

Perceptual distortions of speed at low luminance: Evidence inconsistent with a Bayesian account of speed encoding [☆]

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Abstract

Our perception of speed has been shown to be distorted under a number of viewing conditions. Recently the well-known reduction of perceived speed at low contrast has led to Bayesian models of speed perception that account for these distortions with a slow speed ‘prior’. To test the predictive, rather than the descriptive, power of the Bayesian approach we have investigated perceived speed at low luminance. Our results indicate that, for the mesopic and photopic range (0.13–30 cd m⁻²) the perceived speed of lower luminance patterns is virtually unaffected at low speeds (<4 deg s⁻¹) but is over-estimated at higher speeds (>4 deg s⁻¹). We show here that the results can be accounted for by an extension to a simple ratio model of speed encoding [Hammett, S. T., Champion, R. A., Morland, A. & Thompson, P. G. (2005). A ratio model of perceived speed in the human visual system. *Proceedings of Royal Society B*, 262, 2351–2356.] that takes account of known changes in neural responses as a function of luminance, contrast and temporal frequency. The results are not consistent with current Bayesian approaches to modelling speed encoding that postulate a slow speed prior.

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1. Introduction

How we encode motion in the human visual system has been a topic of research for many years and, although great progress has been made in determining the mechanisms underlying the motion direction, the question of how we compute speed has been harder to answer. Most attempts to understand how we compute speed have taken as a starting point our knowledge about the spatiotemporal filtering characteristics of neurons in visual cortex. By comparing the outputs of these neural filters, speed selective mecha-

nisms can be created. Such ‘ratio’ models of speed perception have a long history, from Exner (1888) through Harris (1980) and Thompson (1982) to Adelson and Bergen (1986). These models have been generally conceptual rather than quantitative in their approach. More recently we have developed a detailed model that assumes that speed is determined by the ratio of two mechanisms “tuned” to different temporal frequencies and with reference to known physiological mechanisms within the early visual pathway. This model can successfully account for the changes in perceived speed that occur following prolonged adaptation to movement and to the effects of reduced contrast on perceived speed (Hammett, Thompson, & Bedingham, 2000; Hammett, Champion, Morland, & Thompson, 2005; Thompson, Brooks, & Hammett, 2006).

Recently, a new type of model has emerged, one that exploits some characteristics of Bayesian statistics, to provide an explanation of some of the phenomena of our

[☆] A preliminary version of some of these findings was first presented at the European Conference on Visual Perception, 2003 (Bedingham, Hammett, & Thompson, 2003).

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speed perception (e.g. Ascher & Grzywacz, 2000; Weiss, Simoncelli, & Adelson, 2002). This development seemed timely; Bayesian models have been particularly influential in computer vision research as well as in experimentally based models of vision, and the notion that our interpretation of the visual world is heavily influenced by our expectations and experience is a commonplace, central to the ideas of vision scientists from Helmholtz, to Gregory, (see Knill & Richards, 1996 for many examples).

The application of this approach to speed perception proposes a speed ‘prior’, an expectation of speed, perhaps based on experience. By multiplying the observed speed distribution and the prior distribution together we generate a ‘posterior’ distribution that determines our perceived speed. Such models are faced with the problem of determining what the prior should be. In their exposition of the Bayesian model Stocker and Simoncelli (2006) concede that ‘*Bayesian models...are difficult to validate experimentally because one does not usually know the prior distribution or the likelihood function.*’ They go on to derive a prior distribution that is maximal at low speed and decreases monotonically with increasing stimulus speed, with the result that any reduction in our certainty about observed speed should be reflected in a lowering of our speed estimate, as the influence of the prior increases as our observed speed information is decreased.

This Bayesian model can, of course, explain why perceived speed is often reduced at low contrast and why speed in peripheral vision may be lower than in central vision, but the prior they derive is not successful in explaining circumstances in which perceived speed is increased under conditions of reduced information about speed. For example it has been shown that at low contrast, although perceived speed is reduced for slow rates of movement, it can be overestimated at faster rates (Thompson et al., 2006). How can this be accommodated within the Bayesian model? The best it can do is to mould the shape of the prior to the observed data. Therefore Stocker and Simoncelli (2006), faced with the possibility that reducing contrast does sometimes lead to increases in perceived speed, and reported that their model ‘*would be able to fit these behaviours with a prior that increases at high speeds.*’

One potential problem for such a Bayesian model is that it might be seen as little more than a re-description of the data with little predictive power, and Stocker and Simoncelli concede that ‘*in order to realize its potential for explaining biology*’ the model needs to make ‘*quantitative experimental testable predictions.*’ We have identified one situation where we feel the Bayesian model can make at least a qualitative prediction. If the influence of the ‘slow’ prior increases as the reliability of speed measurement decreases, then this Bayesian model must expect perceived speed to drop at low luminance. Encouragingly for the Bayesian approach, there is evidence that perceived speed is slowed at low luminance. Gegenfurtner, Mayser, and Sharpe (1999, 2000) have reported that rod-isolating patterns appear to move at about 75% of the speed of cone-de-

tected motion stimuli. However, rather than appealing to a Bayesian model, they suggest that this slowing down of rod-isolating stimuli may be due to retinal low-pass filtering that attenuates the subsequently extracted high velocity signal: They propose that the reduction in perceived speed is due to a relative increase in temporal averaging of rod signals compared with cone signals.

In this study we report here, we have measured the effect of altering luminance upon the perceived speed of sinusoidal gratings. We have restricted our measurements to photopic and mesopic light levels (Wyszecki & Stiles, 1982) rather than investigating the rod- and cone-isolating stimuli previously studied by Gegenfurtner et al.

Methods

1.1. Apparatus and stimuli

All stimuli were 1 cycle/deg horizontally orientated sinusoidal gratings generated on a VSG 2/3 W (Cambridge Research Systems) waveform generator and displayed on an EIZO 6600-M monochrome monitor at a frame rate of 100 Hz. The monitor was gamma corrected using the CRS optical photometric system. The Michelson contrast of all gratings was 0.5. Mean luminance was 30 cd m^{-2} for the high luminance conditions and 2.5 cd m^{-2} for the low luminance conditions. During test conditions a 1.3 log unit neutral density filter (NDF) was placed over the standard pattern to reduce its luminance further. To ensure ambient luminance was kept to a minimum the monitor was placed inside a near light-proof case with a light-protected viewing slot for observing. The active display was masked such that the stimuli were presented through two 6° diameter circular windows with hard edges. Each window was located equidistant from the horizontal centre of the screen and divided by a 1° septum. The viewing distance was 57 cm.

1.2. Procedure

Two patterns were presented simultaneously for 500 ms to the right and left of a central fixation point. The standard patterns (always presented on the left) were drifting in an upward direction at one of five speeds (1, 2, 4, 8, and 16 deg/sec). The speed of the test pattern was altered by a PEST routine (Taylor & Creelman, 1967) depending upon the subject’s responses. The PEST procedure was set to converge upon the 50% point. A blank screen of mean luminance was presented between each test pair and subjects had to press a mouse button in order for each test pair to be presented. In the baseline conditions both patterns were presented at the same luminance. In test conditions, the standard pattern’s luminance was decreased using a NDF of 1.3 log units, thus, reducing the luminance of the standard pattern to 0.13 cd m^{-2} for the low luminance condition and 1.5 cd m^{-2} for the high luminance condition. The subject’s task was to indicate which pattern appeared faster, by pressing a mouse button. Before beginning the experiment subjects were dark adapted for at least 5 min. Each block consisted of 30 presentations and the 50% point of the resultant psychometric function was estimated by Probit analysis (Finney, 1971). The mean of four such estimates was taken as the point of subjective equality.

The experiments were conducted binocularly in a semi-darkened room, no head restraint was used but subjects were required to view through an observation slot in the light-tight case. One of the subjects (SB) was aware of the general aims of the experiment, the other two were naive to the purpose of the experiment.

2. Results

Two baseline luminances were used in the speed matching experiment. Fig. 1 shows the results of the speed match-

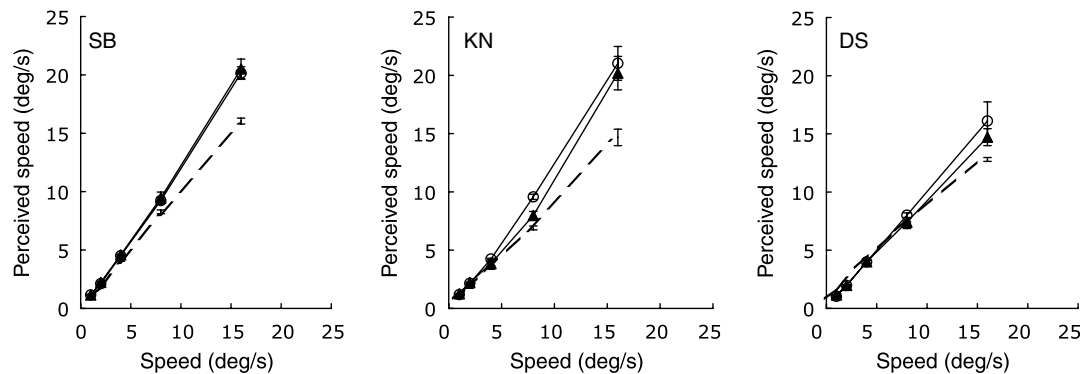


Fig. 1. Perceived speed at 1.5 cd m^{-2} relative to a standard pattern of 30 cd m^{-2} (open circles) and at 0.13 cd m^{-2} relative to a standard pattern of 2.54 cd m^{-2} (solid triangles). The results for three subjects are shown in separate panels. The broken line (no symbols) represents the average baseline performance where subjects were asked to match speeds at equal luminance (either 2.54 cd m^{-2} or 30 cd m^{-2}). Error bars represent $\pm 1 \text{ SEM}$.

ing task in which subjects were asked to judge the relative speed of two patterns, one at low luminance and the other at a higher luminance. The two different high luminances were 2.54 and 30 cd m^{-2} , with the respective low luminance gratings being 0.13 and 1.5 cd m^{-2} . This ensured that our measurements covered a wide range of luminance and that our highest luminance was well within the photopic range (where cones operate). The results indicate that whilst at slow speeds ($<4 \text{ deg s}^{-1}$) perception of speed is virtually unaffected by luminance, at higher speeds the lower luminance pattern appears to be moving significantly *faster* than the high luminance pattern. We find very little evidence for a reduction in the perceived speed of low luminance patterns under these conditions, even at the relatively slow speeds measured by Gegenfurtner et al. However, Gegenfurtner et al. were concerned with rod-isolating stimuli and their stimulus conditions were, therefore, very different from ours.

3. Discussion

The results presented here have received independent support from a recent conference presentation by Vaziri-Pashkam and Cavanagh (2006) who found similar increases in the perceived speed of radial gratings at low luminance. Encouragingly, a plausible interpretation of the results of a recent study of speed tuning in monkey MT cells (Pack, Hunter, & Born, 2005) is that MT cells' responses are consistent with an increase in perceived speed at lower luminance; however it should be noted that an unambiguous interpretation of these results is difficult due to methodological details. Thus, our present results have received independent support using radial stimuli and appear to be consistent with recent physiological findings. Taken together with our previous findings, it appears that the perception of speed can be distorted so that things look slower or faster depending upon ambient lighting, contrast and temporal frequency.

The finding that perceived speed increases at low luminance is difficult to reconcile with Bayesian models that propose a slow speed prior, e.g. Stocker and Simoncelli (2006).

Nor can differences in receptor properties explain our results since these would predict qualitatively similar distortions in perceived speed as found by Gegenfurtner et al using rod-isolating stimuli. To account for our findings we have developed a simple post-receptor model that is based upon some known properties of visual neurones. This is a straightforward extension of a ratio model of speed encoding that we have described elsewhere to account for adaptation effects on perceived speed (Hammett et al., 2000; Hammett et al., 2005) and the effects of contrast on speed (Thompson et al., 2006). At the heart of the model (see appendix for a full description and discussion of physiological relevance) lies the assumption that speed is encoded as the ratio of the responses of two mechanisms, one temporally low-pass and the other band-pass. The contrast responses of these mechanisms, given by a Naka-Rushton equation (Naka & Rushton, 1966), vary independently as a function of luminance and speed; the precise manner in which each mechanism responds to changes in luminance and speed being determined by two free parameters. We found the best least squares fit of the model to the data presented in Fig. 1 using an error minimisation routine ('fminsearch') in Matlab 7.0.4 (Mathworks Inc.). The model fit and data are shown in Fig. 2.

The model is able to characterise the data well – the model predicts little or no effect of luminance upon perceived speed below 4 Hz and a sharp increase in perceived speed for frequencies above this.

Of course we accept that the role of the prior in a Bayesian model is akin to that of the free parameters of the model we have presented here, but we feel that the Bayesian approach has value only when the prior is predictable. Thus our predisposition to see a hollow face as a normal face can be seen as the result of the intervention of a 'prior' based on long experience that noses tend to stick out from faces and not recede inwards (Gregory, 2006). Therefore the results we have presented here pose a challenge to the utility of Bayesian models of speed perception; not because such models cannot adequately *describe* our data by adopting an appropriate and arbitrary 'prior', but, rather, because it is not clear that they could sensibly *predict* these effects of low luminance on perceived speed.

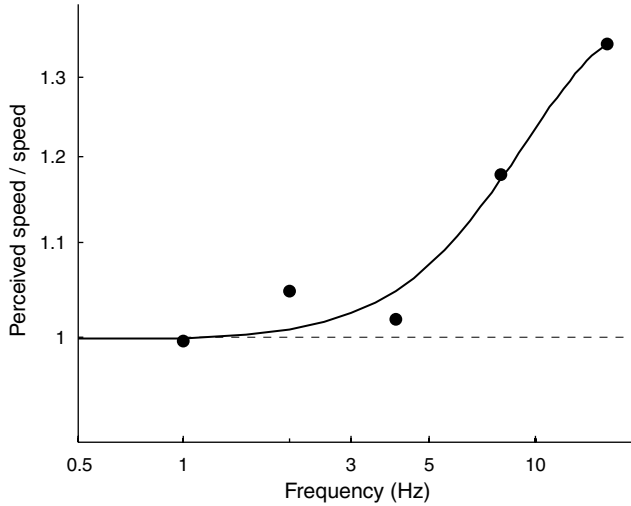


Fig. 2. The best fit of the model (solid line) to the data averaged across subjects and luminance conditions (symbols). The vertical axis represents the ratio of perceived speed to physical speed, thus a value of 1.0 indicates veridical perception and values above 1 indicate an overestimation of perceived speed.

The key point that we wish to draw here is that physiologically plausible models, based on sound experimental findings relating to the early parts of the visual system, can adequately account for the data we have gathered on perceived speed. We have presented one such model in some detail that can account not only for the results presented here, but also a wide range of other effects, including the effects of contrast on speed and the effects of speed adaptation. We conclude that speed perception can be understood without the need to invoke any prior and there is little evidence to suggest that this is the strategy adopted by the visual system when computing speed.

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Appendix A. The model

We have modelled the effect of luminance upon perceived speed by assuming that perceived speed is based upon the ratio of the outputs of the low-pass (p) and band-pass (m) temporal filters proposed by Perrone (2005). The low-pass filter takes the form

$$p(\omega) = \sqrt{a^2 + b^2} \quad (1)$$

where

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

and the high-pass filter is given by

$$m(\omega) = \frac{\omega}{k} p(\omega) \quad (2)$$

where ω is temporal frequency and, following Perrone, τ_1 , τ_2 and k are constants of 0.0072, 0.0043 and 4 respectively. These filters provide a good fit to typical tuning functions in macaque V1 (Foster, Gaska, Nagler, & Pollen, 1985). Note that there are no free parameters at this stage of the model.

The model assumes that the response of each mechanism is determined by the sensitivity of the filter at any particular temporal frequency (ω) and that the linearity of their contrast response functions varies as a function of contrast, luminance and frequency such that their responses are given by:

$$P(\omega, l, c) = \frac{c \cdot p(\omega)}{|c| \cdot p(\omega) + \alpha_p / \omega l} \quad (3)$$

and

$$M(\omega, l, c) = \frac{c \cdot m(\omega)}{|c| \cdot m(\omega) + \alpha_m / \omega l} \quad (4)$$

where l and c are luminance and contrast respectively and α_m and α_p are free parameters that determine the rate at which the function compresses as l and/or ω increases. Speed, S , is determined by the ratio of these two functions such that:

$$S(\omega, l, c) = \frac{M(\omega, l, c)}{P(\omega, l, c)} \quad (5)$$

Thus the response of each mechanism is given by a Naka and Rushton (1966) equation whose semi-saturation constant is inversely proportional to speed and luminance. The model assumes that the contrast response of both mechanisms becomes more compressive as a function of speed and luminance: The free parameters α_m and α_p determine the rate that this compression increases with speed and or luminance for m and p respectively.

A.1. Physiological relevance

There is good reason to believe that the inverse relationship between speed and semi-saturation constant assumed by the model exists for both retinal and geniculate M and P cells in the monkey (Kaplan & Shapley, 1986). The contrast gain of the model's filters is considerably smaller at 1.5 cd m⁻² than at 30 cd m⁻². Purpura, Kaplan, and Shapley (1988) have shown that contrast gain of macaque M and P cells is indeed modulated by mean luminance such that gain decreases as mean luminance decreases. The model's contrast response functions also reveal that response tends to become more compressive as frequency increases. The model's quasi-linear response to lower temporal frequencies (particularly for the p filter) and larger, compressive response to higher temporal frequencies (the m filter) is qualitatively very similar to the known differences in mean contrast response of parvocellular and magnocellular layers

of the Macaque LGN (Sclar, Maunsell, & Lennie, 1990). Given that, it is also known that the optimal temporal frequency for these populations of cells differs such that m cells are more responsive to higher frequencies, one possibility is that the model's reliance upon the assumption of frequency-dependent changes in the value of the semi-saturation constant (α) may reflect a switch in the predominance of m and p responses as speed increases. Hammett, Georgeson, and Gorea (1998) proposed a similar scheme in relation to motion sharpening. Note that this is not equivalent to proposing that the model's filters are equivalent to magno- and parvo-cellular populations but rather that these populations' temporal tuning properties may form the substrate of the frequency-dependent shift in their response functions.

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