert, 2011; Johnston, McOwan, & Buxton, 1992), the evidence is overwhelming that first- and second-order motion are processed by separate low-level mechanisms (e.g., Chubb & Sperling, 1989; Derrington & Badcock, 1985; Ledgeway & Smith, 1994; Nishida & Sato, 1995). While this particular question seems all but settled, it is still useful to characterize the differences between the spatial and temporal properties of the first- and second-order motion systems, as observed differences may provide insights into how information from first and second is subsequently used by the visual system.

For instance, there is extensive evidence that second-order motion cannot subserve tasks that involve relative motion perception, such as structure from motion (Dosher et al., 1989) and induced motion (Nishida et al., 1997). Similarly, visual search for a second-order target stimulus that moves in the opposite direction from second-order distractors is inefficient, while the same task with first-order stimuli is an effortless pop-out task (Ashida, Seiffert, & Osaka, 2001). What these tasks have in common is that they require high sensitivity to local velocity differences. Spatial suppression has been hypothesized to be important for detection and enhancement of such differences (Buračas & Albright, 1994, 1996; Nakayama & Loomis, 1974; Tadin & Lappin, 2005a). Further, it has been demonstrated that center–surround suppression in area MT is important for segregation of figure and background motion (Born et al., 2000), a task that also requires sensitivity to relative motion. Our finding that second-order motion does not exhibit spatial suppression may provide a mechanistic explanation for poor sensitivity to relative motion of second-order stimuli. More broadly, this may indicate different functional roles of first- and second-order motion systems.

Our data raise a potentially interesting direction for future research: investigating how higher order motion cues might actually contribute to the perception of large, high-contrast moving stimuli. While luminance-modulated stimuli are commonly referred to as "first-order stimuli," it is possible that second-order or attentional tracking mechanisms are sensitive to their motion as well (Cavanagh, 1992; Clifford, Freedman, & Vaina, 1998; Lu & Sperling, 1995; but see Wilson, Ferrera, & Yo, 1992). Contributions from second-order cues or attentional tracking would normally be moot due to the perceptual dominance of the first-order motion system. However, if the first-order system is compromised, as we demonstrate with spatial suppression, the contributions of higher level motion systems may become relevant and perhaps important in defining the perceptual limits of such stimuli. Results reported in this paper indicate that the second-order cues become progressively more important as the stimuli size increases, which suggests that the second-order system may be contributing significantly to the perception of large luminance-modulated stimuli. Careful further investigation will be needed to explore this hypothesis.

Conclusion

We have demonstrated that spatial suppression does not affect first- and second-order motion perception equally. While increasing the size of first-order motion stimuli strongly impairs observers' ability to discriminate them, second-order motion perception is largely unaffected by the same spatial manipulation. This asymmetry is also reflected in observers' percepts when the two types of motion cues are set in conflict in a compound stimulus: As the stimulus size increases, the perceived motion direction is largely determined by the direction of second-order cues. These findings provide further evidence for existence of separate systems for processing of first- and second-order motion. Additionally, absence of spatial suppression for second-order motion suggests that the second-order processes may have distinct functional roles from first-order mechanisms—roles that do not require high sensitivity to relative motion.

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