The effect of contrast on perceived speed and flicker

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Slowly moving low contrast patterns appear to drift more slowly than higher contrast patterns. It has been reported that this effect of contrast is reversed for flickering patterns such that they appear to flicker faster than high contrast patterns. This apparent difference in the effect of contrast on perceived speed and flicker may place important constraints upon models of speed encoding in the human visual system. We have measured perceived speed and flicker over a range of spatial and temporal frequencies. The results indicate that contrast has qualitatively (but not quantitatively) similar effects upon perceived speed and flicker. The results also indicate that the effect of contrast upon perceived speed is likely to be inherited from the effect of contrast upon perceived flicker. These findings allow a relaxation of previous constraints upon models of speed encoding.

Keywords: speed, flicker, temporal frequency, contrast

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Introduction

The cortical pathway responsible for motion processing is relatively well documented, but the mechanisms that underlie the encoding of *speed* are still poorly understood. Early visual processing is characterized by neurones whose receptive fields are spatio-temporally separable (e.g., Foster, Gaska, Nagler, & Pollen, 1985; Tolhurst & Movshon, 1975), and thus their responses cannot provide unambiguous speed information. A unifying characteristic of most mechanistic models of speed processing is the assumption that the code for speed is extracted by combining the responses of these early spatio-temporally separable units in some manner (e.g., Adelson & Bergen, 1985; Hammett, Champion, Thompson, & Morland, 2007; Smith & Edgar, 1994; Thompson, Brooks, & Hammett, 2006; Watson & Ahumada, 1985). There is now considerable behavioral evidence that is consistent with such a scheme (see Burr & Thompson, 2011 for a comprehensive review). For instance, the perceived speed of lower contrast gratings is underestimated at temporal frequencies below around 8 Hz (Brooks, 2001; Gegenfurtner & Hawken, 1996; Hürliman, Kiper, & Carandini, 2002; Müller & Greenlee, 1994; Stocker & Simoncelli, 2006; Stone & Thompson, 1992; Thompson, 1982; Thompson, Brooks, & Hammett, 2006). These distortions in perceived speed are readily accommodated in a simple two-channel model whereby the code for speed is derived from the ratio of temporal mechanisms tuned for low and high frequencies. Other distortions in perceived speed induced by both adaptation and luminance have also been found to be consistent with such a ratio model (e.g., Hammett, Bedingham, & Thompson, 2000; Hammett, Champion, Morland, & Thompson, 2005; Hammett et al., 2007; Smith & Edgar, 1994; Thompson, 1981; Vaziri-Pashkam & Cavanagh, 2008).

However, Thompson and Stone (1997) reported that reducing contrast has opposite effects upon perceived speed and perceived flicker. They found that reducing contrast increases the perceived temporal frequency of counterphase sinusoidal gratings but decreases the perceived speed of drifting sinusoidal gratings. This apparent difference between speed and flicker processing poses a serious problem for many models of speed encoding since the majority of models share the assumption that speed is computed from the spatio-temporally separable signals generated in the retina (e.g., Adelson & Bergen, 1985; Smith & Edgar, 1994; Thompson et al., 2006; Watson & Ahumada, 1985). Should this be the case then one would predict that the effect of contrast upon perceived speed should mimic its effect upon perceived flicker.

Thompson and Stone (1997) suggested that the difference between flicker and speed may not rule out such models by proposing that their finding may be due to the effect of contrast on perceived spatial frequency. Georgeson (1980) previously showed that perceived spatial frequency increases as contrast decreases. Since speed is the ratio of temporal and spatial frequency,

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this could indeed lead to a reduction in perceived speed, but not, presumably, temporal frequency. However, this seems an unlikely explanation since Smith and Edgar (1990) reported that both perceived temporal frequency and speed are reduced at high spatial frequencies and suggested that they are likely to be mediated by a single substrate. Moreover, while Parker (1983) reported that perceived spatial frequency increases as both drift speed and counterphase frequency increase, McKee, Silverman, and Nakayama (1986) reported that velocity *discrimination* is virtually unaffected by random changes in spatial frequency. Thus the differential effect of contrast on flicker and speed reported by Thompson and Stone (1997) is unlikely to be mediated by changes in perceived spatial frequency.

The precise relation between perceived flicker and perceived speed is critical to informing future models of motion and speed encoding. Thompson and Stone's (1997) finding places important constraints upon such models and constitutes a strong challenge to both ratio models of speed encoding and motion energy models (e.g., Adelson & Bergen, 1985; Watson & Ahumada, 1985). Since both classes of model rely upon the responses of separable spatio-temporal filters, any effect of contrast on perceived speed should also be evident in perceived flicker. However, Thompson and Stone (1997) used only one temporal frequency (4 Hz) and one spatial frequency. It is known that reducing contrast can both decrease and increase perceived speed depending upon temporal frequency: Whilst at low speeds, reducing contrast reduces perceived speed; at higher speeds reducing contrast increases perceived speed (e.g., Thompson, 1982; Thompson et al., 2006). Therefore, it is possible that, rather than contrast having opposite effects upon perceived flicker and speed, the effect of contrast may be qualitatively similar but shifted with respect to temporal frequency such that at 4 Hz, perceived flicker increases at low contrast but perceived speed decreases. In order to investigate this possibility and the full extent of the effect of contrast upon perceived flicker, we have therefore measured perceived speed and flicker for a larger range of spatial and temporal frequencies.

Methods

Apparatus and stimuli

All stimuli were horizontally orientated sinusoidal gratings of 0.5, 1, or 2 c deg^{-1} generated on a VSG 2/3W (Cambridge Research Systems, Rochester, Kent, UK) waveform generator and displayed on an EIZO 6600-M (Hakusan, Ishikawa, Japan) monochrome monitor at a frame rate of 100Hz. The monitor was gamma corrected using the CRS OPTICAL photometric system and internal look-up tables. In experimental conditions the Michelson contrast of the standard (fixed speed) grating was 0.7, and the contrast of the test (variable speed) grating was 0.2. In control conditions the contrast of all stimuli was 0.7. In order to provide a direct comparison with Stone and Thompson's (1997), an initial auxiliary experiment used a standard contrast of 0.7 and a test contrast of 0.1 at 4 Hz and 2 c/°. In control conditions the contrast of all stimuli was 0.7. The display subtended 28° × 23° at a viewing distance of 57 cm. Mean luminance was 32 cd m^{-2}. Stimuli were presented foveally in a circular window at the center of the display. The diameter of the stimulus window subtended 6°. The spatial and temporal windows of the stimuli were hard. A small dark fixation spot was situated at the center of the display. A schematic of the stimulus configuration is shown in Figure 1.

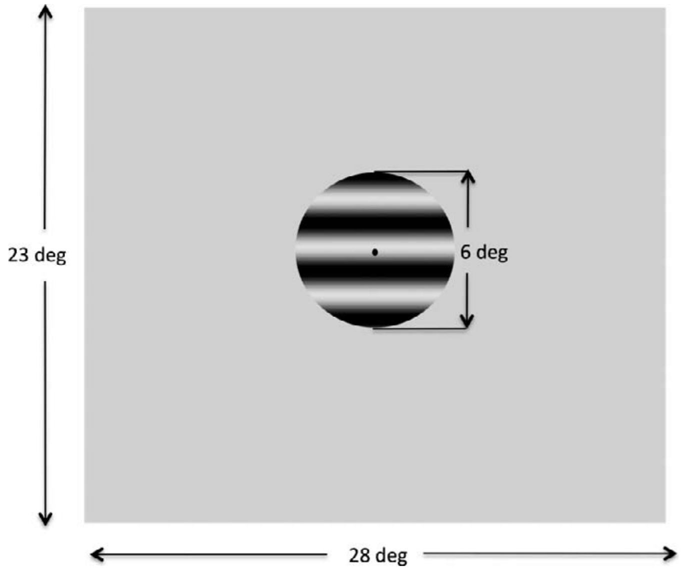

Figure 1. Schematic of the stimulus configuration.

Procedure

Two patterns of the same spatial frequency were presented sequentially for 500 ms with an interstimulus interval of 200 ms that contained a homogeneous gray screen of mean luminance. The order of presentation of the standard and test pattern was pseudorandomized from trial to trial. In the speed conditions, the standard patterns drifted in an upward direction at one of four temporal frequencies (2, 4, 8, or 16 Hz). In flicker conditions, the contrast of the gratings was sinusoidally modulated (counterphased) in time at the same frequencies. The speed or temporal frequency 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 stimulus pair presentation, and subjects pressed a mouse button in order for each test pair to be presented. The subject's task was to indicate which pattern appeared to drift or flicker faster by pressing a mouse button. Each block consisted of four randomly interleaved staircases of forty presentations of one standard spatio-temporal frequency. 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 blocks for all spatio-temporal frequency pairs were pseudorandomized and each block was preceded by at least a three-minute rest period.

The experiments were conducted binocularly in a semidarkened room using a chin and headrest. All three subjects (CP, OH, and EM) were naïve as to the purpose of the experiment and had normal or corrected-to-normal acuity.

Results

In our main experiment we used a contrast ratio of 0.7:0.2. We employed this ratio in order to ensure that our stimuli were visible at higher temporal frequencies (16 Hz). However, Thompson and Stone's (1997) results were obtained using a ratio of 0.7:0.1, but only at 4 Hz. In order to make a more direct comparison between our results and theirs, we therefore conducted an auxiliary experiment that measured the perceived speed and flicker of 2 c/° drifting and counterphasing sinusoidal gratings of 4 Hz for a contrast ratio of 0.7:0.1 (i.e., the same spatio-temporal frequency and contrast ratio as used by Thompson & Stone, 1997). Figure 2 plots the ratio of physical speed or flicker to match speed or flicker for patterns of 0.1 contrast relative to patterns of 0.7 contrast. A ratio of 1.0 (the broken horizontal line) represents a veridical match, values below 1.0 represent a reduction in the perceived speed or flicker of the lower contrast pattern, and values above 1.0 represent an increase in perceived speed or flicker. The results indicate that both perceived speed and flicker are reduced at low contrast. Unlike Thompson and Stone's (1997) results, we find no evidence for an increase in perceived flicker at low contrast under these conditions. However, our results do indicate that the effect of contrast upon perceived flicker is significantly less than its effect on perceived speed ($t = 5.747$ $df = 2$, $p = 0.029$, two-tailed). Thus sampling at this one spatio-temporal frequency leaves open the question of whether the effect of contrast upon perceived flicker is qualitatively different to its effect upon perceived speed.

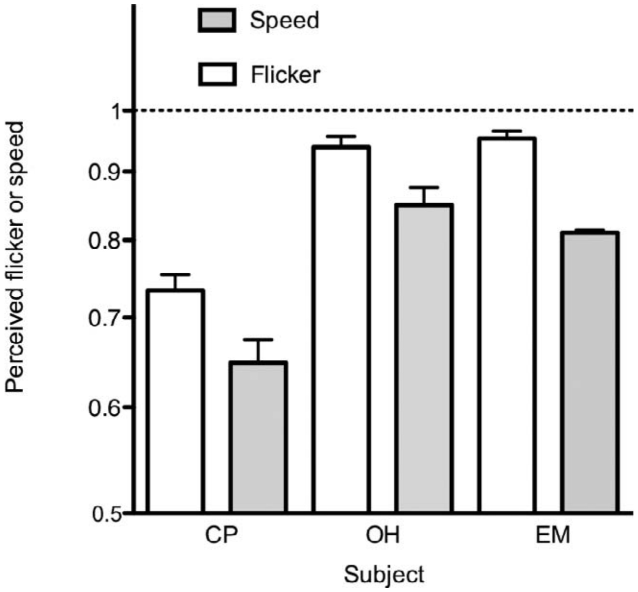

Figure 2. Perceived speed (open columns) and flicker (gray columns) at 4 Hz for a 2 c deg^{-1} sinusoidal grating for three subjects (CP, OH, and EM). Error bars represent ±1 *SEM*. The broken line represents a veridical match.

In order to address this issue we conducted the main experiment that measured the effect of low contrast upon perceived speed and flicker at a range of spatial and temporal frequencies (0.5, 1, and 2 c deg^{-1} and 2–16 Hz). One-sample *t*-tests for the control (equal contrast) conditions indicated that there was no significant deviation from a veridical match for any subject in any of the conditions (lowest p-value > 0.15). The results of this main experiment are plotted in Figure 3. For all spatial frequencies tested, perceived flicker is reduced at low contrast at 2 Hz. This reduction in perceived flicker rate is also evident at 4 Hz at 1 c deg^{-1} and for two subjects at 2 c deg^{-1}. There is no evidence of any reduction in perceived flicker at 8 Hz and above, and two subjects show evidence of a modest increase in perceived flicker at higher temporal frequencies. Thus for low temporal frequencies, reducing contrast resulted in a reduction of perceived flicker akin to that seen for speed. Similarly, perceived speed is also reduced at low temporal frequencies, but this effect is evident for a wider range of temporal frequencies than for flicker. Indeed, at 2 c deg^{-1}, the perceived speed of the lower contrast grating is reduced for all frequencies other than 16 Hz. At 0.5 c deg^{-1}, both perceived speed and flicker is reduced for all frequencies below 16 Hz. There is no evidence of an increase in either perceived speed or flicker at this spatial frequency. At 1 and 2 c deg^{-1}, perceived flicker is reduced at 2 and 4 Hz with evidence of a modest increase in perceived flicker at higher frequencies for

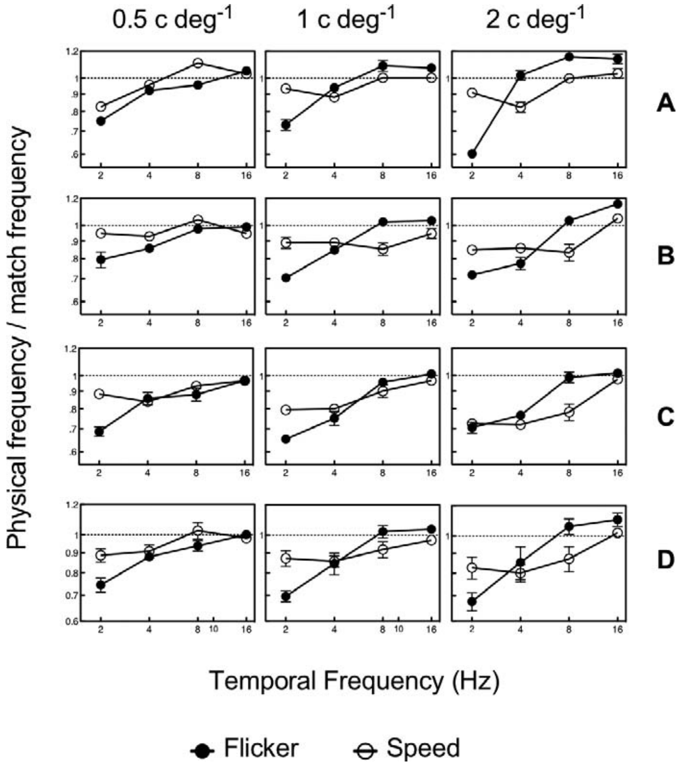

Figure 3. Perceived speed (open symbols) and flicker (closed symbols) as a function of temporal frequency for subject EM (row A), OH (row B), and CP (row C). The average across subjects is plotted in row D. Spatial frequency is indicated above panels. Error bars represent ±1 *SEM*. The broken line represents a veridical match.

two of the three subjects. However, perceived speed is reduced for all frequencies tested below 16 Hz.

Figure 4 replots the data shown in Figure 3 averaged across subjects for each spatial frequency. The results indicate that there is little effect of spatial frequency on perceived flicker. However, there is a modest but systematic trend such that reduction in perceived speed is greater at higher spatial frequencies. There is also a modest trend in the data such that the contrast-induced reduction appears to persist at higher temporal frequencies for perceived speed than for perceived flicker. Despite these quantitative differences between speed and flicker, the effect of contrast on flicker and speed matches is qualitatively similar and significantly positively correlated within each spatial frequency ($r = 0.7$, $p = 0.01$ at 0.5 c/°; $r = 0.69$, $p = 0.01$ at 1 c/°, and $r = 0.61$, $p = 0.03$ at 2 c/°) and across all spatial frequencies and subjects ($r = 0.58$, $p = 0.0002$). Figure 5 plots perceived speed as a function of perceived flicker for all spatial frequencies and subjects. A linear regression (solid line, Figure 5) indicates a positive slope of 0.35 that is significantly different from zero, $F(1, 34) = 17.21$, $p = 0.0002$.

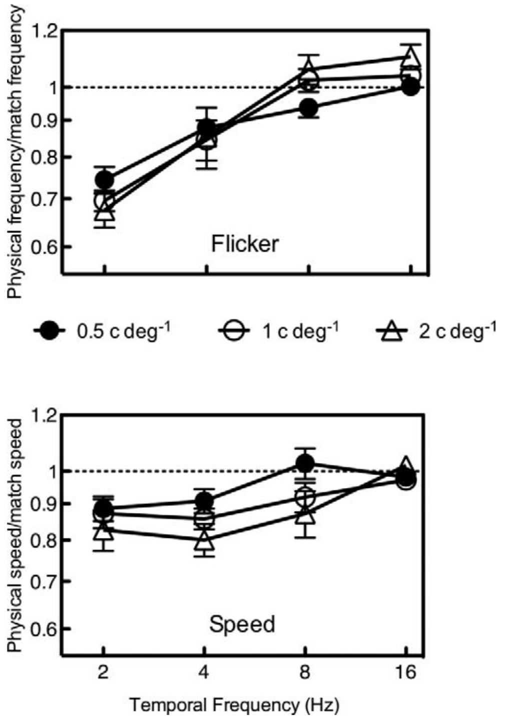

Figure 4. Perceived flicker (upper panel) and speed (lower panel) as a function of temporal frequency for 0.5 c deg^{-1} (closed circles), 1 c deg^{-1} (open circles), and 2 c deg^{-1} (open triangles). Data are averaged across subjects. Error bars represent ±1 *SEM*. The broken line represents a veridical match.

In order to establish whether the effect of contrast on perceived flicker is present in the absence of spatial structure, we conducted a second auxiliary experiment that measured perceived flicker of a spatially homogeneous field at low contrast. The stimuli were presented in two circular windows of the same dimension as in the previous experiment but contained no spatial structure. Two of the subjects were the same as in the main experiment and a third was one of the authors (SH). All other aspects of the procedure were the same as that of

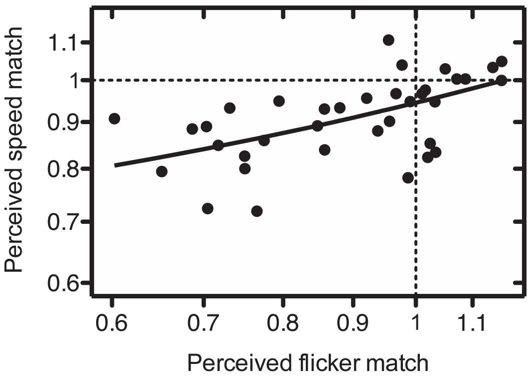

Figure 5. Perceived speed plotted as a function of perceived flicker for all spatial frequencies and observers. The solid line represents the linear regression.

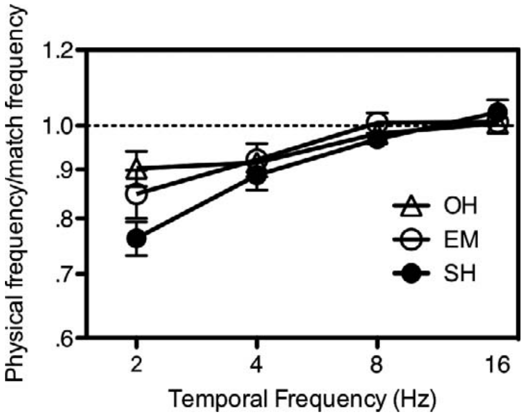

Figure 6. Perceived flicker of a spatially homogeneous field as a function of temporal frequency for three subjects (indicated in panel). The broken line represents a veridical match. Error bars represent ±1 *SEM*. The broken line represents a veridical match.

the main experiment. Figure 6 plots the results of this second auxiliary experiment. All three subjects show a reduction in perceived flicker at low contrast at both 2 and 4 Hz. Perceived flicker matches at 8 and 16 Hz are near-veridical. A one-way ANOVA indicated a significant difference between temporal frequencies, $F(3, 8) = 12.98$, $p = 0.0019$, Tukey's multiple comparison test indicated significant differences between 2 and 8 Hz, 2 and 16 Hz, and 4 and 16 Hz ($p < 0.05$).

Discussion

The results of the first auxiliary experiment indicated that both perceived speed and flicker were reduced at low contrast at 4 Hz with the stimulus configuration employed. Although we failed to find an *increase* in perceived flicker at low contrast, the results of our first auxiliary experiment indicated that low contrast reduced perceived speed significantly more than perceived flicker. Our main results clearly show that both perceived flicker and speed are similarly affected by a reduction in contrast. At low temporal frequencies, reducing contrast reduced both perceived speed and flicker. At higher frequencies, reducing contrast resulted in either a veridical percept or a modest increase in perceived flicker and a veridical percept of speed. At the spatial frequency (2 c deg^{-1}) employed by Thompson and Stone (1997), perceived flicker increases modestly at 8 Hz but perceived speed is underestimated (see Figure 3D). This pattern of results is qualitatively similar to those reported by Thompson and Stone (1997) at 4 Hz. Our second auxiliary experiment indicated that the reduction in perceived flicker at low contrast is present for a spatially homogeneous stimulus.

Unlike Thompson and Stone (1997), we find little evidence for an increase in perceived speed at high frequencies and no increase in perceived flicker at 4 Hz. This lack of quantitative agreement is, however, not unusual within the literature. For instance, other studies have failed to detect increases in perceived speed (e.g., Hawken, Gegenfurtner, & Tang, 1994; Stone & Thompson, 1992). It has long been known that a vast range of parameters including size, background, and luminance can affect perceived speed (Brown, 1931), and it is therefore likely that the effect of contrast is highly susceptible to stimulus configuration. For instance, we note that many of those studies (e.g., Thompson et al., 2006; Thompson & Stone, 1997; Thompson, Stone, & Swash, 1996) that find contrast-induced increases in perceived speed used relatively small patches (<2°) of stimuli, whereas those that have failed to find such an effect (e.g., Hawken et al., 1994; Stone & Thompson, 1992) have used larger (>4°) stimuli. Thus, our failure to replicate the increase in perceived flicker at 4 Hz reported by Thompson and Stone (1997) may well be due to differences in stimulus parameters such as stimulus size, number of cycles, and mean luminance, all of which differed considerably across the studies.

The results of the main experiment reveal that while there are clear quantitative differences in the effect of contrast upon perceived speed and flicker, contrast affects perceived flicker and speed in a qualitatively similar manner, and these effects are significantly correlated. The positive correlation between these contrast effects is precisely the opposite of that which would be expected from Thompson and Stone's (1997) assertion that contrast affects speed and flicker differently. This has important consequences for models of speed encoding. Primarily, it indicates that it is reasonable to assume that speed sensitive mechanisms may be derived from the output of earlier temporal mechanisms. However, since the counterphase gratings we employed can be considered as the sum of two gratings drifting in opposite directions, it could equally be argued that our results are due to an inherent speed effect. In other words, the reduction in perceived flicker we found may be due to at least a partial encoding of counterphase flicker by speed-tuned mechanisms. Indeed, upon the basis of the relatively poor temporal frequency discrimination they found and the fact that subjects could perform velocity discrimination in the presence of random variation in spatial frequency and contrast, McKee, Silverman, and Nakayama (1986) proposed that flicker was encoded solely by speed sensitive units. However, Smith and Edgar (1991) demonstrated that temporal frequency discrimination is similarly unaffected by random changes in velocity. Our second auxiliary experiment demonstrated that perceived flicker is reduced at low contrast in the absence of spatial structure. This stimulus cannot provide a systematic cue for speed-tuned mechanisms. Thus the findings of Smith and Edgar (1991) and the results of our second auxiliary experiment vie strongly against the notion that flicker is only encoded via motion sensitive mechanisms. We conclude that the effect of contrast upon perceived flicker is inherent in early temporal filters rather than inherited from motion sensitive mechanisms. Smith and Edgar (1991) suggested that both flicker and speed information is explicitly represented within the visual system rather than one dimension being extracted from the other. Henning and Derrington's (1994) finding of shallower slopes of psychometric functions for temporal frequency than speed judgments led them to a similar conclusion. Our results are entirely consistent with this suggestion and with a range of other behavioral and physiological findings (e.g., Priebe, Lisberger, & Movshon, 2006; Reisbeck & Gegenfurtner, 1999).

The main emphasis of these results is to demonstrate that, contrary to the conclusions of Thompson and Stone (1997), models of speed encoding need not exclude the possibility of deriving speed information from earlier separable temporal frequency tuned units. Our results do not speak to the veracity of this class of model, nor to which variant of this class (or any other) may prove optimal. However, for the sake of completeness, we modeled our averaged speed data using a simple ratio model in order to evaluate the consistency of a ratio scheme with our behavioral data. The model assumes that speed is derived from the ratio of the outputs of a low-pass (p) and band-pass (m) temporal filter. We used the filters proposed by Perrone (2005). Perrone has previously shown that these filters provide a good fit to typical tuning functions in macaque V1 (Foster et al., 1985). The low-pass filter takes the form:

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

where

$$a = \left((2\pi\omega\tau_1)^2 + 1\right)^{-\frac{9}{2}} \quad \text{and}$$

$$b = \left((2\pi\omega\tau_2)^2 + 1\right)^{-\frac{10}{2}}$$

and the high-pass filter is given by

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

where ω is temporal frequency, and following Perrone, τ_1, τ_2, and k are constants of 0.0072, 0.0043, and 4 respectively. There are no free parameters at this stage of the model.

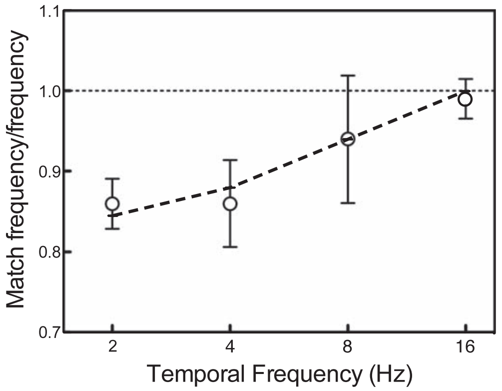

Figure 7. The model's predicted speed at low contrast (broken line) is plotted as a function of temporal frequency. The average perceived speed at low contrast (averaged across subjects and spatial frequencies) is plotted as open symbols. Error bars represent ±1 *SEM*.

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 response of each mechanism is given by a Naka-Rushton (1966) equation such that:

$$P(\omega, c) = \frac{c.p(\omega)}{|c|.p(\omega) + \alpha_p} \tag{3}$$

and

$$M(\omega, c) = \frac{c.m(\omega)}{|c|.m(\omega) + \alpha_m/\omega} \tag{4}$$

where c is contrast and α_p and α_m are the semi-saturation constants. Following, Kaplan, Lee, and Shapley (1990) we set the value of α_p to 1.74, the average value of the semisaturation constant they report for parvocellular cells in the macaque. Note that we have chosen this value to minimize the number of free parameters whilst capturing physiologically plausible values of other parameters. The semisaturation constant for the band-pass mechanism, α_m, was a free parameter, and following Hammett, Georgeson, and Gorea (1998), we assume that its contrast response becomes more compressive as frequency increases such that its value is inversely proportional to frequency. Speed, S, is determined by the ratio of these two functions such that:

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

The best fit of the model, found using the error minimization routine *fminsearch* in Matlab 7.80.347 (The Mathworks Inc., Natick, MA), is plotted in Figure 7. The broken line represents the ratio of the model's predicted speed at low and high contrast, i.e., the ratio of the model's predicted speed at a contrast of 0.2 to 0.7. The model provides an adequate fit to our averaged behavioral data and demonstrates that a simple ratio model is consistent with the contrast dependency of perceived speed. The best fit of the model yields a value of the free parameter α_m of 2.88. Thus at 2 Hz the semisaturation constant for the bandpass mechanism takes a value of 1.44, whereas at 16 Hz the semisaturation constant takes a value of 0.18, close to the average magnocellular semisaturation constant of 0.13 reported by Kaplan et al. (1990). It should be noted that neither our results, nor the model, speak directly to how speed is encoded. Rather, we show here that the effect of contrast upon perceived flicker is consistent with a class of model that extracts speed from early spatiotemporally separable units and that this class of model can account for our behavioral data with physiologically plausible parameters.

Conclusions

We have found that perceived flicker is reduced at low contrast in a manner that is qualitatively similar to contrast's effect upon perceived speed. Our results indicate that the effect occurs at an early level of temporal filtering. Given the similarity of the effect of contrast upon perceived flicker and speed, we conclude that it is likely that the effect of contrast upon perceived speed is at least in part inherited from its effect upon earlier temporal filters.

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