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Perceived speed in peripheral vision can go up or down

Omar Hassan
Department of Psychology,
Royal Holloway University of London, London, UK

Peter Thompson
Department of Psychology, University of York, York, UK

Stephen T. Hammett
Department of Psychology,
Royal Holloway University of London, London, UK

We measured the perceived speed and contrast of patterns in peripheral vision relative to foveal patterns for a range of eccentricities at both mesopic and photopic levels. The results indicate that perceived speed varies with eccentricity, speed, and luminance. At high (photopic) luminance, patterns appear slower when viewed peripherally rather than foveally, but at low (mesopic) luminance fast-moving patterns can appear faster when viewed peripherally. When perceived contrast is equated, perceived speed reduces as a function of eccentricity in a speed-independent manner. Peripheral stimuli appear faster or slower than foveal stimuli depending upon luminance—an image parameter known to influence the gain of magno and parvocellular cells. We conclude that speed encoding in the periphery is consistent with a ratio-type speed code that is weighted by ganglion cell density.

Introduction

Peripherally viewed moving stimuli often appear slower than their foveal analogues. This effect may have been reported first by Czermak (1854), (see LeGrand, 1967; Tynan & Sekuler, 1982) and has been "rediscovered" several times since (Campbell & Maffei, 1979, 1981; Cohen, 1965; Lichtenstein, 1963). MacKay (1982) confirmed that moving stimuli in near-peripheral vision (<10° from the fixation point) can slow and stop and yet their spatial structure can still be resolved. Moving into the far periphery (30°–70°), Hunzelmann and Spillmann (1984) confirmed the slowdown in the perceived speed of moving stimuli in peripheral vision and also observed that the apparent contrast of these stimuli was reduced. Johnston and Wright (1986) also reported that perceived speed reduced in the periphery and demonstrated that, at least within the range of speeds tested, the reduction in perceived speed can be accounted for by the reduction in spatial grain in peripheral vision. Indeed, they report that the spatial scaling factor required to account for the reduction in perceived speed is proportional to the change in mean cortical receptive field area of the macaque (Dow et al., 1981) as a function of eccentricity. Thus they conclude that the reduction in perceived speed in the periphery is determined by changes in spatial scale. Indeed, a range of findings are consistent with the notion that biases in motion can be accounted for by M scaling, for instance, nulling of the motion aftereffect (Johnston & Wright, 1983) and velocity discrimination thresholds (McKee & Nakayama, 1984) are found to be consistent across eccentricity once M scaling is accounted for.

However, there may be other ways in which the reduction in perceived speed that is typically found in the periphery may be accounted for. One possibility is that the encoding of nonspatial image attributes known to bias perceived speed may vary with eccentricity. For instance, if it is the case that peripherally viewed moving stimuli appear reduced in contrast (Hunzelmann & Spillmann, 1984) then their slowed speed might, at least in part, be due to the well-established finding that slowly moving patterns (< 8 Hz) generally appear to move more slowly at low contrast (Stone & Thompson, 1992; Thompson, 1976, 1982). Moreover, the notion that changes in perceived speed are determined by changes in spatial scale overlooks the heterogeneity of temporal filtering as a function of eccentricity. As well as mean receptive field area, the proportion of midget-parasol cells also varies greatly with retinal eccentricity (Dacey, 1994) and the consequent changes in temporal filtering may well have a bearing upon the encoding of speed. This change in the ratio of midget-parasol cells may be particularly important if, as has previously been suggested (e.g., De Valois, Cottaris, Mahon, Elfar, & Wilson, 2000; Hammett, Thompson, & Bedingham,

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2000; Harris, 1986; Smith & Edgar, 1994; Tolhurst, Sharpe, & Hart, 1973), speed is encoded as the ratio of two mechanisms tuned to low (slow) and high (fast) temporal frequencies. Clear physiological candidates for these slow and fast mechanisms are the magnocellular and parvocellular pathways that are driven by the parasol and midget cells respectively (Kaplan & Shapley, 1986). Findings consistent with such a ratio scheme include the effects of adaptation and contrast upon perceived speed (e.g., Thompson, 1976, 1982; Thompson, Brooks, & Hammett, 2006) and the increase in perceived speed found at low luminance (Hammett, Champion, Thompson, & Morland, 2007; Hassan & Hammett, 2015). Hammett et al. (2007) found that the perceived speed of mesopic gratings drifting at moderate and higher speeds (> 4 Hz) was greater than that of photopic stimuli. Given that the sensitivity of the parvocellular pathway is significantly compromised at low luminance but that of the magnocellular pathway is relatively unaffected (Purpura, Kaplan, & Shapley, 1988), they reasoned (assuming that speed is encoded by the ratio of magnocellular and parvocellular activity) that the increase in perceived speed found at low luminance is consistent with the relative increase in magnocellular activity at mesopic levels. Similarly, assuming that the ratio of magnocellular and parvocellular activity contributes to the code for speed, we predict that the increase in the proportion of active magnocellular cells in peripheral vision should yield an increase in the perceived speed of eccentric stimuli at low luminance relative to that found at the same eccentricity at higher luminance.

In Experiment 1 we tested the hypothesis that the perceived slowing of stimuli in peripheral vision can be accounted for entirely in a reduction in perceived contrast by measuring the effect of eccentricity upon perceived speed under conditions where perceived contrast was constant as eccentricity varied. In Experiment 2 we measured perceived speed at a range of eccentricities at both photopic and mesopic levels to establish whether perceived speed increased in peripheral vision at low luminance.

Experiment 1a: Perceived contrast in the periphery

Methods

Subjects

Four subjects (two female) aged between 22 and 27 years participated in this experiment. One of the subjects (OH) was an author; the other three were naïve to the purpose of the experiment. All subjects had normal or corrected-to-normal acuity.

Apparatus and stimuli

All stimuli were horizontally oriented sinusoidal gratings of 2 c/° generated using MATLAB 7.11 (MathWorks, Cambridge, UK) and displayed on an EIZO 6600-M (Hakusan, Ishikawa, Japan) monochrome monitor at a frame rate of 100 Hz and a resolution of 1152×864 (dot pitch $= 0.33$). The monitor was gamma corrected using the CRS Optical photometric system (Cambridge Research Systems, Rochester, UK). The display subtended $68° \times 47°$ at a viewing distance of 28.5 cm. Viewing distance was controlled by use of a headrest and chinrest. Mean luminance was 25 cd m^{-2}. On each trial stimuli were presented simultaneously for 500 ms in elliptical windows with sharp edges that subtended 2° horizontally by 4° vertically. A small bright fixation spot was situated at the center of the display. The standard pattern was situated at the center of the display and the test pattern was situated to the right of the standard pattern centered at one of four eccentricities (6°, 12°, 24°, and 32°). The stimuli drifted downward at one of four speeds (1, 2, 4, and 6°/s). The Michelson contrast of the standard pattern was 0.1 and the contrast of the test pattern was altered by a QUEST routine (Watson & Pelli, 1983) depending on the subject's responses.

Procedure

Subjects adapted to a blank screen of mean luminance for at least 5 min at the beginning of each session. The subject's task was to indicate which pattern (standard or test) appeared to have greater contrast by pressing a mouse button. A blank screen of mean luminance was presented between each trial and subjects pressed a mouse button in order to initiate each trial. For each block the QUEST procedure was terminated after 50 trials, the data were fit to a cumulative Gaussian function using the method of least squares and the 50% point of the function was estimated. The average of five such estimates was taken as the point of subjective equality (PSE) for each speed and eccentricity. The order of each speed and eccentricity estimate was randomized.

A control, foveal condition also was run in which stimuli were presented sequentially at the center of the display for 500 ms with an interstimulus interval of 500 ms; the mean of three estimates was taken as the PSE for each speed. The experiments were conducted binocularly in a semidarkened room using a chinrest and headrest.

Results and discussion

Figure 1 plots the average contrast match as a function of speed for each eccentricity. Consistent with the qualitative reports of Hunzelmann and Spillmann

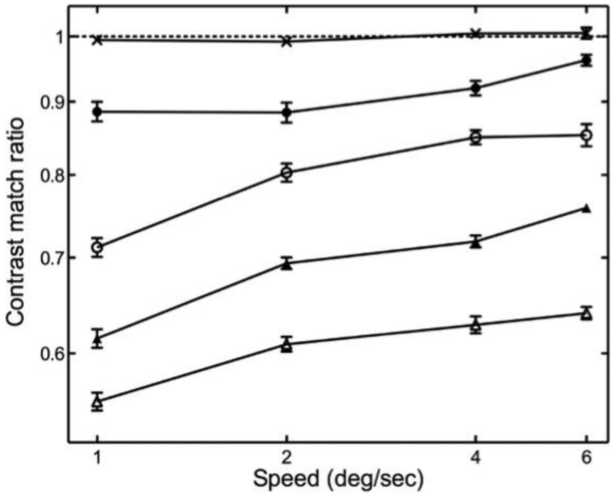

Figure 1. The ratio of physical and matched contrasts is plotted as a function of speed at four eccentricities: 0° the control condition (crosses), 6° (closed circles), 12° (open circles), 24° (closed triangles), and 32° (open triangles). A value of 1.0 (broken line) represents a veridical estimate. Values greater than 1 indicate an overestimation of contrast, values less than 1 indicate an underestimation of contrast. Symbols represent the mean of four subjects; error bars represent ±1 *SEM*.

(1984), we find that perceived contrast is reduced in peripheral vision. The results indicate that subjects accurately matched the contrast of patterns in foveal vision but underestimated the contrast of patterns in the periphery. A two-way repeated-measures analysis of variance (ANOVA) revealed a significant main effect of speed, $F(3, 9) = 99.53$, $p < 0.001$; a significant main effect of eccentricity, $F(4, 12) = 383.24$, $p < 0.001$; and a significant interaction between speed and eccentricity, $F(12, 36) = 7.29$, $p < 0.001$. The further into the periphery the test stimuli were, the greater the underestimation of contrast. Furthermore, at all eccentricities the slower the speed of the stimuli, the more their contrast is underestimated. Thus, changes in perceived contrast as a function of eccentricity and speed may play a role in the known perceptual biases in speed that accompany peripheral viewing. We test this possibility in Experiment 1b.

Experiment 1b: Perceived speed in the periphery at equal physical and perceived contrast

Methods

The experimental details were identical to those described for Experiment 1a except that the subject's task was to indicate which pattern appeared faster, and the speed of the test pattern was altered by a QUEST routine depending upon the subject's response. Perceived speed was measured for stimuli of both equal physical and equal perceived contrast. In the equal physical contrast condition, the contrast of both patterns was fixed at 0.1. In the equal perceived contrast condition, the contrast of the standard pattern was set at 0.1 and the contrast of the test pattern was set to that of the subject's contrast match value estimated in Experiment 1a. Five (three in the control condition) estimates were taken for each speed and eccentricity, the order of each being effectively randomized.

Results

Figure 2 plots the perceived speed matches at equal physical and equal perceived contrast as a function of speed for each eccentricity. The results indicate that subjects progressively underestimated the speed of patterns as eccentricity increased. Equalizing the perceived contrast of the patterns reduced the effect of peripheral viewing on this perceptual slowdown at slower speeds such that all speeds suffered a similar reduction in perceived speed at any particular eccentricity. For foveal stimuli (0°) there was no significant difference between speed matches and veridical speed ($t = -0.94$, $df = 15$, $p = 0.358$, one sample, two-tailed). However, at all eccentricities tested, the perceived speed of stimuli with equalized perceived contrast was significantly lower than veridical ($t = -5.05$, $df = 15$, $p <$

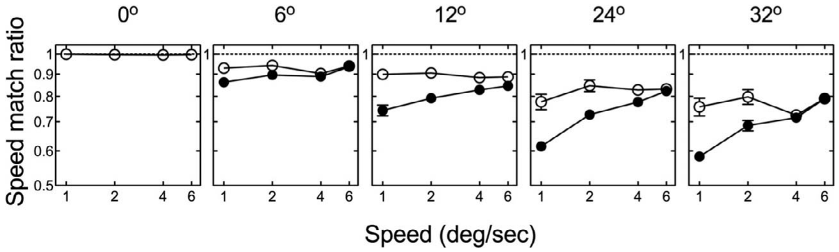

Figure 2. Average perceived speed at equal physical contrast (closed symbols) and equal perceived contrast (open symbols) as a function of physical speed for a range of eccentricities (indicated above panels). A value of 1 (broken line) represents a veridical speed estimate. Values less than 1 indicate an underestimation of matched speed. Error bars represent ±1 *SEM*.

0.001 at 6°; $t = -7.20$, $df = 15$, $p < 0.001$ at 12°; $t = -7.23$, $df = 15$, $p < 0.001$ at 24°; and $t = -9.24$, $df = 15$, $p < 0.001$ at 32°, one sample, two-tailed). Thus changes in perceived contrast as a function of eccentricity cannot exclusively account for the reduction in perceived speed in peripheral vision.

A three-way (speed, contrast, and eccentricity) repeated-measures ANOVA revealed no significant main effect of speed, $F(3, 9) = 2.43$, $p = 0.132$; a significant main effect of contrast, $F(1, 3) = 16.77$, $p < 0.05$; a significant main effect of eccentricity, $F(3, 9) = 57.92$, $p < 0.001$; a significant interaction between speed and contrast, $F(3, 9) = 12.76$, $p < 0.010$; no significant interaction between speed and eccentricity, $F(9, 27) = 1.70$, $p = 0.137$; no significant interaction between contrast and eccentricity, $F(3, 9) = 2.58$, $p = 0.118$; and no significant interaction between speed, contrast, and eccentricity, $F(9, 27) = 1.25$, $p = 0.306$. This pattern of results suggests that there are two components contributing to the reductions in perceived speed observed. First there appears to be a component that is independent of speed and contrast but increases with eccentricity. Secondly there is a component that can be ascribed to the well-known effect of low contrast on perceived speed. Its effect is greatest at the lowest speeds and appears to make no contribution at 6°/s.

Experiment 2: Effect of luminance on peripheral speed perception

Introduction

The results of Experiment 1 indicate that the reduction in perceived contrast that accompanies increasing eccentricity can account for some of the perceptual slowing down of moving patterns in the periphery. However, when one accounts for this contrast-induced reduction in perceived speed by equalizing the perceived contrast of peripherally presented patterns the results indicate that eccentric patterns are still perceived as slower—around 10% slower at 6° and 20% slower at 32°.

How might one account for this residual effect of eccentricity upon perceived speed? One possibility is that the known changes in the ratio of M and P cells with eccentricity (Dacey, 1994) contribute to this effect. It is known that the contrast gain of P cells is more greatly reduced than that of M cells as luminance is reduced (Purpura et al., 1988). Should the effect of eccentricity on perceived speed be in part mediated by the changing ratio of M and P cells, this should result in an increase rather than decrease in perceived speed under conditions where the response of M cells prevails—at low luminance (Purpura et al., 1988), low spatial frequency (Derrington & Lennie, 1984), and large eccentricities (Dacey, 1994). To investigate this notion further we estimated perceived speed as a function of eccentricity at both high and low luminance at the relatively low spatial frequency of 1 c/°.

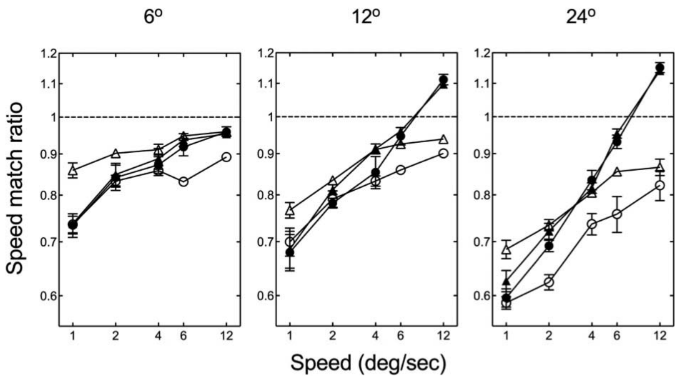

Figure 3. Average speed matching at high (open symbols) and low (closed symbols) luminance for 0.1:0.1 (circles) and 0.7:0.7 (triangles) contrast stimuli plotted as a function of speed. Test grating eccentricity is indicated above panels. The broken horizontal line represents a veridical speed estimate. Speed match values greater than 1 indicate an overestimation of matched speed; values less than 1 indicate an underestimation of matched speed. Error bars represent ±1 *SEM*.

Methods

The experimental details were essentially similar to those of Experiment 1b except that all stimuli had a spatial frequency of 1 c/°, perceived speed was estimated for two (physical) contrasts (0.1 and 0.7), at two luminance levels (2.5 cd m^{-2} and 25 cd m^{-2}), and three eccentricities (6°, 12°, and 24°). During the low luminance conditions 1 log unit neutral density filters (NDF; Thorlabs Inc., Newton, NJ) were inserted into optometrist drop-cell trial frames (Skeoch, Sussex, UK) that were worn by the subjects in all conditions.

Results

Figure 3 plots the speed matches as a function of speed for high and low luminance and contrast at three eccentricities. At high luminance (open symbols), as the test stimuli moved further into the periphery, there was an increase in the underestimation of perceived speed for all speeds tested, confirming the results of Experiment 1b, Figure 2. At low luminance (closed symbols), in the near-periphery (6° eccentricity) the data showed similar underestimation of perceived speed as at high luminance. Further into the periphery (12° and 24°) an underestimation of perceived speed occurred only for slow moving stimuli ($< 6°/s$). For faster moving stimuli (12°/s), perceived speed was overestimated.

At high luminance (open symbols) a reduction in contrast of both the standard and test gratings from 0.7 (open triangles) to 0.1 (open circles) showed an increase in the underestimation of perceived speed, across all eccentricities and for all speeds tested. At low luminance (filled symbols) the reduction in contrast did not appear to affect the perceived speed.

These effects of eccentricity, speed, contrast, and luminance proved to be significant: A four-way repeated-measures ANOVA revealed a significant main effect of eccentricity: $F(2, 6) = 104.34$, $p < 0.00$; contrast: $F(1, 3) = 336.49$, $p < 0.001$; luminance: $F(1, 3) = 24.70$, $p < 0.05$; and speed: $F(4, 12) = 206.73$, $p < 0.001$. Significant interactions between eccentricity and luminance, $F(2, 6) = 121.37$, $p < 0.001$, and eccentricity and speed, $F(8, 24) = 16.09$, $p < 0.001$, indicated that the effect of varying luminance and speed was contingent upon eccentricity and significant interaction between luminance and contrast, $F(1, 3) = 169.15$, $p < 0.010$; and luminance and speed, $F(4, 12) = 62.14$, $p < 0.001$, indicated that the effect of varying speed and contrast was contingent upon luminance.

Discussion

Moving stimuli in peripheral vision appear to move slower and have reduced contrast compared with foveally presented stimuli. In Experiment 1 we measured whether this perceived slowing of eccentric stimuli might be due to a concomitant reduction in perceived contrast. The results indicate that, consistent with Hunzelmann and Spillmann's (1984) report, perceived contrast is attenuated in the periphery. However, when perceived contrast is equalized across eccentricities, perceived speed is still significantly slower in peripheral vision, indicating that the perceived slowing of peripheral stimuli is not just an artefact of reduced perceived contrast. When perceived contrast is equalized, this reduction in perceived speed is roughly equal at all speeds at any given eccentricity but increases with eccentricity.

In Experiment 2 we measured perceived speed in the periphery at both high and low luminance. The results of Experiment 2 indicate that at high luminance perceived speed was reduced as eccentricity increased, consistent with previous research (Campbell & Maffei, 1979, 1981; Cohen, 1965; Hunzelmann & Spillmann, 1984; Lichtenstein, 1963; MacKay, 1982; Tynan & Sekuler, 1982). This underestimation of speed was greater at low contrast. At lower luminance, the speed of slower moving stimuli ($< 6°/s$) was similarly underestimated with increasing eccentricity. However, the speed of faster moving stimuli was overestimated ($> 6°/s$) at the two highest eccentricities. At low luminance, the pattern of results was essentially similar at both low and high contrast. We can discern no clear explanation for these differences in contrast dependency across luminance conditions.

How may the general reduction in perceived speed found at high luminance come about? We and others (e.g., De Valois et al., 2000; Hammett et al., 2000; Harris, 1986; Smith & Edgar, 1994; Tolhurst et al., 1973) have previously speculated that the code for speed may be related to the relative activity of magnocellular and parvocellular populations. Since these are driven by retinal parasol and midget cells, respectively (Kaplan & Shapley, 1986) changes in the ratio of these populations should yield at least a qualitative prediction of how perceived speed changes with eccentricity. However, inspection of the relative densities of midget and parasol cells as a function of eccentricity poses a serious problem for such ratio models. The proportion of midget cells decreases from around 90% near the fovea to around 50% in the far periphery (approximately 52°), whereas the density of parasol cells increases from around 6% in the fovea to around 25% in the far periphery (Dacey, 1994; see also Watson, 2014 for corroborative estimates of midget cell densities). Thus traditional ratio models would predict that perceived speed in the periphery should increase given the increased proportion of parasol cells. Johnston and Wright (1986) have suggested that the reduction in perceived speed may be a result of the changing spatial scaling with eccentricity. Although their findings and ours (at high luminance) are entirely consistent with such a scheme, they cannot be easily reconciled with our additional finding that perceived speed in the periphery can *increase* at low luminance. Thus neither extant ratio models, nor spatial scaling approaches can account for our current findings alone.

However, it is possible to reconcile both approaches by postulating that *absolute* levels of neural activity may bias speed encoding such that speed is underestimated if fewer units are active. Although the *proportion* of parasol cells increases with eccentricity, total ganglion cell density falls from around 27,860 cells/mm^2 in the fovea to 1080 cells/mm^2 at 24° eccentricity (estimated from figure 3A of Dacey, 1994). Moreover, since ganglion cell density is inversely proportional to ganglion cell receptive field area (Peichl & Wassle, 1979), any change in absolute levels of neural activity also would be accompanied by a change in spatial scaling. If absolute levels of neural activity serves to modulate the speed code with eccentricity then speed-dependent biases in perceived speed would also correlate well with changes in spatial scale in the periphery. However, if the relative activity of magnocellular and parvocellular pathways also is implicated in speed encoding, then increases in perceived speed should be observable under conditions where parvocellular activity is reduced. We find clear evidence for such an increase in perceived speed in the periphery under conditions (low luminance and spatial frequency) designed to reduce parvocellular activity. Since reducing luminance reduces the contrast gain of the parvocellular system far more than that of the magnocellular system (Purpura et al., 1988), we predicted that reducing luminance should lead to an increase in perceived speed in the periphery. The present results are consistent with a scheme whereby a local code for speed reflects both the absolute level of neural activity and the relative activity of magnocellular and parvocellular pathways. However, we cannot rule out the contribution of other mechanisms to the biases in perceived speed found in the periphery. Two clear possibilities are the influence of perceived spatial frequency (Georgeson, 1980) and centrifugal bias to perceived peripheral speed (Zhang, Kwon, & Tadin, 2013). Zhang et al. (2013) have reported large biases in the perception of the direction of motion away from the fovea. Their stimuli were at very large eccentricities (40°) and presented for very brief durations but we cannot rule out the possibility that such direction biases do not modulate perceived speed in our stimuli. It is also possible that changes in perceived spatial frequency with eccentricity (Georgeson, 1980) could induce biases in perceived speed since perceived speed is known to be increased by increasing spatial frequency (e.g., Brooks, Morris, and Thompson, 2011). However, it seems this is unlikely to explain both the *reduction* in perceived speed found at high luminance and the *increase* found at low luminance given that perceived spatial frequency increases with both increases in eccentricity and reductions in luminance (Georgeson, 1980).

We conclude that while the precise source(s) of the biases in perceived speed in peripheral vision are uncertain, they are consistent with a scheme whereby a local code for speed is derived from the ratio of low and high temporal frequency filters that is weighted by absolute cell density.

Keywords: speed, contrast, luminance, periphery

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Corresponding author: Stephen T. Hammett.
Email: s.hammett@rhul.ac.uk.
Address: Department of Psychology, Royal Holloway University of London, UK.

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