Vision Research 201 (2022) 108124

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Perceived speed at low luminance: Lights out for the Bayesian observer?

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ARTICLE INFO

Keywords:
Motion perception
Perceived speed
Luminance
Bayesian models

ABSTRACT

To account for perceptual bias, Bayesian models use the precision of early sensory measurements to weight the influence of prior expectations. As precision decreases, prior expectations start to dominate. Important examples come from motion perception, where the slow-motion prior has been used to explain a variety of motion illusions in vision, hearing, and touch, many of which correlate appropriately with threshold measures of underlying precision. However, the Bayesian account seems defeated by the finding that moving objects appear faster in the dark, because most motion thresholds are worse at low luminance. Here we show this is not the case for speed discrimination. Our results show that performance improves at low light levels by virtue of a perceived contrast cue that is more salient in the dark. With this cue removed, discrimination becomes independent of luminance. However, we found perceived speed still increased in the dark for the same observers, and by the same amount. A possible interpretation is that motion processing is therefore not Bayesian, because our findings challenge a key assumption these models make, namely that the accuracy of early sensory measurements is independent of basic stimulus properties like luminance. However, a final experiment restored Bayesian behaviour by adding external noise, making discrimination worse and slowing perceived speed down. Our findings therefore suggest that motion is processed in a Bayesian fashion but based on noisy sensory measurements that also vary in accuracy.

1. Introduction

There are two broad categories of explanation for perceptual bias. The first is 'bottom-up' and suggests that systematic errors are present in early sensory measurements. Some of these errors can depend on the way basic stimulus properties affect sensor output, and others on the way different sensors interact with each other. Examples of the former include the influence of contrast, spatial frequency and retinal location on perceived speed (Johnston & Wright, 1985; Smith & Edgar, 1991; Thompson, 1982); examples of the latter include the many types of simultaneous contrast illusion known to exist (Bosten & Mollon, 2010). The second broad category of explanation is 'top-down' and appeals to the influence of higher-level factors, such as prior knowledge about the world (Gregory, 1997; Teufel & Fletcher, 2020). A contemporary and much debated example is Bayesian perceptual inference (Ernst & Bulthoff, 2004; Geisler & Kersten, 2002; Knill & Richards, 1996; Purves, Wojtach, & Lotto, 2011). Bayesian models trade perceptual accuracy in favour of increased precision by using an optimal 'best-guess' that combines noisy incoming sensory evidence with prior knowledge about the world.

Many of the core claims of Bayesian models have been tested using moving stimuli, where an observer's prior knowledge of movement is relatively easy to justify. The world is largely stationary, so the most probable interpretation of noisy motion sensors is that movement is slow (Weiss, Simoncelli, & Adelson, 2002), a claim supported by the statistics of movies and videos (Dong & Atick, 1995). The 'slow-motion' prior has been used to explain a variety of movement phenomena across the senses, such as the effects of contrast and background sound on perceived visual speed and auditory speed (Senna, Parise, & Ernst, 2015; Sotiropoulos, Seitz, & Seriés, 2014; Stocker & Simoncelli, 2006), the misperception of visual motion during eye movement (Freeman, Champion, & Warren, 2010), misperceptions of auditory and tactile motion during head and arm movement (Freeman, Culling, Akeroyd, & Brimijoin, 2017; Moscatelli, Hayward, Wexler, & Ernst, 2015; Wallach, 1940), judgements of collisions (Welchman, Lam, & Bülthoff, 2008) and the interpretation of dynamic cues to depth (Wexler, Panerai, Lamouret, & Droulez, 2001). The generality of the approach captures some of the appeal of the Bayesian account.

Contrary to 'bottom-up' explanations of perceptual bias, most Bayesian models are built on an assumption that early sensory measurements are accurate. The initial neural signals are assumed to be internally consistent with each other and independent of changes to

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https://doi.org/10.1016/j.visres.2022.108124
Received 6 April 2022; Received in revised form 21 July 2022; Accepted 6 September 2022

basic stimulus properties such as contrast and luminance (Burge, Girshick, & Banks, 2010; Moscatelli et al., 2015). Consider the way perceived visual speed changes in different contexts, such as the speeding up of perceived object motion and self-movement at higher contrasts (Blakemore, 1996; Snowden, Stimpson, & Ruddle, 1998; Thompson, 1982; Thompson, Brooks, & Hammett, 2006). Bayesian models propose that higher contrasts increase sensory precision by virtue of an increased signal-to-noise ratio, thereby reducing the influence of the slow-motion prior and consequently increasing the perceived-speed estimate (Ascher & Grzywacz, 2000; Hurliman, Kiper, & Carandini, 2002; Powell, Meredith, McMillin, & Freeman, 2016; Sotiropoulos et al., 2014; Stocker & Simoncelli, 2006). Crucially, the accuracy of the encoded speed cue is assumed to be fixed, such that its average does not vary with contrast. More traditional 'bottom-up' models, on the other hand, appeal to the influence of contrast on sensory measurements of speed, thus affecting the average. For example, in the ratio-model (Hammett, Champion, Morland, & Thompson, 2005; Harris, 1986), a change in contrast acts to selectively alter the output of one temporal-frequency channel with respect to another. In doing so, perceived speed goes up or down depending on the ratio of the activity between one channel and the other (Hammett et al., 2005; Hammett, Thompson, & Bedingham, 2000; Harris, 1980; Hassan & Hammett, 2015; Smith & Edgar, 1994; Thompson et al., 2006).

A key finding in support of the Bayesian explanation is the fact that speed discrimination, a simple measure of sensory precision, often becomes harder in situations where perceived speed slows. In the case of contrast, this is true for a range of stimuli, from simple and complex gratings (Champion & Warren, 2017; Powell et al., 2016) to movies of real scenes (Horswill & Plooy, 2008). Importantly, this relationship between speed discrimination and perceived speed generalises to other senses, such as hearing (Senna et al., 2015), touch (Moscatelli et al., 2015), and extra-retinal information from the eye-movement system (Freeman et al., 2010; Powell et al., 2016). Yet despite its generality, the Bayesian framework struggles to explain some motion phenomena (for review, see Park & Tadin, 2018). The one we consider here is the increase in perceived speed at low luminance, which can occur for both object motion and self-movement (Hammett, Champion, Thompson & Morland, 2007; Hammett, Smith, Wall, & Larsson, 2013; Pritchard & Hammett, 2012; Vaziri-Pashkam & Cavanagh, 2008).

The luminance effect challenges the Bayesian account because many fundamental aspects of spatiotemporal sensitivity decline in the dark (for review, see Watson, 1986). If the ability to discriminate speed followed the same pattern, then according to the Bayesian framework, perceived speed should slow down not speed up, because poorer discrimination implies lower precision (Hammett et al., 2007). On the face of it, therefore, the effect of luminance on perceived speed appears to be an easy to demonstrate perceptual bias that calls into question the generality of the Bayesian approach.

However, very few studies have measured the effect of luminance on speed discrimination, and of those that exist, the findings are mixed. Orban et al. (1984) found speed discrimination declines with luminance at very low light levels in the scotopic range, a finding echoed by Takeuchi and De Valois (2000), who compared scotopic to much brighter photopic stimuli. However, Raghuram, Lakshminarayanan and Khanna (2005) found the opposite when comparing mesopic to photopic stimuli. The latter light levels are where the effect of luminance on perceived speed has mostly been studied; potentially, therefore, Raghuram et al's result supports the Bayesian model. Crucially, however, they did not explicitly control whether their observers were light or dark adapted, which could confound the ability to discriminate the speed of light or dark stimuli. We therefore compared performance in observers who were either light or dark-adapted, and tested the Bayesian model by collecting both speed discrimination and perceived speed measures at the same time.

Our results showed that speed discrimination improved in the dark by the same amount regardless of adaptation state, an effect that disappeared once differences in perceived contrast were removed. Contrary to the Bayesian prediction, however, the effect of luminance on perceived speed remained unchanged regardless of the condition investigated. Lights out for the Bayesian observer? A final experiment showed that perceived speed slowed, and speed discrimination became poorer, when external noise was added to our displays. Our findings therefore suggest the operation of a Bayesian observer, one dealing with noisy sensory measurements that vary in accuracy.

2. Experiment 1: The effect of luminance on perceived speed and speed discrimination

2.1. Methods

2.1.1. Stimuli

All stimuli were presented on a ViewSonic P225f colour CRT at 120 Hz and pixel resolution of 1280 × 960 using custom software written with PsychToolbox in MatLab. Gamma-correction was used throughout, based on fitting a standard gamma correction curve to readings from a Minolta LS-100 photometer and then updating the LUTs using PsychToolbox's 'LoadNormalizedGammaTable' function. Stimuli were viewed from 70 cm using a forehead and chin rest.

Each trial consisted of two sinusoidal gratings simultaneously presented either side of a fixation point for 500 msec. Gratings had a spatial frequency of 1 cycle / degree, a contrast of 50%, and were displayed through hard circular windows (dia 6°). The window centres were separated by 8°. The local mean luminance of the gratings was 10.2 cd/m^2 but could be reduced using small circular patches of neutral density filter (Rosco E-Colour #299) mounted on horizontal rods, as shown in the schematics of Fig. 1. The neutral density filter (NDF) lowered luminance by 1.2 log units (0.64 cd/m^2), which we checked using a photometer. The rest of the screen was set to either to a high or low luminance depending on the adaptation condition described later. The horizontal rods with or without NDF were present in all conditions. A small side light illuminated the black wall behind the screen. All other lights in the lab were switched off.

2.1.2. Procedure

On each trial, a 'standard' grating was shown at a fixed speed of 8°/s, and a 'test' grating was shown at a speed defined by a Method of Constant Stimuli. Both gratings were shown moving in the same direction, which alternated from trial to trial. The left–right direction on the first trial was randomly selected. The speeds were chosen to bracket the Point of Subjective Equality (PSE) and differed depending on whether speed discrimination or speed matching was being investigated (for values, see below). Observers had to judge which of two gratings appeared faster. No trial-to-trial feedback was given.

For speed matching, the test speeds depended on whether the standard or test appeared behind the NDF. When the test grating was behind the filter, the 7 speeds ranged from 3.8 to 9.8°/s in 1°/s step; when the standard was behind the filter, the tests ranged from 6.2 to 12.2°/s. This yielded two psychometric functions per session. Ten replications of each speed were carried out per psychometric function, yielding 140 trials in total. The left–right position of the test and standard was randomly chosen on each trial. In all experiments, speed-matching conditions always had the NDF placed over the left-hand grating. No attempt was made to counterbalance NDF position.

To measure speed discrimination at low or high luminance, test and standard were shown either with two patches of NDF in place, or with none. Low and high luminance conditions were tested in separate sessions. Test speeds ranged from 5 to 11°/s in 1°/s step, irrespective of the luminance being investigated or the side the standard and test appeared. To make the sessions the same length as the speed-matching condition, two psychometric functions were collected per session despite the fact they were identical.

Adaptation state was manipulated by adapting observers for 2 min to

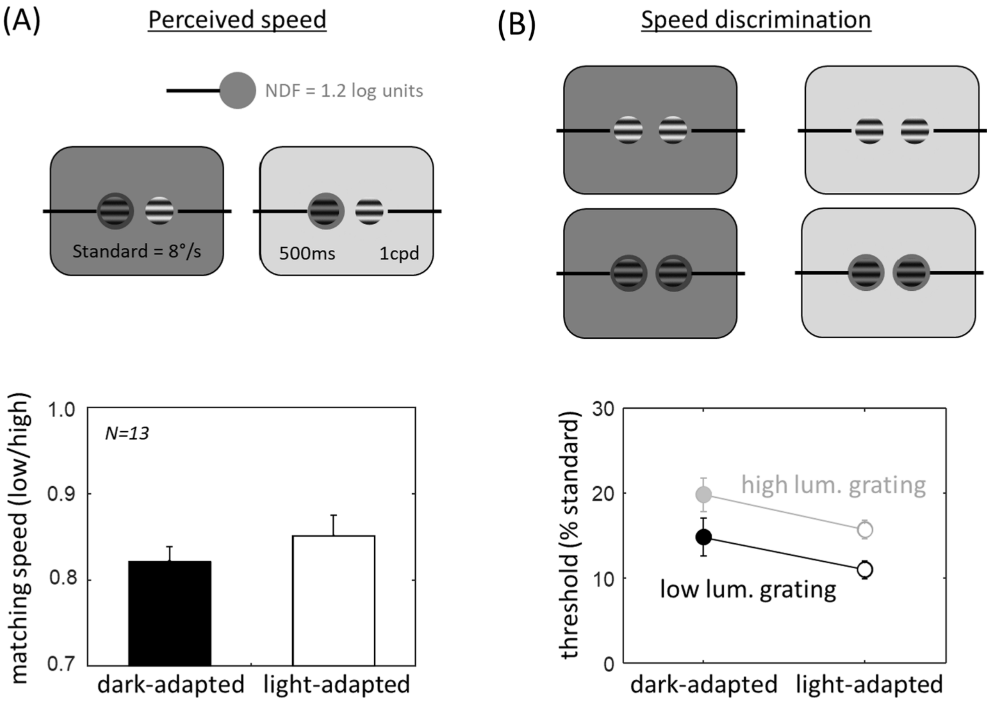

Fig. 1. (A) The effect of luminance on the perceived speed of moving stimuli. Data is expressed as the ratio of speeds of the low to high luminance gratings at the Point of Subjective Equality (PSE). Ratios less than 1 indicate that darker stimuli appear faster. (B) The effect of luminance on speed discrimination for light-adapted and dark-adapted observers. The data are expressed as a percentage of the standard speed (8°/s). Error bars are ±1SE.

the display configuration appropriate for the luminance manipulation (i.e. 0, 1, or 2 NDFs) but without any gratings present. The screen's background was set to the mean luminance of either the filtered or unfiltered grating, yielding dark or light adaptation, respectively. During data collection, the display background was then maintained at the appropriate luminance. All six conditions (light and dark adaptation crossed with speed matching and low and high luminance speed discrimination) were run in a random order just once per observer.

Prior to the main experiment each observer was given a short practice session using either the low luminance or high luminance speed discrimination condition, with the choice counterbalanced across observers. Half the observers practiced with the NDF covering both gratings and half without.

2.1.3. Analysis

The two separate psychometric functions per run were fit with individual cumulative Gaussians, using a standard maximum likelihood procedure, which included a lapse rate parameter constrained to be 6% or less (Wichmann & Hill, 2001). The PSE and threshold were defined as the mean and standard deviation of the underlying Gaussian, respectively. The PSE therefore corresponds to the speed yielding 50% faster responses. The threshold corresponds to the speed yielding the difference between 50% and 84.1% faster responses.

2.1.4. Observers

The research was approved by the School of Psychology's Ethics Committee (ec.05.10.04.521 g). Fifteen undergraduate observers were recruited as part of their course credit requirement and had little if any experience of running in psychophysical experiments. Outliers were detected across the fifteen observers using a modified z-score based on the median absolute deviation. Values > 3.5 were categorised as outliers (Iglewicz & Hoaglin, 1993). Two observers exhibited one or more outliers across the six dependent measures and were therefore excluded, leaving $N = 13$.

2.2. Results and conclusions

The results in Fig. 1A replicate the finding that perceived speed increases at low luminance, albeit with more spatially localised changes to luminance than has previously been used. In both adaptation conditions, the low-luminance grating had to be moved roughly 15–20% slower to achieve a perceived-speed match with the high-luminance grating. The adaptation state of the observers did not change the effect ($t(12) = 1.12$, $p = .28$).

Fig. 1B shows that speed discrimination was much improved in the dark ($F(1,12) = 16.22$, $p = .002$). Light-adapted observers were better at speed discrimination than dark-adapted observers ($F(1,12) = 6.44$, $p = .026$). There was no interaction between adaptation and luminance ($F < 1$). On the face of it, therefore, a standard Bayesian model could explain the increase in perceived speed at low luminance. The discrimination data suggest that precision improved, thereby reducing the putative influence of a slow-motion prior.

3. Experiment 2: Perceived contrast as a function of luminance and speed

The support for the Bayes model obtained in Experiment 1 assumes the difference in discrimination found for low and high luminance reflects differences in precision (i.e. reliability, or internal noise) associated with the encoding of speed feeding the Bayes estimate. However, our impression was that perceived contrast varied more with speed at low luminance than high, a factor known to contribute to the perception of speed in the retinal periphery (Hassan & Hammett, 2015). Perceived contrast could have potentially acted as an additional cue to speed in Experiment 1, explaining the discrimination difference we obtained but not in terms of signal precision. In Experiment 2 we therefore measured perceived contrast as a function of speed and luminance.

3.1. Methods

3.1.1. Stimuli

For this experiment and all those remaining, a more traditional 'split-screen' technique was used to compare percepts simultaneously across low and high luminance (see schematics in Fig. 2). This was achieved by placing the left half of the screen behind the NDF. When comparisons within luminance were called for, the NDF was placed over the whole screen or removed.

We measured perceived contrast in all three luminance contexts. The NDF lowered luminance by 1.8 log units, as opposed to the 1.2 log units used in Experiment 1. The gratings were presented within a large circular patch (dia. 18°) with the rest of the display set to black. All other stimulus details were the same as before.

3.1.2. Procedure

Perceived contrast was measured using 1-up 1-down staircases that adjusted the contrast of a test grating to match that of the standard grating. The standard contrast was fixed at 50% as in Experiment 1, a value equal to the initial contrast of the test grating. The staircase then adjusted the test's contrast using larger steps of 10% and 5% for the first two reversals, and then 2.5% over the remaining ten reversals. Contrast values were prevented from moving beyond the range 0–100%. The PSE was based on the mean contrast over the final ten reversals.

In Experiment 2A, two full-screen conditions were used to determine within-luminance comparisons of perceived contrast. The standard grating always moved at 8°/s. The test grating moved at one of five speeds, ranging from 4 to 12°/s in 2°/s steps. Three replications of each luminance condition were run in sequence (e.g. 3 × low followed by 3 × high), with the sequence counterbalanced across observers. We did not light or dark adapt observers at the start of each sequence, instead relying on the length of time each sequence placed observers within the appropriate prevailing illumination (approx. 40 mins).

Experiment 2B used the split-screen condition to compare perceived contrast across luminance. The standard was presented either at low luminance or high luminance, corresponding to the left or the right of the screen, respectively; at the same time, the test grating was shown at either high or low luminance. All ten conditions (five speeds × two luminance combinations) were randomly interleaved from trial to trial within the same testing session. Three replications were carried out. Again, we did not light or dark adapt observers priors to data collection, this time because all luminance conditions of Experiment 2B were intermingled in the same session.

All observers completed Experiment 2A before Experiment 2B.

3.1.3. Observers

Five observers took part. They consisted of one of the authors (TCAF), members of the lab and postgraduates within the school, all giving their time for free. All were experienced psychophysical observers and were unaware of the hypotheses of the experiments except TCAF.

3.2. Results and conclusions

Fig. 2A shows the contrast matches for the two full-screen conditions. Each panel corresponds to a different observer. Perceived contrast varied little with speed when both gratings were shown at high luminance (open symbols). However, at low luminance, perceived contrast varied a

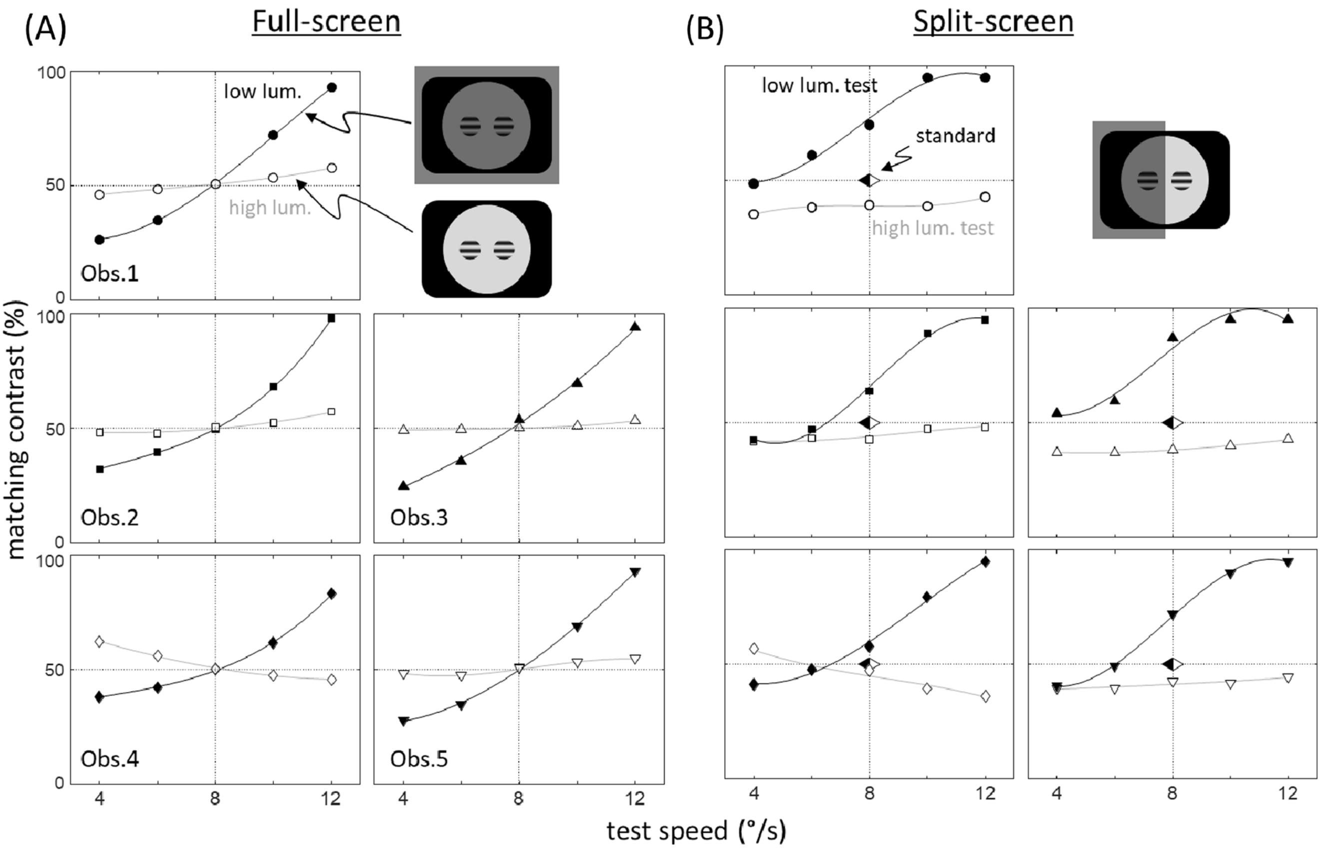

Fig. 2. The effect of luminance on the perceived contrast of moving stimuli at different speeds. (A) Contrast matches for individual observers using full-screen manipulation of luminance. Perceived contrast varied a lot at low luminance (closed symbols) but little at high luminance (open symbols). (B) Contrast matches for a split-screen condition. Again, perceived contrast varied a lot with speed when a low-luminance test was visually compared to a high-luminance standard. However, perceived contrast varied little when a high-luminance test was compared to a low-luminance standard. Lines in each panel show fits of a 3rd order polynomial as detailed in Section 4.1.1.

lot. Specifically, at low luminance, the perceived contrast of the test grating declined with increasing speed, requiring increases in its contrast to achieve a match. The general pattern across the two luminance conditions was echoed by the split-screen condition shown in Fig. 2B. When the perceived contrast of a high luminance test was compared to a low luminance standard (open symbols), test contrast had to be lowered, but by roughly the same amount for all test speeds investigated. However, for a low luminance test (closed symbols), perceived contrast varied a lot more. Indeed, at the highest speed investigated, the system could not deliver enough contrast to achieve a match in the split screen condition. Hence most of the PSEs were fixed to the highest contrast value. But apart from this small region of the data, the contrast matches were very consistent within observers. For instance, observer 4 is the only observer who showed a small increase in perceived contrast with speed at high luminance, an idiosyncrasy that did not depend on the use of a full-screen or split-screen (compare open symbols in bottom left panels of Fig. 2A,B).

Potentially, therefore, the improved speed discrimination found at low luminance in Experiment 1 was due to the presence of a more powerful perceived contrast cue. To test this idea, Experiment 3 controlled perceived contrast using a similar technique to Hassan, Thompson and Hammett (2016). Specifically, we used the data in Fig. 2 to create a set of stimuli with the same perceived contrast regardless of luminance or speed, and then compared the results to stimuli that had the same physical contrast.

4. Experiment 3: Perceived speed and speed discrimination with and without changes in perceived contrast

4.1. Methods

4.1.1. Stimuli and procedure

‘Equicontrast’ stimuli were created using calibration curves fit to each observer’s contrast matches from Experiment 2. These were then used to produce a set of individually tailored stimuli whose perceived contrast was now independent of luminance or speed. The calibration curves are shown as lines in Fig. 2, and were obtained by fitting a 3rd order polynomial to each participant’s contrast matches, using MatLab’s ‘polyfit’ function. Equicontrast stimuli were created by choosing a pair of calibration curves linked by a common standard. We selected the low luminance standard, corresponding to the calibration curves labelled ‘low lum.’ in Fig. 2A, and ‘high lum. test’ in Fig. 2B. The choice was based on the finding in Experiment 2 that perceived contrast saturated at high speeds when using a low luminance test in the split-screen condition. This ruled out the use of a common high luminance standard.

Six conditions were investigated in Experiment 3: two contrast types (equicontrast versus unequal contrast) crossed with three speed judgements (speed matching and low vs high luminance speed discrimination). Each involved the same procedure as Experiment 1. Conditions were run in a random order, with each condition repeated three times per observer. In between each run, observers adapted to the prevailing lighting condition in the absence of the two gratings for 2 min: either no NDF (speed discrimination at high luminance), split-screen (speed-matching) or NDF over the entire screen (speed discrimination at low luminance).

4.1.2. Analysis

For each condition and observer, the two psychometric functions were obtained by collating trials across all three replications. The PSE and threshold were then estimated using the fitting procedure described in Experiment 1.

4.1.3. Observers

The observers were the same as Experiment 2.

4.2. Results and conclusions

Fig. 3A shows the increase of perceived speed at low luminance did not depend on contrast type ($t(4) = 0.28$, $p = .792$). However, Fig. 3B shows a significant interaction between luminance and contrast type for speed discrimination ($F(1,4) = 8.08$, $p = .047$). Simple effects showed that the interaction was driven largely by the difference found for the darker gratings across the two types of contrasts ($p = .001$), with a weaker effect of luminance for the unequal contrast condition ($p = .06$). Neither the simple effects of contrast on the high luminance nor luminance on equicontrast gratings were significant ($p = .47$ and $p = .2$, respectively). The weaker effect of luminance for the unequal contrast condition was surprising given the strong effects found in Experiment 1. Indeed, in an earlier version of the experiment, we found 20/21 observers showed better speed discrimination at low luminance using the same stimuli but a slightly different procedure (Freeman & Powell, 2020). The weaker effect of luminance for unequal contrast gratings found in Experiment 3 seems to be driven by one observer, who showed a small improvement in speed discrimination at high luminance. The remaining 4 observers replicated the speed discrimination effect found in Experiment 1. Overall, therefore, the findings indicate that any luminance-based differences in speed discrimination depend on perceived contrast as opposed to differences in sensory precision.

The effect of luminance was smaller than that obtained in Experiment 1, despite the stronger NDF. Several factors could explain this difference, such as the experience of the observers taking part and the use of localised versus more global changes in mean luminance. It is also possible that the relationship between luminance and perceived speed is non-monotonic. Gegenfurtner and colleagues have shown that perceived speed slows by about 20% when purely rod-based vision is compared to cone-based, a finding based on deuteranopes viewing moving stimuli in a silent substitution paradigm (Gegenfurtner, Mayser, & Sharpe, 1999; Gegenfurtner, Mayser, & Sharpe, 2000). While the lowest luminance used here ($\sim$0.17 cd/m^2) is still firmly in the mesopic range, their results imply that the effect of luminance on perceived speed is non-monotonic, reversing somewhere in the mesopic to scotopic range.

The effects we report here are difficult to explain using a standard Bayesian model because there is little evidence for the changes in sensory precision that are needed to reweight the influence of the slow-motion prior. Our results suggest the effect of luminance on perceived speed is largely determined by changes in the accuracy of early motion sensors. This runs counter to a key assumption of the standard Bayesian model but agrees with the ‘bottom-up’ models discussed earlier. The results therefore question whether a Bayesian estimation stage is present at all. In a final experiment, we sought evidence for Bayes-like behaviour by adding external noise to enforce differences in precision. In doing so, the Bayesian model predicts specific changes in perceived speed as detailed below.

5. Experiment 4: Perceived speed and speed discrimination in the presence of external noise

There are a number of ways of adding external noise to moving stimuli, such as adding random changes in position over the course of the stimulus’s trajectory (Bentvelzen, Leung, & Alais, 2009). In keeping with the key manipulation of the current paper, we decided to add software-controlled switches in mean luminance, drawn from a Gaussian distribution. Crucially, these were applied to the high luminance grating only. According to the Bayesian framework, this should increase the difference in perceived speed at the two light levels we investigated, but only if the external noise also gives rise to a change in speed discrimination for the noise-affected grating. To measure the latter, we did not run separate speed discrimination conditions as carried out in Experiments 1 and 3. Rather, we inferred the effect of the external noise on speed discrimination from the psychometric function used to assess perceived speed in the presence of the split screen. The

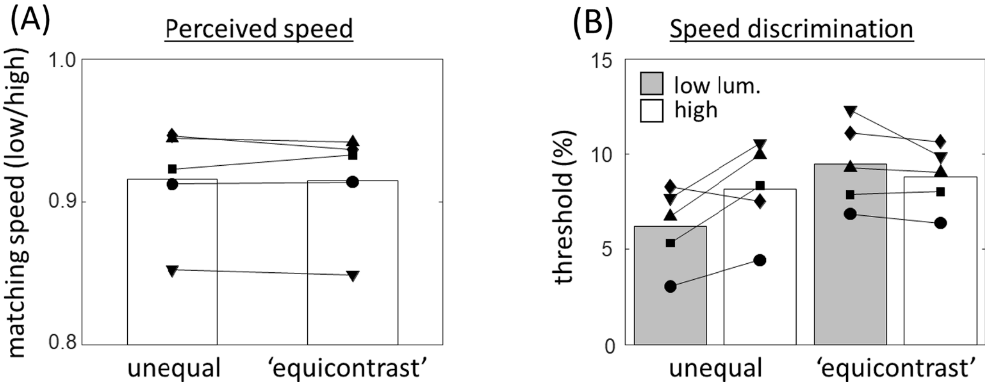

Fig. 3. (A) The effect of luminance on perceived speed for unequal contrast and equicontrast stimuli. Darker stimuli always appeared faster regardless of contrast type. Bars correspond to the mean across the five observers. Individual data use the same symbol convention as Fig. 2. (B) The effect of luminance on speed discrimination for unequal contrast and equicontrast stimuli.

psychometric function in this case is limited by two noise sources, one corresponding to the low luminance grating and one corresponding to the high. Assuming the noise for the low luminance grating remains the same throughout the experiment, then any difference in the slope of the psychometric function (i.e. threshold) reflects changes in the external noise added to the high luminance grating (see Rideaux & Welchman, 2020, for a similar strategy).

5.1. *Methods*

5.1.1. *Stimuli and procedure*

The stimuli were the same as Experiment 3 save for the addition of external noise to the high luminance grating. The noise consisted of software-controlled switches in the mean luminance at a rate of 8 Hz (i.e. every 125msec), with the values drawn from a Gaussian distribution. Expressing the mean luminance as a proportion of the total light level deliverable by our system (L_{prop}), the standard deviation of the Gaussian was set to $L_{prop} = 0.1$, with the additional constraint that the value returned remained within the range $0.25 < L_{prop} < 0.75$ in order to prevent clipping. The grating amplitude was fixed to $L_{prop} = 0.5$. This meant that Michelson contrast also varied with mean luminance, from close to 100% for the lowest possible value to 33% for the highest. Assuming the effect of the added noise was to alter encoded speed, then the fluctuation in contrast correlated exactly with the direction of the speed-change induced by the switching of mean luminance. For example, when mean luminance was momentarily low, contrast would be momentarily high, both of which increase perceived speed as discussed throughout the paper. This issue is explored in more detail the General Discussion.

Each observer carried out three replications of the experiment.

5.1.2. *Observers*

Four of the five observers from Experiments 2 and 3 took part in Experiment 4, including the observer who appeared to show different behaviour from the rest. To equate the number, an additional inexperienced observer was recruited for course credit.

5.2. *Results and conclusions*

Fig. 4A plots individual and mean PSEs and shows that adding external noise to the high luminance grating made it appear slower (t(4) = 4.47, p =.011). Thus, to achieve the perceived speed match, this grating had to be moved faster and hence the ratio of speeds at the PSE (low/high) becomes smaller. Fig. 4B shows that the lowering of perceived speed was accompanied by a decline in speed discrimination (t(4) = 3.07, p =.027). Thus, when differences in discrimination truly reflect differences in underlying precision, Bayesian behaviour is revealed.

6. General discussion

6.1. *Summary*

The fact that moving objects appear faster in the dark has been

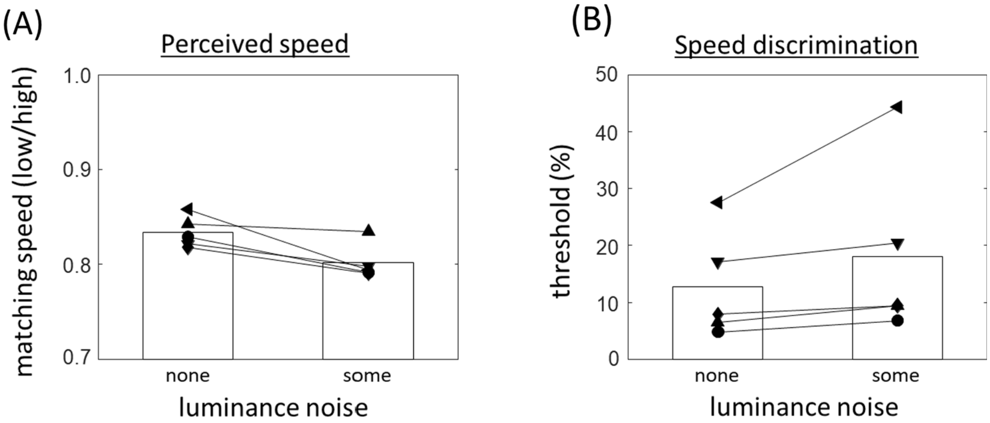

Fig. 4. (A) Adding external noise to the high luminance grating reduced its perceived speed, leading to the shift in PSE shown. Bars correspond to the mean across the five observers. Individual data are shown as points, using the same symbol convention as Figs. 2 and 3 for 4/5 of the observers. (B) The added external noise increased the slope of the psychometric function.

identified as a challenge to Bayesian explanations of perceptual biases in motion perception (Hammett et al., 2007; Hassan & Hammett, 2015; Park & Tadin, 2018). This is because many types of spatiotemporal sensitivity are worse at low luminance (Watson, 1986). Perceived speed should slow down not speed up because the slow-motion prior should dominate more. In fact, our results show that speed discrimination improves as luminance decreases from photopic to mesopic light levels. This result confirms the findings of Raghuram et al (2005), with further experiments showing that the better performance is driven by a speed-dependent perceived contrast cue that is more salient in the dark. With this cue removed, we found speed discrimination was similar for the different light levels tested, yet the change in perceived speed remained the same. The latter result echoes the findings of Hassan & Hammett (2015), at least when their stimuli were presented more centrally. With no difference in discrimination there is no difference in precision, limiting the influence of a Bayesian estimation stage. We conclude that the accuracy of early motion signals depends on certain contexts like prevailing light level, challenging one of the key assumptions of standard Bayesian models.

6.2. *The effects of external noise*

These findings could be used as evidence to rule out a Bayesian stage in the processing of visual motion (Hammett et al., 2007; Hassan & Hammett, 2015). However, the results of our final experiment do not support this conclusion. We manipulated speed discrimination using external noise, which both decreased precision and lowered perceived speed, as predicted by the Bayesian account. This leaves open the question of how switching luminance at 8 Hz produces a less precise low-level sensing of speed. The most direct route is via the temporary changes in luminance itself, which produce robust changes in perceived speed that are difficult to explain with a Bayesian observer (see the findings using equicontrast stimuli in Experiment 3). Switching luminance in this fashion is therefore akin to switching physical speed, both of which would increase the variability of low-level speed sensing about some fixed mean. However, as noted in the Methods section of Experiment 4, the luminance noise also produces a simultaneous change in contrast. These could act in the same way as the switches in luminance because contrast increased when luminance decreased. However, the standard grating moved at 8 Hz, which sits on the cusp of reported reversals in the contrast effect (Thompson et al., 2006). Hence it is possible that the change in contrast either had no effect on speed sensing, or the opposite effect to the switches in luminance. Whichever is the case, Experiment 4 showed that the noise lowered speed discrimination and decreased perceived speed. This is a hallmark of Bayesian processing.

A potential challenge to this conclusion concerns the temporal edges created by the hard switching of luminance. These produce temporal transients into the stimulus, a factor known to affect perceived speed (Castet, 1995; Treue, Snowden, & Andersen, 1993). It is possible therefore that the luminance noise could change low-level speed sensing and so explain the change in perceived speed. However, the effect of adding temporal transience is opposite to that reported in Experiment 4. Transience increases perceived speed, whereas we found it lowered. Whether this means that the effect of transience was absent is debatable. For instance, one possibility is that the change in perceived speed we found was the result of two competitive processes, with the influence of a slow-motion prior outweighing the effect of transience.

As we noted in the introduction to Experiment 4, other forms of noise could have been used to test the Bayesian model. One of the more obvious is to add random fluctuations in speed, which can be achieved by adding positional jitter along the path of moving stimulus (in this case, changes in speed would be fleeting, occurring only around the time that position was updated). Two recent studies have shown that this type of noise increases speed discrimination thresholds; however, they draw very different conclusions when investigating Bayes-like behaviour. Bentvelzen et al (2009) used speed noise to investigate the integration of audiovisual motion and found support for a standard optimal integration model based on maximum likelihood estimation. They found their participants were more optimal when the precision of the audio and visual signals was similar, such that the noise within each modality was used to weight audiovisual bias and enhance audiovisual precision. On the other hand, Rideaux & Welchman (2020) failed to find any influence on speed noise on perceived speed, while at the same time showing that lower contrast reduces perceived speed. It's worth noting that they also failed to find that lowering contrast made speed discrimination worse, contrary to previous reports (Champion & Warren, 2017; Horswill & Plooy, 2008; Powell et al., 2016). Rideaux & Welchman concluded that perceived speed was not influenced by a slow-motion prior. To explain the contrast effect, they appealed to a correlation they found between contrast and speed, a discovery based on the output of a neural network trained on a diet of images of natural scenes. While a detailed discussion of this idea is beyond the scope of the current paper, their finding that speed noise does not influence perceived speed seems to contrast markedly with the Bayes-like behaviour reported by Bentvelzen et al (2009), as well as the results of Experiment 4. Clearly more work is needed to understand why some types of external noise lead to behaviour that support certain aspects of Bayesian behaviour, while some do not.

6.3. *A hybrid model based on signals that are both imprecise and inaccurate*

Our findings suggest a hybrid model in which a Bayesian observer makes an optimal best guess in the face of sensory evidence that varies in both precision and accuracy. To explain the vagaries of motion perception (and potentially other dimensions), one therefore need to understand (1) how early sensors produce biases in the way speed is encoded in different contexts and (2) how the observer deals with the noisy encoding in a statistical fashion. Neither low-level engineering nor higher-level Bayesian operations seem able to provide a complete explanation. Sotiropoulos, Seitz and Series (2014) draw a similar conclusion for the effect of contrast on motion perception, though their evidence relating precision to perceived speed is less direct than ours. Their model introduces low-level inaccuracies using an initial ratio-model stage to form the early sensory estimate of image speed, which in turn offsets the mean of symmetric distributions representing the likelihood. They emphasised that such a model could account for the finding that the effect of contrast depends on the standard speed, declining then reversing for motion around 8 Hz and beyond (Hawken, Gegenfurtner, & Tang, 1994; Thompson et al., 2006). The fact that the relationship between speed, bias and context can be non-monotonic is also important when placing our findings in context. We only investigated a single standard speed, so await to see whether the relationship between perceived speed, speed discrimination, luminance and indeed external noise holds for other speeds. We chose 8 Hz mainly because the effect of luminance is less pronounced at lower speeds (Hammett et al., 2007).

There are other ways low-level inaccuracies could be introduced, such as combining asymmetric likelihood distributions with an appropriate loss function (Wei & Stocker, 2015). It is also possible that the prior distribution changes with stimulus properties such as luminance – to explain our data, the prior would need to flatten as luminance declined. However, we think this unlikely, especially given our finding in Experiment 1 that the effect of luminance is spatially localised. More likely is the need to account for both low-level inaccuracy and the influence of a relatively global prior expectation. This conclusion that has been drawn for other fundamental dimensions, such as spatial frequency and orientation (Wei & Stocker, 2015), and audiovisual localisation (Odegaard, Wozny, & Shams, 2015).

Some care is needed in interpreting what is meant by 'inaccurate'. In an influential Bayesian model of speed perception, Stocker and colleagues proposed that speed is transformed logarithmically before any further processing (Jogan & Stocker, 2015; Stocker & Simoncelli, 2006). The main reason they did this was to capture the Weber's law like behaviour of speed discrimination over a substantial range of speeds, although there are other ways to model this, such as using variable noise (Freeman et al., 2010; Georgeson & Meese, 2006; Gorea & Sagi, 2001; Kontsevich, Chen, & Tyler, 2002). According to their model, therefore, motion sensors do not exhibit "external accuracy" (Burge et al., 2010). However, they do maintain "internal consistency" because the logarithmic transform does not depend on stimulus properties such as contrast, luminance and so forth. It is this internal consistency that lies at the heart of most Bayesian models, and it is this internal consistency that our data challenge. Similar assumptions underpin models of optimal cue combination, where it is typically asserted that internal estimates of various cues to X (e.g. depth) are unbiased with respect to each other (Scarfe & Hibbard, 2011).

6.4. Some consequences of the hybrid model

If the sensory evidence feeding the Bayesian stage is not internally consistent as our findings suggest, then this calls into question a number of claims made in the literature. Here we point out just two. The first is the idea that prior distributions can be reverse-engineered from psychophysical data (Sotiropoulos et al., 2014; Stocker & Simoncelli, 2006). In order to do so, one needs to fix the parameters that determine the accuracy of the sensory evidence feeding the Bayesian stage, but it may not be that easy to tease these apart (Freeman et al., 2010; Odegaard et al., 2015). The second claim relates to the idea that atypical perceptual biases exhibited by certain clinical populations arise from the way they learn and/or use prior knowledge about the world (Pellicano & Burr, 2012; Teufel et al., 2015). One example relates to autism spectrum disorder, with the proposal that those with ASD have flatter priors and therefore are less susceptible to certain perceptual biases (Pellicano & Burr, 2012). While this idea has some support (Powell et al., 2016; Skewes, Jegindø, & Gebauer, 2015; Zaidel, Goin-Kochel, & Angelaki, 2015), the evidence again rests on the assumption that the sensory evidence encoded by individuals with ASD, or those who are higher on subclinical dimensions such as the autism quotient, is unbiased when compared to those who are not. While the flatter prior hypothesis is an appealing idea, the current data suggest that there are other ways to view how differences in perceptual bias arise within the Bayesian framework.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank Jagminder Kaur for her help in collecting the data in Experiment 1, and two anonymous reviewers for their suggested improvements to the manuscript.

References

Ascher, D., & Grzywacz, N. M. (2000). A Bayesian model for the measurement of visual velocity. *Vision Research, 40*, 3427–3434.

Bentvelzen, A., Leung, J., & Alais, D. (2009). Discriminating audiovisual speed: Optimal integration of speed defaults to probability summation when component reliabilities diverge. *Perception, 38*(7), 966–987.

Blakemore, M. S., & Snowden, R. J. (1996). The changing of perceived speed as a function of stimulus contrast: an attempted replication with a variety of stimuli. *Perception, 25*, 34.

Bosten, J., & Mollon, J. (2010). Is there a general trait of susceptibility to simultaneous contrast? *Vision Research, 50*(17), 1656–1664.

Burge, J., Girshick, A. R., & Banks, M. S. (2010). Visual–haptic adaptation is determined by relative reliability. *Journal of Neuroscience, 30*(22), 7714–7721.

Castet, E. (1995). Apparent speed of sampled motion. *Vision Research, 35*(10), 1375–1384.

Champion, R. A., & Warren, P. A. (2017). Contrast effects on speed perception for linear and radial motion. *Vision Research, 140*, 66–72.

Dong, D. W., & Atick, J. J. (1995). Statistics of natural time-varying images. *Network: Computation in Neural Systems, 6*(3), 345.

Ernst, M. O., & Bulthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences, 8*(4), 162–169.

Freeman, T. C. A., Champion, R. A., & Warren, P. A. (2010). A Bayesian model of perceived head-centred velocity during smooth pursuit eye movement. *Current Biology, 20*, 757–762.

Freeman, T. C. A., Culling, J. F., Akeroyd, M. A., & Brimijoin, W. O. (2017). Auditory compensation for head rotation is incomplete. *Journal of Experimental Psychology: Human Perception and Performance, 43*, 371–380. https://doi.org/10.1037/xhp0000321

Freeman, T. C. A., & Powell, G. (2020). Perceived Speed at Low Luminance: Lights Out for the Bayesian Observer? *Perception, 49*(6), 705–706.

Gegenfurtner, K. R., Mayser, H., & Sharpe, L. T. (1999). Seeing movement in the dark. *Nature, 398*(6727), 475–476.

Gegenfurtner, K. R., Mayser, H. M., & Sharpe, L. T. (2000). Motion perception at scotopic light levels. *Journal of the Optical Society of America A, 17*(9), 1505–1515.

Geisler, W. S., & Kersten, D. (2002). Illusions, perception and Bayes. *Nature Neuroscience, 5*(6), 508–510.

Georgeson, M. A., & Meese, T. S. (2006). Fixed or variable noise in contrast discrimination? The jury's still out. *Vision Research, 46*, 4294–4303.

Gorea, A., & Sagi, D. (2001). Disentangling signal from noise in visual contrast discrimination. *Nature Neuroscience, 4*(11), 1146–1150.

Gregory, R. L. (1997). Knowledge in perception and illusion. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 352*(1358), 1121–1127.

Hammett, S. T., Champion, R. A., Morland, A. B., & Thompson, P. G. (2005). A ratio model of perceived speed in the human visual system. *Proceedings of the Royal Society B, 272*, 2351–2356.

Hammett, S. T., Champion, R. A., Thompson, P. G., & Morland, A. B. (2007). Perceptual distortions of speed at low luminance: Evidence inconsistent with a Bayesian account of speed encoding. *Vision Research, 47*, 564–568.

Hammett, S. T., Smith, A. T., Wall, M. B., & Larsson, J. (2013). Implicit representations of luminance and the temporal structure of moving stimuli in multiple regions of human visual cortex revealed by multivariate pattern classification analysis. *Journal of Neurophysiology, 110*(3), 688–699.

Hammett, S. T., Thompson, P. G., & Bedingham, S. (2000). The dynamics of velocity adaptation in human vision. *Current Biology*, 1123–1126.

Harris, M. (1980). Velocity specificity of the flicker to pattern sensitivity ratio in human vision. *Vision Research, 20*(8), 687–691.

Harris, M. (1986). The perception of moving stimuli: A model of spatiotemporal coding in human vision. *Vision Research, 26*(8), 1281–1287.

Hassan, O., & Hammett, S. T. (2015). Perceptual biases are inconsistent with Bayesian encoding of speed in the human visual system. *Journal of Vision, 15*, 1–9. https://doi.org/10.1167/15.2.9.doi

Hassan, O., Thompson, P., & Hammett, S. T. (2016). Perceived speed in peripheral vision can go up or down. *Journal of Vision, 15*, 20. https://doi.org/10.1167/15.2.9.doi

Hawken, M. J., Gegenfurtner, K. R., & Tang, C. (1994). Contrast dependence of colour and luminance motion mechanisms in human vision. *Nature, 367*, 268–270.

Horswill, M. S., & Plooy, A. M. (2008). Reducing contrast makes speeds in a video-based driving simulator harder to discriminate as well as making them appear slower. *Perception, 37*(8), 1269–1275.

Hurliman, F., Kiper, D. C., & Carandini, M. (2002). Testing the Bayesian model of perceived speed. *Vision Research, 42*, 2253–2257.

Iglewicz, B., & Hoaglin, D. (1993). How to detect and handle outliers. In E. F. Mykytka (Ed.), *The ASQC Basic References in Quality Control: Statistical Techniques*.

Jogan, M., & Stocker, A. A. (2015). Signal integration in human visual speed perception. *Journal of Neuroscience, 35*(25), 9381–9390.

Johnston, A., & Wright, M. J. (1985). Matching velocity in central and peripheral vision. *Vision Research, 26*(7), 1099–1109.

Knill, D. C., & Richards, W. (1996). *Perception as Baysian Inference*. Cambridge: Cambridge University Press.

Kontsevich, L. L., Chen, C.-C., & Tyler, C. W. (2002). Separating the effects of response nonlinearity and internal noise psychophysically. *Vision Research, 42*, 1771–1784.

Moscatelli, A., Hayward, V., Wexler, M., & Ernst, M. O. (2015). Illusory Tactile Motion Perception: An Analog of the Visual Filehne Illusion. *Scientific Reports, 5*.

Odegaard, B., Wozny, D. R., & Shams, L. (2015). Biases in visual, auditory, and audiovisual perception of space. *PLoS Computational Biology, 11*(12), Article e1004649.

Orban, G. A., de Wolf, J., & Maes, H. (1984). Factors influencing velocity coding in the human visual system. *Vision Research, 24*(1), 33–39.

Park, W. J., & Tadin, D. (2018). Motion perception. *Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience, 2*, 1–73.

Pellicano, E., & Burr, D. (2012). When the world becomes 'too real': A Bayesian explanation of autistic perception. *Trends in Cognitive Sciences, 16*(10), 504–510.

Powell, G., Meredith, Z., McMillin, R., & Freeman, T. C. A. (2016). Bayesian models of individual differences: Combining autistic traits and sensory thresholds to predict motion perception. *Psychological Science, 27*(12), 1562–1572.

Pritchard, S. J., & Hammett, S. T. (2012). The effect of luminance on simulated driving speed. *Vision Research, 52*, 54–60.

Purves, D., Wojtach, W. T., & Lotto, R. B. (2011). Understanding vision in wholly empirical terms. *Proceedings of the National Academy of Sciences, 108*(Supplement 3), 15588–15595.

Raghuram, A., Lakshminarayanan, V., & Khanna, R. (2005). Psychophysical estimation of speed discrimination. II. Aging effects. *JOSA A, 22*(10), 2269–2280.

Rideaux, R., & Welchman, A. E. (2020). But still it moves: Static image statistics underlie how we see motion. *Journal of Neuroscience, 40*(12), 2538–2552.

Scarfe, P., & Hibbard, P. B. (2011). Statistically optimal integration of biased sensory estimates. *Journal of Vision, 11*(7).

Senna, I., Parise, C. V., & Ernst, M. O. (2015). Hearing in slow-motion: Humans underestimate the speed of moving sounds. *Scientific Reports, 5*.

Skewes, J. C., Jegindø, E.-M., & Gebauer, L. (2015). Perceptual inference and autistic traits. *Autism, 19*(3), 301–307.

Smith, A. T., & Edgar, G. K. (1991). The separability of temporal frequency and velocity. *Vision Research, 31*(2), 321–326.

Smith, A. T., & Edgar, G. K. (1994). Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception. *Vision Research, 34*(2), 253–265.

Snowden, R. J., Stimpson, N., & Ruddle, R. A. (1998). Speed perception fogs up as visibility drops. *Nature, 392*(6675), 450.

Sotiropoulos, G., Seitz, A. R., & Seriés, P. (2014). Contrast dependency and prior expectations in human speed perception. *Vision Research*. https://doi.org/10.1016/j.visres.2014.01.012

Stocker, A. A., & Simoncelli, E. P. (2006). Noise characteristics and prior expectation in human visual speed perception. *Nature Neuroscience, 9*(4), 578–585.

Takeuchi, T., & De Valois, K. K. (2000). Velocity discrimination in scotopic vision. *Vision Research, 40*(15), 2011–2024.

Teufel, C., & Fletcher, P. C. (2020). Forms of prediction in the nervous system. *Nature Reviews Neuroscience, 21*(4), 231–242.

Teufel, C., Subramaniam, N., Dobler, V., Perez, J., Finnemann, J., Mehta, P. R., … Fletcher, P. C. (2015). Shift toward prior knowledge confers a perceptual advantage in early psychosis and psychosis-prone healthy individuals. *Proceedings of the National Academy of Sciences, 112*(43), 13401–13406.

Thompson, P. (1982). Perceived Rate of Movement Depends On Contrast. *Vision Research, 22*(3), 377–380.

Thompson, P., Brooks, K. R., & Hammett, S. T. (2006). Speed can go up as well as down at low contrast: Implications for models of moiton perception. *Vision Research, 46*, 782–786.

Treue, S., Snowden, R., & Andersen, R. A. (1993). The effect of transiency on perceived velocity of visual patterns: A case of `temporal capture'. *Vision Research, 33*(5/6), 791–798.

Vaziri-Pashkam, M., & Cavanagh, P. (2008). Apparent speed increases at low luminance. *Journal of Vision, 8*((16):9), 1–12.

Wallach, H. (1940). The role of head movements and vestibular and visual cues in sound localization. *Journal of Experimental Psychology, 27*(4), 339.

Watson, A. B. (1986). Temporal sensitivity. *Handbook of Perception and Human Performance, 1*(6), 1–43.

Wei, X.-X., & Stocker, A. A. (2015). A Bayesian observer model constrained by efficient coding can explain'anti-Bayesian'percepts. *Nature Neuroscience, 18*(10), 1509.

Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience, 5*(6), 598–604.

Welchman, A. E., Lam, J. M., & Bülthoff, H. H. (2008). Bayesian motion estimation accounts for a surprising bias in 3D vision. *Proceedings of the National Academy of Sciences, 105*(33), 12087–12092.

Wexler, M., Panerai, F., Lamouret, I., & Droulez, J. (2001). Self-motion and the perception of stationary objects. *Nature, 409*, 85–88.

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics, 63*(8), 1293.

Zaidel, A., Goin-Kochel, R. P., & Angelaki, D. E. (2015). Self-motion perception in autism is compromised by visual noise but integrated optimally across multiple senses. *Proceedings of the National Academy of Sciences, 112*(20), 6461–6466.