Motion direction, luminance contrast and speed perception: An unexpected meeting

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Abstract

Motion direction and luminance contrast are two central features in the representation of visual motion in humans. In five psychophysical experiments, we showed that these two features affect the perceived speed of a visual stimulus. Our data showed a surprising interaction between contrast and direction. Participants perceived downward moving stimuli as faster than upward or rightward stimuli, but only at high contrast. Likewise, luminance contrast produced an underestimation of motion speed, but mostly when the stimuli moved downward. We explained these novel phenomena by means of a theoretical model, accounting for prior knowledge of motion dynamics.

Keywords: Speed perception, Motion direction, Luminance contrast.

Introduction

Speed, direction, and luminance contrast are central features in the representation of visual motion in humans (Palmer, 1999). The axis of motion affects the discrimination of motion direction, with the precision of the response being higher along the two cardinal axes compared to the oblique axes (Matthews & Qian, 1999). Luminance contrast plays a role in the perceived direction of coherent motion(Adelson & Movshon, 1982). A plaid arising from the combination of two moving gratings can be perceived either as a coherent motion, or as two gratings sliding over each other: The probability of perceiving a coherent motion of the plaid is strongly affected by the luminance contrast of the two gratings. This has been explained by assuming the existence of multiple channels sensitive to different motion orientation (Adelson & Movshon, 1982). Accordingly, classical studies in electrophysiology showed that neurons in early visual areas respond selectively to motion direction of the individual components or the combined pattern of a moving grating (Movshon, Adelson, Gizzi, & Newsome, 1985). While these results can be explained by the selective tuning of early visual neurons, other stimuli, such as the observation of gravitational motion, likely reflect the role of prior knowledge of physics that is stored in multimodal areas (Indovina et al., 2005). Our previous studies showed that humans account a priori for the effects of Earth's gravity in motor and perceptual tasks—see (Lacquaniti et al., 2013; Zago, McIntyre, Senot, & Lacquaniti, 2009) for a review. For instance, the discrimination of flight duration of accelerated targets is more precise for downward motion, which is consistent with Earth's gravity, than upward or horizontal motion (Moscatelli & Lacquaniti, 2011). Observers perceive as uniform a quasi-harmonic velocity profile that is consistent with a pendulum accelerated by physical gravity (La Scaleia, Zago, Moscatelli, Lacquaniti, & Viviani, 2014). Likewise, when judging rolling motion, observers are accurate at finding the match between slope angle and ball acceleration congruent with physics (Ceccarelli et al., 2018). Studies on motor control are also in accordance with the hypothesis of an internal model of gravity (Zago et al., 2009). Astronauts initiate catching movements earlier in microgravity than on Earth, as if they expected a priori the effects of gravity on target motion even when absent (McIntyre, Zago, Berthoz, & Lacquaniti, 2001). Likewise, motion direction with respect to gravity and target acceleration influence the estimate of the time to contact in catching tasks in virtual reality (Russo et al., 2017; Senot, Zago, Lacquaniti, & McIntyre, 2005; Zago et al., 2004).

In addition to the direction of motion and the representational gravity, luminance contrast also provides important information on object motion, depth, and shape (Adelson & Movshon, 1982; Kandel, 2012; O'Shea, Blackburn, & Ono, 1994). Due **to** the contrast attenuation by water droplets in air, which is even augmented in fog, objects having lower luminance contrast are perceived as farther in space (O'Shea et al., 1994; Pretto, Bresciani, Rainer, & Bülthoff, 2012). A change in stimulus contrast causes a bias in the perceived speed, which is perceived as slower at lower contrast (Thompson, 1982; Weiss, Simoncelli, & Adelson, 2002). **This phenomenon has been evaluated with different types of stimuli—including sinusoidal gratings, random dot patterns, translating and expanding disks—and for a wide range of motion speed and temporal frequencies** (Blakemore & Snowden, 1999; Champion & Warren, 2017; Hassan & Hammett, 2015; Stocker & Simoncelli, 2006; Thompson, Brooks, & Hammett, 2006)**. The effect is robust for slow speed (typically, between 0.5–4** $\deg s^{-1}$**) and low temporal frequencies (up to 6 Hz), is small or approximately zero between 8–10** $\deg s^{-1}$ **and between 6–10 Hz, and even reverse for higher temporal frequencies.** Different hypotheses have been proposed to explain this phenomenon. According to a first hypothesis, visual speed would be encoded as the signal ratio of two channels tuned to low and high temporal frequencies (Adelson & Bergen, 1986; Hassan & Hammett, 2015; Thompson, 1982). **The response of each channel would be a function of both, the temporal frequency and the luminance contrast of the stimulus. Reducing contrast would reduce the influence of the high speed channel at low speeds, and reduce the influence of the low speed channel at high speeds. It has been suggested that** these two channels **could be** identified with the Magno- and the Parvocellular cells in the primate lateral geniculate nucleus (Hassan & Hammett, 2015). Alternatively, a Bayesian model implying a prior for stationarity would account for this phenomenon (Sotiropoulos, Seitz, & Seriès, 2011; Stocker & Simoncelli, 2006; Weiss et al., 2002). According to this model, observers assume a priori that—statistically speaking—inanimate objects are generally at rest (the "static prior", sometimes also referred to as "slow motion prior"). The noisy sensory measurements (corresponding to the likelihood distribution in the Bayesian framework) and the prior distribution are multiplied and the weighting between them depends on the relative variance of the distributions. Under reduced visibility, **as for example at low contrast**, the sensory measurements are noisier **(variance are larger)** and therefore the relative weight of the prior increases. Thus, objects seem to move slower in such condition. **However, other studies did not**

find that reducing luminance contrast is associated with noisier sensory measurements; that is, changing contrast does not lead to a change in Weber Fraction for speed (Hassan & Hammett, 2015; McKee, Silverman, & Nakayama, 1986)**.**

Here, we evaluated the interaction of motion direction and luminance contrast on the perceived speed. To our knowledge, this is the first study investigating this specific issue. We advanced the hypothesis that observers combine their sensory measurements with a motion prior accounting for the effects of Earth's gravity (Jörges & López-Moliner, 2017; Lacquaniti et al., 2013). On Earth, **inanimate and not self-propelled** objects on average move faster when they are in free fall than when rolling or sliding on a plane. Hence, the observer's motion prior would change in mean depending on the direction of motion with respect to gravity. We tested whether the perceived speed changed with the orientation of motion: If observers take gravity into account, downward motion would be perceived as faster than horizontal or upward motion. **According to** (Stocker & Simoncelli, 2006)**, the likelihood variance would be larger at lower contrast, and therefore its relative weight on the mean of the posterior would be lower. If this relationship between contrast and variance were true,** a change in luminance contrast would affect the weighting between the likelihood distribution and the putative gravity prior. We tested these hypotheses by means of psychophysical experiments and we proposed a theoretical model to account for our findings.

Experiment 1: Speed Perception in Horizontal and Vertical Motion

In experiment 1, we evaluated whether the perceived speed of a moving target changes across the two cardinal directions of motion. We asked participants to compare the perceived speed of downward and rightward moving stimuli. Across trials, we manipulated the luminance contrast of the reference and the comparison stimuli to evaluate the effect of the signal reliability on the putative bias.

Participants

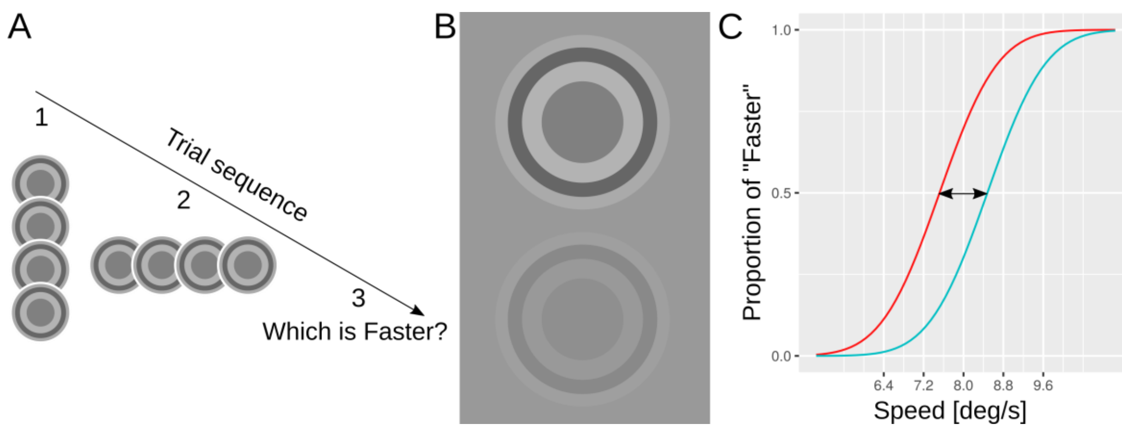
Ten participants (8 naïve participants plus authors AM and BL) took part to the experiment. The age was 23 $\pm$ 6 years (mean $\pm$ standard deviation). The experimental procedures were approved by the Ethical committee of the Santa Lucia Foundation, in accordance with the guidelines of the Declaration of Helsinki for research involving human subjects. Informed written consent was obtained from all participants involved in the study.

Stimuli and Procedure

Participants sat on an office chair, resting their head on a head-and-chin rest placed approximately 50 cm from a computer monitor (LCD Monitor ViewSonic VG920; 1280 x 1024 at 75 Hz). A black tube (diameter: 15.35 cm, length: 50 cm) in front of the participant delimited a circular aperture on the screen, subtending an angle of 17.5 deg at the eye distance of 50 cm. The stimuli consisted of a grey-textured disk (referred to as “the target” in the following) moving with a constant speed across the circular aperture (Fig. 1A-B). The diameter of the disk was equal to two deg. **We used a moving disk, instead of other motion stimuli like gratings or dots, because it might evoke the sensation of motion of natural stimuli** (Blakemore & Snowden, 1999)**. Previous studies showed that effects related to the representation of gravity are modulated by the relative naturalness of the scene and stimuli** (Ceccarelli et al., 2018; Miller et al., 2008; Moscatelli & Lacquaniti, 2011)**.** Luminance was measured using a digital photometer (Tektronix J17 LumaColor). The average luminance of the target was equal to 30 $cd\ m^{-}2$, and was the same as the luminance of the background. A fixation cross was located at the center of the screen. The tube occluded the onset and the offset of the target’s motion. **That is, the target appeared outside the tube, crossed the circular viewing window along its diameter, and finally stopped past the opposite border of the tube. This was to avoid the misperception of constant velocity immediately after motion onset** (Runeson, 1974)**.** Motion stimuli were generated with XVR software (eXtreme Virtual Reality, VR Media S.r.l.).

Each trial consisted of a reference and a comparison stimulus (ISI = 500 ms). Participants reported whether the target moved faster in the reference or in the comparison stimulus interval, by clicking the left or right button of a PC mouse. The next trial started 1500 ms after the response. The motion speed was equal to 8.0 deg s^{-1} in the reference stimulus, whereas in the comparison stimulus it was sampled among five possible values, equally spaced within a range of 8.0 $\pm$ 1.6 deg s^{-1}. **These values of speed are within the range used in luminance contrast literature, typically between 0.5 and 10** deg s^{-1}**. We excluded higher values of speed to**

avoid a zero effect or the reversal of the luminance contrast bias. On the other hand, due to the constant of gravity, in daily-life experience, the slower stimuli in the range are unlikely along the vertical direction; we hypothesized that a reference speed of 8 $\deg s^{-1}$ was "fast enough" to evoke the sensation of a falling object when moving downward. Within each trial either the reference stimulus moved rightward and the comparison moved downward (comparison-downward trials), or vice versa (comparison-rightward trials). The reference and the comparison stimuli were presented either both at high or low luminance contrast (Michelson contrast equal to 83% and 18% respectively). Each combination of luminance contrast, motion direction and speed was replicated 14 times in a pseudo-random order across the experiment.



Stimuli and Procedure. A) The experimental procedure (Experiment 1). For each luminance contrast condition, participants compared the speed of motion of two stimuli, moving either downward or rightwards. B) Visual target were presented at either high or low luminance contrast. C) Categorical responses were analyzed by means of psychometric functions (example of model fit). The relative shift of the function between the two motion conditions, comparison downward (red) and comparison rightward (azure), provided a measurement of the perceptual bias (black arrow). The task was replicated for the two luminance conditions.

Analysis

We analyzed the results using a two-level algorithm and with the Generalized Linear Mixed Model (Moscatelli, Mezzetti, & Lacquaniti, 2012). The two-level algorithm was the following. First, we fit the results of each single participant and for each direction and contrast condition by using a psychometric function (**also referred to as General Linear Model**) of the form,

$$\Phi^{-1}[P(Y=1)] = \eta_0 + \eta_1 v$$

where, $P(Y=1)$ is the probability of reporting that the comparison stimulus was moving faster than the reference, $\Phi^{-1}[\cdot]$ is the probit link function, and v is the motion velocity (Fig. 1C). The parameters η_0 and η_1 are the intercept and the slope of the General Linear Model, respectively. We estimated the Point of Subjective Equivalence (PSE) and the Just Noticeable Difference (JND) from equation , as explained in (Moscatelli, Mezzetti, & Lacquaniti, 2012). For each participant and contrast condition, we computed the difference in PSE between comparison-rightward and comparison-downward trials. By means of one-sample t-test we tested if the difference in PSE was significantly different from zero, separately in each contrast condition. We used a linear regression to evaluate the relationship between the high and the low contrast condition.

We confirmed the results of the two-level analysis by using a Generalized Linear Mixed Model (GLMM). **The GLMM is an extension of the General Linear Model to clustered data, which in psychophysics typically consist of the collection of repeated responses in a group of participants** (Agresti, 2002; Moscatelli, Mezzetti, & Lacquaniti., 2012)**. The GLMM is a hierarchical model, including fixed and random effect parameters. The fixed effect parameters, akin to the parameters of a classical psychometric function, estimate the effect of the experimental variables on the predicted response. Random-effect parameters estimate the heterogeneity between different participants. The GLMM assumes that the random-effect parameters are normally distributed random variables. Advantages of the GLMM with respect to the two-level analysis are the clear distinction between the between- and the within-participants variability and the higher statistical power.** We fit simultaneously the data from the different participants and conditions, with a GLMM of the form:

$$\Phi^{-1}[P(Y=1)] = \beta_0 + u_0 + (\beta_1 + u_1)v + (\beta_2 + u_2)d + \beta_3 c + \beta_4 d{:}c$$

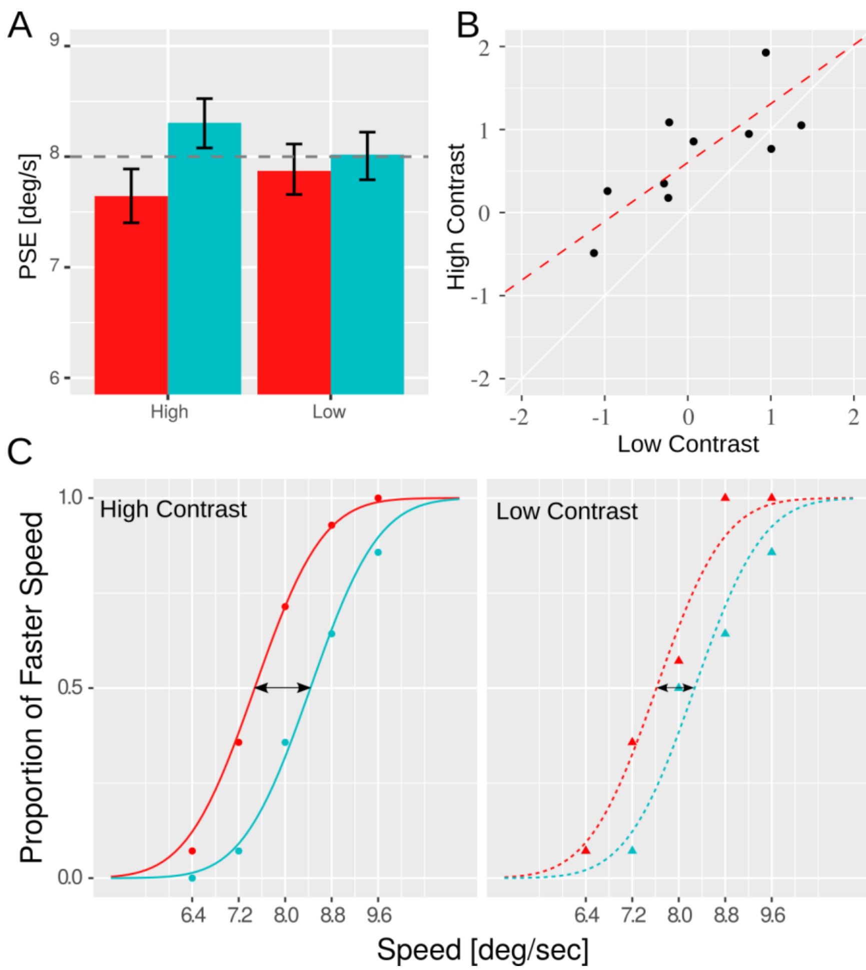
Equation is similar to the psychometric function in equation , with the following differences. On the right side of the equation, v, d, c represent the multiple predictor variables, i.e., the velocity and the direction of motion of the comparison stimulus, and the luminance contrast. The parameters β_* and u_* account for the experimental effects (fixed-effect parameters) and random variability between participants (random-effect parameters), respectively. The GLMM in equation was selected from a pool of nested models based on the Bayesian Information Criterion

(BIC). We estimated the PSE and the JND from the GLMM, as illustrated in (Moscatelli, Mezzetti, & Lacquaniti 2012). **Data analysis was performed in R** (R Core Team, 2018)**. GLMM fitting was performed using the R packages *lme4*** (Bates, Mächler, Bolker, & Walker, 2015) **and *MixedPsy* (Moscatelli, Mezzetti, & Lacquaniti 2012). The same set of analyses, including the two-level analysis and the GLMM, has been replicated in experiment 1–5.**

Results

First, we analyzed the data at high luminance contrast. In this condition the target was perceived as faster when it was moving downward ($t_9 = 3.34$; $p = 0.008$, Fig. 2A "High"). The PSE was equal to 7.64 deg s^{-1} in comparison-downward (with the 95% Confidence Interval, CI, ranging from 7.40 to 7.88 deg s^{-1}), and to 8.30 deg s^{-1} in comparison-rightward (95% CI ranging from 8.08 to 8.52 deg s^{-1}). That is, the values of PSE were significantly smaller than the reference speed in the first experimental condition, and significantly larger in the other (see also Table S1). **The numerical difference between conditions was consistent in 9 out of 10 participants**. Next, we analyzed the data at low contrast and evaluated whether the luminance contrast modulated the speed bias. Unlike in the high contrast condition, the effect of motion direction was not statistically significant at low contrast ($t_9 = 0.47$; $p = 0.65$, **the numerical difference** occurred in 5 out of 10 participants) and the 95% CI crossed the value of the reference speed (Fig. 2A "Low"). The PSE was equal to 7.87 deg s^{-1} in comparison-downward (95% CI ranging from 7.66 to 8.11 deg s^{-1}), and to 8.01 deg s^{-1} in comparison-rightward (95% CI ranging from 7.79 to 8.22 deg s^{-1}). In Eq. , the parameter β_4 accounting for the interaction between direction and contrast was statistically significant ($\beta_4 = 0.55$, $p < 0.001$), supporting the result of a larger bias at high luminance contrast. The perceptual bias was linearly related between the two contrast conditions (Fig. 2B). In accordance with the previous analyses showing a larger effect for the high contrast condition, the regression line was shifted above the identity line. Instead, the slope of the GLMM, accounting for the precision of the response, was not significantly different between the low and the high contrast condition (p = 0.77). Therefore, this parameter was not considered in Eq.. The average JND was equal to 0.63 deg s^{-1} (95% CI ranging from 0.56 to 0.75 deg s^{-1}), corresponding to a Weber Fraction of 7.9% (95% CI ranging from 6.9 to 9.4), which is close to the value of 7% reported in (de Bruyn & Orban, 1988). Results of a representative participant are illustrated in Fig. 2C. **Statistically speaking, population results do not change without the inclusion of the two authors.**

The main result that downward motion was perceived as faster than rightward is consistent with our hypothesis that, in perceiving motion, observers take into account the effect of gravity. Surprisingly, the directional bias was significantly smaller at lower contrast. **In accordance with previous studies using the same value of reference speed of** $8 \deg s^{-1}$**, we failed to reject the null hypothesis that the reliability of the response was the same between the two contrast conditions** (Champion & Warren, 2017; Hassan & Hammett, 2015; McKee et al., 1986; Stocker & Simoncelli, 2006)**. Hence, it is unlikely that the interaction between direction and contrast depends on a change in the weighting between the likelihood and the prior.** We performed a second experiment to evaluate if the well-established phenomenon of the stimulus contrast affecting the perceived speed is modulated by the direction of motion.



Results Experiment 1: The PSE estimates and the 95% *CI (see also Tables S1-S5). A) The PSE in the high and the low contrast condition. The red and the azure bars represent the PSE estimates for downward and rightward comparison direction, respectively. The dashed line is the reference speed. B) The linear relationship of the perceptual bias, computed as* $PSE_{left} - PSE_{down}$*, between high and low contrast condition. Raw data and orthogonal linear regression fit (slope = 0.7; p = 0.01). The oblique line of the white grid shows the identity line. C) Psychometric functions in a representative participant. The left and the right panel illustrated the high and the low contrast condition, respectively.*

Experiment 2: Motion Direction Modulates the Luminance Contrast Bias

According to previous studies discussed above, the luminance contrast affects the perceived speed of a moving target. Within a low speed range (typically below 10 deg s^{-1}), stimuli at lower contrast are perceived as slower that stimuli at higher contrast having the same physical speed. In experiment 2, we evaluated whether this bias changes across the downward and rightward direction of motion.

Participants

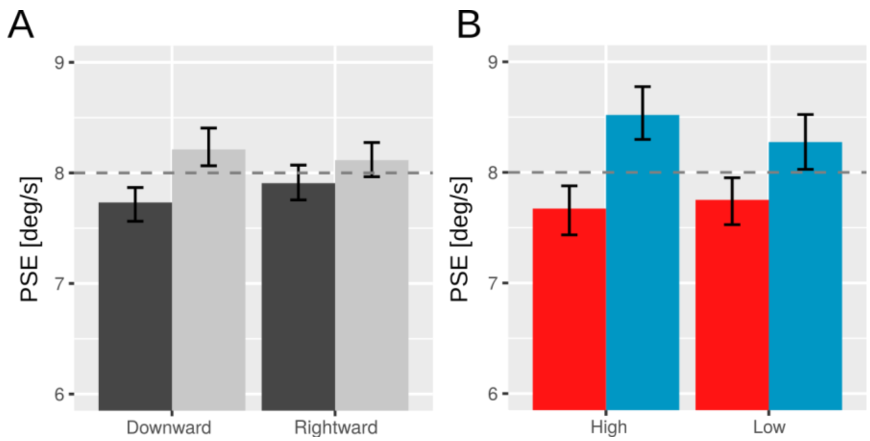
Fourteen participants (12 naïve participants plus authors AM and BL) participated in the experiment. The age was equal to 29 $\pm$ 7 years (mean $\pm$ standard deviation).

Stimuli and Procedure

The experimental setup and the procedures were the same as in experiment 1. This time the direction of motion was the same between the reference and the comparison stimulus, whereas the luminance contrast changed. Within each trial, either the reference stimulus was high contrast and the comparison was low contrast (comparison-low trials), or vice versa (comparison-high trials). The reference and the comparison stimuli moved either both downwards or both rightwards. We evaluated the protocol using a small aperture (diameter = 8.75 deg; N = 7) and a large aperture (diameter = 17.5 deg; N = 7). As the size of the aperture did not produce a significant effect on the responses, data were pooled for further analyses.

Results

In accordance with the previous experiment, experiment 2 confirmed the relationship between luminance contrast, motion direction, and the perceived speed. **The stimuli were perceived as faster** at high compared to low luminance contrast, but only for downward stimuli ($t_{13} = 3.0129$, $p = 0.01$. The effect occurred in 10 out of 14 participants). Instead, the effect was significantly smaller for rightward stimuli (the parameter of interaction between contrast and motion direction was different from zero; estimate = 0.26; $p = 0.01$). Luminance contrast did not produce a significant effect for rightward moving stimuli ($t_{13} = 1.7$; $p = 0.11$. Albeit small, **the numerical difference between conditions** occurred in 10 out of 14 participants), however, the trend was the same as in downward condition. The 95% CI did not include the reference speed for downward stimuli, whereas it crossed the reference for rightwards (Fig. 3B and Table S2). We did not find a significant difference in the slope of the GLMM between rightward and downward (p = 0.28). The average JND was equal to $0.65 \deg s^{-1}$ (95% CI ranging from 0.61 to $0.68 \deg s^{-1}$), corresponding to a Weber Fraction of 8.1% (95% CI ranging from 7.7 to 8.5).



Results Experiments 2-3: A) Experiment 2, PSE estimates and 95% CI. The dark and the light gray bars represent the PSE estimates for comparison stimuli presented at high and low contrast, respectively. B) Experiment 3, PSE estimates and 95% CI. The red and the blue bars represent the PSE estimates for downward and upward comparison direction, respectively.

Experiment 3: Speed Perception in Vertical Motion

The first two experiments showed that the perceived speed depends on contrast, direction (downward Vs rightward), and the interaction of these two factors. We **ran** a third experiment to evaluate whether the perceived speed changes between downward and upward motion, in accordance with the hypothesis of a gravity prior.

Participants

Ten participants (8 naïve participants plus authors AM and BL) participated in the experiment. The age was equal to 25 ± 7 years (mean $\pm$ standard deviation).

Stimuli and Procedure

The experimental setup and the procedure were the same as in experiment 1. This time the direction of motion of the target was always vertical: the target moved either upward in the reference and downward in the comparison stimulus (labelled a *comparison-downward* trials), or vice versa (*comparison-upward* trials).

Results

As in the first experiment, reference and comparison were presented either both at high or both at low luminance contrast. At high luminance contrast, **the stimuli were perceived as faster** in the downward compared to the upward direction ($t_9 = 4.46$; $p = 0.0016$; **numerical difference between conditions in** 9 out of 10 participants). This time, the effect was statistically significant also at low luminance contrast, although the effect size was smaller than at high contrast ($t_9 = 2.41$; $p = 0.039$; **numerical difference between conditions in** 7 out of 10 participants). The average difference between PSE_{up} and PSE_{down} was 0.93 deg s^{-1} and 0.63 deg s^{-1} at high and low contrast, respectively. The interaction between contrast and motion direction was statistically significant (estimate = 0.27, $p = 0.015$). The 95% CI did not include the reference speed, either at high, or at low luminance contrast (Fig. 3B and Table S3). We did not find a significant difference in slope between the low and the high contrast condition. The average JND was equal to 0.80 deg s^{-1} (95% CI ranging from 0.70 to 0.93 deg s^{-1}), corresponding to a Weber Fraction of 10.0% (95% CI ranging from 8.0 to 11.7).

Experiment 4 and 5: Control on Fixation and Path Length

We run two additional experiments to control fixation (experiment 4) and to randomize path length, to reduce the reliability of motion duration as a cue to speed (experiment 5).

Participants

Eleven participants (9 naïve participants plus authors AM and BL) participated in experiments 4 and 5, in two blocks within the same experimental session. The age was equal to 25 ± 7 years (mean $\pm$ standard deviation). The order of the two experiments within the experimental session was counterbalanced across participants.

Stimuli and Procedure

The experimental setup and the motion stimuli were similar to the ones used in experiment 3 (vertical motion). The target moved either upward in the reference and downward in the comparison stimulus (labelled a *comparison-downward* trials), or vice versa (*comparison-upward* trials). In both experiment 4 and 5, only high contrast stimuli were tested.

In *experiment 4*, the speed discrimination task was randomly alternated with a secondary control task (similar to the one used (Dupin, Hayward, & Wexler, 2017)) to ensure that participants maintained the fixation on the central cross. The control task involved Landolt-like stimuli, consisting in a gray square with either the left or the right side missing (Michelson contrast: 17%). The square could either appear once (catch trials) or not appear (speed discrimination trials) during either the reference or the comparison stimulus, with a probability of appearance of 1/15. In catch trials, the square was displayed for 200 ms centered on the stationary fixation cross. The onset of the square stimulus was pseudo-randomly chosen between 200 and 900 ms from the motion onset of the target. The square size was 3 deg (1-pixel line width, corresponding to 0.3 mm). In catch trials, participants were not inquired on the speed of the moving target but reported the orientation of the square.

Experiment 5 consisted of a speed discrimination task, similar to the one tested in experiment 3. In each stimulus interval, the length of the motion path was pseudo-randomly chosen from a uniform distribution (lower limit equal to 8 cm and upper limit equal to 15.35 cm), and centered on the fixation cross. This way, motion duration changed pseudo-randomly between stimuli, making it unreliable as cue to speed. Overall, each participant performed 150 trials in the fixation experiment (140 speed discrimination trials plus 10 catch trials) and 140 trials in the random-path experiment.

Results

The two control experiments confirmed the overestimation of target speed in downward compared to upward motion at high luminance contrast. In experiment 4, the PSE was equal to 7.58 deg s^{-1} in comparison-downward (95% CI ranging from 7.37 to 7.78 deg s^{-1}), and to 8.49 deg s^{-1} in comparison-upward (95% CI ranging from 8.28 to 8.73 deg s^{-1}). In experiment 5, the PSE was equal to 7.57 deg s^{-1} in comparison-downward (95% CI ranging from 7.43 to 7.70 deg s^{-1}), and to 8.50 deg s^{-1} in comparison-upward (95% CI ranging from 8.29 to 8.68 deg s^{-1}).See also Table S4-S5. In both Exp. 4 and 5, **the numerical difference between conditions** was present in all participants.

Discussion

Visual motion plays a fundamental role in our daily life behaviour: To say it in Marr's words, "Motion pervades the visual world" (Marr & Ullman, 1981). Despite decades of studies on this topic—see (Burr & Thompson, 2011) for a comprehensive review—psychophysical experiments are still producing unexpected results. Here, we showed a novel phenomenon, where the perceived speed is affected by the direction of cardinal motion, such as downward moving stimuli are perceived as faster than those moving either rightward (experiment 1) or upward (experiment 3–5). Surprisingly, the effect is modulated by luminance contrast, being stronger at high contrast. In the same vein, the well-established phenomenon of contrast biasing the perceived speed is modulated by motion direction, with the effect being larger for downward motion (experiment 2).

Previous studies revealed other anisotropies in discrimination and detection of visual motion. For instance, centripetal motion can be detected and discriminated better than centrifugal motion (Giaschi, Zwicker, Young, & Bjornson, 2007). **Directional anisotropies are opposite at low and high speed conditions** (Naito, Sato, & Osaka, 2010)**. At low speed ($<$ 4 deg s^{-1}), centrifugal directional anisotropy was observed, while at high speed ($>$ 16 deg s^{-1}), centripetal directional anisotropy was observed in the peripheral upper visual field. The perceived depth of moving random dots depends on its motion directions, and this preferred direction is usually either downward or rightward** (Mamassian & Wallace, 2011). Direction discrimination of moving random dots depends on the axis-of-motion, with the response being **more precise for objects moving cardinally compared to oblique motion stimuli** (Matthews & Qian 1999). Instead, no systematic differences across the cardinal directions have been reported in direction detection and discrimination experiments (Gros, Blake, & Hiris, 1998). A recent study investigated whether motion direction produced a speed bias (Manning, Thomas, & Braddick, 2018). The authors found that stimuli moving along an oblique axis are perceived on average as faster than those moving along cardinal directions (with some differences in this result between the four experiments of the study). Instead, the authors did not find any systematic difference between downward motion and the other cardinal directions. Two possible reasons may explain the difference with our findings. (Manning, Thomas, & Braddick 2018) used two sets of random dots presented side by side for a short time window, equal to 300 ms. Instead, we presented grey-shaded disks moving across a circular aperture that, when moving downwards, might evoke the sensation of a falling object. Accordingly, previous studies showed that effects related to the representation of gravity are modulated by the realism of the visual scene (Miller et al., 2008; Moscatelli & Lacquaniti, 2011). Additionally, in (Manning, Thomas, & Braddick 2018) the repetition of vertical and oblique directions in the reference stimuli may have led to adaptation inducing shifts in perceived speed. Instead, in our protocol the reference and the comparison stimulus appeared each in %50 of the stimuli: Hence, a putative adaptation affected equally the two motion directions. The neural basis of motion anisotropies has been deeply studied—refer to (Maloney & Clifford, 2015) for a review of the literature. Interestingly, anisotropies in the activity of early visual areas depends on stimulus contrast: (Maloney & Clifford 2015) reported an orientation preference for vertical orientations at low contrasts, which instead shifted towards oblique orientations at high contrast. To the best of our knowledge, our study is the first showing a speed bias associated with downward motion. We hypothesized that this downward bias may depend on prior expectations on the effects of gravity on object's motion. Previous studies involving perceptual and motor tasks provided strong **evidence** about the role of prior knowledge of gravity in motion processing in vision (La Scaleia et al., 2014; McIntyre et al., 2001; Moscatelli & Lacquaniti, 2011; Senot et al., 2005; Zago et al., 2004). Adaptation to downward visual motion produces a tactile motion aftereffect, which is stronger than after upward visual motion adaptation (Konkle, Wang, Hayward, & Moore, 2009). **Humans take gravity into account to estimate the stability of a pile** (Battaglia, Hamrick, & Tenenbaum, 2013)**, and in shape judgement tasks our visual system partially relies on a gravitational frame of reference where the light-source is assumed as roughly overhead** (Adams, 2008; Adams, Graf, & Ernst, 2004)**.** Imaging studies shed light on the neural correlates of the representation of gravity with respect to target motion (Indovina et al. 2005; Lacquaniti et al. 2013). Because vision is **weakly** sensitive to accelerations, prior knowledge accounting for the effects of gravity is derived from graviceptive information, is stored in the vestibular cortex, and is activated by visual motion that appears to be coherent with natural gravity (Indovina et al. 2005). Additionally, the over-representation of downward direction in mammals' visual cortex may also partially explain anisotropies in motion perception (Konkle et al., 2009; Ribot, Tanaka, O'Hashi, & Ajima, 2008).

Alike directional anisotropies, the effect of luminance contrast on the perceived motion also received the attention of several studies in the last forty years (Blakemore & Snowden 1999; Weiss, Simoncelli, & Adelson 2002; Stocker & Simoncelli 2006; Thompson, Brooks, & Hammett 2006; Pretto et al. 2012; Hassan & Hammett 2015). This phenomenon occurs with a variety of motion stimuli, including sine-wave gratings, random dot patterns, and discs (similar to those used in the present study). A recent study shed light on the neural basis of this speed bias. Using fMRI, (Vintch & Gardner, 2014) measured speed and temporal frequency-selective responses in early cortical visual areas and found that, at low contrast, the representation shifted toward slow speeds, matching perception rather than the physical stimulus. However, the functional mechanism of this phenomenon is still debated, with different studies supporting either the hypothesis of the combination of two channels with different frequency and contrast sensitivity, or the Bayesian model implying a static prior.

Models for speed perception

First, we will evaluate to which extent previous models predict results of the current study. Next, we will propose how to extend the Bayesian model, based on the hypothesis that perceptual judgements account for prior knowledge of motion dynamics.

According to a first hypothesis, visual speed would be encoded as the signal ratio of two channels tuned to different temporal frequencies, and having different contrast threshold (Thompson et al., 2006)**. This model predicts the contrast bias at low range of temporal frequency and speed. The effect would reduce in size, and even reverse, for faster speeds. In accordance with that,** (Champion & Warren, 2017) **did not find a significant effect of luminance contrast on the perceived speed for a reference speed equal to 8 deg s^{-1}. Instead, for the same value of reference speed, we found that high contrast stimuli were perceived as faster than lower contrast stimuli, but only when moving downward. The**

two-channel model does not account for this result, unless we hypothesize that the response of each channel were frequency-, contrast-, and direction-dependent.

Alternatively, other studies proposed a Bayesian model where the observer assumes *a priori* that objects are stationary. Because of the change in stimulus noise, the weight of the static prior would be relatively higher in low- compared to high-contrast stimuli, accounting for the observed bias (Weiss, Simoncelli, & Adelson 2002). To explain the dependency of the effect on the reference speed, (Stocker & Simoncelli 2006) hypothesised that the variance of the prior may be larger as the reference speed increases. An important prediction of this model is that the perceptual bias would be always associated with a difference in sensory noise between low- and high-contrast stimuli. Previous studies produced mixed results on this point. For instance, in (McKee, Silverman, & Nakayama 1986; Hassan & Hammett 2015), the authors did not find evidence for a difference in discrimination threshold between low- and high-contrast stimuli. Other studies found a difference in discrimination threshold at slow speeds, and a non-significant difference for a reference speed equal to 8 deg s^{-1} or higher (Champion & Warren 2017; Stocker & Simoncelli 2006). In accordance with that, for the same reference speed we failed to reject the null hypothesis that the reliability of the response was the same between the two contrast conditions (experiment 1, 3–5). Nevertheless, we found a perceptual bias, such as low-contrast stimuli were perceived as slower than high-contrast stimuli when both were moving downward (experiment 2). As the model proposed in (Thompson, Brooks, & Hammett 2006), also the Bayesian model does not predict the effect of motion direction, and interaction between motion direction and contrast.

In alternative to the previous models, we advanced the hypothesis that the observed biases in visual speed depend on prior assumptions on scene dynamics. Prior expectations about object dynamics play an important role in perceptual judgements (Battaglia, Hamrick, & Tenenbaum 2013; La Scaleia et al. 2014; Ceccarelli et al. 2018). Accordingly, we suggest that the two visual features of direction and contrast would change the internal representation of the implied gravity and the perceived medium, respectively (Fig.4 and Supplementary Materials). We hypothesised the existence of a prior for downward motion, because on Earth this motion component is more likely, due to gravity. A ball will

move much faster in free fall than when rolling on a plane, and the observer may account for that by changing her expectation on object speed accordingly. In addition to that, downward direction may be over-represented in the retina for the combined effects of optic flow and the unbalanced distribution of objects between lower and upper visual field during self-motion through natural scenes (Calow, Kruger, Worgotter, & Lappe, 2004)**. The downward bias may depend on a combination of retinotopic and world-centred environmental statistics. In both cases, in the Bayesian account for perception, the mean of the prior would change depending on motion direction, generating the perceptual bias. This is illustrated in Fig. 4 where the prior mean changed between reference (downward motion) and comparison (rightward), biasing the perceived difference between the two.**

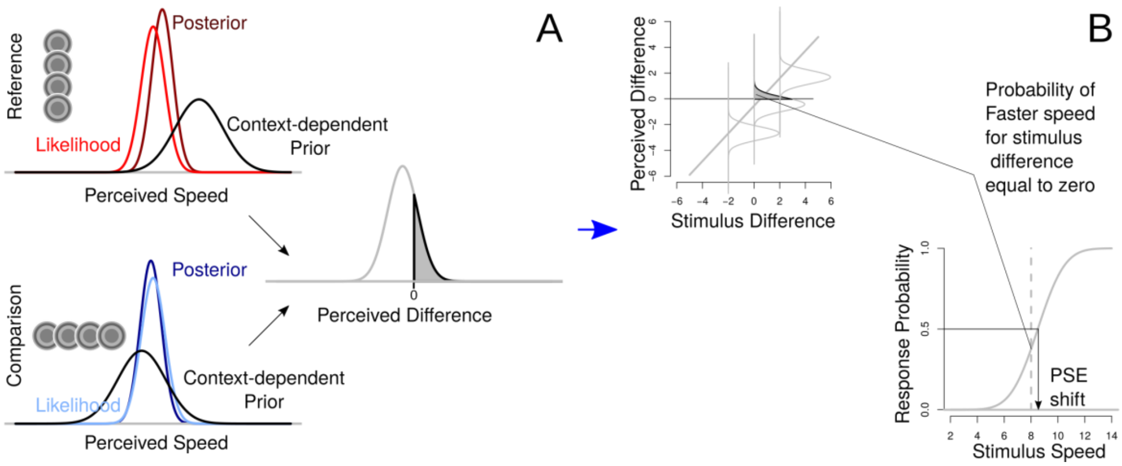
In experiment 1 and 3, we changed the luminance contrast across trials: If sensory noise were higher at lower contrast, the effect of the putative downward prior would be relatively stronger for this condition. Unexpectedly, we found the opposite, with the effect being stronger for the higher contrast condition. Even assuming that our experiment failed to detect a difference in sensory noise between the two contrast conditions, this latter result could not be easily explained if contrast only affected the variance of the two distributions.

Instead, we hypothesise that luminance contrast may change the internal representation of the medium (e.g., air or water). The medium affects the visual appearance and the motion dynamics of immersed objects—as we experience in familiar situations. In natural environments, contrast is lower when objects are underwater than in air, as a consequence of the light scattering by particles in water (Jonasz & Fournier, 2007)**. Human observers take into account the effect of contrast attenuation due to particles in water in perceptual judgements. Due to water droplets in air, which is even augmented in fog, objects having lower luminance contrast are perceived as farther in space (O'Shea, Blackburn, & Ono 1994; Pretto et al. 2012). Observers consider the effects of a water medium on the deformation in shape of an object** (Dövencioglu, van Doorn, Koenderink, & Doerschner, 2018)**, and take into account buoyancy to estimate object motion** (Castillo, Waltzer, & Kloos, 2017; Masin & Rispoli, 2010)**. For example, when we drop a lump of sugar**

into a cup of tea or a pebble in an aquarium, we expect that it will move slower in the aqueous medium than when mid-air.

A prior assumption that low contrast stimuli are moving in an aqueous medium, having higher viscosity than air, may explain the underestimation of their motion speed reported in previous studies. The implied buoyancy may account for the observed interaction between contrast and motion orientation with respect to gravity. If so, the putative effect of gravity would be partially compensated by the implied buoyant force and viscosity, that is, the observer may assume that, at lower contrasts, a downward moving target is "sinking" rather than "falling".

To demonstrate the feasibility of our approach, we provide in the supplementary information the model equations and the fit to the data. Albeit speculative at the present stage, our model is potentially appealing because it may explain two seemingly unrelated motion illusions in a unified framework. As other Bayesian models, it postulates the existence of a latent distributions (i.e., the prior and the likelihood distributions) that we can characterise only indirectly. The proposed model has three degrees of freedom accounting for the change in the prior mean across the experiments. To partially constrain the choice of the parameters, we linked them to natural environment statistics. For our reasoning, it is not relevant whether contrast would also affect sensory noise—in case, this would require an additional free parameter for the likelihood variance. In future work, it will be possible to test the predictions of our model, specifically with respect to expectations about multisensory properties of gravity and of a body immersed in a fluid.



The Bayesian observer model accounting for participant's behaviour. A) The perceived speed arose from the combination of sensory measurements (Likelihood) and prior expectations on object's motion (Prior). The representation of object's dynamics, e.g. due to the implied gravity in the figure, produced a shift on the mean of the prior. B) We related the probability distributions in the left panel to the psychometric functions by posing $P(Y = 1) = P(Perceived\ Difference > 0)$, *as illustrated in Supplementary Materials.*

Conclusions

We presented an unexpected phenomenon in speed perception that we explained by postulating that the observer updates the motion prior based on critical features of the visual target. We assumed that prior knowledge does not affect velocity *per se*, but the implied dynamics causing motion. This assumption is in accordance with previous studies showing that constant velocity is not perceived as such (Runeson 1974), and that the trajectory affects the perceived motion profile of a target (La Scaleia et al. 2014). To a broader extent, our findings revealed an unexpected interaction between visual features of the stimulus, which partially mirrors the relationship between physical properties of the World.

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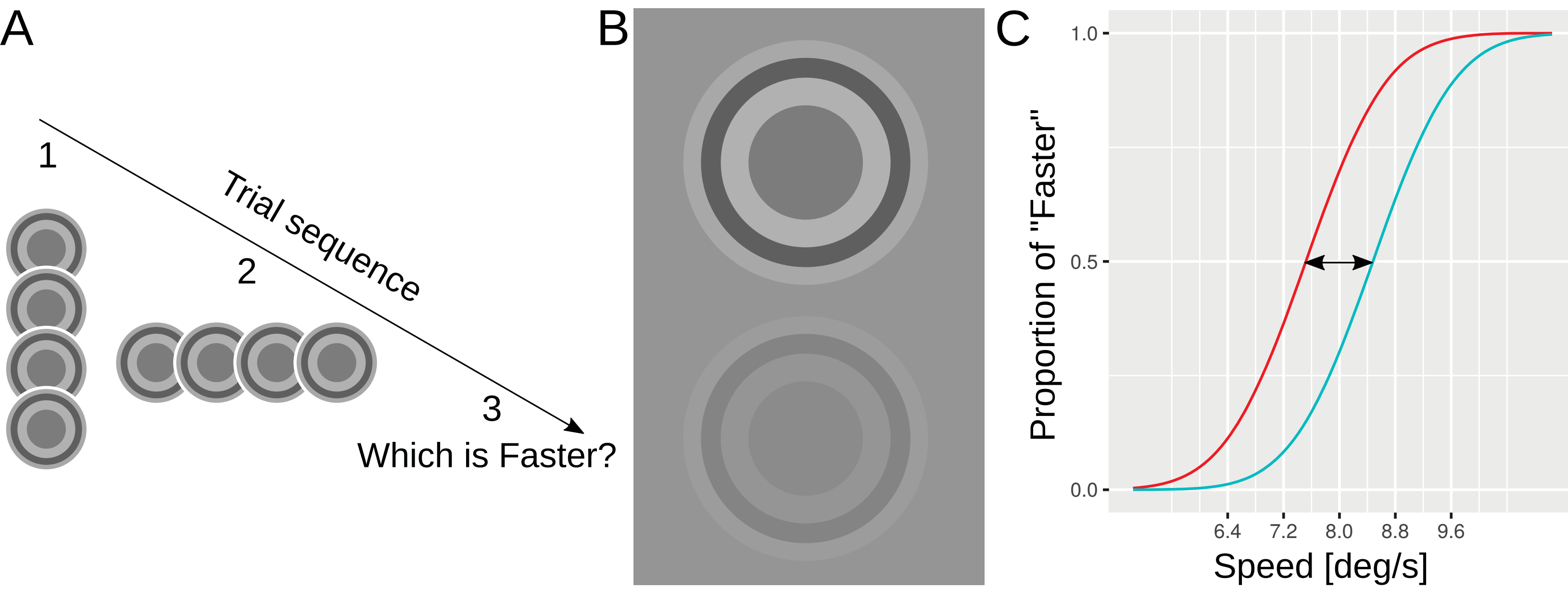
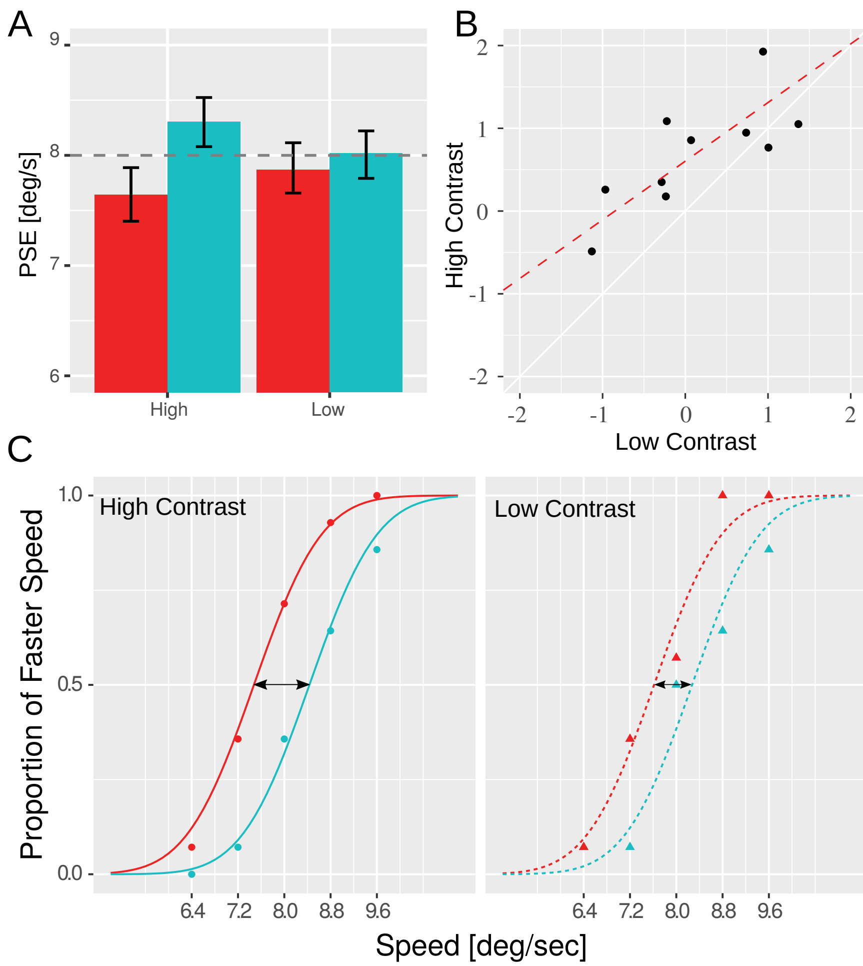
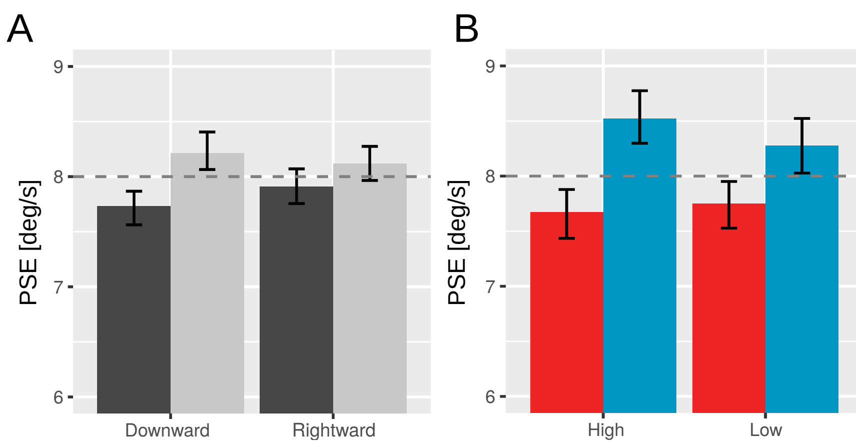


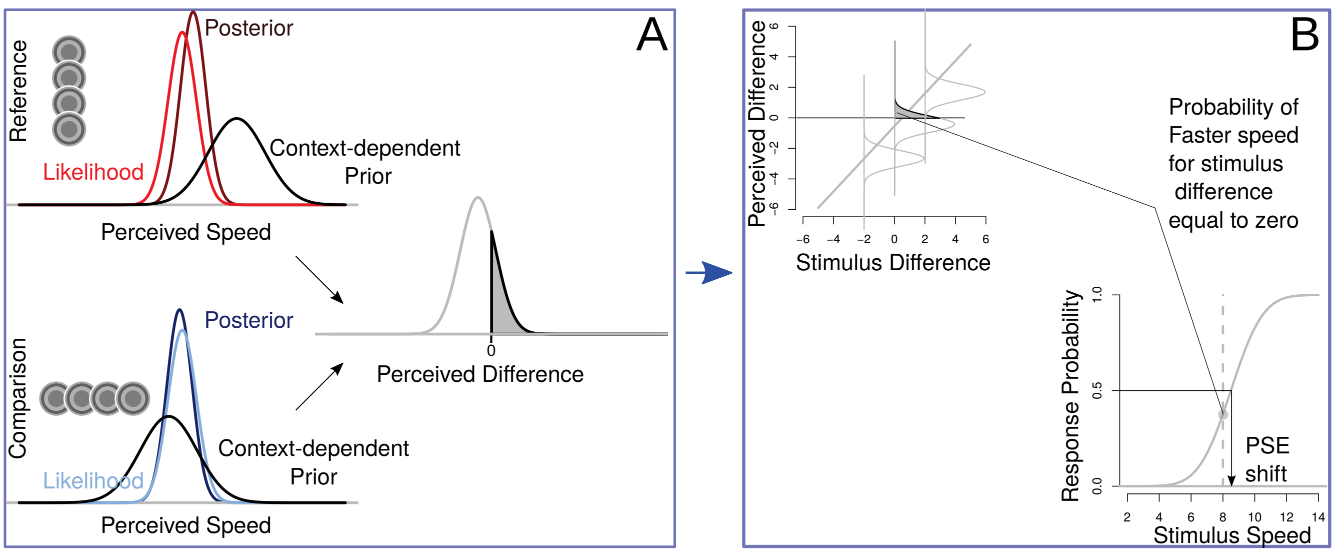
A
1
Trial sequence
2
3
Which is Faster?
B
C
1.0
0.5
0.0
Proportion of "Faster"
6.4
7.2
8.0
8.8
9.6
Speed [deg/s]



A
B
C
9
8
7
6
PSE [deg/s]
High
Low
2
1
0
-1
-2
High Contrast
Low Contrast
1.0
0.5
0.0
Proportion of Faster Speed
High Contrast
Low Contrast
6.4
7.2
8.0
8.8
9.6
Speed [deg/sec]



A
B
PSE [deg/s]
9
8
7
6
Downward
Rightward
High
Low



A
Reference
Posterior
Likelihood
Context-dependent
Prior
Perceived Speed
0
Perceived Difference
Comparison
Posterior
Likelihood
Context-dependent
Prior
Perceived Speed
B
Perceived Difference
Stimulus Difference
Probability of
Faster speed
for stimulus
difference
equal to zero
Response Probability
PSE
shift
Stimulus Speed