Low-level mechanisms may contribute to paradoxical motion percepts

Craig R. Aaen-Stockdale

McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Canada

Benjamin Thompson

McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Canada

Pi-Chun Huang

McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Canada

Robert F. Hess

McGill Vision Research, Department of Ophthalmology, McGill University, Montreal, Canada

A recent series of experiments demonstrated a surprising deterioration of visual motion discrimination with increasing stimulus size for stimuli of high contrast. This counterintuitive finding was explained as a result of surround suppression in visual area V5. Equally paradoxical was the finding that older observers showed better performance than younger observers. This second result was explained as an age-related reduction in surround suppression due to changes in GABA-mediated inhibition. Using an opponent motion stimulus, we find an analogous effect and also find that this effect is much reduced in older observers, to the point where they perform better than younger observers. Our long duration stimulus should be beyond the range at which surround-suppressed neurons in V5 are preferentially activated. Having normalized our stimuli relative to contrast threshold, we show that our results can be entirely explained by the relative contrast of the stimulus and speculate that contrast sensitivity may play a role in previously reported results. Our older observers’ data similarly can be explained by the relative contrast of the stimulus. The difference between older and younger observers appears to be a result of a weakening of spatial summation at high contrast in younger observers, perhaps caused by earlier saturation of motion mechanisms.

Keyword: contrast sensitivity, detection/discrimination, visual cortex, motion—2D, temporal vision


Introduction

A paradoxical increase in motion-discrimination thresholds with increasing stimulus size has been reported for high-contrast moving stimuli (Tadin, Lappin, Gilroy, & Blake, 2003). As the size of a stimulus increases, one would expect detection and discrimination of the stimulus to improve according to spatial summation of contrast and/or probability summation as the outputs of more local motion sensors are recruited and integrated. Contrary to this idea, Tadin et al. noted that, as the size of a high-contrast moving Gabor patch was increased, observers counterintuitively required longer presentation durations or larger phase shifts to discriminate its direction of motion. If the patch was low contrast, spatial summation occurred as expected. Tadin et al. propose that their psychophysical results are a perceptual correlate of surround suppression in the receptive fields of motion-selective neurons and suggest that the locus of this surround suppression is likely visual area V5. Indeed, the size of the effect seems correlated with the speed preferences of V5 neurons (Lappin, Tadin, Nyquist, & Corn, 2009). The rationale is that, at high contrasts, motion in the inhibitory surround would be sufficiently strong to suppress the motion signals from the excitatory center, while at low contrasts this surround antagonism would be weaker.

There is much physiological evidence for surround suppression in the animal homologue of V5, the middle temporal visual area (MT), for both motion and disparity (Allman, Miezin, & McGuinness, 1985; Born, 2000; Bradley & Andersen, 1998; DeAngelis & Uka, 2003) and it no doubt serves an important role in reducing redundancy in the visual field (Born & Bradley, 2005). The psychophysical effect noted by Tadin et al. (2003) bears some similarity to electrophysiological recordings of neurons in MT. Cells, which showed similar surround-suppressive interactions (Pack, Hunter, & Born, 2005), were found. These neurons respond more to large low-contrast stimuli than to large high-contrast stimuli. However, the population of neurons in this study was heterogeneous in their level of surround suppression.
Although surround suppression was reduced at low contrast in the majority of cells, most cells showed little or no surround suppression and only a minority switched from summation to suppression. It was initially unclear why this subpopulation in particular should dictate perception and, therefore, whether the psychophysical effects seen by Tadin et al. were indeed a direct result of surround suppression. However, recent work has suggested that surround-suppressed neurons are selectively targeted by very brief presentation durations (approximately 40 ms) in the macaque (Churan, Khawaja, Tsui, & Pack, 2008).

Tadin and colleagues (Lappin et al., 2009; Tadin et al., 2006, 2003) measured motion discrimination thresholds by varying the duration of the stimulus or the size of a single phase shift systematically until observers could no longer discriminate the motion direction. Other studies have since used the same technique to contend that there is weaker surround suppression in schizophrenics (Tadin et al., 2006) and older subjects (Betts, Taylor, Sekuler, & Bennett, 2005; Tadin & Blake, 2005), infant observers (Lewis, Sekuler, & Bennett, 2008), and observers with a history of depression (Golomb et al., 2008). Age-related changes in GABA-mediated inhibition are hypothesized to be responsible for the weaker surround suppression in older subjects. Degradation of GABA-mediated inhibitory mechanisms has been found in aging monkey cortex (Leventhal, Wang, Pu, Zhou, & Ma, 2003) and this decline in inhibitory mechanisms could theoretically lead to the weaker surround suppression shown in older observers using the duration threshold measure (Betts et al., 2005). However, this argument rests on the assumption that poorer motion discrimination for large, high-contrast stimuli—defined by longer duration thresholds—is indeed a result of surround suppression.

**Contrast-dependent effects**

The size of the receptive field of individual local motion sensors has been estimated by measuring the size of the area over which spatial summation of contrast occurs linearly (Anderson & Burr, 1987, 1991). The size of the receptive field of a single local motion sensor decreases as spatial frequency increases. Below 1 c/deg, receptive field size decreases with the square root of spatial frequency, varying from 0.07 cycles of the stimulus to 1 cycle. Above 1 c/deg, receptive field size decreases linearly, remaining constant at 1 cycle. Above these maximum receptive field sizes, contrast sensitivity continues to increase according to probability summation as the outputs of multiple sensors are pooled (Anderson & Burr, 1987, 1991). Contrast is also integrated over time, with contrast thresholds for moving stimuli decreasing as stimulus presentation is lengthened, up to 100–200 ms (Burr, 1981). This spatial and temporal integration of motion means that contrast sensitivity and, correspondingly, contrast thresholds for discrimination of a moving stimulus will vary with stimulus size and duration.

Tadin et al. presented stimuli of differing sizes at a variety of contrasts between 2.8% and 92%. However, since contrast sensitivity varies with stimulus size, the stimulus contrast relative to threshold covaries with size. This means that, for the largest stimulus, a contrast of 5.5% could be many times higher than the contrast threshold for detection, while for the smallest stimulus the same contrast (5.5%) may be just above contrast threshold. If the motion energy required to discriminate motion is proportional to the suprathreshold contrast of the stimulus, then motion discrimination performance may be predictable from the observer’s contrast threshold. We therefore felt that it was important to attempt to replicate these findings with stimuli that are appropriately normalized for differences in contrast sensitivity.

---

**Short duration motion stimuli preferentially target surround-suppressed neurons**

In monkey visual area MT (thought to be equivalent to human area V5), sudden onset of a moving stimulus results in transient (~30 ms) bursts of neural activity in area MT, which are not initially direction-selective and indiscriminately signal both the preferred and anti-preferred directions of the cell (Churan, Khawaja, Tsui, Richard, & Pack, 2008; Churan, Khawaja, Tsui, & Pack, 2008). Eventually, the response pattern settles into that signaling the preferred direction.

Churan, Khawaja, Tsui, and Pack (2008) found that the disruptive effect of initial responses to non-preferred directions affected non-surround-suppressed MT neurons more than those that were surround-suppressed, which means that psychophysical performance on tasks utilizing short duration (40 ms) stimuli would preferentially reflect the operation of these neurons. At longer durations (100 ms), this distinction had disappeared. A good test of whether surround suppression is responsible for the psychophysical effects could therefore be to test motion discrimination using longer duration stimuli that would activate both V5 populations.

The findings of Churan et al. may seem at first difficult to reconcile with the fact that similar paradoxical patterns of performance are found in studies that use the motion aftereffect (MAE) as a measure (Falkenberg & Bex, 2007; Tadin et al., 2003). The adaptation stimulus in these studies is of very long duration and therefore must stimulate both surround-suppressed and non-surround-suppressed neurons. However, the MAE is the result of adaptation occurring at many levels of the motion processing hierarchy simultaneously (for a review, see Niedeggen & Wist, 1998) and surround suppression may be occurring at any (or several) of these levels. Since we have not used an adaptation paradigm, the current study limits itself to investigating the hypothesis that surround suppression is responsible for paradoxical patterns of motion discrimination.
Recent work has collapsed the covarying variables of contrast and size into a single metric, contrast energy, the sum of the stimulus squared contrast (Betts, Sekuler, & Bennett, 2009). Betts et al. show that the contrast energy metric is a good predictor of their data but contend that surround suppression is still responsible. The contrast energy metric provides a description of the information content of the stimulus, but if contrast sensitivity is variable across size, it may not perfectly reflect the contrast or motion energy in the visual system.

**The current study**

The paradoxical motion percept measured psychophysically in human observers by previous studies may be a result of surround suppression in V5. Since short duration stimuli such as those used in previous studies appear to preferentially target surround-suppressed neurons, a good test of this hypothesis is to attempt to reproduce the effect using longer duration stimuli. We first set out to investigate whether the basic effect (Tadin et al., 2003) and the reduction of the effect in older observers (Betts et al., 2005) could be replicated with a motion energy stimulus (Ledgeway, 1994; Levinson & Sekuler, 1975) that was of a fixed, long (800 ms) duration.

Our stimulus was composed of two, temporally interleaved, Gabor patches (a sinusoidal grating multiplied by a 2-dimensional Gaussian window) moving in opposite directions. When the contrast of the two component Gabors was equal, the stimulus would flicker with no net motion. The contrast of one component could be increased (and the other decreased by the same amount) to create a percept of motion in one direction. The contrast imbalance necessary to perceive consistent motion in one direction, rather than the minimum duration measure used by previous studies (Betts et al., 2005; Lappin et al., 2009; Tadin et al., 2006, 2003), provides a measure of the sensitivity of motion discrimination mechanisms that is relatively uncontaminated by non-direction-selective onset transients, which typically last for ~30 ms (Churan, Khawaja, Tsui, Richard et al., 2008; Churan, Khawaja, Tsui & Pack, 2008). This stimulus allows us to probe motion discrimination mechanisms using stimuli that are presented for longer than the period during which the activity of surround-suppressed cells dominates performance. We find a suppression-like impairment of performance with increasing size at high contrasts with a stimulus that reflects the activity of both surround-suppressed and non-surround-suppressed V5 neurons. This seems to exclude surround suppression in V5 as solely responsible for these interesting effects.

We next investigated the effect of normalizing the stimulus at multiples of contrast threshold and find that variations in contrast sensitivity with stimulus size and differences in the pattern of spatial summation between younger and older observers explain the majority of our data. Although we cannot exclude surround-suppressive mechanisms elsewhere in the visual system, our results suggest that contrast sensitivity may play a role in other similar results.

### Experimental procedures

#### Participants

The four younger participants (mean age = 29.5, SD = 2.6 years) were one of the authors (CAS) and three experienced psychophysical observers naive to the hypothesis (JS, GM, and AY). The four older subjects (mean age = 63 years, SD = 2.2 years) were also experienced in psychophysical tasks and naive to the hypothesis. All observers were reimbursed for their participation.

#### Apparatus

The stimuli were presented on a Sony Trinitron monitor driven by the VSG 2/5 graphics board (Cambridge Research Systems, Rochester, UK) with 15 bits of contrast resolution, housed in a Pentium PC computer running Windows XP. The screen resolution was 1024 × 768 pixels with frame rate of 120 Hz and mean luminance of 71 cd/m². Subjects viewed the monitor in a dimly lit room and responded by pressing a button on a CT3 button box (Cambridge Research Systems, Rochester, UK). The computer was gamma-corrected using software lookup tables implemented in the VSG.

#### Stimuli

**Drifting Gabor**

The basic stimulus was a sinusoidal grating multiplied by a 2-dimensional Gaussian envelope (often referred to as a “Gabor patch”). A single Gabor patch is defined by the following equation:

\[
L(x,y,t) = L_0 + L_0 \times c \times \cos(2\pi f_s (x - x_0) + \tau_s) \exp\left(-\left(\frac{x^2 + y^2}{2\sigma^2}\right)\right) \times \cos(2\pi f_t (t - t_0) + \theta_t),
\]

where \(L_0\) is the mean luminance, \(c\) is the contrast of the Gabor, \(f_s\) is the spatial frequency of the carrier, \(\sigma\) is the standard deviation of the Gaussian envelope, \(\tau_s\) is the phase of the carriers with respect to the center of a Gaussian window, \(f_t\) is the temporal modulation frequency, and \(\theta_t\) is the temporal phase. The spatial frequency of the sinusoidal component was 1 cycle per degree (c/deg) and the drift rate was 2 Hz.
**Opponent Gabor**

A directionally ambiguous stimulus was created by interleaving, on alternate frames, two Gabor patches drifting in opposite directions. The interleaving of the Gabors on alternate frames allowed us to control the contrast of each drifting Gabor independently. When the contrast of each Gabor patch was identical, the observers would perceive a counterphase, or flickering, Gabor with no net motion in either direction. The contrast of the two components could be manipulated in a seesaw fashion to bias the motion energy in either direction, while maintaining constant absolute contrast. As the components drifted at 2 Hz, the resulting opponent Gabor flickered at 4 Hz. The advantage of this stimulus, which has previously been used as a test stimulus for measuring the motion after effect (Ledgeway, 1994; Levinson & Sekuler, 1975), is that motion-selective mechanisms can be tested without curtailing the presentation duration or varying the speed of a simple grating. Since it is presented for long durations (800 ms), this stimulus should also produce estimates of motion sensitivity that are relatively uncontaminated by onset transients, which typically last for ~30 ms (Churan, Khawaja, Tsui, Richard et al., 2008).

The size of the Gabor patches is expressed as 4 SD of the Gaussian component to give some idea of the total visible extent of the stimulus. Size was varied between 0.92° and 7.4° of visual angle at a viewing distance of 100 cm. This closely matches the same range used in previous studies (Betts et al., 2005; Tadin et al., 2006, 2003).

**Procedure**

Subjects were required to determine the dominant direction of motion and did so by responding with the left or right button on a response box. The stimuli were presented for 0.5 s within a temporal Gaussian envelope of 133 ms. A two-down/one-up staircase method was used to obtain thresholds. The initial reversal was discarded and the last five reversal points in each staircase were averaged. The final reported threshold was an average of at least three separate staircase measures.

**Constant absolute contrast condition**

Data were collected at arbitrarily high, low, and medium contrasts for all observers, covering the available range of contrast. The selected contrast was maintained across all stimulus sizes. Table 1 shows the exact contrasts at which each observer was tested.

<table>
<thead>
<tr>
<th>Observer</th>
<th>Age group</th>
<th>Low</th>
<th>Medium</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>CAS</td>
<td>Younger</td>
<td>0.013</td>
<td>0.13</td>
<td>0.26</td>
</tr>
<tr>
<td>JS</td>
<td>Younger</td>
<td>0.012</td>
<td></td>
<td></td>
</tr>
<tr>
<td>GM</td>
<td>Younger</td>
<td>0.02</td>
<td>0.21</td>
<td>0.42</td>
</tr>
<tr>
<td>AY</td>
<td>Younger</td>
<td>0.015</td>
<td>0.03 and 0.08</td>
<td>0.15</td>
</tr>
<tr>
<td>EW</td>
<td>Older</td>
<td>0.04</td>
<td>0.21</td>
<td>0.41</td>
</tr>
<tr>
<td>SW</td>
<td>Older</td>
<td>0.04</td>
<td>0.19</td>
<td>0.38</td>
</tr>
<tr>
<td>AB</td>
<td>Older</td>
<td>0.04</td>
<td>0.2</td>
<td>0.4</td>
</tr>
<tr>
<td>JB</td>
<td>Older</td>
<td>0.02</td>
<td>0.12</td>
<td>0.36</td>
</tr>
</tbody>
</table>

Table 1. Contrasts at which observers were tested in the constant absolute contrast condition.

to the contrast threshold for the particular sizes of stimuli. The contrast threshold for discriminating the motion direction of a single drifting Gabor was first measured using the staircase technique outlined above and the contrast of the opponent stimulus was set to a multiple of that threshold.

**Constant relative contrast condition**

To control for differences in perceived contrast at different stimulus sizes, data were also collected relative to the contrast threshold for the particular sizes of stimuli. The contrast threshold for discriminating the motion direction of a single drifting Gabor was first measured using the staircase technique outlined above and the contrast of the opponent stimulus was set to a multiple of that threshold.

**Results**

**Constant contrast**

Figure 1 plots the absolute contrast imbalance necessary to correctly discriminate the motion direction of the opponent Gabor stimulus. The y-axis shows the contrast increment added to one component of the stimulus and subtracted from the oppositely moving component. Higher values mean that a greater imbalance between the two components was necessary to disambiguate the motion direction.

We tested both younger and older observers at high, medium, and low contrasts, the value of which remained constant across the different stimulus sizes. The exact values used varied for each subject (see Table 1) and were chosen to cover as much of the range of contrast as possible with our experimental setup. When the younger observers were tested at a constant high contrast, performance was impaired (i.e., a greater difference in contrast between the two oppositely moving components was required to disambiguate motion) for large stimuli as compared to small stimuli (Figure 1). For a constant low contrast, on the other hand, performance improved (less difference in contrast was required) with increasing size. Medium constant contrasts fell predictably between these functions. These data are similar to the findings of Tadin et al., but they are obtained with a stimulus of constant, long duration. That we can produce a spatial suppression-like effect with a long duration stimulus, which does not preferentially target surround-suppressed V5 neurons, suggests that the activity of these cells is not solely responsible...
for this paradoxical result. It should be noted that the increase in thresholds for the high-contrast condition is quite substantial, although it may not appear so on the log-scale plot. Previous authors have calculated a “suppression index”, defined as \( \log_{10}(\text{threshold at largest size}) - \log_{10}(\text{threshold at smallest size}) \), to summarize the strength of the surround suppression effect at the highest contrast. By calculating the suppression index for our effect, we can more quantitatively compare our results to the previous literature. For the younger observers, the average suppression index is 0.456 log units (SD 0.114). This value is very similar to that obtained for stimuli of a similar speed and similar contrasts (Betts et al., 2005; Lappin et al., 2009; Tadin et al., 2003).

One aspect of Tadin et al.’s results that does not at first appear to be replicated is the crossover of the functions evident in the duration threshold data. This is a result of the fact that thresholds increase proportionally in a Weber’s Law-like fashion as the base contrast is progressively increased. The thresholds shown in Figure 1 are expressed as absolute contrast, but the base contrast of these stimuli is very different. If the thresholds are expressed as a proportion of the stimulus contrast, essentially a measure of how “unbalanced” the stimulus is regardless of its contrast, we see a clear crossover of the functions akin to that obtained by previous studies for younger observers (Figure 2).

Similarly, the crossover interaction obtained in the original study is simply a consequence of the units of measurement utilized. Duration is not an absolute measure of performance on motion tasks and is perhaps not very appropriate in this context. Stimulus discrimination requires signal accumulation over time and thought of in these terms, performance is actually vastly better for the low-contrast stimuli in the original paper, because less contrast (and motion energy) is available in the low-contrast stimuli, yet the information is accumulated and reaches threshold in roughly the same amount of time. If Tadin et al.’s original results are replotted as the threshold stimulus energy (contrast * time) rather than simply the integration period (time), they also show a proportional upward shift in threshold with increasing stimulus contrast that eliminates the crossover interaction (see Figure 3). As with our data, the higher the baseline contrast, the larger the amount of contrast energy that needs to be accumulated to discriminate motion direction. The data plotted in
this fashion look identical to our results when plotted by absolute contrast (see Figure 1), which reassures us that the same mechanisms are being tapped using these two very different measures.

For the older observers, we see much flatter functions with very little suppression and only mild summation (Figure 4). When these data are plotted as proportional to the baseline contrast (Figure 5), they fall on top of each other, and although there is some evidence of an interaction, it is much weaker than the younger observers. Although one observer shows strong spatial summation for low contrasts (AB), none show particularly strong spatial suppression at high contrasts or summation at low contrasts. The average suppression index for the older observers is 0.095 log units (SD 0.037), which is very similar to the weak effect reported previously (Betts et al., 2005).

Betts et al. showed that for a large stimulus at high contrasts, older observers counterintuitively performed better than younger observers. We have shown here that older observers need proportionally less imbalance in large, high-contrast stimuli to reliably disambiguate motion, but does this translate into an age-related advantage at certain stimulus configurations? Although our subjects were tested at slightly different contrasts (see Table 1), for three younger observers and three older observers, the “high” contrast value was chosen to be 20× threshold at the smallest stimulus size. It is therefore reasonable to average these observers’ data for the high-contrast condition (see Figure 6), and as can be seen, for larger sizes at high contrast, older observers indeed perform better than younger observers at the same suprathreshold contrast. This reproduces very well the paradoxical age effect found by Betts et al. and significantly strengthens our case, i.e., that we are tapping the same mechanisms with our stimulus.

Here we have a genuinely perplexing set of results, namely that large, high-contrast stimuli need proportionally greater imbalance in order to disambiguate their motion and older observers perform better with these stimulus configurations than younger observers. Very similar effects have been reported before (Betts et al., 2005; Tadin et al., 2003) and ascribed to surround suppression. Neurons have been identified in MT with these properties (Pack et al., 2005), but here we have a long duration stimulus that is
beyond the point at which these surround-suppressed neurons dominate the signal (Churan, Khawaja, Tsui, & Pack, 2008). So could the variations in contrast sensitivity to the progressively larger stimuli be playing a role?

Relative contrast

Contrast sensitivity increases with stimulus extent, therefore for two stimuli of the same contrast but different sizes, the contrast of the larger stimuli would be much higher than threshold compared to the smaller stimulus. It may be that the motion energy required to discriminate a stimulus is proportional to the suprathreshold contrast. If this is the case, then the higher motion energy thresholds obtained for larger, high-contrast stimuli may simply reflect this lawful relationship. We therefore felt it important to control for any effects upon motion discrimination that were purely related to contrast.

When tested at similar suprathreshold contrasts, subjects’ performances showed summation with increasing size, combined with the previously discussed Weber’s Law-like increase in the contrast imbalance necessary to detect the dominant direction of motion (Figures 7 and 8). The younger observers also showed a weakening of spatial summation at higher contrasts, whereas this was not...
evident in the older observers’ data, in which spatial summation remained constant across different relative contrasts.

When the constant absolute contrast data are superimposed upon this threshold-relative data, it becomes clearer what may be causing the paradoxical deterioration of motion perception for large, high-contrast stimuli and why this is not observed for older observers. Figure 9 shows sample data from two younger (left) and two older (right) observers. Thresholds for a constant absolute contrast are predicted quite well by the contrast relative to threshold at any particular size. For younger observer GM, the low constant contrast stimulus is $1/C^2$ threshold at the smallest size, and $3/C^2$ threshold at the largest size. The high-contrast stimulus, however, covers a range from $20/C^2$ threshold at the smallest size to $57/C^2$ threshold at the largest size. At successively larger sizes, more contrast energy is needed to disambiguate motion because the stimulus is proportionally higher above threshold. For the low-contrast stimulus, this proportional increase in contrast energy needed to disambiguate motion at successively larger sizes is not sufficient to overcome the effects of spatial summation, so performance improves with increasing size. At high constant contrasts, however, the larger stimuli are far higher above contrast threshold than the smaller stimuli and thus require a proportionally larger motion energy imbalance to disambiguate their motion. This effect also seems to be exacerbated by the lessening
Figure 7. Contrast imbalance thresholds for four younger observers across a range of stimulus sizes for stimulus contrasts relative to contrast threshold. Darker markers signify higher contrasts.

Figure 8. Contrast imbalance thresholds for four older observers across a range of stimulus sizes for stimulus contrasts relative to contrast threshold.
When tested relative to threshold, the older observers (AB and SW) show more closely packed spatial summation functions of more constant slope, without the weakening of spatial summation shown by the younger observers. These factors result in flatter functions when tested at a constant absolute contrast, which could be interpreted as weaker spatial suppression, but since our stimuli are presented for much longer than the period during which spatially suppressed neurons are preferentially activated, we favor an explanation based on the variations in the suprathreshold contrast of the stimulus.

Discussion

There is much physiological evidence that surround-suppressive mechanisms exist in MT/V5 (Allman et al., 1985; Born, 2000; Bradley & Andersen, 1998; DeAngelis & Uka, 2003) and elsewhere in the visual system. This surround suppression undoubtedly serves an important function by reducing redundancy in a visual scene (Born & Bradley, 2005). Center–surround inhibition may explain the fact that the motion aftereffect (MAE) is weaker in the presence of a high-contrast surround moving in the same direction (Tadin et al., 2003) but stronger if the surround moves in a sufficiently different direction (Falkenberg & Bex, 2007) and similar center–surround effects may explain the modulation of binocular rivalry by surrounds moving in the same direction (Paffen, Tadin, te Pas, Blake, & Verstraten, 2006; Paffen, van der Smagt, te Pas, & Verstraten, 2005). In this paper, we have not examined evidence for center–surround antagonism obtained using the MAE or binocular rivalry as a probe, although whether there exist any contrast sensitivity-dependent effects in these experiments obviously warrants investigation. It may well be that the effects of surround suppression have a psychophysical correlate in terms of the MAE or binocular rivalry, but it seems unlikely that these effects result from surround suppression in V5, since both of these techniques use long duration stimuli that are beyond
the interval over which surround-suppressed neurons dominate (Churan, Khawaja, Tsui, & Pack, 2008). In addition, we do not think that the direction discrimination data, obtained with short duration stimuli, are necessarily a perceptual consequence of surround suppression. The very similar results presented here cast some doubt on whether the duration threshold technique of Tadin et al. (2003) is actually measuring the action of surround-suppressed neurons in V5 (Churan, Khawaja, Tsui, & Pack, 2008; Pack et al., 2005), since qualitatively and quantitatively similar effects appear to be possible at durations longer than those that preferentially activate these cells.

Human motion detection has been variously and successfully modeled as direction-selective motion sensors with space–time oriented receptive fields (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). Contrast thresholds for motion detection and discrimination decrease as the size of the stimulus increases according to summation within the receptive field and then probability summation beyond the receptive field (Anderson & Burr, 1987, 1991). The previous findings, in which performance gets worse with increasing size at constant absolute high contrasts, may be the result of the fact that performance is tested at contrasts that are increasingly higher above contrast threshold as size increases. Our results with a long duration, opponent motion stimulus, presented at a contrast that is relative to the subjects’ contrast threshold, show a Weber’s Law-like increase in the contrast imbalance necessary to discriminate motion proportional to the total stimulus contrast, spatial summation with increasing stimulus size, and weakening of spatial summation at high contrasts for younger observers only. These data suggest that the psychophysical functions produced at a constant absolute contrast (see Figures 1 and 4) combine performance across several suprathreshold contrast functions, which results in the impression that performance is getting worse. In fact, performance on our task is almost exactly predicted by the proportional increase in the motion energy required to discriminate direction at progressively higher suprathreshold contrasts.

It is difficult to conclusively test whether this suggestion is indeed responsible for the data of Tadin et al. and other groups using their same technique. Contrast is integrated over time and this temporal integration means that varying the stimulus duration, to obtain a duration threshold, changes the corresponding contrast threshold for motion discrimination (Burr, 1981). Likewise, varying the phase (and therefore speed/temporal frequency) of the stimulus would mean testing relative to different points on the spatiotemporal contrast sensitivity function (Kelly, 1979; Robson, 1966; van Nes, Koenderink, Nas, & Bouman, 1967). This makes it problematic to control for contrast thresholds using their approach and we opted to use a modified version of their stimulus. The fact that we can reproduce qualitatively similar effects in younger and older observers with this, rather different, stimulus and that suppression indexes obtained with this measure are quantitatively similar reassures us that we are accessing the same basic mechanisms.

A possible objection to the use of our stimulus is that MT does not respond to, or is suppressed by, flicker. While it has been reported that a subset of monkey MT neurons, and perhaps V5 as a whole, demonstrate a suppressed response when presented with counterphase stimuli that have perfectly balanced local motion energy (Heeger, Boynton, Demb, Seidemann, & Newsome, 1999), our stimuli do not fall into this category. We deliberately imbalance the local motion energy in order to produce direction-selective responses. Although we are unaware of any physiological data on the effects of contrast imbalance between opposing directions, other similarly subtle forms of local motion imbalancing such as very small spatial separation of paired dots (Qian & Andersen, 1994) have been shown to restore the responses of MT motion opponent neurons. By extrapolation from these results, we have no reason to believe that our contrast-imbalanced stimuli would suppress direction-selective cells in MT, in fact from the literature it seems very difficult to suppress MT and this area is exquisitely sensitive to imbalanced directional information. With regard to the response of V5 as a whole, Muckli, Singer, Zanella, and Goebel (2002) showed, using the paired-dot stimulus, that very small local imbalances result in strong activation in V5 as measured by fMRI.

In addition, there is evidence that many neurons in MT show little or no opponency in response to counterphase gratings. The physiological data of Heeger et al. (1999) show that there are many neurons that respond as well to a counterphase grating as they do to a drifting grating, although on average the population was opponent. Other authors have similarly found that only a minority of MT neurons are suppressed by counterphase stimuli (Krekelberg & Albright, 2005; Thiele, Dobkins, & Albright, 2000).

**Clinical implications**

Tadin and colleagues have used duration threshold measurements to argue for weaker surround suppression in patients with schizophrenia (Tadin et al., 2006) and other groups have used the same technique to make a case for weaker surround suppression in older observers (Betts et al., 2005), children (Lewis et al., 2008), and observers with a history of depression (Golomb et al., 2008).

The physiological work carried out by Churan, Khawaja, Tsui, and Pack (2008) suggest that the methods used by Tadin et al. (2003) to measure motion discrimination performance may preferentially activate surround-suppressed neurons in V5. However, our work seems to suggest that similar effects can be acquired in motion discrimination tasks that utilize much longer duration stimuli. This has implications for whether or not other factors are contributing to measurements of surround suppression acquired with this method and, if so, whether it provides a valid
estimate of surround suppression in V5. If it does not, it has further implications for research carried out with clinical populations (Betts et al., 2005; Golomb et al., 2008; Lewis et al., 2008; Tadin & Blake, 2005; Tadin et al., 2006) and conclusions drawn from these studies.

Using a similar stimulus, which can be presented at a fixed duration, contrast, and speed, we have produced an analogous effect of contrast and size and an analogous reduction of this effect in older subjects. However, our data suggest that these effects are predictable from stimulus contrast and we therefore favor a low-level explanation of these effects.

Our results relative to contrast threshold show spatial summation combined with a Weber’s Law-like proportional increase in the amount of motion energy required to discriminate direction as the overall contrast of the stimulus is increased. This proportional increase in motion energy thresholds with increasing stimulus suprathreshold contrast may be interpreted as performance getting worse when stimuli are presented at a constant contrast across different sizes. We argue that thresholds for the individual observers are predicted very well by the suprathreshold contrast of the stimulus.

With regard to the counterintuitive effect of age on motion perception, the more constant slope of the older observers’ relative contrast functions results in flatter functions when tested at constant absolute contrast. The older observers therefore show weaker or non-existent deterioration of motion discrimination with stimulus size at high constant contrasts, but this result is again predicted by the individual observer’s contrast sensitivity at any particular size. What has been interpreted as weaker surround suppression in older observers (Betts et al., 2005) appears, from our results, to be the result of more constant spatial summation at all suprathreshold contrasts, while for younger observers, spatial summation is stronger at low contrast than at high contrast. It remains to be seen what is causing this reduction of spatial summation at progressively higher suprathreshold contrasts. We speculate that the younger observers’ functions flatten because of saturation at high contrasts (Derrington & Goddard, 1989). If the contrast is so high that a single motion sensor is performing maximally, then perhaps there is no great advantage of pooling additional sensors. We speculate that older observers do not show this flattening of the spatial summation functions because the output of single motion sensors is less reliable and therefore there is always an advantage to be gained by pooling.

These interacting low-level factors produce a genuinely paradoxical pattern of results in which motion discrimination performance for older observers is indisputably superior to that of younger observers. Although we feel confident that we have excluded the possibility that surround-suppressed V5 neurons are directly responsible for these effects, we cannot entirely rule out surround suppression elsewhere in the visual system, but our data do not seem to require it.

## Conclusion

Motion discrimination thresholds obtained with an opponent motion stimulus while keeping contrast constant across all stimulus sizes are predicted almost entirely by the observer’s contrast sensitivity and the contrast of the stimulus relative to threshold at each successive size. Differences between younger and older observers on our motion discrimination task seem to be likewise explicable by the fact that the thresholds of younger observers show earlier saturation. This leads us to conclude that our results are a low-level effect of stimulus contrast and we speculate that perhaps those of other studies using similar methods may be explained in this way. We note that recent work on this phenomenon has begun to acknowledge the role of contrast energy in the stimulus (Betts et al., 2009) and the importance of the observer’s contrast sensitivity (Lappin et al., 2009), although this has so far only been investigated in the context of summation at low contrast, not suppression at high contrast.

## Acknowledgments

These data were first presented at the Optical Society of America, Fall Vision Meeting, 24–26 October 2008 (Aaen-Stockdale, Thompson, Huang, & Hess, 2008). This work was supported by a Natural Sciences and Engineering Research Council of Canada Grant (# 46528-06 to RFH). The authors would like to thank Dr. Goro Maehara for invaluable programming support.

Commercial relationships: none.
Corresponding author: Craig Aaen-Stockdale.
Email: c.aaen-stockdale@bradford.ac.uk.
Address: School of Optometry and Vision Science, University of Bradford, Bradford, BD7 1DP, UK.

## References


