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Center–surround effects on perceived speed

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ABSTRACT

We investigated whether center–surround interactions affect perceived speed in a manner similar to their effects on direction discrimination thresholds [e.g. Tadin, D., Lappin, J. S., Gilroy, L. A., & Blake, R. (2003). Perceptual consequences of center–surround antagonism in visual motion processing. Nature, 424, 312–315]. Observers were asked to match the speed of a test stimulus (a grating, with fixed contrast and no surround) to that of a reference stimulus of variable contrast and with a variably sized surround, moving at one of two possible velocities (1 and 12 cps). At 1-cps, both lowering contrast and increasing surround-size resulted in a decrease in perceived speed, except for very low contrast stimuli, where a larger surround resulted in an increase in perceived speed. Although the effect of surround-size was comparable in the two velocity conditions, the effect of contrast was different at 12-cps. That is, in the 12 cps condition, a decrease in perceived speed was observed only for the lowest contrast used. Our results suggest that, at least for the lower velocity used, center–surround interactions affect perceived speed in a manner analogous to their effect on direction discrimination.

1. Introduction

Speed and direction are the two main parameters that define the velocity of a moving stimulus. Not surprisingly, cells in Macaque MT/V5, where ~80% of the cells are direction selective, also appear to be selective for different speeds (e.g. Mikami, Newsome, & Wurtz, 1986a, 1986b; Rodman & Albright, 1987; Snowden, Treue, & Andersen, 1992). Therefore, these two parameters appear intertwined, not only at the physical, but also at the neuronal level.

A well-known characteristic of neuronal responses to a moving stimulus is that they can be modulated by stimulation of the area surrounding the classical receptive field (CRF). This modulatory effect of the surround on the center has been shown to be often antagonistic (e.g. Allman, Miezin, & McGuinness, 1985; Raiguel, Van Hulle, Xiao, Marcar, & Orban, 1995) but can be integrative as well (e.g. Allman et al., 1985; Born & Tootell, 1992; Huang, Albright, & Stoner, 2007). That is, the influence can be of inhibitory or facilitatory nature, and/or related to segmentation or integration. Contrast of the center stimulus (over the CRF) (Pack, Hunter, & Born, 2005) or its ambiguity (for instance in direction of motion; Huang, Albright, & Stoner, 2008) are major factors in determining the nature of these neuronal center–surround interactions. In a psychophysical experiment, Tadin and his colleagues elegantly demonstrated a perceptual correlate of such center–surround interactions. They also showed these interactions to be mainly antagonistic, except for very low contrast stimuli where they become integrative (Tadin, Lappin, Gilroy, & Blake, 2003).

These studies, however, were mainly concerned with motion *direction* discrimination. Apart from direction, velocity also has a speed component. The question whether these two parameters are processed independently, as has been suggested in a number of recent studies (e.g. Curran & Benton, 2006; Edwards & Grainger, 2006; Matthews, Luber, Qian, & Lisanby, 2001; Matthews & Qian, 1999), is still a matter of debate. Therefore, here we are specifically interested in whether center–surround interactions are also likely to influence perceived *speed*. Similar center–surround interactions, i.e. antagonistic interactions except for very low contrast stimuli, for both speed and direction would be support for the hypothesis that speed and direction are not processed independently.

The present study was inspired by three seemingly independent observations. First, the classic finding by Thompson (1982), showing that observers underestimate the speed of a moving stimulus (e.g. a grating) when that stimulus is presented at low contrast, relative to a reference (higher contrast) stimulus. Accordingly, when comparing the speed of two moving stimuli, the one with the higher contrast is judged as the faster one. The second classic observation, documented by Brown (1931) and elaborated on more parametrically by i.a. Ryan and Zanker (2001), is that a larger stimulus is usually perceived as moving more slowly than a smaller stimulus when, in fact, their speeds are identical. The third observation, investigated by i.a. Snowden and Hammett (1998), is that the perceived *contrast* of a (counter phasing) stimulus is decreased when surrounded by a similar stimulus, although for moving stimuli this only appears to apply when center and surround move with

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similar direction and speed (Takeuchi & De Valois, 2000). In a similar vein, center–surround interactions in general have been interpreted such that the inhibitory influence of a moving surround acts by *decreasing effective contrast* in the center, for instance during binocular rivalry (Paffen, van der Smagt, te Pas, & Verstraten, 2005). In other words: lowering contrast reduces perceived speed, as does increasing the size of a stimulus. However, increasing the size of a stimulus can also be interpreted as increasing the modulatory effect of neuronal center–surround interactions, which has a measurable effect on its perceptual manifestation (e.g. Tadin et al., 2003): stimuli of increasing size will increasingly activate the suppressive non-classical receptive fields. These suppressive center–surround interactions lead to a decrease in perceived contrast (or at least a decrease in *effective* contrast) of the stimulus, and hence a decrease in perceived speed. The three observations thus appear all sides of the same coin (i.e. including the rim). One could wonder, then, whether such a decrease in perceived contrast, induced by the surrounding stimulus (as documented by Snowden and Hammett (1998) and Takeuchi and De Valois (2000)), might cause the center to be perceived as moving slower (i.e. a serial process), or whether the influence of a surround stimulus on perceived contrast and on perceived speed might be more or less independent of one another (which would imply a more parallel process).

We asked our observers to compare the speed of a moving grating in a central patch to a test stimulus, equal in all parameters except speed and contrast, in a two-interval forced choice paradigm. The central patch was either presented in isolation, or surrounded by an annulus of variable width containing an identical grating, which was moving in the same direction and speed as the center. The contrasts of center and surround were identical, but were varied parametrically.

2. Methods

2.1. Observers

Ten observers participated in the experiment, including two authors (MS and CP). The other eight observers were naïve as to the purpose of the experiment. Nine of the observers were included in the data analysis (see below). All observers had normal or corrected to normal visual acuity. Experiments were in accordance with the declaration of Helsinki, and the protocol was approved by the ethical committee of the faculty of Social and Behavioural Sciences of Utrecht University.

2.2. Apparatus and stimuli

Stimuli were presented using an Apple dual 2 GHz PowerPC G5 and a linearized LaCie Electron blue 22 in. monitor running at 100 Hz, using MATLAB and the Psychtoolbox extensions. Stimuli were shown as schematically represented in Fig. 1. The stimuli consisted of drifting sine-wave gratings with a spatial frequency of 2 cpd. The edges of stimuli were filtered with half a period of a raised cosine with a width of 0.31°. The stimuli were presented on a gray background with a luminance of 35.5 cd/m^2. A drifting grating always comprised a center region with a radius of 1.5°. In some conditions, a surrounding annulus (3° or 8° wide, resulting in a stimulus with a 4.5° or 9.5° radius) was also present (see Section 2.3). The filtered edges introduce a gap between center and surrounding annulus. Such a gap was not apparent in the Tadin et al. (2003) study or other mentioned studies where stimulus size was manipulated. This gap ensured, however, that participants always matched the same part of the reference stimulus (i.e. the center) to the test stimulus irrespective of a surround being present or absent. The direction of motion (and thus orientation) of the grating was randomly varied between eight possible directions (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315° clockwise from upward) in order to prevent motion adaptation effects. Speed, direction, orientation, spatial frequency, phase, and cosine filter were the same for center and surround regions of a stimulus.

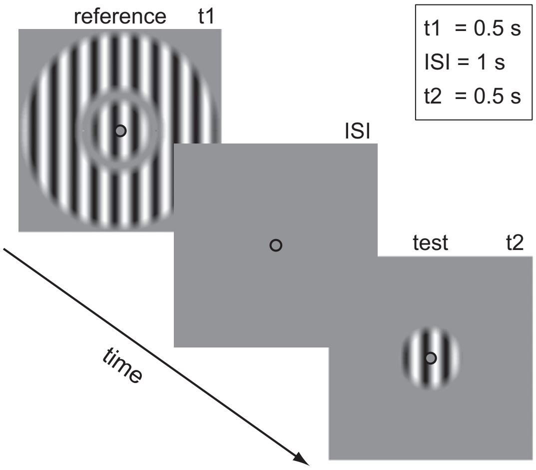

Fig. 1. Example of a stimulus sequence in one trial. The reference stimulus (in this example with a 3° annulus surrounding the center and with a contrast equal to that of the test stimulus) is presented in the first interval, followed by an ISI and the second interval containing the test stimulus.

2.3. Procedure

Observers sat in front of the monitor at a distance of 57 cm in a darkened room. To prevent head movements, the observer's head was kept steady by a chin and a forehead rest. The observer was required to maintain fixation at a red fixation point and refrain from making eye-movements. Completing the experiment took about 1.5 h for each observer, but observers could take breaks between blocks (see below).

A single trial consisted of two 0.5 s intervals separated by an inter-stimulus-interval of 1 s. In the first interval the reference stimulus was presented, in the second interval the test stimulus. An observer initiated a trial by pressing the space bar. The task of the observer was to indicate whether the test stimulus moved faster (left key) or slower (right key) than the reference stimulus. In a full-factorial design we varied the speed (1 or 12 cps; i.e. 0.5 or 6° s^{-1}, since only a single spatial frequency (2 cpd) was used), the width of the annulus (0°, 3° or 8°), and the contrast (1.4%, 9.5%, 38.0% and 66.4% Michelson contrast) of the reference stimulus. The size (1.5°) and contrast (38.0% Michelson contrast) of the test stimulus was the same in all conditions. Within a trial, motion direction and orientation of the test stimulus was identical to that of the reference stimulus.

To investigate how perceived speed is affected by stimulus velocity, -size and -contrast we determined Points of Subjective Equality (PSEs) using a one-up, one-down staircase in which the speed of the test stimulus was varied. Until the second reversal of a staircase, the speed was adjusted by an average factor of 2 (a 'slower' response would increase the speed by on average a factor of 2, a 'faster' response would decrease the speed by that same factor). For the subsequent trials, speed was changed by an average factor of 1.05. The exact factor with which the speed was adjusted each trial was randomly jittered between ±10% of the two factors (i.e. ranging from 1.8 to 2.2 until the second reversal and ranging from 0.945 to 1.155 for the remaining trials). The different conditions (different reference speeds, contrasts and surround widths) were presented in different blocks. A single block (one speed, contrast and surround width) consisted of three interleaved staircases. Individual staircases terminated after 10 reversals. The starting-point of each staircase (the speed of the test stimulus) was randomly chosen within an interval of 30% of the speed of the reference stimulus.

2.4. Data analysis

To determine the PSEs for each observer, the responses from the three staircases for one condition (one contrast, size and speed of the reference stimulus) were sorted ('slower' or 'faster') in ascending order of speed of the test stimulus. Subsequently, the range of test speeds was binned into five bins comprising the same number of trials for each of the bins, and the fraction 'faster'-responses per speed bin was calculated. The PSE for a condition was acquired by fitting these fractions of 'faster' responses with a cumulative normal distribution, its μ-parameter value representing the PSE. Note that observers indicated whether the test stimulus moved slower or faster compared to the reference stimulus and that the contrast and size of the test stimulus was always constant. A change in PSE therefore reflects changes in perceived speed of the reference stimulus compared to that of the test stimulus. The slope (or σ-parameter) of the cumulative normal distribution function was determined as well. For one observer the slope turned out to be too shallow to reliably determine the PSE in some conditions, and therefore this observer's data was omitted from the statistical analyses.

The statistical analyses involved a multi-factorial Repeated-Measures ANOVA. Where the homogeneity associated with the covariance matrix was violated, the p-values associated with the F-statistic were Greenhouse-Geisser adjusted. Where applicable, pair-wise comparisons applied the Sidak-adjustment for multiple comparisons.

3. Results

The matched test speeds as a function of reference contrast and reference size (parameter) are depicted in Fig. 2. The left panel shows the results of the 1-cps condition and the right panel shows the results of the 12-cps condition. The length of the black bar (38% contrast condition without a surrounding stimulus) shows nicely that subjects were well able to match the speed of two similar stimuli presented in consecutive intervals, as it lies very close to the to be matched (veridical) speed (dashed line). A repeated-measures ANOVA with speed, contrast and surround-size as within subject factors revealed significant main effects of (as expected) speed [$F(1, 8) = 262.92$, $p < 0.001$] and surround-size [$F(2, 16) = 7.13$, $p = 0.01$], as well as significant two-way interactions of speed $*$ contrast [$F(3, 24) = 3.31$, $p = 0.037$] and speed $*$ surround-size [$F(2, 16) = 8.68$, $p = 0.012$]. There was no significant main effect of contrast [$F(3, 24) = 2.23$, $p = 0.111$], nor a significant two-way interaction of contrast $*$ surround-size or three-way interaction of speed $*$ contrast $*$ surround-size ([$F(6, 48) = 1.55$, $p = 0.227$] and [$F(6, 48) = 0.81$, $p = 0.568$] respectively). These results indicate that perceived speed of the central patch is affected by the size of the surround and (to a lesser extent) the contrast of the stimulus, but that the effect of these magnitudes differs between the different stimulus speed conditions.

If we focus on the 1-cps conditions (Fig. 2, left panel), it is clear that the perceived speed of a stimulus without a surround (white and black bars) decreases with decreasing stimulus contrast, which replicates Thompson's (1982) results. This is underlined by significant pair-wise comparison differences for these conditions between stimuli of 1.4% and 38% as well as 1.4% and 66.4% and between 9.5% and 38% Michelson contrast ($p = 0.013$ and <0.001 and 0.024 respectively). Except for the two lowest contrast conditions, it is also clear that adding a surrounding stimulus results in a decrease in perceived speed, with significant pair-wise differences at 38% and 66.4% contrast between conditions without and with an 8-deg surround ($p = 0.001$ and $p = 0.004$ respectively) and at 66.4% contrast between the 3- an 8-deg surround conditions as well ($p = 0.031$).

Interestingly, in the 1.4% contrast condition, the PSEs hint at an integrative rather than antagonistic influence of the surround, resulting in a significant *increase* in perceived speed for the 8-deg surround compared to the 3-deg surround condition ($p = 0.038$).

For the 12-cps condition (Fig. 2, right panel), the results are different. The effect of contrast is less clear than for the 1-cps conditions. Without a surrounding stimulus, the only significantly different pair-wise comparison is that between the 1.4% and 9.5% Michelson contrast conditions ($p = 0.006$), denoting a decrease in speed with decreasing contrast. Interestingly, this lowest contrast

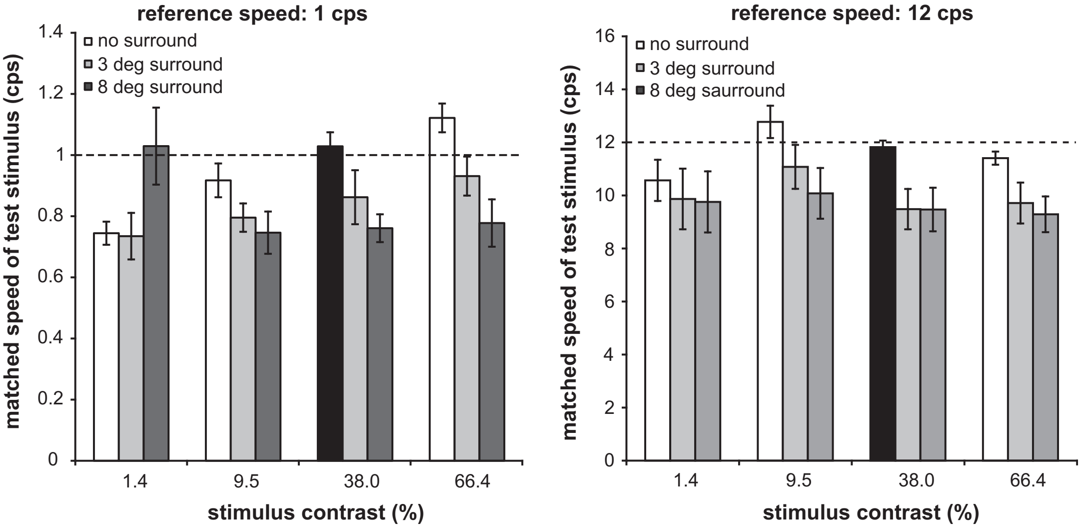

Fig. 2. PSEs (speeds of the test stimulus (38% contrast, no surround) when matched to that of the reference stimulus) for all contrast–size combinations in the 1-cps reference speed (left panel) and the 12-cps reference speed (right panel) conditions, averaged across 9 observers. Error bars depict ±1 SEM. The horizontal dashed lines represent the reference speed and the black bars the condition where the reference and test stimulus were identical in contrast and size.

condition appears to be the odd-one out compared to the other three contrast conditions: in the latter conditions, a decrease in contrast appears to (slightly) *increase* perceived speed. We will return to this issue in Section 4. Increasing the stimulus size by adding a surrounding annulus results in a decrease in perceived speed for all but the lowest contrasts used ($p < 0.028$ for all comparisons between 8-deg surround and no-surround conditions, $p = 0.016$ for the comparison between a 3-deg surround and no surround at 38% contrast), but the size of the annulus appears to be of less importance than in the 1-cps conditions. Again, in the lowest contrast conditions there is no significant effect of the surround, but there is no apparent increase in perceived speed with increasing surround-size either (as was observed for the 1 cps condition).

4. Discussion

We investigated whether center–surround interactions affect speed perception in manner analogous to their effects on direction discrimination (e.g. Tadin et al., 2003). Our results suggest this is indeed the case. Adding a surround stimulus to a central patch decreases the perceived speed of a stimulus, and this decrease varies with surround width and stimulus contrast. For very low contrasts, the effect of adding a surround appears to reverse; that is, addition of a surrounding stimulus results in an increase in perceived speed.

However, there are some caveats in comparing our results to that of previous studies on direction discrimination. The above mentioned results only hold for the lower velocity used (1 cps; comparable to the stimulus of Tadin et al. (2003)), and the integrative interaction at the lowest contrast was only significant for the comparison between the 3-deg and 8-deg surround. More importantly, the currently presented effect of the surround represents a *bias* in perceived speed, not a change in speed discrimination threshold, and as such is not necessarily related to the change in threshold reported in the Tadin et al. study, which is generally assumed to represent a change in *sensitivity*. As the observers' task in our experiment was to match a test speed to a reference speed and speed itself was varied, our data are not easily analyzed in terms of speed discrimination thresholds.[1] In addition, experiments using adaptation have shown that a decrease in perceived speed can be accompanied in *improved* speed discrimination (e.g. Bex, Bedingham, & Hammett, 1999; Krekelberg, van Wezel, & Albright, 2006) both psychophysically (in humans and macaques) as in neuronal responses in macaque MT (Krekelberg et al., 2006). Notwithstanding these caveats, our results for both the 1-cps and 12-cps conditions show a pronounced effect of a surround stimulus on perceived speed and are indicative of oppositely directed surround effects for very low contrasts (at least for the 1-cps condition).

4.1. Influence of contrast

Our results in the 1-cps conditions without a surround, of a decrease in perceived speed with decreasing stimulus contrast, resemble those of Thompson (1982) and subsequent studies linking stimulus contrast to perceived speed (e.g. Blakemore & Snowden, 1999; Gegenfurtner & Hawken, 1996; Stone & Thompson, 1992). Our 12-cps conditions, however, show no effect of contrast for the higher (9.5–66.4%) contrasts used or (if anything) even a slight increase of perceived speed with decreasing contrast. Thompson (1982) already reported little effect of contrast on perceived speed at higher velocities, but he recently showed quite a profound increase in perceived speed with decreasing contrast when higher velocities were used (Thompson, Brooks, & Hammett, 2006). Comparing our 9.5–66.4% Michelson contrast – no-surround – 12-cps conditions, yields a similar perceived speed ratio as they reported (their Fig. 1A, 12 cps condition): perceived speed is *higher* at 9.5% compared to 66.4% contrast. However, for very low contrast (1.4% Michelson contrast; not tested by Thompson et al. (2006)) this trend is reversed: perceived speed is *lower* at 1.4% compared to 9.5% contrast (note that the contrast *ratio* for 1.4–9.5% and 9.5–66.4% contrast comparisons is the same). This is an interesting finding as this reversal was not apparent for the 1-cps conditions. Moreover, this finding appears at odds with the ratio-model proposed by Thompson et al. (2006), as at high temporal frequencies in their model the lower contrast stimulus is perceived as faster, irrespective of the overall or mean contrast level. It should be noted that even in the 1.4% contrast condition the grating and its motion were clearly visible in both the 1 and 12 cps conditions. This is not surprising, as previous studies have found the contrast detection thresholds in the (para-) fovea for these spatio-temporal frequency combinations to be similar (e.g. Koenderink, Bouman, Bueno de Mesquita, & Slappendel, 1978a, 1978b).

4.2. Influence of size

Except for very low contrast conditions, adding a surround resulted in a lower perceived speed when compared to the conditions with no surround, and this effect again differed slightly for the two velocity conditions. For the 1-cps conditions, an increase in the annular width of the surround resulted in a larger decrease of the perceived speed, while this was less apparent for the 12-cps condition. Others have described such an effect of stimulus size on perceived speed for random dot stimuli (e.g. Norman, Norman, Todd, & Lindsey, 1996; Ryan & Zanker, 2001). One could argue that attention plays a role in this effect. As attention to a moving stimulus results in an increase in perceived speed compared to a non-attended stimulus (Turatto, Vescovi, & Valsecchi, 2007), the presence of a surround stimulus might attract attentional resources away from the center, hence the lower perceived speed. However, Pavlova and Sokolov (2000) have shown that the perceived speed of a stimulus in an identical central aperture can be modulated by differential Ebbinghaus–Titchener configurations. A larger and more conspicuous surround configuration that – arguably – will attract more attentional resources, resulted in a lower perceived central aperture size and a higher perceived speed in their experiment. Moreover, for the very low contrast stimuli in our experiment the effect of the surround was absent (for the 12-cps condition) or even in the opposite direction (for the 1-cps condition). It should be noted that for lower contrast stimuli in our experiment, the surround contrast was, of course, also lower and analogous to experiments on perceived contrast (e.g. Snowden & Hammett, 1998; Takeuchi & De Valois, 2000) might have exerted a smaller influence on the perceived speed in the center. Apart from this very low (1.4% Michelson) contrast case, however, the effect of surround-size appeared similar in most conditions; that is, independent of stimulus contrast.

In disregard of the lowest contrast used, our 12-cps conditions showed, on average, a slightly smaller surround effect (compare the 8-deg surround to the no-surround conditions) than our 1-cps conditions. This is interesting in that a previous study on the effect of speed on surround suppression (Lappin, Tadin, Nyquist, & Corn, 2009) showed a clear suppression increase with increasing stimulus speed. In a separate experiment, they demonstrated facilitation at 'low contrast' (as in the Tadin et al., 2003 paper) for a range of stimulus speeds, using a variable ('low') contrast contingent on each observer's speed-dependent contrast-response function. Comparing our present results to those of Lappin et al. suggests that the relationship between speed, contrast and sup-

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[1] Of course, the slope (or σ-parameter) of the cumulative normal distribution function can serve as some measure of sensitivity as well. However, apart from a (non-surprising) main effect of speed, the slope did not differ significantly between any of the contrast or surround conditions.

pression differs when measuring perceived speed (i.e. a bias) rather than discrimination thresholds.

4.3. Influence of contrast and size

As hinted at in the Introduction, a decrease in perceived speed as a result of a surround stimulus could be mediated by the lower perceived contrast of the center induced by the surround (i.e. a serial process): the presence of the surround decreases the perceived contrast of the center (e.g. Snowden & Hammett, 1998; Takeuchi & De Valois, 2000), which in turn decreases the perceived speed of the center stimulus. Our results clearly show that such a simple notion cannot explain the data. While the surround stimulus results in a reduction of perceived speed in both the 1-cps and 12-cps conditions, stimulus contrast shows differential effects for these two velocities used. If the effect of perceived speed in the center would be mediated by a change in perceived contrast induced by the surround, one would expect contrast in the no-surround conditions to have similar effects on the PSE for both the 1-cps and 12-cps conditions, which is clearly not the case. In addition to our results, Takeuchi and De Valois (2000) showed that a surround moving in the same direction and with the same speed has the largest effect on perceived contrast of the center, while Norman et al. (1996) have demonstrated the effect of the surround on perceived speed of the center to be invariant over surround–motion direction (same or opposite to the motion of the center). These two results, though tested with different stimulus-setups are also hard to reconcile with a serial, surround influences perceived contrast – influences perceived speed, mechanism.

We can of course only speculate on what might be the cause of the decrease in perceived speed as a result of the surround stimulus. The strength of surround suppression in, for instance, area MT has been shown to be modulated by the speed of the surround stimulus, with the identical speed showing the maximum suppression (e.g. Xiao, Raiguel, Marcar, & Orban, 1998). Still this would affect *sensitivity* to a certain speed, not an underestimation of this speed per se. Such a change in sensitivity for a certain speed at a certain retinal location *might* have an effect on the level of population coding (e.g. Priebe & Lisberger, 2004). Whether this would result in the pattern of results observed in the present study, however, remains unclear.

To conclude, we have shown that the addition of a surround stimulus reduces the perceived speed of a central stimulus and does so in a way that can be interpreted as an analog to psychophysically measured correlates of center–surround interactions, which can be found in for instance macaque area MT (e.g. Pack et al., 2005; Paffen et al., 2005; Tadin et al., 2003). In addition, we have shown that a decrease in stimulus contrast influences perceived speed differentially, depending upon stimulus velocity (e.g. Thompson et al., 2006) and whether a very low or higher contrasts are used. Clearly, the modulatory influence of the surround stimulus on perceived speed in the center is not mediated by a serial process, instead the surround affects perceived contrast and perceived speed through (at least partly) independent processes.

References

Allman, J., Miezin, F., & McGuinness, E. (1985). Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local–global comparisons in visual neurons. *Annual Review of Neuroscience, 8*, 407–430.

Bex, P. J., Bedingham, S., & Hammett, S. T. (1999). Apparent speed and speed sensitivity during adaptation to motion. *Journal of the Optical Society of America A, 16*, 2817–2824.

Blakemore, M. R., & Snowden, R. J. (1999). The effect of contrast upon perceived speed: A general phenomenon? *Perception, 28*, 33–48.

Born, R. T., & Tootell, R. B. H. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature, 357*, 497–499.

Brown, J. F. (1931). The visual perception of velocity. *Psychologische Forschung, 14*, 199–232.

Curran, W., & Benton, C. P. (2006). Test stimulus characteristics determine the perceived speed of the dynamic motion aftereffect. *Vision Research, 46*, 3284–3290.

Edwards, M., & Grainger, L. (2006). Effect of signal intensity on perceived speed. *Vision Research, 46*, 2728–2734.

Gegenfurtner, K. R., & Hawken, M. J. (1996). Perceived velocity of luminance, chromatic and non-Fourier stimuli: Influence of contrast and temporal frequency. *Vision Research, 36*, 1281–1290.

Huang, X., Albright, T. D., & Stoner, G. R. (2007). Adaptive surround modulation in cortical area MT. *Neuron, 53*, 761–770.

Huang, X., Albright, T. D., & Stoner, G. R. (2008). Stimulus dependency and mechanisms of surround modulation in cortical area MT. *The Journal of Neuroscience, 28*, 13889–13906.

Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E., & Slappendel, S. (1978a). Perimetry of contrast detection thresholds of moving spatial sine wave patterns. I. The near peripheral visual field (eccentricity 0 degrees–8 degrees). *Journal of the Optical Society of America, 68*(6), 845–849.

Koenderink, J. J., Bouman, M. A., Bueno de Mesquita, A. E., & Slappendel, S. (1978b). Perimetry of contrast detection thresholds of moving spatial sine wave patterns. II. The far peripheral visual field (eccentricity 0 degrees–50 degrees). *Journal of the Optical Society of America, 68*(6), 850–854.

Krekelberg, B., van Wezel, R. J., & Albright, T. D. (2006). Adaptation in macaque MT reduces perceived speed and improves speed discrimination. *Journal of Neurophysiology, 95*, 255–270.

Lappin, J. S., Tadin, D., Nyquist, J. B., & Corn, A. L. (2009). Spatial and temporal limits of motion perception across variations in speed, eccentricity, and low vision. *Journal of Vision, 9*(1). 30, 31–14.

Matthews, N., Luber, B., Qian, N., & Lisanby, S. H. (2001). Transcranial magnetic stimulation differentially affects speed and direction judgments. *Experimental Brain Research, 140*, 397–406.

Matthews, N., & Qian, N. (1999). Axis-of-motion affects direction discrimination, not speed discrimination. *Vision Research, 39*, 2205–2211.

Mikami, A., Newsome, W. T., & Wurtz, R. H. (1986a). Motion selectivity in Macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. *Journal of Neurophysiology, 55*, 1308–1327.

Mikami, A., Newsome, W. T., & Wurtz, R. H. (1986b). Motion selectivity in Macaque visual cortex. II. Spatiotemporal range of directional interactions in MT and V1. *Journal of Neurophysiology, 55*, 1328–1339.

Norman, H. F., Norman, J. F., Todd, J. T., & Lindsey, D. T. (1996). Spatial interactions in perceived speed. *Perception, 25*, 815–830.

Pack, C. C., Hunter, J. N., & Born, R. T. (2005). Contrast dependence of suppressive influences in cortical area MT of alert macaque. *Journal of Neurophysiology, 93*, 1809–1815.

Paffen, C. L., van der Smagt, M. J., te Pas, S. F., & Verstraten, F. A. (2005). Center–surround inhibition and facilitation as a function of size and contrast at multiple levels of visual motion processing. *Journal of Vision, 5*, 571–578.

Pavlova, M., & Sokolov, A. (2000). Speed perception is affected by the Ebbinghaus–Titchener illusion. *Perception, 29*, 1203–1208.

Priebe, N. J., & Lisberger, S. G. (2004). Estimating target speed from the population response in visual area MT. *Journal of Neuroscience, 24*(8), 1907–1916.

Raiguel, S., Van Hulle, M. M., Xiao, D. K., Marcar, V. L., & Orban, G. A. (1995). Shape and spatial distribution of receptive fields and antagonistic motion surrounds in the middle temporal area (V5) of the macaque. *European Journal of Neuroscience, 7*, 2064–2082.

Rodman, H. R., & Albright, T. D. (1987). Coding of visual stimulus velocity in area MT of the macaque. *Vision Research, 27*, 2035–2048.

Ryan, J., & Zanker, J. M. (2001). What determines the perceived speed of dots moving within apertures? *Experimental Brain Research, 141*, 79–87.

Snowden, R. J., & Hammett, S. T. (1998). The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination. *Vision Research, 38*, 1935–1945.

Snowden, R. J., Treue, S., & Andersen, R. A. (1992). The response of neurons in areas V1 and MT of the alert rhesus monkey to moving random dot patterns. *Experimental Brain Research, 88*, 389–400.

Stone, L. S., & Thompson, P. (1992). Human speed perception is contrast dependent. *Vision Research, 32*, 1535–1549.

Tadin, D., Lappin, J. S., Gilroy, L. A., & Blake, R. (2003). Perceptual consequences of centre–surround antagonism in visual motion processing. *Nature, 424*, 312–315.

Takeuchi, T., & De Valois, K. K. (2000). Modulation of perceived contrast by a moving surround. *Vision Research, 40*, 2697–2709.

Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research, 22*, 377–380.

Thompson, P., Brooks, K., & Hammett, S. T. (2006). Speed can go up as well as down at low contrast: Implications for models of motion perception. *Vision Research, 46*, 782–786.

Turatto, M., Vescovi, M., & Valsecchi, M. (2007). Attention makes moving objects be perceived to move faster. *Vision Research, 47*, 166–178.

Xiao, D. K., Raiguel, S., Marcar, V., & Orban, G. A. (1998). Influence of stimulus speed upon the antagonistic surrounds of area MT/V5 neurons. *Neuroreport, 9*(7), 1321–1326.