The perceptual dynamics of the contrast induced speed bias*

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Abstract

In this article we present a temporal extension of the slow motion prior model to generate predictions regarding the temporal evolution of the contrast induced speed bias. We further tested these predictions using a novel experimental paradigm that allows us to measure the dynamic perceptual difference between stimuli through a series of manual pursuit open loop tasks. Results show a great deal of agreement with our model's predictions. The main findings reveal that hand speed dynamics are affected by stimulus contrast in a way that is consistent with a dynamic model of motion perception that assumes a slow motion prior. The proposed model also confirms observations made in previous studies that suggest that motion bias persisted even at high contrast as a consequence of the dynamics of the slow motion prior.

In this article we present a temporal extension of the slow motion prior model to generate predictions regarding the temporal evolution of the contrast induced speed bias, which were further experimentally tested. For this purpose, we designed a novel experimental paradigm that allows us to measure the dynamic perceptual difference between stimuli through a series of manual pursuit open loop tasks. Results show a great deal of agreement with our model's predictions. The main findings reveal that hand speed dynamics are affected by stimulus contrast in a way that is consistent with a dynamic model of motion perception that assumes a slow motion prior. The proposed model also confirms observations made in previous studies that suggest that motion bias persisted even at high contrast as a consequence of the dynamics of the slow motion prior.

Keywords: Bayesian models, Speed perception, Temporal dynamics, Contrast Speed prior, Manual pursuit, Continuous psychophysics

1. Introduction

The perceived speed of a stimulus is influenced by its contrast. This perception bias, originally reported by Thompson (Thompson, 1976, 1982), has been extensively studied since then (Blakemore & Snowden, 2000; Champion & Warren, 2017; de'Sperati & Thornton, 2019; Hawken et al., 1994; Snowden et al., 1998; Sotiropoulos et al., 2014; Stocker & Simoncelli, 2006; Stone & Thompson, 1992; Thompson, 1982) for different types of stimuli (Blakemore & Snowden, 2000; Brooks, 2001; Champion & Warren, 2017), time frames and experimental devices (Champion & Warren, 2017; Stocker & Simoncelli, 2006; Stone & Thompson, 1992; Thompson, 1982). For most cases and scenarios, low contrast stimuli are seen as moving more slowly than those of high contrast.

Many studies argue that this bias of the human perceptual system is actually the consequence of an observer that needs to infer the current status of the world through noisy or incomplete measurements and relies on her/his past knowledge of the external world to achieve this. This idea, originally formulated by Helmholtz (Helmholtz, 1962), has been reformulated in recent years in terms of a Bayesian framework (Knill & Pouget, 2004; Knill & Richards, 1996; Maloney & Zhang, 2010), where past experience of the world can be expressed as a probability distribution (known as the prior) that represents the probability of encountering some event in the real world, and current measurements as a second distribution (known as the likelihood), whose width represents the amount of noise present in the signal. Our perception of a given stimulus, the argument goes, is dependent on the signal-to-noise ratio of the measurement, which determines the reliance of our perceptual system on prior experience: the lower the ratio, the higher the reliance on past knowledge. In Bayesian terms, our perception is represented by the posterior distribution which is the product of the prior and likelihood distributions. Studies that attribute this underestimation of speed observed with low contrast stimuli (Hürlimann et al., 2002; Sotiropoulos et al., 2014; Stocker & Simoncelli, 2006) assume that (i) when contrast is reduced, the signal-to-noise ratio decreases, making measurements less reliable, and (ii) objects in the external world tend to move slowly or remain still. Under these two assumptions perceiving lower contrast stimuli as moving more slowly is in fact the optimal behavior.

This Bayesian approach as a model of perception has received much attention in the last two decades. By stating its premise in terms of measurement noise or uncertainty (and not contrast specifically), which in turn is modeled as a probability distribution's width, the result is an intuitive framework that is highly flexible but also mathematically rigorous. The slow motion prior in particular, has provided an elegant explanation for a number of different and seemingly unrelated phenomena, e.g. motion biases related to the aperture problem (Weiss et al., 2002; Weiss & Adelson, 1998), or to 3D signals such as speed of motion in-depth (Aguado & López-Moliner, 2019; Lages, 2006; Rokers et al., 2018; Welchman et al., 2008) or path integration during self movement (Lakshminarasimhan et al., 2018) to cite a few. Moreover, some studies have created more sophisticated models that combine the slow motion prior with other assumptions, such as Kwon et al., 2015Kwon et al. (2015), who presented a dynamic object tracking model that employs the slow motion prior --along with a set of other assumptions-- that explains perceptual biases such as the motion induced position shift (De Valois & De Valois, 1991) and the curve-ball illusion (Shapiro et al., 2010). A series of studies (Bogadhi et al., 2011; Dimova & Denham, 2009; Montagnini et al., 2007) presented another dynamic extension of the slow motion prior, this time as a plausible model to explain motion integration in smooth pursuit eye movements, that successfully accounts for the temporal evolution of a tracking error that occurs when visually tracking a moving target with ambiguous 1D motion, i.e. with the aperture problem (Born et al., 2006; Masson & Stone, 2002; Wallace et al., 2005).

The ability to explain such a wide variety of phenomena through a small and simple set of premises is certainly the main appeal of this model. This is not only parsimonious, but also a powerful tool to generate novel predictions. In this regard, the aforementioned dynamic models led us to wonder about the temporal nature of the Contrast Induced Speed Bias (from now on referred to as CISB). Despite being extensively studied, we could not find any study that has consistently studied the CISB for several stimulus durations. On the one hand, although psychophysical studies show that the effect is present for a wide range of stimulus durations -- from 280 ms (Thompson et al., 1996) up to several seconds (Snowden et al., 1998; Thompson, 1982)-- the large experimental differences between these studies do not allow us to make even a qualitative comparison of results. On the other hand, eye movement studies also show significant effects of the CISB during smooth pursuit (SPEMs) (Fallah & Reynolds, 2012; Priebe & Lisberger, 2004; Spering et al., 2005) and saccades (de'Sperati & Thornton, 2019; Etchells et al., 2011). In particular, smooth pursuit studies (Spering et al., 2005) report an increase in pursuit latency, and a decrease in steady state pursuit gain and initial acceleration (also reported in Priebe & Lisberger, 2004), all consistent with the CISB. Although these findings suggest that this bias is present from the beginning of motion integration, we cannot infer from these results what its temporal evolution is, if any.

The theoretical implications of the Bayesian dynamic models for motion integration we mentioned (Bogadhi et al., 2011; Dimova & Denham, 2009; Kwon et al., 2015; Montagnini et al., 2007) suggest an analogous effect for the CISB that has not yet been established, although some evidence from smooth pursuit studies (Priebe & Lisberger, 2004; Spering et al., 2005) indeed point in this direction. Our purpose in the present study is to test the predictions that a dynamic Bayesian model that fits the existing experimental and theoretical findings makes about the temporal evolution of the CISB.

Following the line of the previously mentioned studies, our model combines prior knowledge of speed with motion signals sampled from the external world from which the percept will derive. In contrast with static Bayesian models, recurrent models update the prior in every time step, using the previous speed estimate (i.e. the posterior probability) as the current prior. This continuous updating produces a prior that may change through time, depending on the specific updating rule and the uncertainties of both prior and observation, as we will address in the next section.

Given the continuous nature of this model, we wished to obtain a continuous and temporally correlated stream of behavioural observations that could be linked to the instantaneous motion perception, so as to mirror the output of our model. Although the most obviousl choice to this end would seem to be through SPEMs, an experimental constraint made this approach less than ideal. SPEMs measurements reliably reflect visual motion in only a short window of time -- during the initial open loop stage, the first ~ 100 ms of eve movement (Lisberger et al., 1987; Tychsen & Lisberger, 1986) -- after which a steady state stage begins where eye motion is driven by a more complex, positive feedback loop between the efferent copy and retinal velocity (Spering & Montagnini, 2011). Because we were interested in testing this phenomenon over a longer time frame (at least 2 seconds), smooth pursuit seems not to be the appropriate approach for our purpose.

To circumvent these issues, we decided to explore a “continuous psychophysics” approach (Bonnen et al., 2015), specifically proposed in recent studies to address experimental demands such as ours (Huk et al., 2018). We chose to use a task in which subjects follow a patch with their unseen hand, known as an open loop manual pursuit (Masson et al., 1995; Rodríguez-Herreros & López-Moliner, 2008; van Donkelaar et al., 1994), and use the instantaneous hand velocity to measure the temporal evolution of motion perception. Open loop manual tracking, in contrast with SPEMs, seems to be guided by visual motion throughout the entire task, showing effects in agreement with perceptual studies at both short (Rodríguez-Herreros & López-Moliner, 2008) and long (van Donkelaar et al., 1994) time windows. However, using the hand’s speed as a proxy for the dynamics of motion perception is not a straightforward task because of the kinematic transformation that underlies the process of turning a perceptual signal into hand movement. To solve this issue, we designed for this study a simple experimental procedure that allows us to obtain the dynamic perceptual bias between two stimuli by simply subtracting the hand’s motion response to each stimulus.

To summarize, in this paper we implemented a temporal extension of the slow motion prior model similar to those proposed in previous studies (Bogadhi et al., 2011; Dimova & Denham, 2009; Kwon et al., 2015; Montagnini et al., 2007) to generate novel predictions regarding the temporal evolution of the CISB. We further tested these predictions, for which we designed a novel experimental paradigm that allows us to measure the dynamic perceptual difference between stimuli through a series of manual pursuit open loop tasks.

2. The model

The main innovation of dynamic models in contrast with static models is that they update their assumptions regarding the current state of the world by incorporating distribution information from their immediate past into their prior. Therefore, during the time course of a stimulus the prior does not remain fixed, but rather changes to incorporate past stimulus information, thus producing a dynamic percept.

The model we use in this study is implemented as a Kalman filter (Kalman, 1960) in a way similar to the one used in previous SPEMs studies (Bogadhi et al., 2011; Dimova & Denham, 2009; Montagnini et al., 2007) and the object tracking model presented by Kwon et al., 2015 (although our model is simpler than Kwon's, since it does not involve object position). A Kalman filter defines the prior function and the measurement process as dynamic equations called the state model and observation model respectively. For our set of assumptions, the state model is defined in equation (1) as follows:

$$X_t^{v-}\hat{} = \beta X_{t-1}^{v}\hat{} + \delta_x^v \Omega;\ 0 < \beta < 1 \quad (1)$$

In the above equation, $X_t^{v-}\hat{}$ represents the motion prior at time t. The parameter β (deceleration coefficient) is a scalar that embodies the slow motion assumption, as it represents how much the stimulus is expected to decelerate from time $t-1$ to t with respect to $X_{t-1}^{v}\hat{}$, which is the posterior motion estimate at $t-1.\delta_x^v$ (state variance) represents the prior's uncertainty level and Ω is unit variance, gaussian white noise.

The observation model, which represents the observers' motion measures of the world, is defined in equation (2).

$$Y_t^v = X_t^v + \delta_y^v \Omega \tag{2}$$

Where Y_t^v represents the sensory measurement of the physical motion X_t^v at time t, corrupted by gaussian noise with zero mean and a standard deviation of δ_y^v (observational variance), which represents the measurement's uncertainty. The final estimate, as a consequence of using a Kalman filter, is calculated with equation (3) :

$$X_t^v\hat{} = X_t^{v-}\hat{} + K\left(Y_t^v - X_t^{v-}\hat{}\right) \tag{3}$$

Where $X_t^v\hat{}$ is the motion perceptual estimate at time t, and K is a recursively updated gain matrix known as the Kalman gain, designed to minimize the posterior error variance: $P = E[X^v - X^v\hat{}]$. The Kalman gain is calculated through equation (4), where P^- is the a priori estimate of motion variance.

$$K = P^-\left(P^- + \delta_y^v\right)^{-1} \tag{4}$$

From equation 3, one can gather that the final perceptual estimate is a combination of prior ($X_t^{v-}\hat{}$) and measurement (Y_t^v) balanced by K.

The model's behavior is governed by two parameters: the observational variance-- that represents the signal-to-noise ratio of the motion stimulus--, and the deceleration coefficient, that determines "how slow" the slow prior is.

2.1 Predictions

To illustrate the model's predictions, consider two moving objects differing in some attribute that modulates uncertainty, for example contrast: the dynamic speed bias is defined as the difference between their perceived speeds at each time step. The model's prediction for this bias can therefore be expressed as equation (5), where $Msb_t$is the model's speed bias at time t, and $S_t^T$and $S_t^R$are the physical motions of T(test) and R(reference) for time t respectively.

$$Msb_t = X_t^v\hat{}(S_t^R) - X_t^v\hat{}(S_t^T) \tag{5}$$

In this scenario, Fig. 1 shows the speed bias' evolution predicted by the model for two stimuli, with medium and low contrast (red and brown lines respectively), with respect to a high contrast stimulus, all moving at equal speed, for three different deceleration coefficient scenarios ($\beta = 1, 0 < \beta < 1$ and $\beta = 0$). Contrast reduction was modelled by increasing the observational variance. Two main conclusions can be obtained from inspecting this figure. On one hand, contrast modulates the magnitude of the bias: as expected, the lower the contrast, the larger the bias, and always biased towards slow motion. On the other hand, β modulates how fast this bias changes, and therefore the trend's overall shape: when $\beta = 1$ the system always stabilizes at the same level, regardless of contrast (i.e. all stimuli are eventually perceived moving at equal speed), and the effect that contrast has on motion bias is seen in a transient stage. As β is reduced towards 0, the transient stage becomes shorter (effectively disappearing when $\beta = 0$, eliminating the dynamic nature of the model), and the CISB is translated to the steady state.

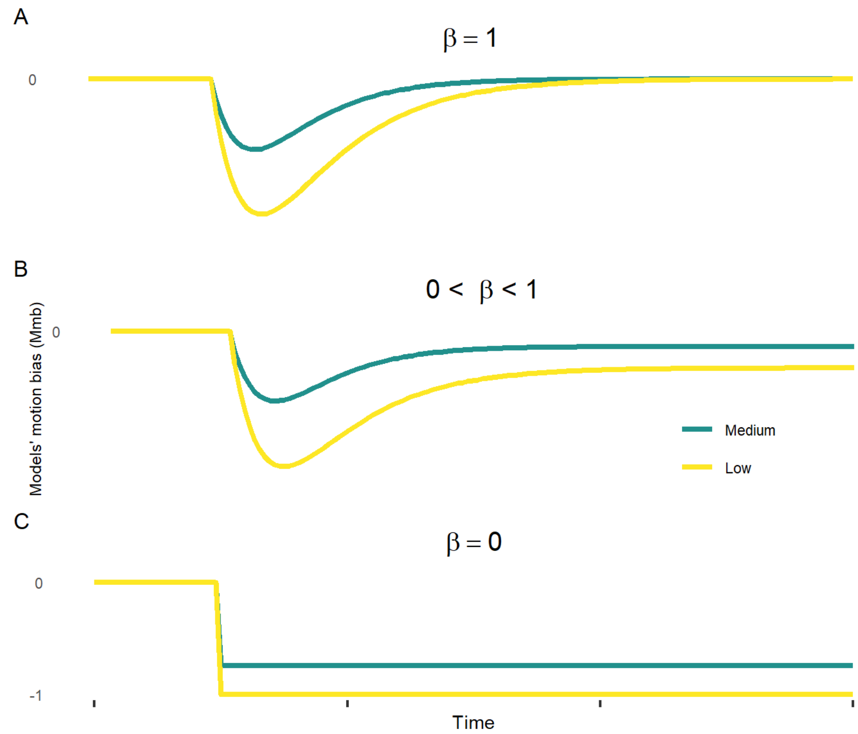

Figure 1:*Perceptual speed bias as a function of time for a medium and low contrast test compared to a high contrast reference moving at equal speed. Each panel corresponds to three deceleration coefficient scenarios. Notice that lower contrasts produce larger bias and take longer to reach steady state.*

3. Methods

Once we obtained the model predictions shown in the last section, we designed an experimental device with which we could continuously obtain estimations of perceived speed, in order to compare them with such predictions.

3.1 Experimental model

Manually pursuing a moving target with no visual feedback from the hand is known to be driven by visual motion information (Masson et al., 1995; Rodríguez-Herreros & López-Moliner, 2008; van Donkelaar et al., 1994). We can therefore think of the hand's motion response as the output of a function that translates the continuous perceptual estimates of the stimulus' motion to motor responses. Our strategy to measure continuous motion perception lies in the assumption that, within a range of motion perceptual estimates, the hand speed response function can be approximated to the sum of the perceptual signal and an invariant motor component. This can be represented as:

$$Hsr_t\big(P_t(S_t)\big) \sim P_t(S_t) + M_t \tag{6}$$

Where Hsr is the hand's speed response, P is the motion perceptual estimate of the physical stimulus S, and M is the invariant motor component. Under these premises, the difference between the Hsr for two stimuli can be approximated to the perceptual difference between the two stimuli, since M_t will be cancelled out as it would be the same for both stimuli. A test and verification process of these assumptions are provided in Appendix A.

Following this rationale (see procedure for details), we instructed subjects to follow a patch with varying contrasts with their unseen hand. The hand's response to a high contrast motion stimulus was used as reference, which was then subtracted from the hand's speed response to lower contrast test stimuli, emulating the process shown in the previous section. The Msb was then fitted to the resulting hand speed bias to estimate the model's parameters and verify our predictions (details provided in the parameters fitting section). Finally, we included in the experiment accelerating and decelerating target speed conditions to further test the model's response to different speed scenarios.

3.2. Participants

Twenty eight participants from the University of Barcelona (24 females, ages 21-35) took part in this study. The study was approved by the local ethics committee, and participants provided informed consent.

3.3. Apparatus

Fig. 2 Panel A shows a sketch of the layout used for this experiment. Stimuli were projected from a Mitsubishi SD220U projector, at a frame rate of 72 Hz with a resolution of 800 by 600 pixels, to a screen located in the axial plane, 103.0 cm wide and 70.2 cm long, 70 cm above the floor. Hand movement was recorded using a Polhemus Liberty attached to the tip of the subject's right hand index finger, which recorded its position at a rate of 240 Hz.

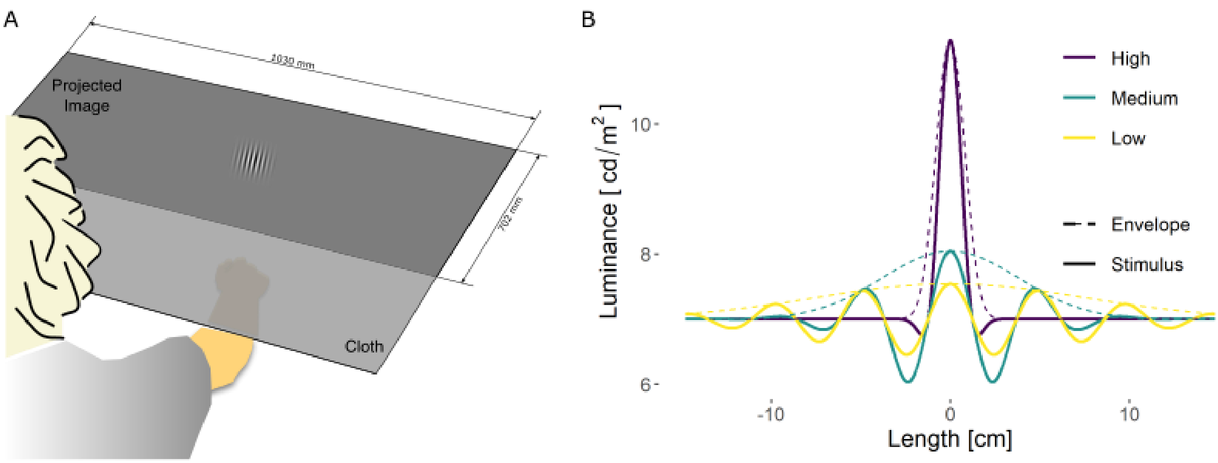

***Figure 2**: **A** General layout of the experiment. Subjects saw the stimulus projected on the screen, and did not have visual feedback of their hand. **B** Stimulus cross section. All three contrast stimuli had the same spatial frequency (0.2 cycles/cm) and contrast was modulated by normalized gaussian envelopes (dashed lines)*

A strip of black cloth extended from the end of the screen prevented subjects from seeing their hand during the experiment. Stimuli were generated using custom software written in C on a Macintosh Pro 2.6 GHz Quad-Core computer.

3.4. Stimulus

For all experimental conditions, the target was a vertical grating with a spatial frequency of 0.2 cycles/cm, with a mean luminance of 7 cd/m^2 modulated by a normalized gaussian envelope of different standard deviations. Three contrast conditions were tested at 41.1% (high contrast), 18.8% (medium contrast) and 9.7% (low contrast) michelson contrast, generated by envelopes of 0.5, 2.5 and 5 cm s.d. Fig. 2 Panel B shows the luminance profiles of each contrast stimulus.

The target would appear on the screen, and after 1.5 s would start moving to the right until it traversed 35 cm. The patch's initial position Y coordinate (corresponding to the sagittal plane) was fixed for all trials at the screen's center. The X coordinate (corresponding to the coronal plane) was selected randomly from a uniform distribution that ranged between 21.5 and 18.5 cm to the left of the screen's center. The initial speed of the stimulus was always 10 cm/s. Throughout the experiment, three acceleration conditions were tested: Decelerated (-1.071 cm/s^2), Constant (0 cm/s^2) and Accelerated (1.786 cm/s^2). The constant speed condition was employed to test the predictions of our model, while the accelerated and decelerated conditions were utilized to test the model's performance under a different set of input signals, in order to analyze its robustness. These specific accelerations were selected so that the final target speed would be 50% higher (for the accelerated condition) or 50% lower (for the Decelerated condition) than the starting speed. The target's traveling time was 4.67 s for the Decelerated condition, 3.50 s for the Constant condition and 2.80 s for the Accelerated condition.

3.5. Procedure

Participants sat in front of the screen with their midline aligned with the screen's center. The mean viewing distance to the stimulus was 71 cm. The subject's task was to pursue the target with their right hand, without having visual feedback from the hand. For this reason, subjects had their right hand under the screen and under the black cloth that extended from the screen (see Fig. 2 A), preventing all visual cues from the arm and hand. Vision was binocular, and no head or body movement restriction was imposed.

At the beginning of each trial, subjects were instructed to align as accurately as possible, the tip of their index finger with the center of the target. After 1.5 s, as the target started moving, they would pursue the target, trying to maintain their hand aligned with the target as it moved right. Once the target traversed 35 cm it would disappear, and after 2.5 s a new trial began.

The entire experiment was divided into 2 separate sessions, with a 1-2 minute break between them. Each session consisted of five repetitions for each acceleration and for each contrast. Thus, each session contained 45 trials (3 accelerations x 3 contrasts. x 5 repetitions). In the end, subjects performed 10 repetitions of all 9 possible combinations, for a total of 90 trials per subject in approximately 15 minutes.

3.6. Experimental data processing

The recorded hand position for each subject was low pass filtered with a Butterworth dual pass filter (cutoff frequency at 5 Hz). Hand speed was computed from this smoothed data, and was temporally averaged for each condition across all subjects. The high contrast - constant speed condition was always the reference, and was temporally subtracted from the test, which could be either low or medium contrast for all three acceleration conditions, thereby obtaining 6 different conditions (3 accelerations x 2 test contrasts). Formally, this operation can be expressed as follows:

$$Hsb_t = Hsr_t(S_t^T) - Hsr_t(S_t^R) \tag{7}$$

Where Hsb_t is the Hand speed bias, Hsr_t is the Hand's speed response and S_t^T and S_t^R are respectively test and reference stimuli for time t. Note that although we are subtracting the hand speed response of target and reference, within our experimental model (tested in Appendix A), the motor signals for these two stimuli are considered equal and separable for both conditions, and therefore cancelled out through this subtraction. Consequently, the resulting Hsb can be regarded as the motion perception bias.

3.7. Parameter fitting

We fitted the model's speed bias Msb-Equation (6)- to the hand's speed bias Hsb-Equation (7)- independently for each test contrast moving at constant speed (i.e. 2 of the 6 conditions). The parameters were estimated using a least square error fit for the time period from stimulus onset (at 1.5 s) to 600 ms before the shortest trial finished. The target speed fed to Msb was lagged 440 ms, which was experimentally determined in order to temporally synchronize peak Hsb with peak Msb. The time step of the model was set to 200 ms.

We fitted the parameters of our model through a grid-search in which we explored the parameter space of β and the observational variances in order to analyze the parameters' regularities in the parameters space. For each of these two conditions, we fitted the test observational variances for a range of β between 0.8 to 1.1 with steps of 0.01, and reference variance δ_R^v between 0.1 and 1 with steps of 0.1. State variance was fixed to 1. Note that although we defined in our model the deceleration coefficient as lower than 1, we tested the model for values higher than 1 to confirm this hypothesis.

4. Results

Fig. 3 presents the time course of mean Hand speed bias (Hsb) for all 28 subjects. The plots show (in blue) the difference between the hand's instantaneous speed response to the test stimulus (medium contrast in panel A, low contrast in panel B) and the reference stimulus as a function of time, for the constant speed condition.

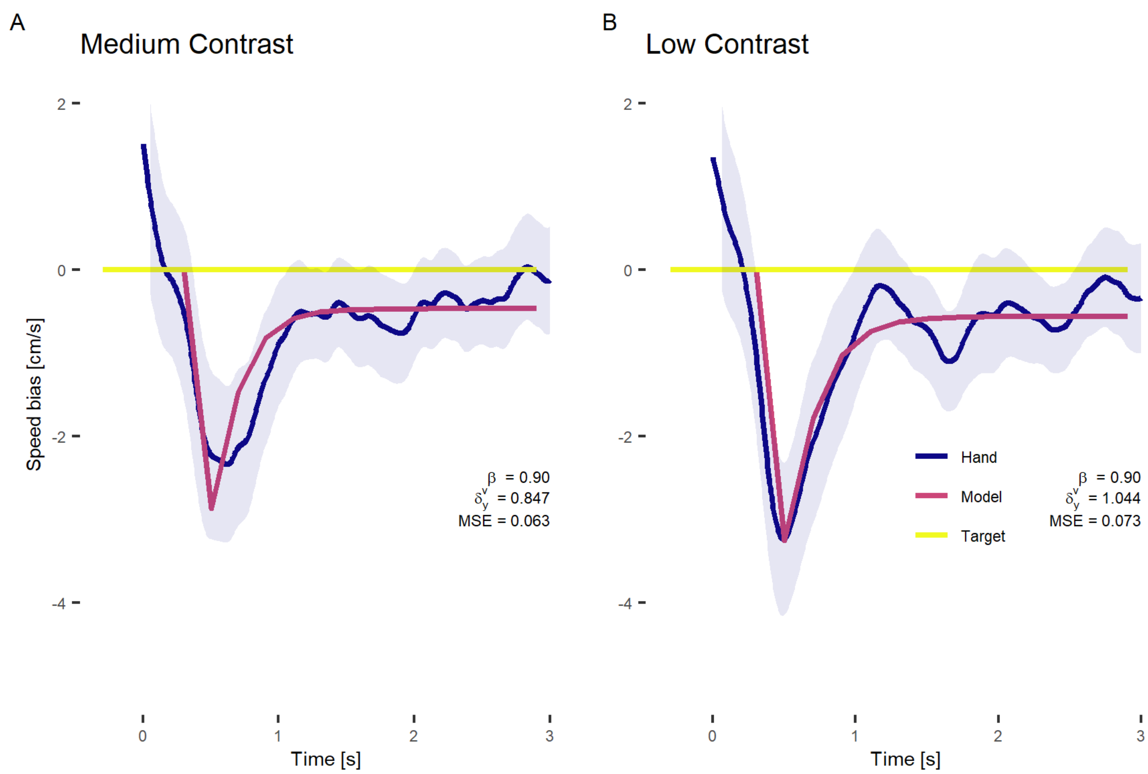

***Figure 3**: General mean of speed bias vs time when test and reference move at equal speed (constant speed condition). Blue lines are the mean hand's response bias, ribbons show standard error. Red lines are the model's speed bias response, and yellow lines are the veridical target motion difference for the medium contrast stimulus (panel A) and low stimulus (panel B)*

At any given instant, a Hsb below 0 indicates that test speeds are perceived slower than reference speeds. The bias' dynamical behavior shown in Fig. 3 is in agreement with our model's prediction, showing an initial transient stage with a strong speed bias (tests between 20 to 35% slower than reference) that gradually reduces with stimulus presentation time, slowly converging to a steady state level, where bias is still present, although much lower (~ 5%). Responses to medium and low contrast stimuli are also consistent, showing an overall larger bias for low contrast than for medium contrast, particularly in the transient phase. The output of the best fit of the models' speed bias for δ_{yR}^{v}= 0.1 to the mean Hsb's are plotted in Fig. 3 as well (red lines). The model fits theHsbstream well in both conditions ($R^2 > 0.85$for both cases), and its parameters confirm our initial premises regarding the deceleration coefficient ($\beta < 1.00$), which confirms the slow motion prior; and the observational variance, which grows as contrast is reduced thus producing stronger biases.

Fig. 4 shows a similar story. Panel A shows the mean MSE, considering all tested reference's variances (δ^{v}_{yR}), as a function of the deceleration coefficient β for each test contrast. We see the MSE rising steeply as β approaches unity. In panel B, we show the mean tests' observational variances (δ^{v}_{yT}) as a function of the entire range of the tested reference's observational variances (δ^{v}_{yR}), for all evaluated β. We see here that high contrast stimulus variance (i.e. reference variance) is always lower than medium contrast variance, which in turn is lower than low contrast variance, regardless of the specific reference variance value. From these results, we find that our parameter fitting strategy confirms our initial insights from Fig. 3 throughout the explored parameter space, namely that the model fits best when β <1 and when high contrast variance < medium contrast variance < low contrast variance.

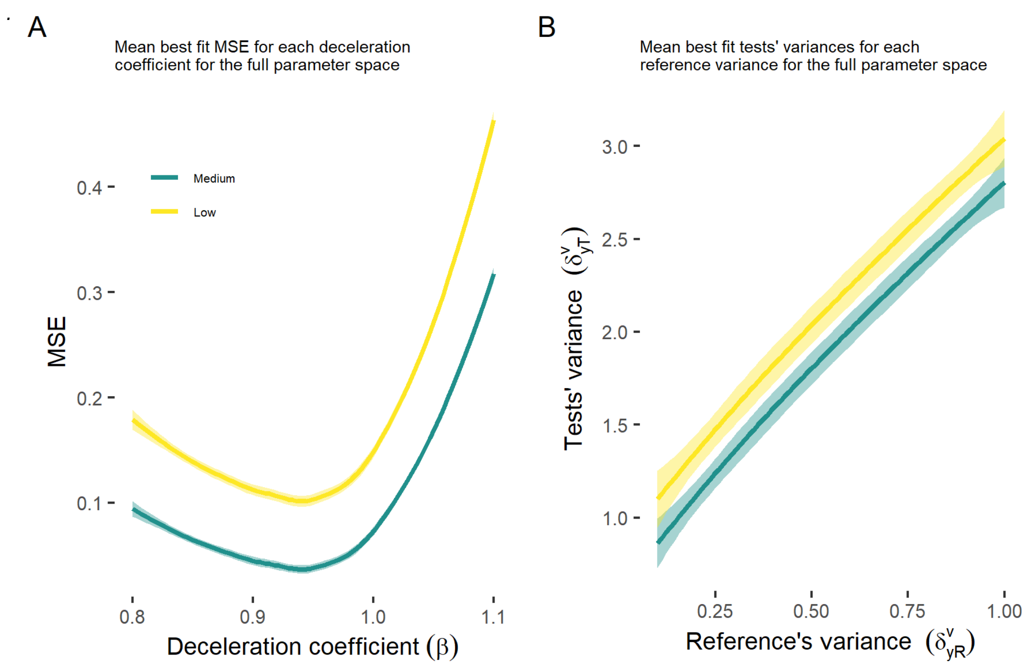

Figure 4*: (A) Mean best MSE for each tested deceleration coefficient(β). (B) Best fit's test variance for all tested reference variance*

To statistically test the value of β and the relationship between all observational variances we employed a bootstrap technique based on 1000 simulations. In each iteration and for each test contrast, the model was fitted to the average Hsb of 28 independently sampled (with replacement) streams from the 28 subject's meanHsb. The fitting procedure was the same as the one used previously, except for the reference's observational variance (δ_{yR}^{v}), which was fixed to 0.1. In Table 1 we show the mean deceleration coefficient (β) and both tests' observational variances for the best fit obtained from this technique (95% 'BCa' confidence interval). As we can see, deceleration coefficients for both conditions are, as expected, not significantly different; and the observational variances for the low and medium contrast conditions are larger than the high contrast case. As for the differences between the low and medium contrast variances, the low contrast variance is greater than the medium contrast variance, although the statistical analysis shows that the significance is marginal (80% CI.

Contrast	Deceleration coefficient (β)	Test observational variance (δ_{T}^{y})
Medium	0.89 CI [0.80, 0.95]	0.85 CI [0.58, 1.27]
Low	0.91 CI [0.80, 0.97]	1.15 CI [0.80, 1.61]

Table 1: *Deceleration coefficient and test observational variance model's estimates for medium and low contrast, obtained through 1000 bootstrap simulations. Confidence intervals are 95% ('Bca')*

To further test our model's performance, we used the parameters from the model shown in Fig. 4 to predict the hand speed bias for accelerated (Fig. 5, panel A and B) and decelerated test stimuli (Fig. 5, panel C and D), for both test contrasts. The resulting prediction matches the hand's response remarkably well, particularly for the decelerated condition. Although it underestimates the absolute bias for the accelerated condition, it captures all the main features of the data with no free parameters.

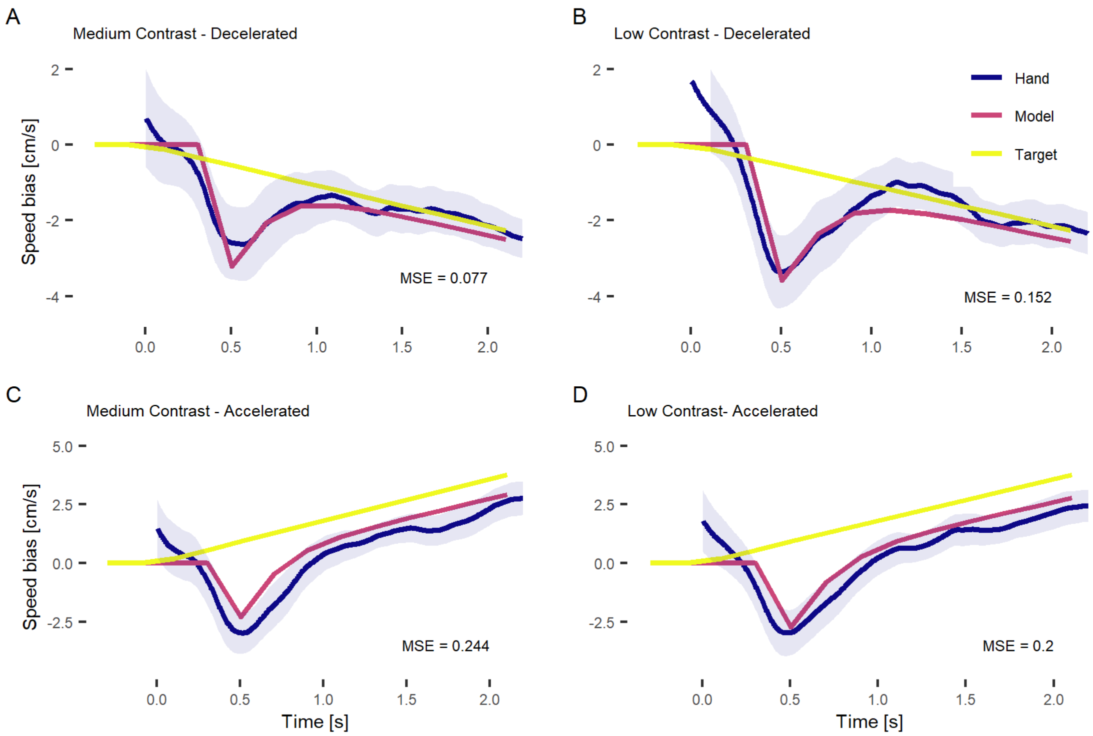

***Figure 5**: General mean speed bias vs time when test is decelerating (Panel's A and B) and accelerating (Panel's C and D). . Blue lines are the mean hand's response bias , ribbons show standard error. Red lines are the model's speed bias response for the model fitted for constant speed condition, and yellow lines are the veridical target motion difference for the medium contrast stimulus (panel's A and C) and low contrast stimulus (panel B and D)*.

Finally, we tested these predictions by extending the bootstrap procedure we employed earlier to compute for each iteration the coefficient of determination between the output of the fitted models for each target acceleration and the corresponding Hsb.

	R^2		
Contrast	Speed		
	Constant	Decelerated	Accelerated
Medium	0.69 CI[0.66,0.89]	0.85 CI [0.91,0.96]	0.91 CI [0.86,0.97]
Low	0.75 CI[0.73,0.89]	0.79 CI [0.73,0.92]	0.89 CI[0.86,0.96]

Table 2: R^2 between the model's speed bias and hand speed response estimates from 1000 bootstrap simulations. Confidence intervals are 95% ('BCa')

5. Discussion

Since it was first introduced (Weiss et al., 2002) the slow motion prior has been employed to explain an impressive variety of perceptual phenomena (Aguado & López-Moliner, 2019; Bogadhi et al., 2011; Kwon et al., 2015; Lakshminarasimhan et al., 2018; Welchman et al., 2008), providing a common framework to connect all of them. Dynamic models in particular have been used to explain the direction bias seen in SPEMs when pursuing ambiguous 1D motion (Bogadhi et al., 2011; Dimova & Denham, 2009; Montagnini et al., 2007) and the perceptual illusion known as the curveball illusion and the motion induced position shift (MIPS)(Kwon et al., 2015). In the present study, we wished to follow a somewhat different approach: we implemented a dynamic Bayesian model with assumptions similar to these models to generate predictions regarding the temporal evolution of the contrast induced speed bias. Considering the dynamic behavior of the direction bias reported in SPEMs (Masson & Stone, 2002; Wallace et al., 2005) and the model proposed to explain these results (Bogadhi et al., 2011; Montagnini et al., 2007), we hypothesized a similar effect for speed, i.e. that the magnitude of the velocity vector will show similar dynamics to that of direction when contrast is reduced. In this study we confirm this hypothesis, quantitatively showing that speed perception presents a dynamic behavior, analogous to that of direction.

In a nutshell, by assuming a dynamic prior rather than a static one, our model predicts that the CISB does not remain constant through time. On the contrary, it predicts a large bias at stimulus onset (when the *slow* motion prior has its largest effect) that slowly decreases as the stimulus progresses, as a consequence of information integration.

Our results show a great deal of agreement with our model's predictions. Most notably, the model quantitatively predicts the hand speed bias to conditions to which it was not specifically fitted, evidence of the model's robustness. Results are also consistent with the existing literature, although experimental conditions make quantitative comparisons a difficult task. For instance, the dynamic bias in SPEMs produced when tracking targets with ambiguous 1D motion found in Bogadhi et al., 2011, although very similar in nature to ours, shows a very different time constant bias decay (150-200 ms in Bogadhi et al., 2011 vs 400-500 ms in ours). This discrepancy is most likely associated with the difference in behavioural tasks, considering that although both manual and smooth pursuits typically show similar responses (Engel et al., 2000), manual pursuit is often "slower", showing both longer latency --~170-200 ms (Engel et al., 2000; van Donkelaar et al., 1994) vs ~100 ms (Engel et al., 2000; Liversedge et al., 2011) for similar speeds-- and time to peak velocity --~330-500 from visual inspection in Rodríguez-Herreros & López-Moliner, (2008) vs ~200-250 ms (Liversedge et al., 2011)- for similar speeds- than SPEMs.

In Bex et al., 1999 (ref) on the other hand, the authors estimated the effect of contrast on speed bias through time in the context of motion adaptation. In this study, contrast induced speed bias is seen to increase- rather than decrease- with time, as a result of the decrease in perceived contrast due to adaptation. Unfortunately, because of the low temporal resolution in this study and the fact that perceived contrast is not static, the transient effect we describe here cannot be observed under Bex et. al.'s experimental conditions. At any rate, within the speed range of our study (approximately 8 deg/s), smooth pursuit studies show that the contrast reduces eye motion in both the initial and steady state phases of pursuit (Bogadhi et al., 2011; Priebe & Lisberger, 2004; Spering & Montagnini, 2011), as well as studies using classical psychophysical methods (Blakemore & Snowden, 1999, 2000; Sotiropoulos et al., 2014; Stocker & Simoncelli, 2006).

In addition to the transient effect we present in our findings, a detailed analysis of the steady-state phase offers some interesting insights regarding an unsolved question in the literature. Previous SPEMs studies have shown that steady-state gain is reduced as contrast decreases, and rather surprisingly, does not reach 1 (i.e. eye velocity equal to target velocity) even at high contrast (Bogadhi et al., 2011; Spering et al., 2005). This evidence by itself of course does not mean that our motion perception does not provide an accurate account of a moving object with full contrast, considering that these measurements of steady state smooth pursuit were done in the initial 500 to 1000 ms after eye movement initiation. Moreover, beyond this time frame SPEMs are well into their closed loop stage, where eye motion cannot be considered a straightforward measure of motion signal; so even if steady-state gain is 1 after 1000 s, results would still be inconclusive.

It is in this regard where this study can offer some clarity: the model we propose presents a deceleration coefficient which is absent in the dynamic Bayesian models proposed for SPEMs (Bogadhi et al., 2011; Dimova & Denham, 2009; Montagnini et al., 2007) --but present in Kwon et al., 2015-- that predicts that even at full contrast, motion signals will not correspond to the actual motion measure. It is worth noting that the absence of this parameter would not have a significant impact when measuring SPEMs because the effect of β is mainly seen well into the steady-state phase, when the SPEMs are already in closed-loop mode. Our simulations shown in Fig. 1 reveal a clear picture regarding this issue: when β is equal to 1, the CISB is only present in a transient stage, i.e. eventually all stimuli are perceived as moving at the same speed, regardless of contrast (Fig. 1 A). On the other hand, when β is lower than 1, the perceived motion to which each stimulus converges does depend on contrast (Fig 1 B). Our results in Fig. 4, where we show for all conditions fitted that the MSE is minimum for β between 0.9 and 1, suggest a significant effect of contrast in the steady state phase.

The time frame for this effect is not a minor issue. Since one of the goals of this study was to explore what the motion estimates would be after a 1 s time frame, we specifically designed our methods to accommodate these needs. Recent studies have proposed new psychophysical experimental designs where perceptual signals are not measured through classical trial-based, forced choice decisions but rather by the continuous measurement of an action through which perception can be inferred. Importantly, the task employed in each study --and its interpretation-- will be specific to the hypothesis and experimental demands. For instance, a number of studies have used a manual tracking task (Bonnen et al., 2015, 2017) similar to our approach, but also other behavioral tasks, such as gaze (Knöll et al., 2018) and navigation (Lakshminarasimhan et al., 2018) have been used in the past. We developed and tested a simple and effective experimental device that allowed us to measure motion perception well beyond the SPEMs open loop phase through an open loop manual pursuit task. Although previous studies showed that this task was efficient in revealing motion perception effects over a wide time range, transduction from the instantaneous motion perceptual signal to hand motion is not straightforward. We designed our experimental model so as to offer a simple solution to bypass this issue, which we consider is one of the main contributions of this study. We assumed that, under our experimental conditions, the hand plant behaved like a linear system. Specifically, we hypothesized that within a range of perceptual inputs, the motor contribution to the velocity output could be considered equal to and independent of the perceptual input, which implies that whatever it may be, the difference of outputs will be equal to the difference between the inputs, regardless of the shape of both inputs' signal. Therefore, the simple subtraction of two hand motion signals can be considered representative of the perceptual difference between the two perceptual signals that feed the hand. The results, shown in appendix A, as well as our main results, provide evidence that our assumptions are sound within the range tested in this study.

This method is not without its limitations. One could expect that the perceptual variability of each stimulus would be reflected in hand motion variability, but this is not the case: for all tested conditions, hand motion variances are not significantly different from each other. However, when we consider both sources of variability in hand movement (i.e. perceptual and motor) we find a simple reason that explains this discrepancy. First of all, motor variabilitiy in this task is much higher than perceptual variability: for spacial discrimination tasks, motor noise can be between 5 to 10 times larger than perceptual noise (Bonnen et al., 2015); for a speed matching task such as ours, this number is probably much higher. Moreover, since motor noise increases with hand velocity, motor and perceptual variance are inversely correlated: low perceptual variability increases speed estimates, which in turn produce high motor noise, cancelling out each other's effect. Given this scenario, it is of no surprise that the difference in perceptual variance is clouded with motor variability. This in fact is what led us to our parameter fitting strategy, in which we explored the parameter space for all the model's variances and analyzed its regularities. Yet, considering that the model is fitted under one specific --constant speed-- condition, and predicts the remaining conditions very well, we feel it is safe to ensure it provides a quantitative account of the underlying perceptual process.

The second limitation our experimental model faces is the speed range in which the linearity assumptions of the hand plant can hold, which of course limits the possibility of interpreting hand motion as a proxy for perceptual motion. Aware of this limitation, we chose our experimental conditions in such a way that their initial speeds would agree, considering that this stage had the highest chance of producing non-linearities. In fact, the model's underestimation of the accelerating condition is very likely caused by this limitation, considering it is also observed in the model's validation provided in appendix A, where the perceptual model would have no significant influence.

All that being said, it is important to consider how the overall conditions imposed on the task impact the above mentioned limitations. We decided to favour a naturalistic approach, thus leaving hand, eye, and head movements unconstrained; an experimental setup specifically designed to minimize variability might look quite different. This design, despite its caveats however, further emphasizes the notion that the CISB effect has very real life consequences, a fact already noted by previous studies (Lakshminarasimhan et al., 2018; Snowden et al., 1998).

One final aspect worth noting is that, by averaging all trials for each condition, we made the implicit assumption that trials are independent. Although this is an accurate assumption given our experimental design, it has been shown that trials can show a temporal correlation with each other(Cicchini et al., 2017; Gekas et al., 2019; Narain et al., 2013), which is especially interesting within the context of this study, since dynamic Bayesian models (in which the prior is updated from trial to trial, rather than within a trial) have been used to explain these trial-history effects

(Burge et al., 2008; Narain et al., 2013). In other words, using the same premises of our model, we can expect a long-term dynamic effect, in which the prior of each individual trial cannot be considered independent. This is left for a future study, one in which the trial-sequence is specifically designed to produce a noticeable long-term effect.

To conclude, our results show that hand speed dynamics are affected by stimulus contrast in a way that is consistent with a dynamic model of motion perception that assumes a slow motion prior. The proposed model also confirms observations made in previous studies that suggest that motion perception would not correspond with physical motion measurements, even at high contrast, due to the dynamics of the slow motion prior.

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Appendix A

As explained in Section 3.1 (Experimental Model) we assumed that the hand speed response function to a visual input can be approximated by the sum of a perceptual and a motor component, the latter being invariant from perceptual variations within the range of our experimental conditions. This was expressed in Equation (6) and rewritten below for clarity:

$$Hsr_t\big(P_t(S_t)\big) \sim P_t(S_t) + M_t \tag{6}$$

Where Hsr is the hand's speed response, P is the motion perceptual estimate of the physical stimulus S, M is the invariant motor component and t is time.

Under these assumptions, if the perceptual estimates of two different stimuli lie within a certain range, the difference between the Hsr to each stimulus can be approximated to the perceptual difference between the two stimuli, since M will be cancelled out.

We tested this claim by comparing the Hsr produced by two motion stimuli for which we could expect a linear correlation between the perceptual difference and the instantaneous physical speed difference. For that purpose, we employed suprathreshold stimuli, identical in all dimensions with the exception of speed, which would begin equal and only differ smoothly in small temporal increments and up to 50%. We followed the same processing detailed in Section 3.6 (Experimental data processing), only this time keeping reference and test at equal contrast. In the end, we had two main conditions: accelerated test minus constant speed reference, and decelerated test minus constant speed reference, for all three contrasts (High, Medium and Low). Should our assumptions hold -namely a) equation 5 and b) linear correlation between perceptual speed difference and physical speed difference-, we expected a high linear correlation between Hand Speed Difference and Target Speed Difference

In Fig. A.1 we show the resulting output for the mean of all subjects for each condition: panel i, ii and iii are for High, Medium and Low contrast respectively. The yellow lines represent the resulting target speed difference as a function of time, the blue lines are Hsr , and the red lines are Hsr linear fit. From visual inspection, Target and Hand signals seem to comply with our assumptions throughout the task for all 6 conditions.

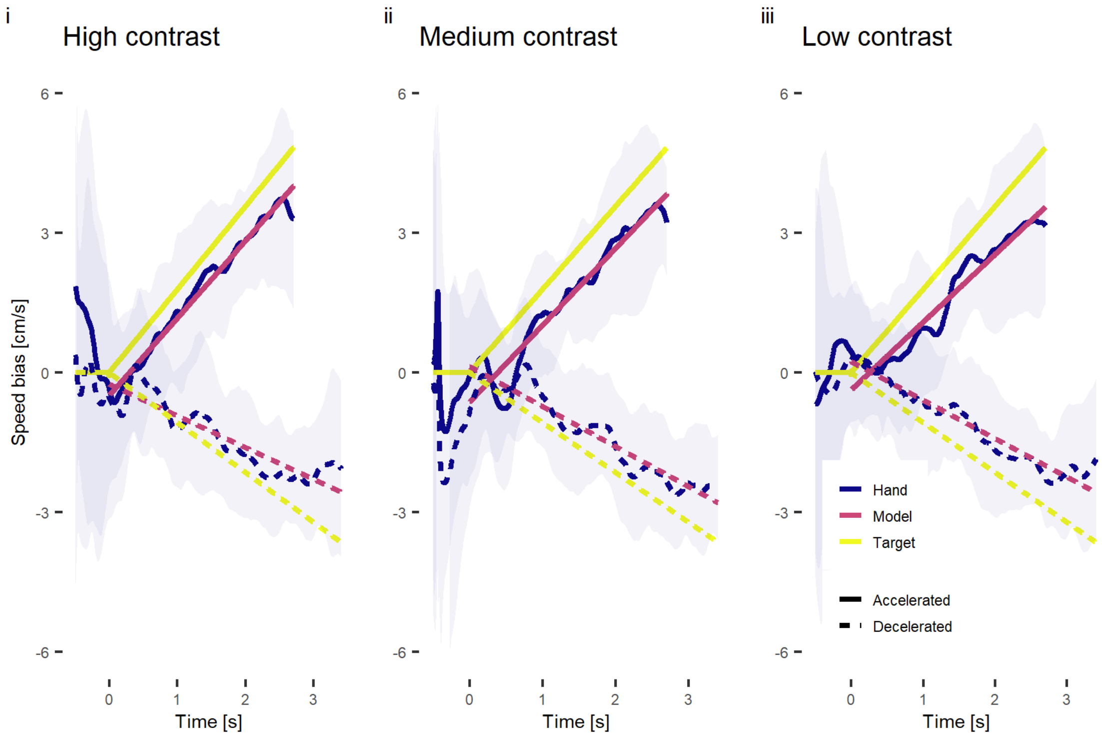

Figure A.1: *General mean of speed difference vs time for decelerating and accelerating tests, with equal contrast for test and reference.. Blue lines are the mean hand's response bias, ribbons show standard error. Red lines are the linear fits for the hand response bias, and yellow lines are the veridical target motion difference. Each panel corresponds to one contrast difference*

Following the same bootstrap technique used in the main article (Section 4 - Results), we computed 1000 simulations for each condition, and fitted a linear model between Hsr and target speed difference. Mean slope, intercept and R^2 are shown in Table A.1, and corroborate our initial insights, with an $R^2 > 0.81$ for all conditions. The parameters of the linear model show small differences among conditions, yet the proposed approximation is accurate enough for the purposes of our study.

Speed difference	Contrast	Intercept	Slope	R^2

Decelerated	High	-0.10 CI[-0.49, 0.32]	0.76 CI[0.60, 0.93]	0.81 CI[0.60, 0.93]
	Medium	0.20 CI[-0.16,0.53]	0.86 CI[0.65,1.05]	0.84 CI[0.69, 0.93]
	Low	0.35 CI[0.03,0.63]	0.87 CI[0.70,1.02]	0.92 CI[0.75, 0.95]
Accelerated	High	-0.56 CI[-0.95, -0.20]	0.98 CI[0.79,1.17]	0.96 CI[0.90, 0.98]
	Medium	-0.66 CI[-1.14, -0.12]	0.95 CI[0.70,1.15]	0.87 CI[0.73, 0.95]
	Low	-0.41 CI[-0.84, -0.07]	0.84 CI[0.66,1.03]	0.88 CI[0.75, 0.95]

Table A.1: Intercept, slope and R^2 linear fits estimates of equal contrast hand speed differences from 1000 bootstrap simulations. Confidence intervals 95%.