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Brief communication

Speed can go up as well as down at low contrast: Implications for models of motion perception

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Abstract

It is well-known that reducing the contrast of a slow moving stimulus reduces its apparent speed. [Thompson, P. (1982). Perceived rate of movement depends on contrast. *Vision Research, 22*, 377–380.] report of this finding also suggested that at speeds above 8 cycles/s reducing contrast increased perceived speed. However in a later report, Stone and Thompson (1992), using a more rigorous, forced-choice procedure, failed to collect reliable data at these higher speeds. Here, we confirm that faster moving stimuli can appear to move faster than their true speed at low contrasts and we propose a physiologically plausible ratio model that unlike recent Bayesian models (e.g. Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience, 5*, 598–604) can account well for the results.
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1. Introduction

Since Thompson (1976, 1982) first reported that perceived speed depends on stimulus contrast there have been more than a dozen papers that have supported his findings that at slow speeds reducing contrast reduces perceived speed (examples being, Blakemore & Snowden, 1999; Brooks, 2001; Hurliman, Kiper, & Carandini, 2002; Muller & Greenlee, 1994).

If the question of the effect of reducing contrast at slow speed is now satisfactorily resolved, what of the effects at higher speeds? Thompson (1976, 1982) reported that as temporal frequency increased the effects of contrast were reduced until at some point, around 8 cycles/s, perceived speed was unaffected by contrast. However at still higher temporal frequencies he reported that reducing contrast results in speed being overesti-

mated. Hawken, Gegenfurtner, and Tang (1994) provide some support for this position in experiments that examined the contrast dependence of both luminance and colour defined moving stimuli. While they write that '*motion perception of moderate to fast movement is invariant to changes in contrast …,*' nonetheless their data (Hawken et al. (1994) Fig. 1C) suggest that lower contrasts might look faster at 8 deg/s.

Although the issue of whether the speed of faster rates of movement is susceptible to contrast is less clear, it is nonetheless a matter of some importance in formulating any model of speed processing. For example, Weiss, Simoncelli, and Adelson (2002) state that their Bayesian model does not predict any increase in speed at reduced contrasts, as reducing contrast always increases the influence of a slow speed 'prior.' Indeed Weiss et al. (2002) state this explicitly: "*One result* (Thompson, 1982) *that is not predicted by our model is the finding that low contrast gratings actually appear to move faster than high-contrast gratings for temporal*

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frequencies above 8 Hz." They continue "*However the same author* (Stone & Thompson, 1992) *later was unable to reproduce this result using a forced choice task, and concluded that the original finding was probably 'an artifact of the experimental method with subjects making 'speed' matches based on some other criterion.*'"

While it is true that Stone and Thompson (1992) failed to find an increase in perceived speed at low contrasts, they did report that "*. . . the task became very difficult for one subject and impossible for another at temporal frequencies above 10 Hz.*" They ran a total of three subjects.

Not all Bayesian models make the same predictions. Ascher and Grzywacz's (2000) model "*shows the same qualitative behaviour as human* observers (see for example Figs. 1 and 2 in Thompson, 1982). *Specifically at low contrast, the model underestimates perceived velocity at low velocities, and overestimates it at high velocities.*" Ascher and Grzywacz (2000, p. 3421). However this seeming support for Thompson's results needs to be treated with caution, as inspection of Ascher and Grzywacz's Fig. 4 reveals. First, their model predicts only marginal shifts from the veridical over a very wide range of velocities (from 2 to 16 cpd according to the figure. We assume the authors intended deg/s). Second, even at more extreme speeds, any significant effect is only predicted at very low contrasts; by contrasts of 8% the velocity effects are little more than 2% at best. Thompson's results were obtained with contrasts over 10%. Further, this model only predicts an effect at very low or high speeds, between 2 and 8 deg/s the model predicts virtually veridical speed perception at all contrast levels. This is clearly not consistent with the psychophysical results. We therefore feel that the Ascher and Grzywacz model does not give a good account of the data.

In the course of other experiments (Thompson, Stone, & Brooks, 1995) we found further evidence that at higher velocities, perceived speed may be over-estimated as contrast falls. Given the theoretical importance of the effects of contrast on faster speeds we have designed the present experiments to re-examine this question in an attempt to resolve the issue.

2. Methods

We measured the effects of contrast on speed in forced-choice experiments with stimuli presented foveally in two successive intervals, separated by a 500 ms period of mean luminance. Stimuli were generated by a Cambridge Research Systems VSG 2.5 and displayed on a Barco Calibrator display. Observers fixated briefly-presented (500 ms) patches of vertically drifting horizontal monochrome (grey) sinusoidal gratings. Each grating patch was an ellipse with sharp edges, 2 deg horizontally by 1 deg vertically, with a small central fixation spot. The mean luminance of the screen was 80 cd/m^2 throughout. On each trial, one of the patches drifted at a 'standard' speed while the speed of the other, 'test,' grating was stair-cased by a PEST routine (Findlay, 1978). The stair-case was terminated after 12 reversals and the mean of the last 8 reversals was taken as the point of subjectively equal speed. The direction of drift of the standard was randomly assigned to be either up or down, with the direction of the test grating being in the same direction. In every trial the order of presentation of the standard and test stimuli was randomised. Four staircases were interleaved in any one session with different contrast pairs; in two baseline conditions both standard and test gratings were of equal contrast, 10 and 70%. Two mixed contrast conditions were also run: one with standard 10% and test 70% contrast, the other with standard 70% and test 10% contrast. Five temporal frequencies of the standard grating (2, 4, 8, 12 and 16 cycles/s) were investigated in separate sessions. The whole experiment was conducted at two spatial frequencies, 2 and 8 cycles/deg. Four subjects (all naïve) repeated each condition four times. The order of all sessions was randomised.

3. Results

The results for both spatial frequencies are shown in Fig. 1. In the baseline conditions, in which both standard and test gratings were of equal contrast, the PSE was always within 5% of the veridical match. However, when gratings of unequal contrast were matched for speed consistent biases emerged. At 2 cycles/deg, lower contrast stimuli appear slower at low temporal frequencies (2 and 4 cycles/s) but appear to move faster at higher temporal frequencies (12 and 16 cycles/s). At low temporal frequencies, these results merely confirm the well-established finding but at high temporal frequencies, the finding that reducing contrast can increase perceived speed provides confirmation of Thompson's (1976, 1982) finding but with a forced-choice procedure. The results at 8 cycles/deg show a similar pattern.

Different models of speed perception make clear and different predictions of what should happen when contrast is reduced at higher speeds. Thompson's original (Thompson, 1982) position was that velocity was computed by a ratio (or at least a comparison) of a putative high speed channel and a slow speed channel (Harris, 1980), and that reducing contrast would reduce the influence of the high speed channel at low speeds and reduce the influence of the low speed channel at high speeds.

No details of this model were given in the original paper but we now present a plausible ratio model based on more recent knowledge. The computation of speed is based on the ratio of a low pass and a band pass
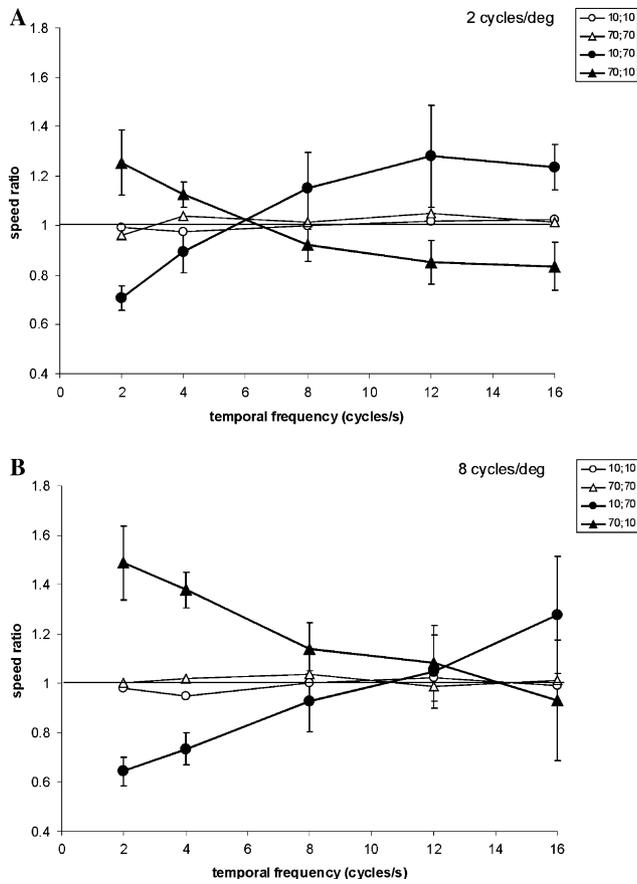
Fig. 1. Speed matching at different contrasts. (A) All stimuli 2 cycles/deg. (B) All stimuli 8 cycles/deg. Results are the mean of the same 4 naïve subjects in both conditions. Error bars show ±1 standard deviation. Open symbols show control conditions matching speeds at equal contrast. Filled circles show speed matches of 0.7 contrast gratings stair-cased to match speed of 0.1 contrast standard. Filled triangles show speed matches of 0.1 contrast gratings stair-cased to match speed of 0.7 contrast standard.

temporal filter described by Perrone (2005) and follows his nomenclature.

Following Perrone (2005) the low-pass filter, p, takes the form

$$p(\omega) = \sqrt{a^2 + b^2},$$

where

$$a = ((2\pi\omega\tau_1)^2 + 1)^{-\frac{9}{2}} \text{ and } b = ((2\pi\omega\tau_2)^2 + 1)^{-\frac{10}{2}}.$$

The parameters τ_1 and τ_2 are time constants, measured in seconds.

The high-pass filter, m is given by

$$m(\omega) = \frac{\omega}{k} p(\omega).$$

We have used Perrone's values of 0.0072, 0.0043 and 4 for τ_1, τ_2 and k, respectively. These filters (see Fig. 2) are in good agreement with tuning properties of cortical cells in the primate (Foster, Gaska, Nagler, & Pollen, 1985; Hawken, Shapley, & Grosof, 1996). We have
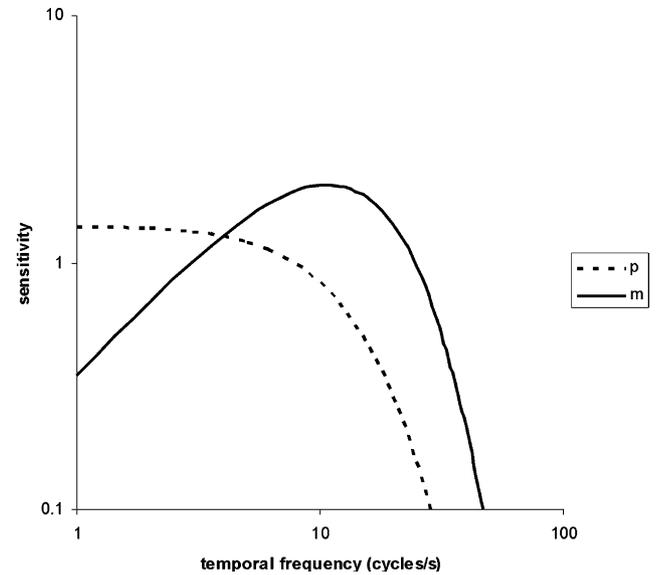

Fig. 2. Temporal sensitivity functions of the Perrone p and m filters used in our model.

assumed that the outputs of these filters are frequency-contrast inseparable. We have therefore used a modified form of the Naka-Rushton equation so that each filter's output is described by a non-linear function of the product of contrast and temporal frequency such that:

$$p(\omega, c) = \frac{\bar{p}(\omega).c}{|\bar{p}(\omega).c| + s_p},$$

and

$$m(\omega, c) = \frac{\bar{m}(\omega).c}{|\bar{m}(\omega).c| + s_m},$$

where $\bar{p}(\omega)$ and $\bar{m}(\omega)$ are the sensitivities of the low- and band-pass filters at frequency ω. The semi-saturation constants of the filters are s_p and s_m, and c is contrast. Speed, S, is given by the ratio of the outputs of these filters such that

$$S = \frac{m(\omega, c)}{p(\omega, c)}.$$

Thus, the model has just two free parameters, s_p and s_m, that represent the semi-saturation constants of the two filters. We found the best (least squares) fit of the model to the data (averaged across all subjects) using the error minimization routine ("solver") in Microsoft Excel 98. Independent fits were calculated for each condition (i.e., for all speeds but independently for contrast polarity and spatial frequency). The resultant fits are plotted in Fig. 3. The model predicts veridical performance for the control conditions and consequently these are omitted for clarity. The fits are very close to psychophysical performance for all conditions and speeds measured. The values of the free parameters (representing the semi-saturation constants, s_p and s_m) ranged from
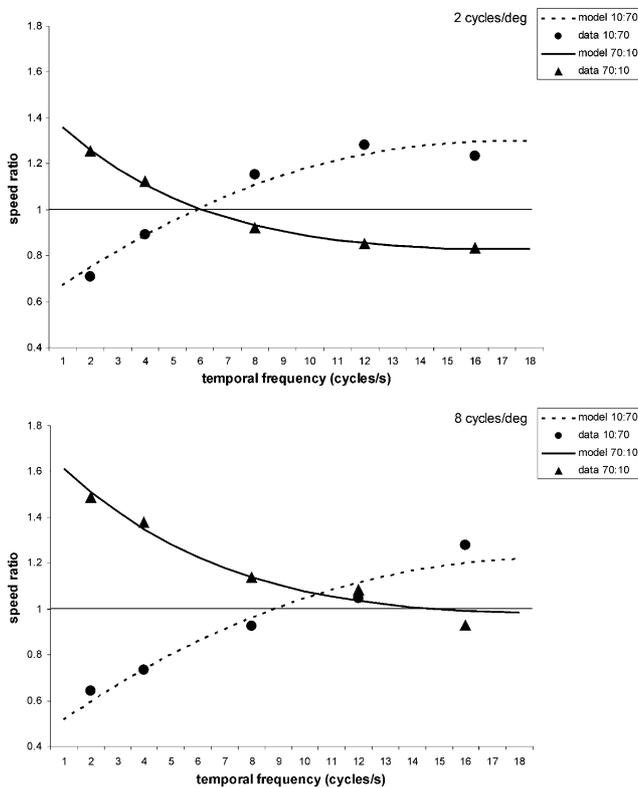
Fig. 3. The best fit of ratio model to the data shown in Fig. 1. Baseline data and fits are not shown as the model predicts veridical perception of speed. Actual matches were within 5% of veridical. Note the model has only two free parameters.

0.44 to 1.48–well within the range of physiologically plausible values of the semi-saturation constants for parvo- and magno-cellular cells (cf. Kaplan & Shapley, 1986, who found average semi-saturation constants of 0.13 and 1.74 for magnocellular- and parvocellular- projecting ganglion cells, respectively).

4. Discussion

The results of this study carried out with somewhat more rigour than Thompson's original work largely support his earlier findings. At rates of movement above about 8 Hz it does seem that reducing contrast can lead to increases in perceived speed. In one regard the earlier work is not completely replicated. Thompson (1982) found that a very similar pattern of results was found over a range of spatial frequencies, from 1 to 8 cycles/deg, leading him to speculate that the effects of contrast on speed were tuned for temporal frequency and not for velocity. The present results are not so clear cut. The results at 2 cycles/deg (Fig. 1A) suggest that there is a rate of movement at which changes in contrast produce no change in perceived speed. This null point lies between 6 and 8 cycles/s, or 3–4 deg/s. The results at 8 cycles/ deg (Fig. 1B) show a null point at 10–14 cycles/s or

1.25–1.75 deg/s. Whether this null point is invariant with temporal frequency only future research will determine but it is certainly not invariant with velocity.

We conclude that a very simple ratio model, incorporating two physiologically plausible temporal filters and a physiologically plausible response function that assumes contrast-frequency inseparability can adequately account for both under- and over-estimations of perceived speed as a function of contrast. Given this, it seems unnecessary to adopt models that seeks to account for the data with ad hoc 'priors' (cf. Weiss et al. (2002)), particularly since such an approach cannot capture both increases and decreases in perceived speed simultaneously. Nor is it necessary to appeal to models where the predictions, though qualitatively in the right direction are far from quantitatively satisfactory e.g., Ascher and Grzywacz (2000).

In presenting our ratio model, we are not claiming that it represents the optimal model to describe the data available but merely that it provides a better description of the data within the framework of physiologically plausible mechanisms than other available models. To detail the model further will require further experiments, particularly experiments that investigate other circumstances where speed perception is non-veridical. We are currently exploring some of these possibilities.

Acknowledgments

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