Vision Research 187 (2021) 85–93

Contents lists available at ScienceDirect

Vision Research

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

The magnitude of monocular light attenuation required to elicit the Pulfrich illusion

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ARTICLE INFO

Keywords:
Anisocoria
Binocular disparity
Depth
Pupil
Retinal Illuminance
Transmission latencies

ABSTRACT

In the Pulfrich illusion, the depth of a moving object is misperceived due to induced retinal disparity and/or interocular velocity differences arising from differences in luminance, contrast, or spatial frequency between the two eyes. These effects have been shown to occur both for visual deficits and for optical corrections that introduce significant binocular differences between the retinal images. However, it remains unknown to what extent the illusion might arise given normal variation between the eyes, such as natural interocular variation in pupil diameter (anisocoria). To assess this, we examined the threshold interocular retinal illuminance difference required to experience illusory depth in two random-dot fields moving in opposite directions in 24 normally-sighted observers with dilated pupils. Interocular difference in retinal illuminance was induced by placing neutral density filters of different intensities before the left eye. A minority of subjects ($n = 8$) did not provide meaningful data on changes in the experience of illusory depth with interocular difference in retinal illuminance and four subjects showed biases $>\pm 10\%$ from the 50% point of subjective equality in the psychometric function. For the remaining 12 participants, the retinal illuminance had to differ by approximately 40% for the depth between the planes to become visible at threshold levels. This difference was approximately constant over a range of absolute luminance levels from 10 to 80 cd/m^2. Our results suggest that while motion-in-depth illusions due to interocular differences in retinal illuminance may be pronounced in certain ophthalmic diseases or following certain optical interventions, it is unlikely to be manifest as a result of normal interocular variations in retinal illuminance. Further, our results also point towards the existence of substantial individual differences in the experience of what is otherwise thought of as a readily appreciable motion-in-depth illusion.

1. Introduction

The Pulfrich motion-in-depth illusion is typically observed by creating an interocular difference in retinal illuminance while watching a pendulum swing in the frontoparallel plane or by using computer generated stimuli whose luminance/contrast to one eye is manipulated relative to the other with neutral density filters (NDF) (Burge, Rodriguez-Lopez, & Dorronsoro, 2019; Howard & Rogers, 2002; Lit, 1960; Min, Reynaud, & Hess, 2020; Mojon, Rosler, & Oetliker, 1998; Petzold & Pitz, 2009; Stadelmann, Jiang, & Mojon, 2009). This illusion has also been shown to occur spontaneously in individuals with ocular disease such as unilateral media opacity (Scotcher, Laidlaw, Canning, Weal, & Harrad, 1997), retinal and neuro-ophthalmic pathology (Reynaud & Hess, 2019; Heng & Dutton, 2011; Heron, Thompson, & Dutton, 2007; O'Doherty & Flitcroft, 2009; Wist, Hennerici, & Dichgans, 1978), amblyopia (Wu, 2020) or following optical correction strategies such as monovision for presbyopia (Burge et al., 2019; Plainis et al., 2012, 2013; Read, 2019). In most of these scenarios, the illusory depth is thought to arise from binocular disparities that arise from a delay in information transmission from the eye experiencing the reduced illuminance to the

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https://doi.org/10.1016/j.visres.2021.06.008
Received 24 August 2020; Received in revised form 17 June 2021; Accepted 19 June 2021

visual cortex, relative to the fellow eye (Emerson & Pesta, 1992; Lit, 1960; Read & Cumming, 2005) or from interocular velocity differences arising from the differences in retinal illuminance in the two eyes (Fernandez & Farell, 2005; Shioiri, Saisho, & Yaguchi, 2000; Wu et al., 2020) (see, however Lages, Mamassian, & Graf (2003)).

While exact formulae relating the extent of illusory depth perceived with the intensity of the interocular difference in retinal illuminance, target velocity, viewing distance, etc, have been developed (Lit & Hyman, 1951; Lit, 1949, 1960; Weale, 1954), surprisingly, it remains uncertain how large the interocular differences need to be to reliably experience the illusion. Thus, the extent to which the illusion might arise given the optical and physiological variations between the two eyes in normally sighted observers remains unknown. Since retinal illuminance is a product of the target luminance and pupil area, both factors are likely to influence the experience of this illusion in real life. Interocular differences in retinal illuminance may arise either because of differences in the size of the two pupils (anisocoria) or because of differences in transmittance of light through the optical elements of the two eyes (e.g. differential light scattering due to different grades of cataract in the two eyes). An anisocoria of up to 1 mm is considered physiological (Steck, Kong, McCray, Quan & Davey, 2018), and, for an average pupil diameter of 3 mm and photopic target luminance of 50 cd/m^2, this magnitude of anisocoria can result in interocular differences in retinal illuminance of as large as 270Trolands (Td). For the same anisocoria, the interocular difference in retinal illuminance would also scale with target luminance and mean pupil diameter. Would such a physiological anisocoria, for instance, lead to the experience of the Pulfrich-type motion in depth illusion?

Previous studies have demonstrated a reliable perception of illusory depth using NDFs with a wide range of different optical densities (typically $\geq$ 0.1log unit that causes a luminance attenuation of $\geq$ 12%) before one eye. (Brauner & Lit, 1976; Burge et al., 2019; Lit & Hyman, 1951; Lit, 1960; Reynaud & Hess, 2017; Rodriguez-Lopez, Dorronsoro, & Burge, 2020) However, the minimum value of NDF and, therefore, the minimum interocular difference in retinal illuminance needed for this illusion to reach detection thresholds is not readily available in the literature. It is also uncertain how this threshold value might depend on the absolute levels of retinal illumination. Here, we addressed these questions to provide insights into the extent to which illusory misperceptions of motion-in-depth might arise within normal variations in vision, or is it a perceptual phenomenon specific to exaggerated conditions of ophthalmic pathology or optical interventions (Heron et al., 2007; Lit, 1949; Mojon et al., 1998; O'Doherty & Flitcroft, 2009; Plainis et al., 2013; Wist et al., 1978; Wu, 2020). In turn, these results provide insights into how sensitive the illusion might be as a test of visual pathology.

2. Methods

2.1. Participants

A total of 24 visually normal adults [18 females and 6males; mean ($\pm$1SD) age of 23 $\pm$ 3yrs], naïve to the Pulfrich phenomenon and the present study protocol, were recruited for this study from amongst the staff and students of the L V Prasad Eye Institute (LVPEI), Hyderabad, India. The study adhered to the tenets of the Declaration of Helsinki and was approved by the Institute Research Board of LVPEI. Participation was with written informed consent. A comprehensive eye examination revealed that all participants were free of any sensory and motor ocular pathology and had best-corrected high-contrast acuity of 20/20 or better and stereoacuity of 40arc sec or better.

3. Stimulus

The stimuli for eliciting the Pulfrich-type motion-in-depth illusion was generated on an Apple iMac LCD monitor (1680 × 1050 pixels resolution) using custom-written Matlab® (R2014a, The MathWorks, Natick, MA) routines on the Psychtoolbox® PTB-3 interface (Brainard, 1997). The display screen had a uniform gray background and was virtually bisected into two hemifields, with the upper hemifield consisting of black dots (dot density = 4dots/cm^2; dot size = 10pixels; 0.07° at 80 cm viewing distance) moving from left end to right end of the monitor at a speed of 90pixels/sec and the lower hemifield consisting of the similar dots moving in the opposite direction (i.e., from right end to left end of the monitor) at the same speed (Fig. 1). The direction of motion of the dots was not randomized between the two hemifields across trials. For a monitor resolution of 38pixels/cm, the dot speed translated into a linear velocity of 2.4 cm/sec and an angular velocity of 1.71°/sec. Subjects viewed this stimulus with their best refractive error correction, if any, from 80 cm (Fig. 1). Nine Kodak Wratten NDFs (Edmund Optics, Singapore) from 0.1 to 0.9log units of optical density in 0.1log unit steps (producing 12% to 79% of light attenuation (Zhang, Gentile, Migdall, & Datla, 1997) were placed before the left eye in a custom-designed circular turret that could be manually rotated to dial-in the desired filter intensity during each trial to induce the motion-in-depth illusion (Fig. 1). This NDF set-up was mounted ~ 4 cm before the subject's left eye such that this eye always viewed the stimulus through one filter or another while the right eye's view remains unfiltered (Fig. 1). The size of the NDF in the turret offered a visual angle of ~ 29°, ensuring that the entire computer monitor was visible to that eye (Fig. 1). One of the slots in the circular turret contained a transparent sheet representing no light attenuation to the left eye.

Since retinal illuminance (in Td) is a product of the monitor luminance (in cd/m^2) and pupil area (in mm^2), a change in either of these parameters would influence the retinal illuminance in an uncontrolled fashion. Therefore, to avoid the interplay between pupil size and monitor luminance, the pupils of both eyes were dilated and kept fixed at ~ 7 mm using 0.5% Tropicamide eye drops. Retinal illuminance was primarily varied by altering the monitor luminance, either by adjusting its display or by using varying intensities of NDFs. The pupil diameters were verified to be within $\pm$ 0.5 mm of the 7 mm value in a sample of subjects using a custom-designed infrared camera with built-in pupil size determining algorithms (Bharadwaj et al., 2013). No artificial pupils were used here to control pupil size as a pilot study indicated subjects having difficulty in binocular fusion and experiencing discomfort due to visual field restriction when these apertures were placed on a trial frame at ~ 14 mm vertex distance, in addition to their spectacle correction, if any.

3.1. Procedure

The interocular difference in retinal illuminance required to elicit a threshold-level motion-in-depth illusion was determined using a method of constant stimuli psychophysical procedure. On each trial, a given intensity of NDF was randomly chosen by the computer algorithm and was manually dialled-in before the subject's left eye by rotating the NDF turret (Fig. 1). Before the start of each trial, subjects binocularly fixated on a black cross at the center of the monitor. The start of each trial was cued by an auditory pulse. This cross disappeared when the trial was initiated. Subjects provided a two-alternate forced choice response of which hemifield of dots – upper or lower – appeared in front of the other, i.e., which one of the two planes appeared closer to the observer than the other. The illusion of motion-in-depth is experienced because the eye with the reduced retinal illuminance perceives targets with a temporal delay, relative to the fellow eye (Emerson & Pesta, 1992; Lit, 1960; Read & Cumming, 2005). For the present task, when the NDF is placed before the left eye, the movement of the dots from the right end to left end in the lower hemifield of the monitor creates a crossed disparity and movement of dots in the opposite direction in the upper hemifield of the monitor creates an uncrossed disparity. This will make the lower hemifield of dots appear closer than the upper hemifield of dots (Fig. 1). Each of the 9 NDF's and the no-filter catch trials were tested 10 times in

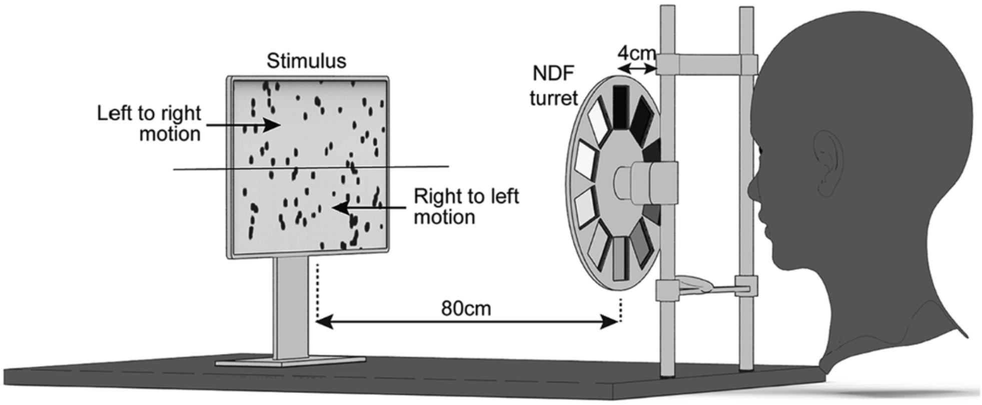

Fig. 1. The experimental set up.

random order, totalling 100 trials for each subject and absolute luminance level. For catch trials (i.e., when the left eye did not have any NDF before it), the frequency of seeing one hemifield of dots closer than the other hemifield is expected to be at 50% chance level. For trials with a NDF before the left eye, it is expected that the percentage of times the lower hemifield of dots would appear closer than the upper hemifield would systematically increase from chance level towards 100% with an increase in the NDF intensity.

The resultant psychometric function was then fit with a cumulative Gaussian distribution function (Eq. (1)), where f(x) was the frequency of perceiving the lower hemifield of dots closer than the upper hemifield of dots as predicted by the fit, x was the range of NDF's used in this study and μ and σ were the mean and standard deviation of the Gaussian distribution, respectively. The mean and variance were kept as free parameters and optimized to fit the data using the fminsearch function in MATLAB based on the maximum likelihood based Nelder-Mead simplex method. Three outcome variables were obtained from this fit (Fig. 2). First, the subjective bias in seeing one hemifield of dots more frequently closer than the other hemifield in the catch trials and the NDF value that was required to eliminate this bias (Fig. 2). The former was obtained from the y-intercept of the psychometric fit and the latter was obtained as the NDF value that corresponded to the point of subjective equality (PSE) of the psychometric function. The NDF value at PSE was obtained by re-arranging Eq. *(2)* to Eq. *(3)*, where the value of 0.5 corresponded to the 50% point in the ordinate scale of the psychometric function. Ideally, the subjective bias should be zero (i.e., one hemifield of dots should appear closer than the other with equal frequency in the catch trials) and the PSE of the psychometric function should be at 50%, corresponding to an NDF value of zero optical density (Fig. 2). Second, the NDF value before the left eye that led to illusory depth exceeding detection of 76% in the psychometric function. This value was calculated using *Eq. (3)*, using the same logic as Eq. *(2)*. The difference in the NDF values from the PSE to the 76% point in the psychometric function was deemed as the threshold NDF required to experience the illusory

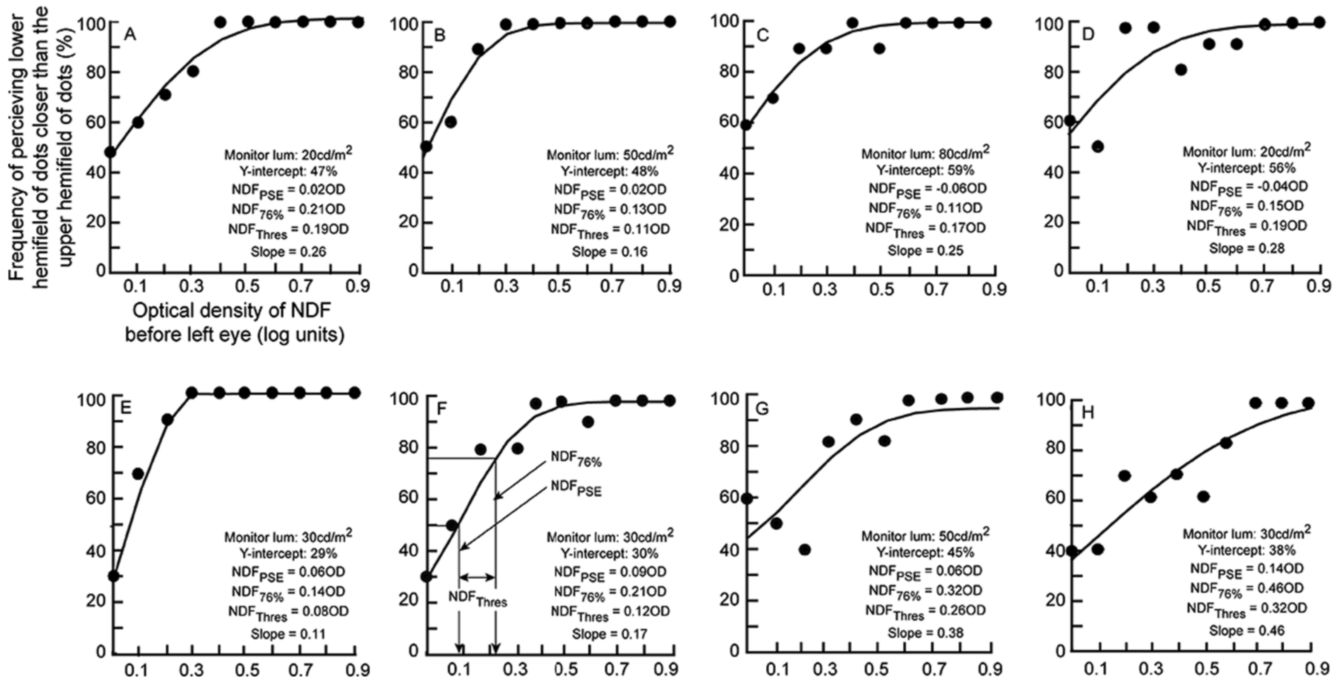

Fig. 2. Psychometric functions from eight subjects across different monitor luminances, illustrating different degrees of bias [Y-intercept and point of subjective equality (PSE)], NDF at PSE (NDF_{PSE}), NDF at 76% point of the psychometric function ($NDF_{76\%}$), threshold NDF (NDF_{Thres}) and slope values. Panels A and B show data of two subjects who did not show any bias, Panels C and D show data of two other subjects that show bias in favour of the lower hemifield of dots appearing closer than the upper hemifields in the catch trials and Panels E – H show psychometric functions from four other subjects with a bias towards the upper hemifields of dots appearing closer than the lower hemifields in catch trials. In panels E – H, subjects are arranged in order of steepest to flattest slopes of the psychometric fit.

depth in this study. For instances where there was no bias in the psychometric function, Y-intercept of this function will be at 50% and the NDF at PSE would be at zero optical density (Fig. 2A and B). The threshold NDF would therefore be equal to the NDF value corresponding to the 76% point in the psychometric function (Fig. 2A and B). For instances with a bias in favour of the lower hemifield of dots appearing closer than the upper hemifield of dots in the catch trials, the Y-intercept of the psychometric function will be > 50% and PSE will be a negative value, as if, the NDF had to be placed before the right eye to reach PSE (Fig. 2C and D). In reality, no NDF's were placed before the right eye during the experiment. The threshold NDF for experiencing illusory depth would therefore be the range from the negative NDF value at PSE to the NDF value at the 76% point in the psychometric function (Fig. 2C and D). For instances with a bias in favour of the upper hemifield of dots appearing closer than the lower hemifield of dots in the catch trials, the Y-intercept of the psychometric function will be < 50% and PSE will be a positive non-zero value of NDF (Fig. 2E – H). The threshold NDF for experiencing illusory depth would therefore range from this positive value of PSE to the NDF value at the 76% point in the psychometric function (Fig. 2E – H). This procedure ensured that the threshold NDF values reported in this study were corrected for any subjective bias occurring in the psychometric function. Third, the slope of the psychometric function as a measure of task precision. Steeper slopes of the psychometric function corresponded to greater task precision than shallower slopes.

$$f(x) = 0.5 \times [1 + \mathrm{erf}((x - \mu)/(\sigma \times \sqrt{2}))] \tag{1}$$

$$\mathrm{NDF}_{pse} = \sqrt{2} \times (\mu/\sigma) \times \mathrm{erfinv}(2 \times (0.5 - 1)) \tag{2}$$

$$\mathrm{NDF}_{Threshold} = \sqrt{2} \times (\mu/\sigma) \times erfinv(2 \times (0.76 - 1)) \tag{3}$$

To calculate the retinal illuminance incident on each eye, the monitor luminance was multiplied by the pupil area corresponding to 7 mm diameter (pupil area = 38.5 mm^2). The effective monitor luminance incident on the left eye was calculated by multiplying the monitor luminance against the percentage attenuation created by the threshold NDF intensity (e.g., for 30 cd/m^2 monitor luminance and a threshold NDF of 0.2log unit intensity that has a light transmission of 63%, the monitor luminance impinging on the left eye was 18.9 cd/m^2). Since there was no filter before the right eye, the monitor luminance was considered as is. The interocular difference in retinal illuminance was calculated as the arithmetic difference in retinal illuminance between the right and the left eye. Weber's constant was calculated for each subject and each monitor luminance by dividing this interocular difference in retinal illuminance by the retinal illuminance reaching the right eye without the filter.

This experiment was performed on each subject at five different monitor luminances (10, 20, 30, 50 and 80 cd/m^2) to derive the Weber's constant for perceiving the illusory depth. The different luminances were verified using a photometer before each session. For a constant 7 mm pupil diameter, these monitor luminances translated into baseline retinal illuminance of 384Td, 769Td, 1153Td, 1923Td and 3077Td, respectively. Each trial took no more than a few seconds for the subject to respond and therefore the NDF's were placed only transiently before the subject's left eye. This, combined with the random order of NDF placement before the eye, avoided any retinal light adaptation that may adversely influence the results shown here.

Data analyses were performed with MATLAB® R2014a, Microsoft Office Excel® 2007and SPSS® v16 (SPSS Inc., Chicago, IL). The Kolmogorov-Smirnov test indicated that the outcome measures were not normally distributed. Therefore, non-parametric statistics were used to analyze the data. The Friedman test, the non-parametric alternative to one-way repeated measures ANOVA, was used to determine the overall statistical significance of the outcome variables across the five different monitor luminances. The Wilcoxon signed rank test with Bonferroni correction was used for pairwise comparison between the groups, wherever necessary. $P \leq 0.05$ was considered statistically significant. Significance values were adjusted by the Bonferroni correction for multiple tests.

4. Results

Of the 24 subjects that participated in the study, only 16 perceived the illusory depth (~67%). The remaining 8 subjects either did not perceive depth between the upper and lower hemifields even with the highest NDF ($n = 4$) or they perceived depth even without any NDF before their eyes ($n = 4$). In either scenario, the psychometric function could therefore not yield a meaningful threshold value. All these subjects were excluded from further analyses.

Fig. 2 shows psychometric functions obtained from eight subjects for different monitor luminances to illustrate different magnitudes of bias, threshold NDF's and slopes obtained in this study. Panels A and B represent psychometric functions of two subjects who did not show any bias, as indicated by the Y-intercept of the psychometric fit at the 50% mark and the NDF's at PSE being very close to zero optical density (Fig. 2A and B). Panels C and D show psychometric functions from two other subjects that show bias in favour of the lower hemifield of dots appearing closer than the upper hemifields in the catch trials. The Y-intercepts of their psychometric fits were above the 50% mark and the NDF at PSE were negative values (Fig. 2C and D). Panels E – H show psychometric functions from four other subjects with a bias towards the upper hemifields of dots appearing closer than the lower hemifields in catch trials, as indicated by the Y-intercepts of their psychometric fits being lower than the 50% NDF mark. The NDF at PSE for these subjects were positive values, indicating that a certain optical density of NDF was required before the left eye to neutralize the bias (Fig. 2E – H). These subjects exhibited different slope values of the psychometric fit, indicating different levels of task precision. Seeing the upper hemifield of dots closer than the lower hemifield in catch trials was the most prominent bias direction seen amongst subjects in this study (Fig. 2E–H).

Fig. 3 shows Box and Whisker plots of the bias observed in the psychometric functions (panel A) and the NDF values needed to eliminate this bias (i.e., NDF's at PSE; panel B) across the five different monitor luminances tested in this study. The median (25th – 75th interquartile range) bias was 43% (40 – 45%) and the median NDF at PSE needed to eliminate this bias was 0.05log units (0.02 – 0.12log units), with no statistically significant differences across monitor luminances [bias: $\chi^2(2) = 3.08$, $p = 0.54$; NDF at PSE: $\chi^2(2) = 4.86$, $p = 0.30$]. As can be seen from Fig. 3, the psychometric functions of some subjects exhibited a strong bias in one direction or the other, for one or more monitor luminances tested here. To eliminate the impact of such subjects on the final calculation of the outcome variables of this study, all subjects with bias values > 60% and < 40% (i.e., greater than ± 10% from the no bias level) for 3 or more monitor luminances were identified and removed from further analysis. These subjects essentially represented the outliers in Fig. 3A and they did not impact the bias and NDF at PSE values reported in Fig. 3. This strategy led to the exclusion of 4 subjects from the final analysis – thus, data from a total of 12 subjects were finally used for calculation of the NDF values required to reach detection thresholds of experiencing illusory depth in this study.

Fig. 4A – C show the threshold NDF before the left eye that led to illusory depth exceeding detection threshold (panel A), the corresponding retinal illuminance of that eye for a constant 7 mm pupil diameter (panel B) and the calculated interocular difference in retinal illuminance (panel C) for the five different monitor luminances used in this study. While there was no statistically significant difference in the threshold NDF value required before the left eye for experiencing illusory depth across the five monitor luminances [$\chi^2(2) = 0.74$, $p = 0.94$] (Fig. 4A), the NDF values did reflect a progressive increase in the attenuation of retinal illuminance in the left eye needed for the illusory depth to reach detectable levels (Fig. 4B). The retinal illuminance in the

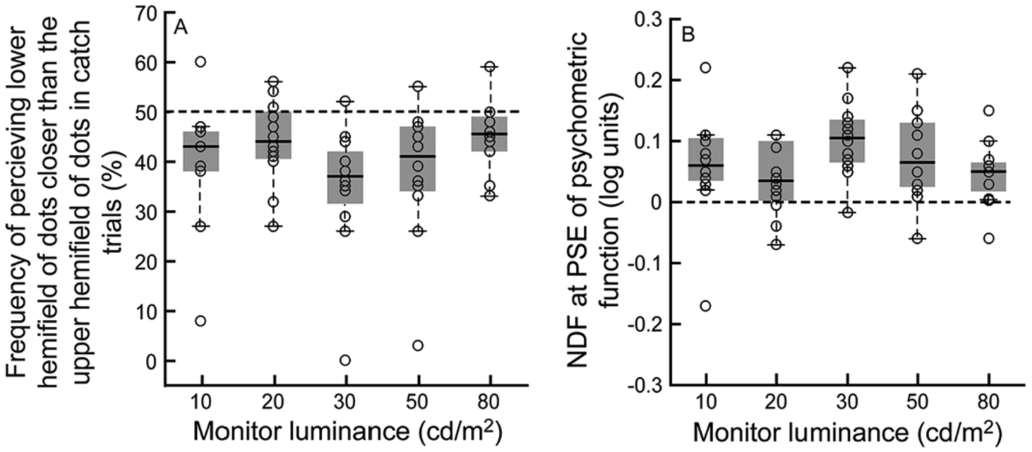

Fig. 3. Box and Whisker plots showing the bias in the psychometric functions (panel A) and the NDF needed to eliminate this bias (i.e., NDF's at PSE; panel B) across monitor luminances tested in this study. The solid black line within each box shows the median value, the lower and upper boundaries of the shaded box show the 25th and 75th quartiles and the error bars indicate the 1st and 99th quartile for that luminance. Individual data points are shown as circles and outliers are indicated as plus symbols. For panels A and B, an ordinate value of 50% and NDF at PSE of zero optical density indicate no bias, respectively. Ordinate values < 50% in panel A and positive values in panel B indicate bias in favour of seeing the upper hemifield of dots closer than the lower field of dots in the catch trials. Ordinate values > 50% in panel A and negative values in panel B indicate the opposite.

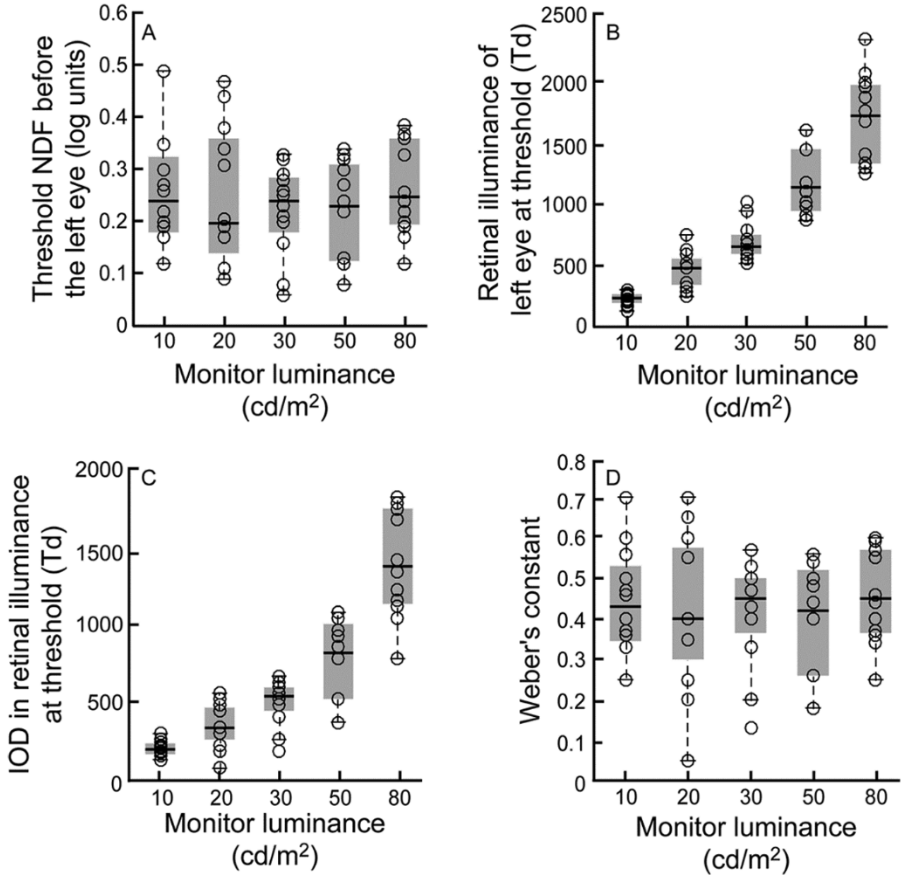

Fig. 4. Box and Whisker plot showing the distribution of the threshold NDF before the left eye that led to illusory depth exceeding the detection thresholds (panel A), the corresponding retinal illuminance in the left eye at threshold (panel B), interocular difference in retinal illuminance (IOD) at threshold (panel C) and the Weber's constants (panel D) across for the five monitor luminances tested in this study. Details of box and whisker plots are same as Fig. 3.

left eye required to experience the illusion was overall statistically significantly different across monitor luminances tested [$\chi^2(2) = 47.04$, $p > 0.001$] (Fig. 4B). Post-hoc analysis showed significant differences across each pair of monitor luminance ($p < 0.001$). The calculated interocular difference in retinal illuminance that led to illusion exceeding detection threshold also increased significantly with monitor luminance [$\chi^2(2) = 57.3$, $p = 0.001$], with post-hoc analyses showing significant differences across all pairwise comparisons ($p < 0.001$), except between 10 and 20 cd/m^2 ($p = 0.88$) (Fig. 4C).

A Spearman's correlation was run to determine if the subject's calculated interocular difference in retinal illuminance at threshold was significantly correlated across the give different monitor luminances tested here. The results indicated a strong statistically significant positive correlation of within-subject data between the 10 cd/m^2 and 30 cd/m^2 monitor luminances ($r = 0.70$, $p = 0.01$) and between 10 cd/m^2 and 50 cd/m^2 ($r = 0.64$, $p = 0.03$). None of the other correlations were statistically significant ($r \leq 0.25$, $p \geq 0.05$).

The median Weber's constants across the five-monitor luminance ranged from 0.40 to 0.45, without any significant trends between them (Fig. 4D). Since the monitor luminance and the pupil diameter was fixed in this study, the main source of intersubject variability in the Weber's constants shown in Fig. 4D was the underlying variability in the threshold interocular difference in retinal illuminance needed for perceiving the illusory depth.

The magnitude of interocular delay (Δt, in milliseconds) arising in the Pulfrich illusion can be ascertained from the magnitude of illusory depth experienced by the subject (D; in cm) for a given interocular difference in retinal illuminance, velocity of target motion (V, in cm/sec), target viewing distance (Vd, in cm) and the subject's interpupillary distance (IPD, in cm) (Eq. (4)) (Lit, 1949, 1960). For a given interocular difference in retinal illuminance, the value of D will be greater when the target appears to move behind the fronto-parallel plane than when it is moving in front of the fronto-parallel plane due to the fundamental properties of space projection (Lit, 1949, 1960). This difference in value of D is however small and ignored in the present study. In the present study, D therefore represents the illusory depth of targets perceived in front of the fronto-parallel plane.

The interocular delay experienced by the visual system at the threshold value of interocular difference in retinal illuminance was obtained using Eq. (4). Since the value of D was not empirically measured in this study, this information was derived from the relation between the perceived depth (D) and interocular difference in retinal illuminance for three different NDF's in Lit (Lit, 1960) (see Table 2 in that paper) (Lit, 1960). A linear regression equation was fit to the average data of the two subjects in Lit's study (Eq. (5)) and used here to calculate the value of D for threshold values of interocular difference in retinal illuminance for each subject and each monitor luminance. The target speed used in the aforementioned Lit study (2.59 cm/sec) was similar to the speed of 2.4 cm/sec used in the present study. D increased linearly with the interocular difference in retinal illuminance. Following this, Eq. (4) was used to calculate Δt (the interocular delay) for threshold values of interocular difference in retinal illuminance (IOD_{RI}), for a constant V of 2.4 cm/sec, Vd of 80 cm and IPD of 6.5 cm. The calculated transmission delay ranged from 12 to 15msec, with no significant differences across all monitor luminances [$\chi^2(2) = 2.36$, $p = 0.66$] (Fig. 5) (Lit & Hyman, 1951).

$$\Delta t = [IPD/V] \times [D/(Vd + D)] \tag{4}$$

$$D = 0.37 \times IOD_{RI} + 0.29 \; (r^2 = 0.91) \tag{5}$$

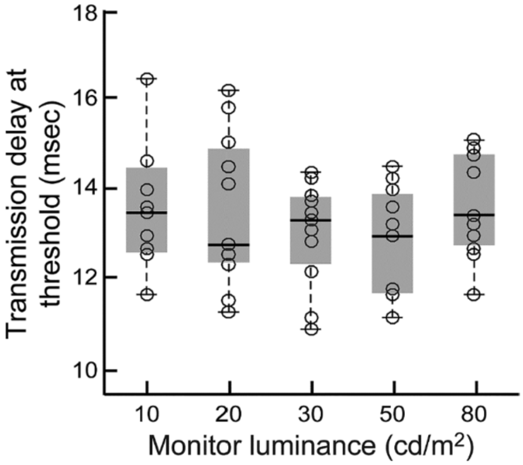

Fig. 5. Box and Whisker plot showing the distribution of the transmission delay arising from the interocular difference in retinal illuminance at which the illusory depth exceeded detection thresholds for different monitor luminances tested in this study. Details of box and whisker plots are same as Fig. 3.

A potential confounding factor for the results shown in this study (Figs. 3 – 5) is the lack of randomization in the direction of dot motion between the upper and lower hemifields of the stimuli on every trial in the experiment. The upper hemifield of dots always moved from left to right while the lower hemifield of dots always moved from right to left. Given the geometry of the Pulfrich illusion (Lit, 1960), dots moving from right to left (i.e., lower hemifield of dots) would appear closer than those moving in the opposite direction. Subjects might quickly notice this pattern during the experiment, adversely influencing the obtained results. To address this, confound, a control experiment was conducted on a subset of five subjects wherein the direction of dot motion was randomized between the upper and lower hemifields during the psychophysical experiment. Like the main experiment, subjects provided a two-alternate forced choice response of whether the upper or lower hemifield of dots appeared closer than the other. All other experimental paradigms and outcome variables were identical to the main experiment. This control experiment was conducted for the 30 cd/m^2 and 50 cd/m^2 monitor luminances. Table 1 shows the range of Y-intercept, NDF at PSE, threshold NDF and the slope of the psychometric functions obtained in these five subjects for the randomized and non-randomized test paradigms. The data varied idiosyncratically across subjects in the two paradigms, with none of the outcome variables showing any systematic differences between the two paradigms (e.g., lowered bias in the psychometric function with the randomized paradigm, vis-à-vis, the non-randomized paradigm) (Table 1). These results suggest that the non-randomization of dot motion in the main experiment did not have a strong influence on the results presented in this study.

5. Discussion

Pulfrich-like effects may represent an important misperception of depth in individuals with ocular pathology or when wearing optical corrections that introduce large interocular differences between the retinal images in the two eyes. In this study, we explored how likely these misperceptions might be in observers without evident visual deficits or differential corrections in their two eyes. Interocular variation could naturally arise from a number of subclinical factors including differences in refractive error, lens opacity, or pupil size, the latter two affecting the relative overall retinal illuminance. Our results suggest that the required luminance differences are likely too large to generate the illusion in natural viewing. At a median level, for the target speed of 2.4 cm/sec used in this study, the interocular difference had to be ~40 – 45% of the baseline retinal illuminance for most individuals to detect the illusion across the range of monitor luminances tested, indicating that considerable amount of monocular light attenuation is required for experiencing this type of motion-in-depth illusion (Fig. 4D). The retinal illuminance attenuation required to appreciate this illusion also scaled with the baseline retinal illuminance (Fig. 4C). Both the monitor luminance and pupil area are likely to influence the experience of this illusion in real life. This relationship is illustrated in Fig. 6 by plotting the interocular difference in retinal illuminance as a function of the interocular difference in pupil diameter (anisocoria) for different baseline pupil diameters and for different monitor luminances used in this study. Gray bands in each of this figure panels show the interquartile range of interocular difference in retinal illuminance empirically obtained in this study to elicit the illusion (Fig. 6). Combinations of baseline pupil diameters and anisocoria that are below the gray band for a given monitor luminance are unlikely to result in this illusion (i.e., small baseline pupil diameters with smaller magnitudes of anisocoria) while those combinations that are within or above these bands may result in this illusion (i.e., larger baseline pupil diameters with larger magnitudes of anisocoria) (Fig. 6). A minimum anisocoria of 2–3 mm is required before the threshold interocular difference in retinal illuminance is reached to perceive the illusion for any given monitor luminance (Fig. 6). Such levels of anisocoria typically signal an ophthalmic pathology (physiological anisocoria is ≤ 1 mm (Wilhelm, 2011), in which the Pulfrich

Table 1
Results of the control experiment. Range of Y-intercepts, NDF’s at PSE, threshold NDF’s and slopes of the psychometric function obtained for the randomized and non-randomized paradigms for the two monitor luminances.

Paradigm	Luminance (cd/m^2)	Intercept (%)	NDF at PSE (log units)	Threshold	Slope
Randomized	30	42 to 74	−0.03 to 0.04	0.14 to 0.38	0.20 to 0.54
	50	47 to 66	−0.05 to 0.02	0.11to 0.59	0.16 to 0.85
Non-randomized	30	32 to 68	−0.006 to 0.13	0.16 to 0.29	0.23 to 0.41
	50	43 to 67	−0.06 to 0.05	0.08 to 0.46	0.11 to 0.52

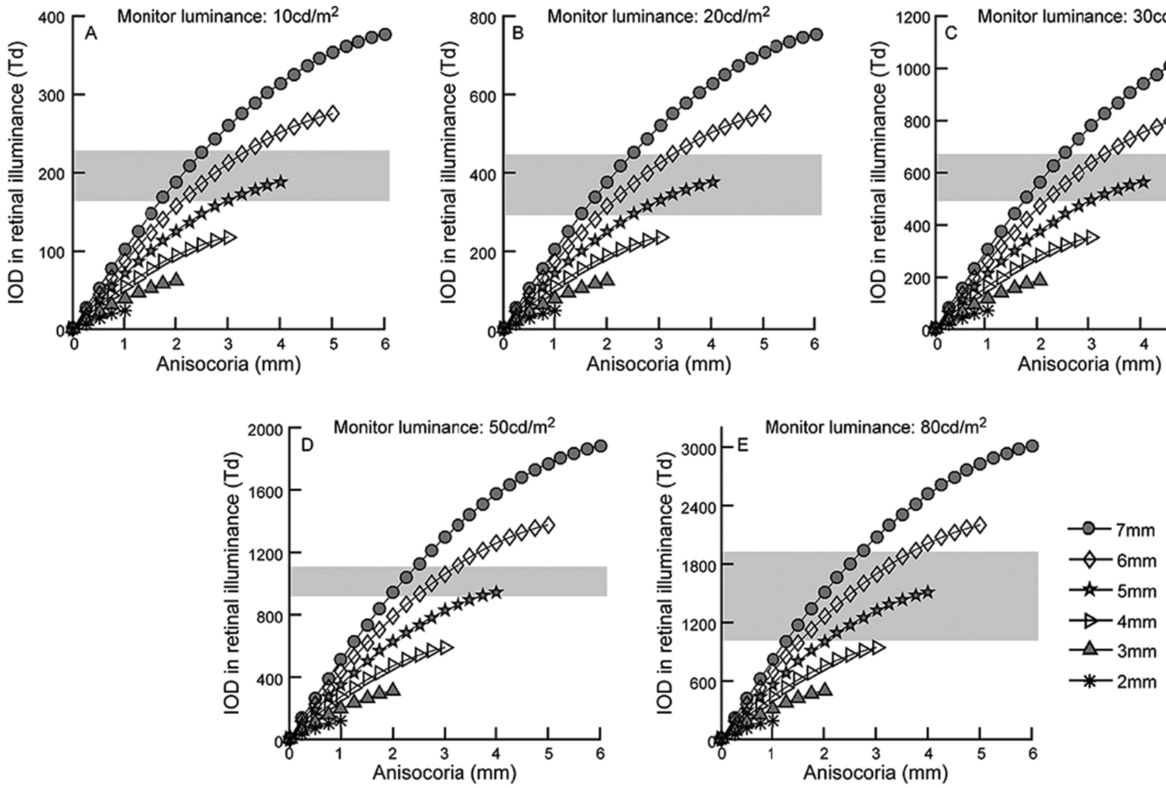

Fig. 6. Theoretical curves plotting the interocular difference (IOD) in retinal illuminance as a function of interocular difference in pupil diameter (anisocoria) for 7 to 2 mm baseline pupil diameters across monitor luminances tested in this study. The gray band in each panel shows the 25th to 75th interquartile range of IOD in retinal illuminance that was required to elicit the motion-in-depth illusion. The ordinate scale in each panel is made different for clarity of data trends.

illusion has been demonstrated previously (Plainis et al., 2012; Wist et al., 1978; Yang, Thompson, & Burns, 2002) and suggests the unlikeliness of experiencing such illusory motion-induced depth under normal physiological conditions and during activities of daily living (e.g. automobile driving (Breyer, 2006). The 7 mm pupil diameter achieved post dilation in this study are larger than habitual pupil sizes seen under natural viewing conditions (~3 – 4 mm) (Yang et al., 2002). For the same monitor luminance, smaller pupil diameters will result in lower retinal illuminance and, therefore, lower interocular difference in retinal illuminance to reach threshold levels for perceiving the Pulfrich illusion (Fig. 6). These values may however still be outside the range of interocular retinal illuminance differences experienced physiologically (Fig. 6) and, therefore, will not alter the study conclusions. Given this, our results suggest that the Pulfrich illusion may not provide a sensitive diagnostic measure of interocular differences in retinal illuminance.

All monitor luminances tested in this study were in the photopic range of light levels (Zele & Cao, 2014). The results of the present study will predict that the interocular difference in retinal illuminance needed to experience illusory depth will be much smaller for mesopic and scotopic levels, increasing the chances of normally sighted individuals with physiological anisocoria experiencing the Pulfrich illusion. This prediction however needs to be tested empirically. Similar analyses could also be performed to determine the level of media opacity in one eye (e.g. unilateral cataract) that would elicit this illusion to support previous empirical observations (Breyer, 2006; Mojon et al., 1998; Yang et al., 2002). However, quantification of media opacity and its impact on retinal illuminance is non-trivial, making this analysis presently untenable.

Our results also point to substantial individual differences in the experience of the Pulfrich illusion, an entity that is otherwise thought of as a readily appreciable motion-in-depth illusion (Howard & Rogers, 2002; Petzold & Pitz, 2009). One-third of our participants could not perform the task and four others showed a strong bias in the psychometric function in at least 3 of the 5 monitor luminances tested here. Only the remaining 12 subjects generated data that were used to derive the aforementioned conclusions. Such inter-subject variability has also been noted in other recent studies (Burge et al., 2019). None of the subjects that participated in the study were trained psychophysical observers and their naivety with the procedure could have reflected in the distribution of performance noted here. The Pulfrich illusion is typically demonstrated by placing a strong neutral density filter that significantly attenuates the retinal illuminance of one eye relative to the other. The experience of illusory motion-in-depth is quite obvious under such conditions. Contrary to this, our experiment was aimed at determining threshold level performance, wherein the experience of motion-in-depth illusion is bound to be subtle, thus challenging our subjects. Non-randomization of dot motion between the two hemifields across trials could have also made the task vulnerable to bias, thus affecting our subject's performance. This may however not be the case because the control experiment performed on 5 subjects with dot motion randomized between the two hemifields did not yield any systematically different results from the non-randomized paradigm (Table 1). The variation in subject's performance in the two paradigms was quite idiosyncratic. Other possibilities for the four subjects experiencing illusory depth even during the catch trials is the presence of subtle differences in the two eyes that remained unmanifest during clinical testing for study inclusion or the spontaneous experience of the Pulfrich illusion, such as those reported in previous literature (Reynaud & Hess, 2019; Heng & Dutton, 2011). Lastly, the inter-subject variability in the results observed here could also partly reflect the underlying sensitivity of the visual system to detect disparity and process stereo information or interocular velocity differences – subjects with higher detection thresholds in this experiment could have poorer disparity sensitivity and poorer stereoacuity or poorer velocity discrimination capabilities, relative to those with lower thresholds. While we screened for normal stereoacuity, we did not quantify disparity sensitivity or velocity discrimination, and how it might relate to sensitivity to the illusion. These would be valuable to address in future research. No specific explanation can be presently offered for the observed bias in majority of subjects in this study (Figs. 2 and 3). The experiment was run in an otherwise dark room with no other extraneous cues obviously visible that could have biased their judgement of depth. Had the subjects learnt that the lower hemifield of dots were much more likely to appear closer than the upper hemifield of dots over the duration of the experiment, the bias would have been in the opposite direction of what was observed here – the point of subjective equality in the psychometric function would have been $>$ 50%. The idiosyncratic results between the randomized and non-randomized dot motion paradigms in the control experiment point against such a possibility as well.

The present study results match well with the observations of Lit (Lit, 1949) that the suprathreshold interocular difference in retinal illuminance needed by his two subjects to elicit a constant impression of illusory depth reduced with the baseline monitor luminance (Lit, 1949). Also, a given magnitude of interocular difference in retinal illuminance produced a larger impression of depth for lower values of background luminance (Lit, 1949). Both observations essentially mean that the impression of illusory depth is more pronounced for lower monitor luminances than for higher monitor luminances (Lit, 1949). The present study found the threshold interocular difference in retinal illuminance required to experience illusory depth scaled with background luminance (Fig. 4C), consistent with the previous observations by Lit (Lit, 1949). In our case this scaling was relative constant, leading to a more or less constant Weber fraction for the thresholds. In contrast to the present study, the Weber's fraction increased progressively with baseline monitor luminance for suprathreshold stimuli in Lit's study (Lit, 1949). These results may reflect methodological or task level differences in the two studies and/or slightly different properties of spatio-temporal disparity coding or coding of interocular velocity difference for threshold and suprathreshold level stimuli. Based on the apparent depth observed, Lit calculated these interocular differences in retinal illuminance to translate into transmission delays of $\sim$ 6 – 22msec for a target velocity of 2.59 cm/sec (Lit, 1960). The calculated transmission delays in the present study ($\sim$12 – 15msec) were in the same range for threshold level interocular differences in retinal illuminance. These values also match other psychophysical and VEP studies of the visual system's sensitivity to temporal delays in retino-cortical information transmission (Heron et al., 2002; 2007;; Prestrude, 1971). As noted in the methods section, the transmission delays in Fig. 5 were derived from the earlier studies by Lit (Lit, 1949) assuming that the parameters in Eq. (1) for suprathreshold retinal illuminance difference apply to threshold level performance. Threshold and suprathreshold performance may be different in other visual functions (e.g. contrast processing in spatial vision (Georgeson & Sullivan, 1975) and perceived depth in stereo vision (Guan & Banks, 1697) and may very well hold true for the illusory depth observed here. The transmission delays shown here are therefore valid only to the extent that the aforementioned assumption is valid. Recently, Burge et al and Rodriguez-Lopez et al observed Pulfrich-like motion-in-depth illusion for interocular differences in retinal illuminance induced by for NDFs of optical density as small as 0.075log units and for optical blur as small as 0.25D simulating monovision corrections for presbyopia (Rodriguez-Lopez et al., 2020). Their subjects were sensitive to interocular temporal delays of as small as 2 – 3 ms, much shorter than what was calculated here for retinal illuminance differences (Rodriguez-Lopez et al., 2020). Similar magnitudes of interocular temporal delays were also observed by Carkeet et al for NDF with optical density of 0.3log units using an interocular temporal asynchrony paradigm (Carkeet et al., 1997). The longer transmission delays observed in this study, vis-à-vis, Burge et al (Burge et al., 2019), Rodriguez et al (Rodriguez-Lopez et al., 2020) and Carkeet et al (Carkeet, Wildsoet, & Wood, 1997) may reflect subject-cohort-level variability, methodological differences between studies [e.g., target speed was substantially faster in Burge et al and Rodriguez et al ($\geq$10°/sec) compared to 1.7°/sec in the present study – the former will translate into smaller disparity and, therefore, lower interocular difference thresholds compared to the present study (Eq. (1))], different points in the psychometric function that was considered as the outcome measure [e.g., Burge et al (Burge et al., 2019) and Rodriguez et al (Rodriguez-Lopez et al., 2020) reported 50% point of subjective equality in the psychometric function while the present study reported 76% threshold level of performance] or any combination of these aforementioned factors.

In conclusion, misperceptions of depth from motion have been recognized as an important perceptual deficit in visual disorders and optical corrections that lead to latency differences in the signals from the two eyes. We examined how large the retinal illuminance differences need to be to induce noticeable perceptual biases in normal vision. Our results suggest that sensitivity to these differences is sufficiently weak that they are unlikely to be manifest in normal vision.

CRediT authorship contribution statement

Vijay Reena Durai: Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Siddhart Rajendran:** Conceptualization, Methodology, Software, Writing - review & editing. **Michael A. Webster:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition. **Sandeep Vempati:** Methodology, Writing - review & editing. **Shrikant R. Bharadwaj:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Acknowledgments

The authors thank all the study participants, Arthur G. Shapiro, Professor of Psychology and Computer Science, American University, Washington, DC for critical feedback on the study design and Ashish Jain for help with the graphic design of the experimental set up in Fig. 1. Vijay Reena Durai also thanks Praveen K. Bandela for support during manuscript writing. This study was financially supported by the Hyderabad Eye Research Foundation, L V Prasad Eye Institute, Hyderabad, India, a partnership grant between the L V Prasad Eye Institute and the Department of Biotechnology, Govt. of India to (BT/PR32404/MED/30/2136/2019) and by NIH grant EY-010834 to Michael Webster.

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