Vision Research 240 (2026) 108729

Contents lists available at ScienceDirect

Vision Research

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

Distortion of perceived visual space after prolonged horizontal eccentric gaze holding☆

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ARTICLE INFO

Keywords:
Gaze holding
Visual space
Eye position
Adaptation

ABSTRACT

Eye movements have long been used as a measure of underlying brain function and pathology. Specifically, rebound nystagmus has provided a behavioral window into the adaptive mechanisms of gaze holding. It is an eye movement aftereffect resulting from maintaining gaze eccentrically for a prolonged duration. Upon returning to central fixation, the eyes drift or "rebound" back toward the previously held gaze location, demonstrating an adaptive process. Little is known about how prolonged eccentric gaze holding, and the accompanying adaptation of the oculomotor system, influences the perception of visual space. Here, we used a variant of the landmark task to assess spatial bias (or lack thereof) with and without prior eccentric gaze holding. We found that perceived spatial bias after prolonged eccentric gaze holding was significantly different between gaze holding to the far left (−40 deg) and the far right (+40 deg). We also found that sensitivity in distinguishing relative distances between objects in space was marginally different between the left and right gaze holding conditions. This suggests that perceived visual space is differentially impacted by where gaze was previously held, reflecting a dependence on the history of eye positions.

1. Introduction

The gaze-holding system enables stable gaze and in turn a stable percept of reality. However, imperfections exist in this system, with studies suggesting that these imperfections are a feature and not a bug. For example, eye drift occurring during fixation has been shown to enhance visual acuity (Intoy & Rucci, 2020; Ratnam et al., 2017; Rucci et al., 2007). Another salient imperfection occurs when trying to hold gaze at eccentric eye positions where the drift motion is not random in direction but tends toward central fixation (Becker & Klein, 1973; Hess et al., 1985). This particular eye movement, commonly referred to as gaze-evoked nystagmus (GEN), exhibits a periodic pattern of slow drift toward the center followed by a saccade in the opposite direction to correct for the drift.

This ocular motor phenomenon is typically interpreted as an imperfection of the gaze-holding system. Specifically, this directional drift arises from the inherent leakiness of the oculomotor integrator in which the accumulated neural drive to hold eye position dissipates over time (Leech et al., 1977; Leigh & Zee, 2015; Otero-Millan et al., 2019). This leakiness property can prove useful in conferring resiliency from perturbation in the presence of noise, since the ideal integrator should avoid accumulating noise.

Gaze-evoked nystagmus is often analyzed by measuring how the drift (or slow-phase) velocity changes as a function of eye position (Bertolini et al., 2013, Bertolini et al., 2019) in the absence of visual cues that could also be used to stabilize gaze via feedback control. The inverse slope of this velocity-position curve (deg/s/deg or in units of seconds) corresponds with the estimated *time constant* (τ) of the leaky integrator. Specifically, analyses of the leaky integrator via eye drift were often modelled as a single exponential decay, with an eye velocity drift that is proportional to eye position, resulting in a slope of $-1/\tau$ for the relationship between eye position and initial velocity (Bockisch et al., 2012; Major, Baker, Aksay, Mensh, et al., 2004; Major, Baker, Aksay, Seung, et al., 2004; Mensh et al., 2004). Becker and Klein showed a time constant of 25 s for horizontal displacements of eye position in humans (Becker & Klein, 1973; Sanchez & Rowe, 2018), reflecting a slow decay back to central fixation.

The performance of the gaze-holding integrator is not constant and

☆ This article is part of a special issue entitled: 'Visual Aftereffects' published in Vision Research.

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https://doi.org/10.1016/j.visres.2025.108729
Received 17 April 2025; Received in revised form 15 November 2025; Accepted 17 November 2025
Available online 10 December 2025
0042-6989/Published by Elsevier Ltd.

can adapt over time. First, the centripetal drift becomes smaller over time during prolonged eccentric gaze holding, suggesting that the gaze-holding system is *adapting* to the current eye position (Zee et al., 2017). Second, evidence of adaptation in the integrator has been shown in the modulation of the gain or phase of the vestibular-ocular reflex (Kramer et al., 1995; Tiliket et al., 1994) via changes in the retinal-slip feedback (Arnold & Robinson, 1991, 1997; Major, Baker, Aksay, Mensh, et al., 2004; Major, Baker, Aksay, Seung, et al., 2004; Turaga et al., 2006). Finally, rebound nystagmus has been used as a behavioral window into the *adaptive* properties of the oculomotor integrator by studying the aftereffect that occurs after holding prolonged fixation at an eccentric point, that is, the eyes would drift toward the previously held gaze when returning to central fixation (Leigh & Zee, 2015; Otero-Millan et al., 2019; Shallo-Hoffmann et al., 1990). Oculomotor behavior has proven to be an insightful measure of adaptive processes in the oculomotor system, specifically of the neural integrator.

Eccentric gaze holding has also been shown to affect perception as well as eye movements. First, it is related to a shift in the perception of straight ahead (Howard, 1991). Observers, while fixating eccentrically, made perceptual errors on the order of several degrees of perceived straight ahead in the direction of the currently held side of eccentric gaze (Hill, 1972), suggesting that gaze holding does indeed play a role in our perception of space. Paap and Ebenholtz (1976) found that prolonged gaze holding at an eccentric eye position showed an aftereffect on perceived straight ahead in which the direction of straight ahead was biased toward the previously held gaze location. Previous studies have also found links between other eye movement adaptation paradigms and perception. For example, saccade adaptation is linked to perceptual spatial remapping (Colby et al., 1995; Duhamel et al., 1992).

There exists a large corpus of findings on spatial bias or asymmetries in perception in both healthy and patient populations using various paradigms (Learmonth & Papadatou-Pastou, 2022), the most common being Milner's landmark task (Milner et al., 1993) and Schekenberg's bisecting line task (Schenkenberg et al., 1980). These approaches have mainly shown a consistent leftward spatial bias where space on the left side of central gaze appears to be larger than it actually is (Jewell & McCourt, 2000); this perceptual asymmetry is often termed as *pseudo-neglect*, signifying that the right hemifield of space is perceptually neglected while the left hemifield garners more perceptual resources (Bowers & Heilman, 1980). Here, we set out to test if holding eccentric gaze also shows an aftereffect on the perceived symmetry of visual space. We probed this potential link using a variant of Milner's landmark task, where the stimulus is already "pre-bisected" and the observer has to determine whether the midline is closer to the left or right line. Observers started the task looking centrally (0 deg eccentricity), and *after* holding their gaze eccentrically either to the left or right at 40 degrees eccentricity, they performed the judgment upon returning to central gaze. We used this experiment to assess whether perception of space changes after the oculomotor integrator adapts to a new eye position.

2. Methods

2.1. Subjects

Twelve subjects completed the study and were compensated for their participation. All subjects completed a consent form that was approved by the institutional review board (IRB) at the University of California, Berkeley and followed the guidelines established by the Declaration of Helsinki. Visual acuity, ocular dominance, and hand dominance were assessed prior to the main task. All subjects had normal or corrected-to-normal binocular visual acuity better than 20/40 Snellen fraction or 0.3 logMAR and were assessed using a Snellen eye chart (Snellen, 1862). For a comprehensive list of subject demographics, see Table 1.

Table 1
Handedness was assessed using a short-form version of the Edinburgh Handedness Inventory (Oldfield, 1971; Veale, 2014). Subjects scoring 61 to 100 were categorized as right-handed, -60 to 60 as mixed-handed, and -100 to -61 as left-handed. The dominant eye was determined using the Miles test (Miles, 1929). The mean (± SD) values across subjects for age and handedness scores are reported in the table.

Subject Demographics	
n	12 (6 females)
Age (years)	30.1 ± 3.5
Handedness Score	81.3 ± 43.1
Dominant Eye	7 OD and 5 OS

2.2. Equipment

For the main experiment, subjects were asked to fix their head within a forehead and chin rest while viewing visual stimuli presented on a display monitor at an 83 cm viewing distance. Stimuli were presented on a 65″ CX LG 4K OLED TV (OLED65CXPUA model; LG Electronics Inc., Seoul, South Korea) with a 60 Hz refresh rate and 3840 x 2160-pixel display resolution. Auditory cues were presented on the display's speaker system to cue the start of the trial and for each change in position of the fixation target. Subjects were placed in a completely dark room and were instructed to complete a perceptual judgment task and provide responses via key presses on a keyboard. The perceptual judgment task was developed in MATLAB™ (R2021b, MathWorks, Natick, MA, USA), utilizing Psychtoolbox (version 3.0.18; Brainard, 1997) and custom MATLAB code for stimulus generation, experiment design, and data acquisition.

2.3. Perceptual judgment task

The current study consisted of a single perceptual judgment task where subjects had to report which among two short vertical lines (0.1 deg wide by 2.6 deg tall) flashed to the left or to the right of the display was closer to a third central line. This variant of Milner's landmark task was used due to its advantage of removing the motor confound that is readily apparent in the line bisection task, with the exception of reporting the two-alternative forced choice response with the right hand via a key press. This is in contrast with an observer having to bisect a line with their hand using a pencil or other bisecting modalities (Bowers & Heilman, 1980; Schenkenberg et al., 1980). Weak within-subject reliability was observed across sensory modalities when using the line bisection task (Mitchell et al., 2020), deeming the landmark task a more robust method for assessing perceptual asymmetries. The distance of one of two lateral lines varied between 15 and 25 deg eccentricity ranging from 0.25 to 1 deg increments while the other lateral line remained fixed at 20 deg, resulting in 11 possible displacements. Specifically, ten subjects were given a stimulus set ranging from 17.5 to 22.5 deg in eccentricity in 0.5 deg increments, one subject was given a range from 18.75 to 21.25 deg in 0.25 deg increments, and another was provided a range from 15 to 25 deg in 1 deg increments. There were two possible tasks for each trial – one with eccentric gaze holding (EGH) and one without (see Fig. 1). Subjects were instructed to report their answer via the left or right arrow key after being briefly shown the three vertical lines.

2.4. Experiment design

Each subject completed two sessions of the perceptual judgment task. The first session consisted of three runs of 176 trials of only the control trials across 11 distance conditions of the lateral lines. The line distances varied between runs in order to establish a set of line distances that would be sufficiently difficult (but not too difficult) for the subject to perform around their threshold performance. After the completion of the three runs, we evaluated the psychometric curves for each run to

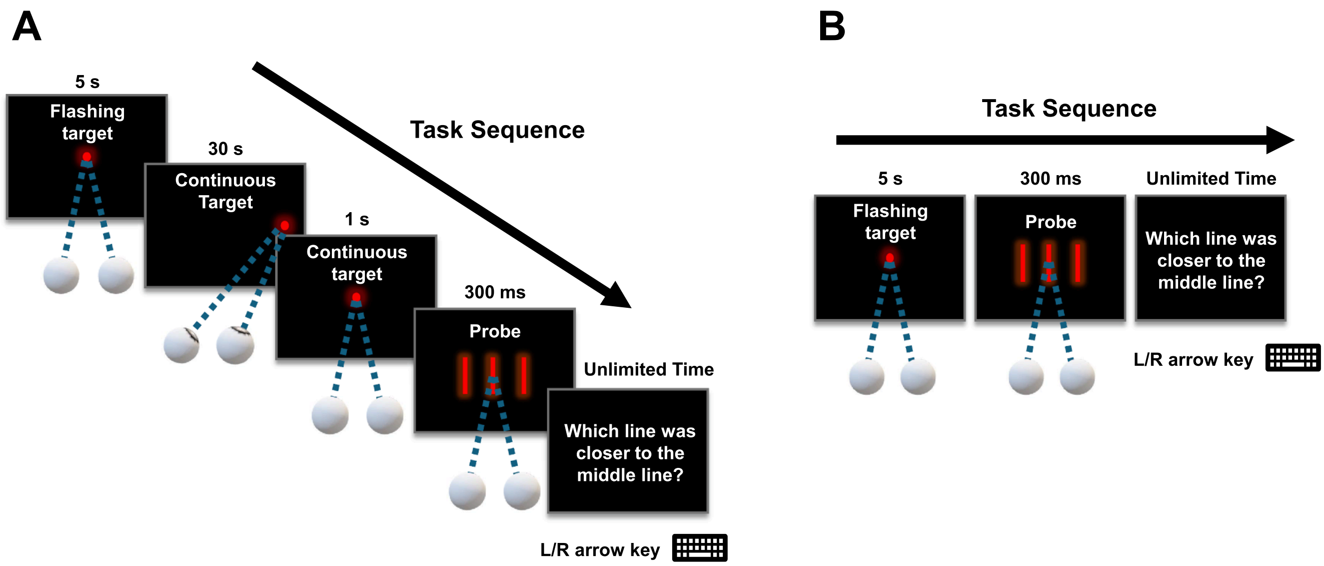

Fig. 1. The experimental task sequence with and without eccentric gaze holding. (A) In the experimental condition, subjects had to gaze at an eccentric point for 30 or 5 s on either the left or right side of the monitor and upon return to central gaze, were presented the three vertical lines. Subjects were given 1 s to return to central gaze before the probe appeared. The fixation spot was presented continuously for the initial 500 ms to facilitate the return to central gaze. Also, note that subjects were not presented with text at the end of the trial and instead were presented with a black screen. Subjects had to make a choice, whether the left or right line was closer to the central line, at the end of the trial. (B) In the control condition subjects performed the same task without a period of eccentric fixation.

determine the appropriate line-distance set that was used in the main experiment for the second session. The data from this session were not included in any of the results that are reported in this paper.

The second session required subjects to complete a randomized trial session of 352 trials with and without EGH (see Fig. 2A); gaze holding trials were split into two possible gaze locations – leftward EGH and rightward, both at 40 deg eccentricity. Subjects were tested on 11-line distance conditions and on two gaze holding conditions (with or without EGH). Trials were grouped into 11-trial blocks totaling 32 blocks, with each block reflecting a specific gaze holding condition and gaze location (leftward or rightward gaze at 40 deg), and each trial presenting one of 11 possible line distance conditions for the bisection probe in a randomized order. The EGH trial blocks were grouped in a manner such that the initial trial would require gaze holding for 30 s and the subsequent 10 trials requiring 5 s. This trial grouping helped maintain the adaptation making the data collection more efficient and less demanding on the subjects. Trials without EGH were blocked in the same manner but without the gaze holding procedure described previously. Block order was randomized for the entire second session.

2.5. Statistical analysis

All analyses were performed using MATLAB™ (R2021b, R2023a, MathWorks, Natick, MA, USA) and Excel (Microsoft Office Professional Plus 2019, Microsoft Corporation, Redmond, WA, USA). Response data for both gaze holding conditions were each fit with a generalized linear model (GLM) using a logit link function to model the predicted responses as a binomial distribution. The estimated parameters from the GLM and the line distance condition for a given trial were then used to generate a psychometric function, a sigmoid, for a given experiment block. Two metrics were estimated from the psychometric fits – *spatial bias* and *discrimination sensitivity*. Spatial bias was defined as the point of subjective equality (PSE), in degrees of visual angle, at a proportion of 50% rightward responses. If the PSE is 0 deg, then the subject's perception reflects the actual relative spacing of the lines, whereas any $|\text{PSE}| > 0$ would reflect a spatial bias or left–right asymmetry in the perceived distance between the vertical lines. Estimates of discrimination sensitivity were defined as the just-noticeable differences (JND; Fechner, 1860), in degrees of visual angle, indicating the degree of steepness of the psychometric curve. This metric reflects how sensitive the subject is to changes in distance between the left or right line from the center one. JNDs were computed nonparametrically using half the interquartile range of the psychometric curve (Bausenhart et al., 2018; R. D. Luce & Galanter, 1963).

3. Results

Here, we report our psychometric results on spatial bias across the different gaze holding conditions. Specifically, we show the across-subjects result on spatial bias (Fig. 3), our main finding, followed by the individual psychometric fits (Fig. 4) and their respective goodness-of-fit statistics. Further, we report on discrimination sensitivity and correlation analyses between perceptual performance and hand dominance.

3.1. Spatial bias

Psychometric analysis was performed for all twelve subjects across the three gaze conditions, i.e., left and right EGH, and without EGH. Fig. 2B shows three sigmoidal curves for one subject, each representing a gaze condition. Curve fits for each subject are shown in Fig. 4.

Since half of the trials for a given EGH condition have the left line adjusted while the right line remains fixed at 20 deg and vice-versa for the other half, the PSE can be visualized in a combined plot by relative changes in visual angle. Subjects, overall, showed average spatial biases of 0.2 ± 0.8 deg (mean $\pm$ SD), 0.3 ± 0.8 deg, and -0.2 ± 0.7 deg for the no EGH (control), left EGH, and right EGH conditions, respectively. For our primary finding, we found that the spatial bias was significantly different between the left and right EGH conditions with a moderate effect size ($t(11) = 2.36$, $p = 0.038$, $d = 0.63$; see Fig. 3A). However, spatial biases in the EGH conditions were not significantly different from the condition without EGH ($p \geq 0.15$). Further, spatial bias under no EGH did not show a significant difference from the point of objective equality (i.e., equidistant lines), although descriptively, showed a slight

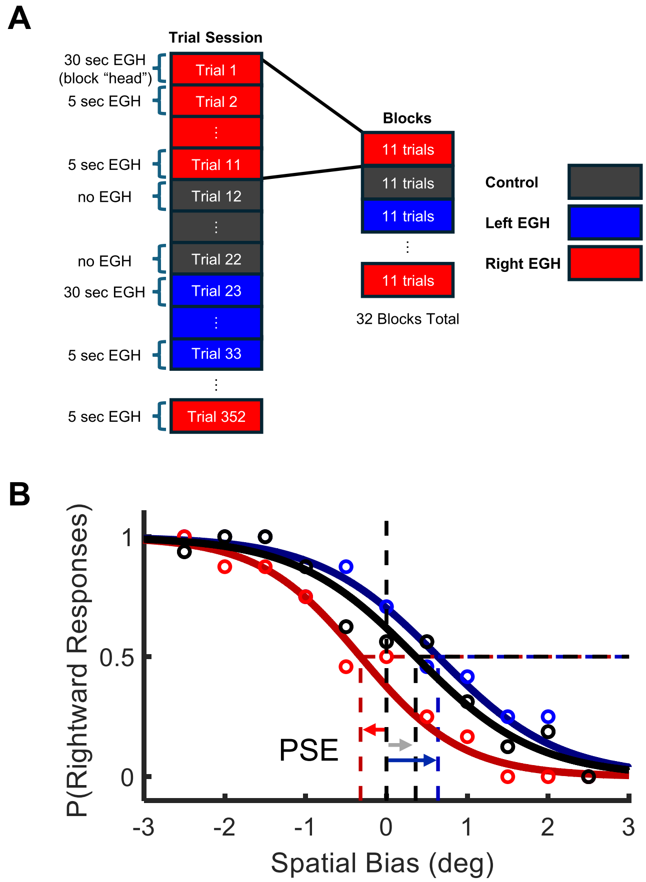

Fig. 2. (A) Experimental block design for the eccentric gaze holding experiment. A trial session is divided into 32 blocks, each containing 11 trials of the same gaze-holding condition reflecting the 11 possible line distances. For the eccentric gaze holding conditions, the "head" of the block or starting trial has a 30-second gaze-holding phase and the proceeding 10 trials a 5-second gaze-holding phase to maintain the effects of eccentric gaze holding while reducing the time spent on trial and alleviating physical fatigue. The 32 blocks are pseudo-randomly ordered within the trial block. (B) Psychometric curves for a specific subject (S11). The intersection of the dashed vertical and horizontal lines is simply the point of subjective equality (PSE) for that particular gaze condition (specified by its color).

leftward spatial bias ($p = 0.33$; see Fig. 3A).

A psychometric curve was fit to each gaze condition for each subject (3 gaze conditions x 12 subjects), resulting in 36 fits (see Fig. 4). We evaluated the psychometric fits using a likelihood-ratio test, where we compared the full psychometric model against a constant model (intercept only). Among the 36 fits, 26 were significantly different ($p < 0.05$) from a constant model. Five of the ten insignificant fits were marginally significant ($p < 0.1$). The deviance between the saturated model (i.e., the model that perfectly fits the data) and the actual model (constant or full psychometric model) was computed for each gaze condition. The median across-subjects deviance between the psychometric model and the saturated model was 0.55, 2.00, and 1.42 for the control, left gaze holding, and right gaze holding conditions, respectively. As expected, the median deviance across subjects for the constant model was larger across all conditions (control: 6.81; left EGH: 7.39; right EGH: 7.86), suggesting that the sigmoid is the appropriate model for a large proportion of our experimental results. Further, we showed that the median adjusted r^2 across subjects was 0.94, 0.76, and 0.84 for the control, left gaze holding, and right gaze holding conditions, respectively. The grand median of the adjusted r^2 was 0.87 (range: 0.38–0.99).

3.2. Secondary findings

The mean ($\pm$ SD) just-noticeable difference was 0.9 ± 0.3 deg, 1.0 ± 0.5 deg, and 0.8 ± 0.4 deg for the control, left EGH, and right EGH conditions, respectively. Discrimination sensitivities between the three gaze conditions were not significantly different, with the minor exception of left versus right gaze holding conditions revealing marginal significance with a moderate effect size ($t(11) = 2.11$, $p = 0.06$, $d = 0.57$), suggesting that prolonged gaze at extreme horizontal eccentricities may have some minor effect on the sensitivity of perceived changes in distance between objects in space between the two eccentric gaze holding conditions. A significant correlation was found between spatial bias and handedness under no EGH ($r^2 = 0.37$, $p = 0.035$); however, no significant correlations between handedness and the EGH conditions were found ($p > 0.56$). Lastly, a marginally significant correlation was found between discrimination sensitivity and handedness without EGH ($r^2 = 0.31$, $p = 0.058$).

4. Discussion

Under the no gaze holding condition, we expected that the subjects would show a leftward spatial bias where the left side of their visual field would appear larger than the right when the three lines are *objectively* equidistant. Another view of this leftward spatial bias would be when the middle line is objectively closer to the left line when subjects *perceive* the three lines as equidistant. This phenomenon has been reported in many studies under a similar viewing condition while using a similar task paradigm (i.e., the landmark task; Milner et al., 1993). With prolonged gaze holding at an extreme eccentricity, we expected a spatial bias on the side of where gaze was held. Our data trended in that direction but did not show statistical significance.

Prolonged holding of gaze at an extreme eccentricity invokes an adaptive change in the oculomotor system. Specifically, the oculomotor integrator seems to adapt the set point to the current gaze location.

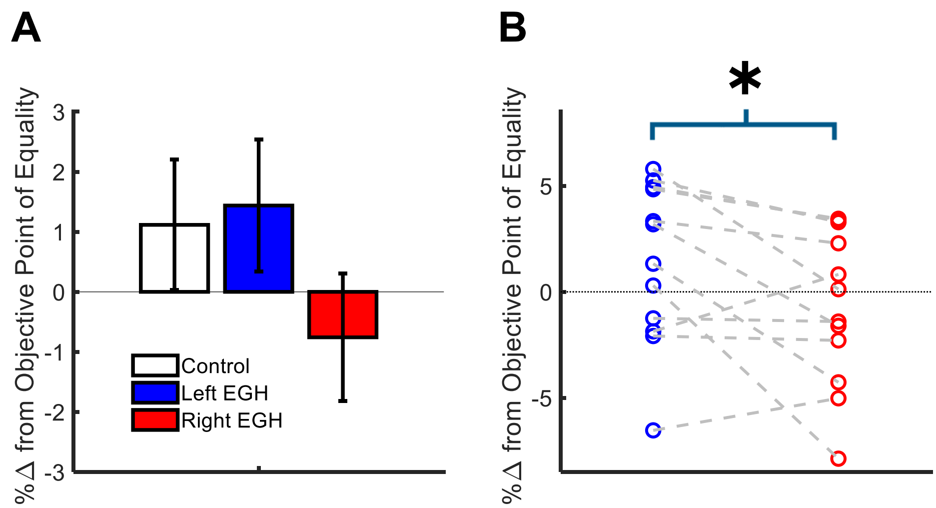

Fig. 3. The left panel (A) shows a bar plot of the across-subject mean (± SEM) of the point of subjective equality for twelve subjects. Units are in percent change from the objective point of equality (when the lateral lines are equidistant to the middle line). The right panel (B) shows the point of subjective equality for each subject for the eccentric gaze holding conditions. Dashed lines indicate the paired differences between the two conditions.

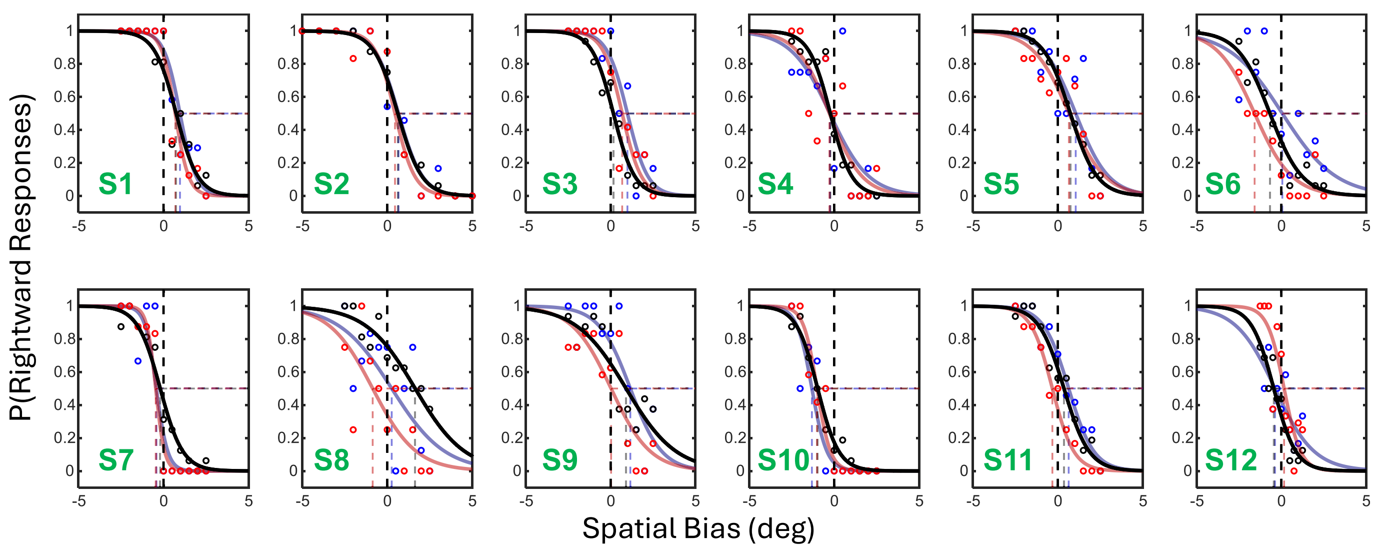

Fig. 4. Psychometric curves of each subject on the relative spatial judgment task. Scatterplots reflect the proportion of rightward responses for a given line distance condition, spanning 11 conditions for each experiment. The S-shaped curves reflect the best-fit sigmoid for a specific experiment. The color scheme indicates the experimental condition for eccentric gaze holding, where blue and red represent the left and rightward gaze holding conditions, respectively; the black color scheme is the control experiment without eccentric gaze holding.

Perceptually, we found that observers showed a spatial bias in the direction of gaze holding upon returning to central fixation. This suggests observers perceived the left eccentric line as further from the center than the right eccentric line and vice-versa. This finding is supported by the significant difference found between the left and right eccentric gaze holding conditions. However, the gaze holding conditions were not statistically significant from the no gaze holding condition. Additionally, differences in the sensitivity to discriminate a range of line displacements were not found across the three gaze holding conditions. This is not surprising since we did not expect gaze holding to necessarily improve or weaken spatial sensitivity upon returning to central gaze. We also did not expect to observe any enhancement or deficits in sensitivity due to directional eye motion (i.e., rebound nystagmus) evoked by prolonged gaze holding since the stimulus probe was brief and did not require the fine visual acuity attributed to the spatio-spectral whitening effects of eye motion (Clark et al., 2022).

4.1. *Spatial perceptual biases*

There exists a large corpus of research that shows this perceptual asymmetry or spatial bias. Biases along the visual horizontal meridian were shown with asymmetric retinal stimulation, where the perceived medial plane of the head is biased toward the center of visual field stimulation (Bruell & Albee, 1955). Another bias was found when a frame was presented within a full-field retinal stimulus, where the perceived straight-ahead was shifted toward the center of the frame and not toward the center of retinal stimulation (Brosgole, 1967). The current study presents a vertical line in both hemifields and the central vertical line at the center, approximating symmetric retinal stimulation. However, the left and right vertical lines are usually placed at different eccentricities, likely stimulating a different number of receptive fields between both sides of the visual field. This can potentially introduce a bias due to the asymmetry in receptive field stimulation.

Spatial bias can also be introduced via rotations of a surface with a symmetric stimulus on the given surface, for example, two parallel lines as shown in the study by Li and colleagues (Li et al., 2001). Here, the observer instructed the experimenter to move a laser target along a meridian that is parallel and in between the two visible lines where they have to find where they believe to be “straight ahead”. Observers reported biases in the direction of rotation – for instance, if the surface with two parallel vertical lines was pitched away from the observer, then the observer would perceive their eye level slightly above their actual eye level. If the surface with two parallel horizontal lines was rotated around a vertical axis, then the observer would perceive straight ahead to be slightly to the right, replicating the leftward pseudoneglect effect found in a large corpus of studies (Jewell & McCourt, 2000; Learmonth & Papadatou-Pastou, 2022).

Another consideration is how the brain interprets the varying horizontal offsets of the vertical lines. Can such differences be interpreted as a slanted surface that the lines occupy? A study by Backus and colleagues have shown that vertical size ratio (VSR), the ratio of the vertical subtended angle of the stimulus between the two eyes, affects the perception of azimuthal slant of a surface patch (Backus et al., 1999). Indeed, VSR deviates from 1 when the vertical lines in the current study are not equidistant, which may introduce a bias from the perception of a slanted surface. Based on the empirical results of this study, the size of the vertical lines in our current study should have less than a 25% correction factor for perceived azimuthal slant, and is more impacted by eye position (> 70% correction factor).

4.2. Neural basis of perceptual biases

Cortical structures have been investigated extensively to unveil the role of these perceptual asymmetries in perceived visual space. The pseudoneglect phenomena in particular have been linked to a possible hemispheric dominance in parietal cortex for visual attentional processes. A structural imaging study has shown a larger volume of the fronto-parietal tract in the right hemisphere for observers with more pronounced pseudoneglect (de Schotten et al., 2011). Our findings could reflect a possible link between visuo-cognitive processing in higher-order cortex and low-level adaptive processing in the brainstem and cerebellum. Specifically, gaze holding to a specific side in space could invoke adaptation in multiple parts of the brain, where the brainstem and cerebellum circuits adapt the oculomotor set point for the new gaze location and the fronto-parietal attentional network adapt the perception of visual space – in this case introducing a perceptual bias in the direction of where gaze is being held as suggested by our results. However, further work is needed to truly establish the coordinated adaptation between these two seemingly disparate neural systems.

4.3. Effect of stimulus characteristics

The eccentricity or spacing of the vertical lines in the current study could also play a role in producing the perception of spatial asymmetry. Previous studies have shown that the length of the line in a line bisection task determines whether the observer would exhibit a pseudoneglect effect or not (Rueckert et al., 2002; Thomas et al., 2012). Specifically, pseudoneglect is more likely to be observed with longer lines than shorter ones. Further, differences in neural activity between the two hemispheres were shown for longer lines (15.3 deg) whereas the shorter lines (1 deg) did not exhibit this difference (Benwell et al., 2014), suggesting that the asymmetry is only present when the stimulus spans a sufficient portion of the visual field. Although, whether this generalizes to horizontal offsets of vertical lines has yet to be seen. Considering that this assumption holds, the eccentricities tested in the current study largely exceed 15 degrees, which in theory should be sufficient to invoke the neural correlates of pseudoneglect.

4.4. Links between motor and perceptual effects of gaze-holding

Prolonged gaze holding at an eccentric position has been shown to have certain effects on perception and motor control. A study by Harris and Smith (2008) found that eye position in the dark was more accurate after prolonged gaze holding at 11 deg to the left versus holding gaze to the right at 11 deg, revealing a left–right asymmetry. Our findings, although marginal in significance, appeared to reflect this left–right asymmetry in the estimated sensitivity of distinguishing relative positions in space. Qualitatively, we found the spatial bias to be more similar between the left EGH condition and control (mean $\pm$ SEM within-subject difference; left EGH – control: 0.1 ± 0.2 deg, right EGH – control: -0.4 ± 0.2 deg), suggesting that perception may deviate from baseline with prolonged gaze holding to the right while also producing a deleterious effect on the accuracy of eye position. However, it is unclear whether prolonged gaze holding harms perceptual performance directly, and consequently, eye-position accuracy, or that the less accurate motor command for eye position impacts perception.

Additionally, other sensory modalities, such as touch, have been found to be coded by eye position signals (Pritchett & Harris, 2011), signifying that eye position is critical for bringing non-visual multisensory information into a visual reference frame. Saccade adaptation in particular has been shown to use an extraretinal reference frame for localization of objects in space, reinforcing the important role of eye position for calibrating spatial coordinates (Zimmermann & Lappe, 2011). This would imply that a spatial mislocalization produced by prolonged gaze holding may transfer to other sensory systems and that perceptual discrimination in these other sensory domains may indeed be impacted.

There is ample physiological and behavioral evidence to suggest that object positions in space are encoded in retinotopic coordinates (Colby et al., 1995; Honda, 1989; Keith et al., 2010; Matin et al., 1969; Sparks, 1988) and the remapping of this coordinate system occurs largely prior to the initiation of a saccade (Moran et al., 2024). The occurrence of remapping before a saccade supports von Holst’s principle of reafference (von Holst & Mittelstaedt, 1950) in which a copy of the motor command is used to influence the remapping of spatial coordinates. Furthermore, remapping is also present during and after a saccade (persisting up to ~150 ms after a saccade), but with a smaller influence (Moran et al., 2024). This is yet another example of how perceptual recalibration can be linked to the oculomotor system. However, how saccade adaptation relates to our findings is unclear.

4.5. Correlation with handedness

We found a correlation between handedness and spatial bias under the no gaze holding condition, an association found in a number of previous studies that investigated the pseudoneglect effect (Brodie & Pettigrew, 1996; De Agostini et al., 1999). In contrast, the correlation dissipates with gaze holding, which could suggest that prolonged gaze holding may play a role in cortical processing of visual space. However, the correlation itself is limited in its interpretability due to the small sample size and the larger proportion of right-handers, which may skew the correlation.

4.6. Conclusions

Without gaze holding, a spatial bias exists where the left eccentric line is perceived as further from the center than the right eccentric line. With eccentric gaze holding, we showed qualitatively that the side with the spatial bias was linked to the side that gaze holding took place; however, this effect was not significantly different from the condition without gaze holding. Despite the lack of significance, we showed that spatial bias was different between the left and right EGH conditions, suggesting that prolonged fixation at extreme eccentricities (40 deg) reveal a differential bias in the perception of space. Although gaze holding invoked differences in the perception of relative distance, it is still unclear whether this perceptual change is causally linked to the change that occurs in the oculomotor neural integrator.

CRediT authorship contribution statement

Terence L. Tyson: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Dennis F. Perez:** Writing – review & editing, Software, Conceptualization. **Jorge Otero-Millan:** Writing – review & editing, Visualization, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation.

Declaration of Competing Interest

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

Acknowledgments

This work was supported by the NASA Ames Research Center Graduate Fellowship Program, the Department of Veterans Affairs (VA) Veteran Readiness and Employment (Chapter 31) Program, National Institute of Health (NIH) R00EY027846 research project grant, and startup lab funds from the University of California, Berkeley. We would like to extend our gratitude to Tiffany Lau for performing a portion of the data collection. We would also like to thank Martin Banks, Brent Beutter, Susana Chung, Emily Cooper, Dennis Levi, Austin Roorda, Clifton Schor, and Eugene Switkes for their feedback on an earlier iteration of the work. We would also like to thank the members of the Berkeley Ocular Motor Lab (Reem Almagati, Stephanie Reeves, Raul Rodriguez, and Roksana Sadeghi) for their invaluable feedback and discussions throughout various stages of the study.

Data availability

Data will be made available on request.

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