# Perceptual biases are inconsistent with Bayesian encoding of speed in the human visual system

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The notion that Bayesian processes are fundamental to brain function and sensory processing has recently received much support, and a number of Bayesian accounts of how the brain encodes the speed of moving objects have been proposed that challenge earlier mechanistic models. We measured the perceived speed of low contrast patterns at both low (2.5 cd m$^{-2}$) and high (25 cd m$^{-2}$) luminance in order to assess these competing models of how the human visual system encodes speed. At both luminance levels low contrast stimuli are perceptually biased such that they appear slower at slow ($<$ 8 Hz) speeds but faster at higher (16 Hz) speeds. However, we find that the reversal of the perceptual bias from under- to overestimation occurred at slower speeds at low luminance. We also found that the bias was greater at slow speeds at high luminance but greater at fast speeds at low luminance. Moreover, discrimination thresholds were found to be similar at high and low luminance. These findings can be predicted by models in which speed is encoded by the relative activity within two broadly tuned temporal channels but are inconsistent with Bayesian models of speed encoding. We conclude that Bayesian processes cannot adequately account for speed encoding in the human visual system.

## Introduction

Whereas knowledge of the speed of objects in the environment is of critical importance, there is still no consensus on the nature of the processes that underlie the encoding of speed in the human visual system. Much of the work that addresses this problem has looked to biases in our perception of speed to inform both formal and informal models of speed encoding. Human speed perception has been shown to be readily influenced by the contrast of the scene viewed (e.g.,

Hammett, Champion, Thompson, & Morland, 2007; Thompson, 1982; Thompson, Brooks, & Hammett, 2006); and it is now well established that, at slow speeds, low contrast stimuli appear to move more slowly than their higher contrast analogues but, conversely, they can appear to move more quickly at higher speeds ($>$ 8 Hz)[1] (e.g., Thompson, 1982; Thompson et al., 2006). For convenience and following others (e.g., Brooks, 2001; Snowden, Stimpson, & Ruddle, 1998), we will refer to these biases in perceived speed as the Thompson Effect. This observation and others has led Thompson (1982) and many others (e.g., Adelson & Bergen, 1986; Hammett, Thompson, & Bedingham, 2000; Harris, 1980; Smith & Edgar, 1994; Tolhurst, Sharpe, & Hart, 1973) to the suggestion that speed may be encoded as the ratio of two mechanisms tuned to low and high temporal frequencies (or "slow" and "fast" mechanisms) (Figure 1, left hand panel). Whereas the physiological substrate of these mechanisms is not known, one clear candidate may be the subpopulations of Magno and Parvocellular cells (hereafter referred to as M and P cells, respectively) in the primate lateral geniculate nucleus (LGN) (De Valois, Cottaris, Mahon, Elfar, & Wilson, 2000). The logic of this ratio class of model rests upon the assumption that speed is encoded as the relative activity of "slow" and "fast" mechanisms—at slow speeds, reducing contrast has proportionately less effect upon the response of the "slow" mechanism (since it is most sensitive to slower stimuli) and thus patterns appear slower. Similarly, at fast speeds, reducing contrast will have proportionately less effect upon the "fast" mechanism and will thus result in a perceptual speeding up. The ratio model can therefore adequately account for the Thompson Effect and other perceptual biases in speed such as those induced by changes in luminance and adaptive state (Hammett, Champion, Morland, &
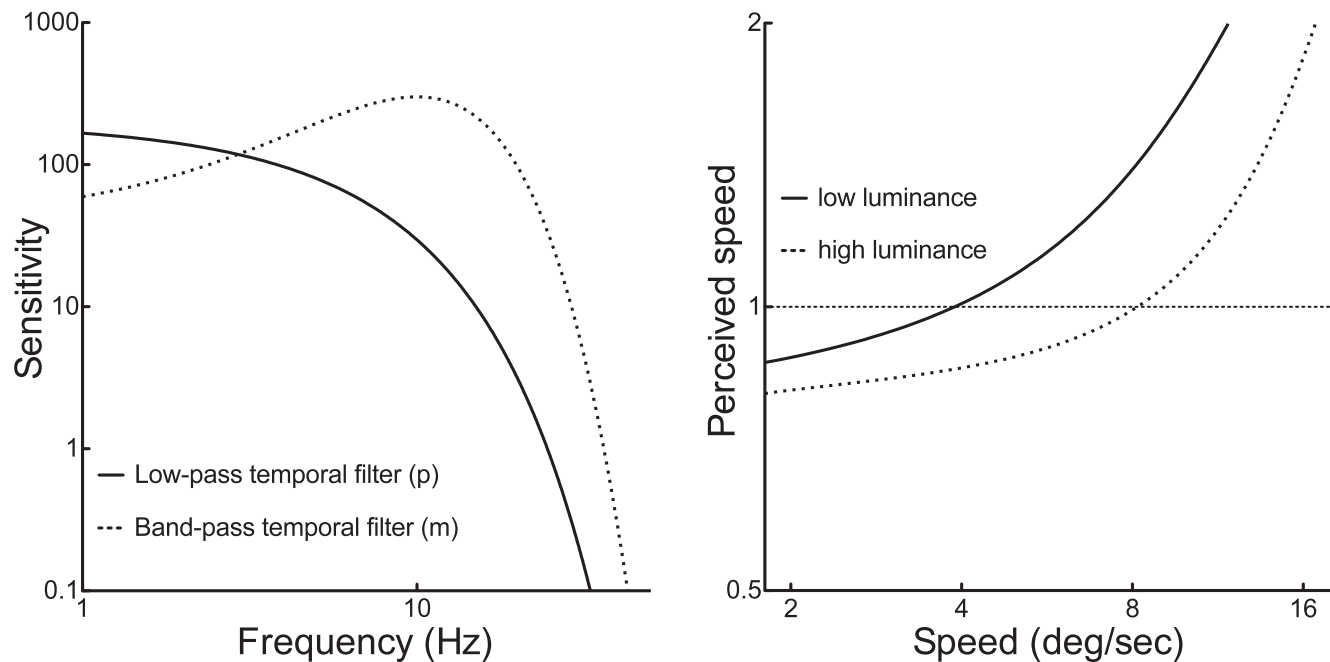
Figure 1. The ratio of the responses of low-pass and band-pass temporal filters (left panel) after Smith and Edgar (1994) provides a monotonic code for speed that is consistent with under- and overestimation of speed at low contrast. Perceived speed of a low contrast pattern encoded by a ratio model at high and low luminance is plotted in the right hand panel: Values below 1 indicate an underestimation of perceived speed at low contrast, and values above 1 indicate an overestimation of perceived speed. The ratio model shows a reduction in the underestimation of slow speeds and an overestimation of higher speeds at reduced luminance. Details of the simulation may be found in the Appendix.

Thompson, 2005; Hammett et al., 2007; Thompson, 1981).

However, subsequent to the popularization of modelling brain processes as Bayesian operations (e.g., Jaynes, 1988) a number of workers (e.g., Ascher & Grzywacz, 2000; Hürlimann, Kiper, & Carandini, 2002; Stocker & Simoncelli, 2006; Weiss & Adelson, 1998; Weiss, Simoncelli, & Adelson, 2002) have proposed an alternative account of how the brain encodes speed. Whereas the details of the models vary, this new class of model shares the assumption that speed is encoded as the product of a likelihood (the sensory signal including noise) and a Bayesian prior that favors slow speeds. The logic of this approach is based upon two key ideas: (a) the observation that as the sensory evidence becomes less precise (e.g., by a reduction in signal-to-noise ratio), the proportional influence of the prior on the product will increase and (b) the assertion that visual experience is dominated by slow speeds and hence the brain deploys a "slow" prior. Given these two assumptions, it follows that reducing the sensory signal (for instance by reducing contrast) must result in a phenomenal slow-down. The well-established Thompson Effect is thus broadly consistent with both the ratio and Bayesian class of models of speed encoding, and both approaches have had some degree of success in modelling it (Ascher & Grzywacz, 2000; Hammett et al., 2000; Stocker & Simoncelli, 2006; Thompson et al., 2006).

Recently Vintch and Gardner (2014) have reported that the fMRI BOLD population response in V1 effectively mirrors the contrast-induced perceptual biases in speed experienced by their subjects and suggest that these biases constitute evidence for the encoding of perceptual priors for slow speed. However, they also note that their results could be interpreted as evidence for a scheme where speed was encoded by two mechanisms whose gains varied differentially as a function of speed.

Thus there are currently two competing accounts of how speed is encoded in the human visual system that are broadly consistent with much behavioral data. One of the problems in resolving which (if either) approach provides a more consonant framework for understanding speed encoding is that both class of models tend to make similar predictions and, where they diverge, can be readily modified to accommodate empirical evidence. For instance, whereas Stocker and Simoncelli's (2006) model does not predict the reversal in perceptual bias frequently found in the Thompson Effect at higher speed, they note that their model "would be able to fit these behaviours with a prior that increases at high speeds" (p. 583).

There is therefore a need to identify cases where the Bayesian and ratio approaches yield unequivocally different predictions. In order to do so, we used the logic and model invoked by Hammett et al. (2007) to derive divergent predictions for Bayesian and ratio class models of speed encoding. Hammett et al. (2007) (see also Vaziri-Pashkam & Cavanagh, 2008) found that low luminance (mesopic) patterns appeared faster than higher luminance (photopic) patterns at fast (> 4 Hz) speeds. They demonstrated that a simple ratio model comprising two temporally tuned mechanisms could account for this perceptual bias if the gain of the lower frequency channel is reduced proportionately more than that of the higher frequency channel at low luminance—an assumption that is consistent with the known properties of retinal ganglion cells that project to the M and P layers of the primate LGN (Purpura, Kaplan, & Shapley, 1988). In such a scheme the response of the lower frequency tuned mechanism is reduced at low luminance (relative to its response to the same contrast at high luminance) and thus the ratio model yields an increase in perceived speed relative to photopic levels. Thus this class of model predicts that at low luminance the reduction in perceived speed at low contrast will be attenuated since a proportionately larger input to the ratio will be derived from the higher frequency-tuned mechanism. Figure 1 shows the qualitative effect of reducing luminance (and concomitantly the gain of the "slow" mechanism) predicted by ratio models: The Thompson Effect is reduced at slow speeds, increases at faster speeds, and the speed at which the perceptual bias reverses is reduced. The Bayesian approach posits that the precision of the speed signal is reduced at low luminance. Since reducing luminance effectively reduces the contribution of the signal input equally for high and low contrast patterns, Bayesian models predict that reducing luminance will have no effect upon the contrast-induced perceptual bias but will increase discrimination thresholds as the precision of the signal is reduced. In order to test these predictions, we therefore measured perceived speed and estimated discrimination thresholds of low contrast patterns over a range of speeds and at high and low luminance.

## Methods

### Subjects

Five (two male and three female) subjects aged between 20 and 29 participated in this experiment. One of the subjects (OH) was an author; the other four were naïve to the purpose of the experiment. All subjects had normal or corrected-to-normal acuity.

### Apparatus and stimuli

All stimuli were horizontally orientated 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. The monitor was gamma corrected using the CRS Optical photometric system (Cambridge Research Systems, Rochester, UK). The Michelson contrast of the standard (fixed speed) grating was 0.7, and the contrast of the test (variable speed) grating was 0.1. During the control conditions both the standard and test gratings were of equal contrast (either 0.1 or 0.7). The spatial and temporal phase of the standard and test gratings was randomized. The display subtended $68° \times 47°$ at a viewing distance of 28.5 cm. Mean luminance was 25 cd m$^{-2}$ for the high luminance conditions and 2.5 cd m$^{-2}$ in the low luminance conditions. In the low luminance conditions 1 log unit neutral density filters (NDF) (Thorlabs Inc., Newton, New Jersey, USA) were inserted into drop-cell trial frames (Skeoch, Sussex, UK) worn by subjects. Stimuli were presented through two 6° diameter circular windows with hard edges. Each window was located equidistant from the horizontal center of the screen and separated by 2°. A small bright fixation spot was situated at the center of the display.

### 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 a downward direction at one of four temporal frequencies (2, 4, 8, and 16 Hz). The speed of the test pattern was altered by a QUEST routine (Watson & Pelli, 1983) depending on the subject's responses. 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 fit, and the 50% point of the function was derived. The mean of five (three in the control condition) such estimates was taken as the point of subjective equality (PSE). Both patterns were presented at equal luminance, in both the high or low luminance conditions. 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. 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. The experiments were conducted binocularly in a semidarkened room using a chin and headrest.
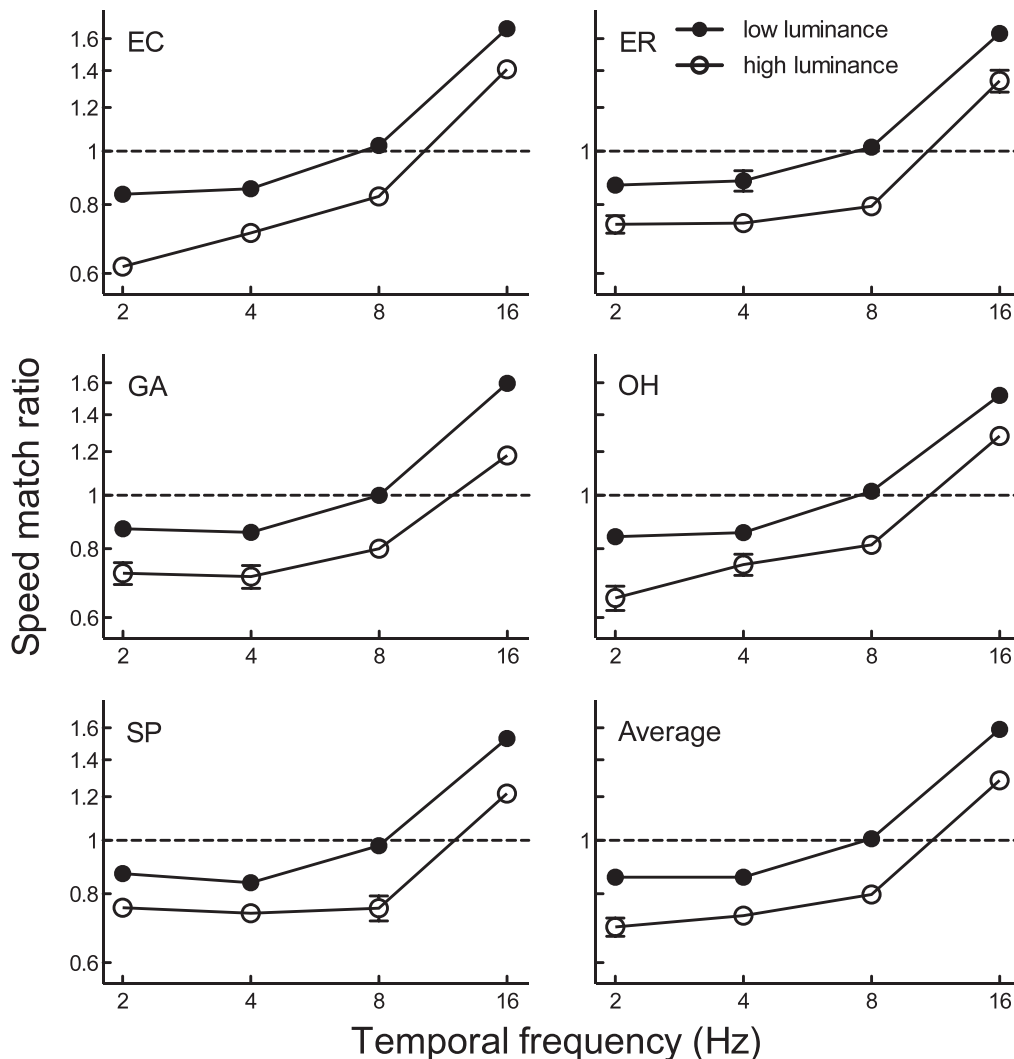
Figure 2. The ratio between perceived speed and physical speed of the low contrast (0.1) pattern is plotted as a function of speed at high (open symbols) and low luminance (closed symbols). Subjects' initials are indicated in the top left of each panel, the average across subjects is indicated in the lowermost right panel. The broken horizontal line represents a veridical match. 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*.

# Results

At all temporal frequencies tested in the control condition speed matching was near veridical at both high and low luminance. For 0.1:0.1 contrast patterns, a two-way ANOVA revealed no significant main effect of temporal frequency, $F(3, 32) = 1.06$, $p = 0.379$; no significant main effect of luminance, $F(1, 32) = 2.93$, $p = 0.096$; and no significant interaction between temporal frequency and luminance, $F(3, 32) = 1.48$, $p = 0.239$. Similarly, for patterns at 0.7:0.7 contrast, a two-way ANOVA revealed no significant main effect of temporal frequency, $F(3, 32) = 1.80$, $p = 0.167$; no significant main effect of luminance, $F(1, 32) = 0.22$, $p = 0.638$; and no significant interaction between temporal frequency

and luminance, $F(3, 32) = 0.17$, $p = 0.916$, on the speed match ratio.

Figure 2 plots the ratio of the match speed for the low contrast stimuli to the standard speed. A value greater than one represents an overestimate of the perceived speed of low contrast with respect to high contrast patterns, and a value less than one represents an underestimate of the perceived speed of low contrast with respect to high contrast patterns. The results clearly indicate that low contrast patterns appear slower for most speeds tested. In line with many other studies, our results also indicate that the perceptual bias in speed reverses at faster speeds such that low contrast patterns appear faster at fast speeds. A two-way ANOVA revealed a significant main effect of temporal frequency, $F(3, 32) = 428.05$, $p < 0.001$; a significant
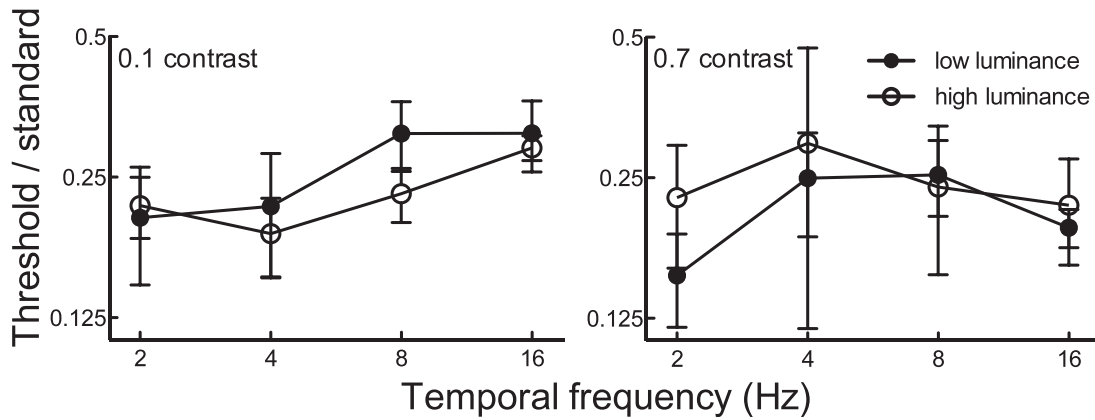
Figure 3. Estimated discrimination thresholds are reported as fractions of the standard speed for test and standard patterns of equal contrast (left panel, 0.1, right panel, 0.7), at high (open symbols) and low (closed symbols) luminance. Data points represent the mean of five subjects. Error bars represent ±1 *SEM*.

main effect of luminance, $F(1, 32) = 177.20$, $p < 0.001$; and a significant interaction between temporal frequency and luminance, $F(3, 32) = 6.50$, $p < 0.010$, on the speed match ratio. The results clearly indicate that the speed at which this reversal in perceptual bias occurs varies with luminance. At high luminance, the perceived speed of low contrast patterns is underestimated for temporal frequencies up to 8 Hz but overestimated at 16 Hz. At low luminance a similar reversal in the bias occurs but at a lower frequency— only frequencies less than 8 Hz were underestimated. One-sample $t$ tests at 8 Hz revealed that there was no significant difference between perceived and veridical speed at low luminance ($t = 0.89$, $df = 4$, $p = 0.422$), but at high luminance, perceived speed was significantly lower than veridical ($t = -16.15$, $df = 4$, $p < 0.001$).

Following Freeman, Champion, and Warren (2010) we calculated the average standard deviations of the underlying cumulative Gaussian psychometric functions for our control conditions in order to estimate speed discrimination thresholds at high and low luminance. Figure 3 plots these thresholds as fractions of the standard speed for test and standard patterns of 0.1 and 0.7 contrast. A two-way ANOVA revealed no significant main effect of temporal frequency, $F(3, 32) = 2.08$, $p = 0.122$; no significant main effect of luminance, $F(1, 32) = 0.79$, $p = 0.379$; and no significant interaction between temporal frequency and luminance, $F(3, 32) = 0.34$, $p = 0.793$.

Similarly, for test and standard patterns with a contrast of 0.7, a two-way ANOVA revealed no significant main effect of temporal frequency, $F(3, 32) = 0.41$, $p = 0.743$; no significant main effect of luminance, $F(1, 32) = 0.30$, $p = 0.587$; and no significant interaction between temporal frequency and luminance, $F(3, 32) = 0.10$, $p = 0.958$, on estimated discrimination thresholds.

At both high and low luminance the estimated discrimination thresholds as fractions of the standard

speed were not affected by changes in contrast. At low luminance, a two-way ANOVA revealed no significant main effect of temporal frequency, $F(3, 32) = 1.42$, $p = 0.253$; no significant main effect of contrast, $F(1, 32) = 1.69$, $p = 0.202$; and no significant interaction between temporal frequency and contrast, $F(3, 32) = 0.70$, $p = 0.553$. At high luminance, a two-way ANOVA revealed no significant main effect of temporal frequency, $F(3, 32) = 0.05$, $p = 0.981$; no significant main effect of contrast, $F(1, 32) = 0.06$, $p = 0.808$; and no significant interaction between temporal frequency and contrast, $F(3, 32) = 0.42$, $p = 0.735$.

## Discussion

There is currently no consensus on how speed is encoded in the human visual system. Both Bayesian and ratio class models have been proposed and previous investigations have found perceptual biases consistent with both class of model. Recently, Sotiropoulos, Seitz, and Seriès (2014) reported that a model that combined Stocker and Simoncelli's (2006) Bayesian model with Thompson et al.'s (2006) ratio model accounted for their measurements of the Thompson Effect better than a Bayesian model alone. However, the model required 10 free parameters, and the resultant best fitting parameters render the temporal filters underlying the ratio stage to be both effectively low-pass with the peak and cut-off of the "m" filter at around 2 Hz and 20 Hz respectively. Thus whereas the large number of parameters does allow for a good fit to the data, the underlying filters lose the physiological plausibility of the original fixed parameter model proposed by Perrone (2005).

Very recently, Vintch and Gardner's (2014) finding that the population response in V1 mirrors the

contrast-induced perceptual biases in speed and flicker gave further weight to a Bayesian approach. However, Vintch and Gardner's measurements were restricted to speeds no faster than 4 °/s (well below the speeds at which a reversal in perceptual bias may be expected) and, whereas pointing to the consistency of their results with a Bayesian prior, they also note that their results are consistent with a two-channel model of speed where the prior can be considered as a frequency-dependent difference in the gain of the mechanisms. We therefore set out to provide a direct test of the predictions of ratio and Bayesian class models of speed encoding by assessing the effect of luminance upon the Thompson Effect: An early slow prior should be readily differentiated from a ratio mechanism upon the basis of the effect of luminance on speed biases. A ratio model of speed encoding that incorporates known luminance-induced changes in gain (Purpura et al., 1988) predicts that the perceptual bias will be greater at slow speeds at high luminance and greater at fast speeds at lower luminance.

In order to evaluate the effect of the luminance reduction upon Bayesian models, we followed the logic of Freeman et al. (2010). They observed that a reduction of the slope of the underlying psychometric function (and thus discrimination threshold) should yield less certainty and therefore a slower perceived speed. We estimated the slopes of the underlying psychometric functions of our control conditions at 0.1 and 0.7 contrast (Figure 3). There is no significant difference between low and high luminance discrimination thresholds, nor is there any significant difference in discrimination thresholds at high and low contrasts. Thus, the Bayesian class of model predicts that luminance should have no effect on the contrast-induced bias in our measurements since the discriminability of the patterns is equally affected by the luminance reduction. Moreover, given the lack of any significant difference in discrimination thresholds between high and low contrast, Bayesian models would also not predict perceptual biases as a function of contrast.

Our results clearly indicate that the perceived speed of low contrast patterns is under-estimated at slow speeds and over-estimated at faster speeds as has previously been reported. We also find that this shift in perceptual bias *is* influenced by the average luminance of the image: At lower luminance there is significantly less reduction in perceived speed, greater increase in perceived speed, and a concomitant reduction in the speed at which the bias is reversed. This increase in perceived speed and the associated reduction in the speed at which the perceptual bias reversed at low luminance is predicted by the ratio class of model (e.g., Hammett et al., 2007) that incorporates the biologically plausible (Purpura et al., 1988) assumption that the

gain of the lower temporal frequency tuned mechanism reduces proportionately more at low luminance.

Others (e.g., Thompson et al., 2006) have pointed out that Bayesian approaches do not predict the reversal in perceptual bias found here and elsewhere, and Hammett et al. (2007) noted that the finding that stimuli appear faster at mesopic than at photopic levels was also inconsistent with Bayesian models. Our new finding that the perceived slowing of low contrast patterns is greater at high luminance provides a strong challenge to the plausibility of Bayesian accounts of speed encoding since they predict that lower contrast patterns should have the same relative perceived speed at either luminance and cannot explain the shift in frequency at which the bias reverses. Conversely, the perceptual biases induced by luminance and contrast (Hammett et al., 2007; Thompson, 1982; Thompson et al., 2006; Vaziri-Pashkam & Cavanagh, 2008) and the effect of luminance we find here are all consistent with a simple, biologically plausible two-mechanism ratio model.

## Conclusions

Bayesian approaches to characterizing brain function have become very popular in recent years and have been used to model a range of processes such as perceived speed under smooth pursuit, sensorimotor learning and tactile perception (Freeman et al., 2010; Goldreich & Tong, 2013; Körding & Wolpert, 2004). Indeed, the impressive range of studies proposing a Bayesian characterization of sensory processes (Geisler & Kersten, 2002; Langer & Bülthoff, 2001) led Körding and Wolpert (2006) to suggest that "the Bayesian process may be a fundamental element of sensory processing" (p. 321). Among the evidence cited by Körding and Wolpert to support this suggestion was Stocker and Simoncelli's (2006) Bayesian model of speed encoding. However, their model (like all pure Bayesian models) fails to predict the reversal in perceptual bias found at higher speeds in the Thompson Effect and is inconsistent with both previous work that has manipulated luminance (e.g., Hammett et al., 2007; Vaziri-Pashkam & Cavanagh, 2008) and the results presented here.

It is important to stress that our data may be consistent with a range of models of speed encoding other than ratio models, and it is not our intention to make any strong claim in support of ratio models upon the basis of our results. Indeed, it is appropriate to acknowledge that the basis of proposed ratio models is itself ad hoc in nature and rests upon assumptions regarding gain changes with luminance that rely upon relatively sparse evidence. However, the evidence we

report here, and previous reports of perceptual biases in speed perception, are not readily reconciled with Bayesian accounts of speed encoding in the human brain.

Keywords: *speed, contrast, luminance, Bayesian, ratio, model*

## Footnote

¹ Not all studies (e.g., Hawken, Gegenfurtner & Tang, 1994; Stone & Thompson, 1992) find evidence of a reversal (i.e., an over-estimation) at high speed, most likely due to disparate stimulus parameters (see Hammett & Larsson, 2012).

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## Appendix

The simulation in Figure 1 used the temporal filters originally proposed by Smith and Edgar (1994) for their close fit to behavioral data. They take the form $m = 300e^{-0.5(\omega - 10)/(24 + \omega)}$ and $p = 15\,000e^{-0.5(\omega-50)^2/(17)}$ where $m$ and $p$ define the sensitivity of the "fast" and "slow" mechanisms. The simulation assumes that their responses ($M$ and $P$) are determined by a modified

Naka-Rushton relation such that sensitivity at any given temporal frequency, $w$, and contrast, $c$, is given by $P(\omega,c) = \frac{c.p(\omega)}{|c|.p(\omega)+\alpha_p}$ and $M(\omega,c) = \frac{c.m(\omega)}{|c|.m(\omega)+\alpha_m/\omega}$ where $\alpha_m$ and $\alpha_p$ are the semisaturation constants. In the high luminance simulation these values were set to 0.13 and 1.79 which is consistent with the known properties of M and P cells (Blakemore & Vital-Durand, 1986; Derrington & Lennie, 1984; Hicks, Lee, & Vidyasagar, 1983; Kaplan, Lee, & Shapley, 1990; Schiller & Colby, 1983). The value of $\alpha_m$ varied inversely as a function of frequency such that the contrast response became more compressive at higher frequencies, consistent with physiological reports (Kaplan & Shapley, 1986). In the low luminance condition the values were set to 0.15 and 8.95 in order to simulate a large reduction in gain of the P mechanism (Purpura et al., 1988). Speed, $S$, at each contrast, $c$, was calculated as the ratio of the two mechanisms' responses such that $S(\omega,c) = \frac{M(\omega,c)}{P(\omega,c)}$.