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Sensory and Motor Systems

Head Orientation Influences Saccade Directions during Free Viewing

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Abstract

When looking around a visual scene, humans make saccadic eye movements to fixate objects of interest. While the extraocular muscles can execute saccades in any direction, not all saccade directions are equally likely: saccades in horizontal and vertical directions are most prevalent. Here, we asked whether head orientation plays a role in determining saccade direction biases. Study participants ($n = 14$) viewed natural scenes and abstract fractals (radially symmetric patterns) through a virtual reality headset equipped with eye tracking. Participants' heads were stabilized and tilted at -30° , 0° , or 30° while viewing the images, which could also be tilted by -30° , 0° , and 30° relative to the head. To determine whether the biases in saccade direction changed with head tilt, we calculated polar histograms of saccade directions and cross-correlated pairs of histograms to find the angular displacement resulting in the maximum correlation. During free viewing of fractals, saccade biases largely followed the orientation of the head with an average displacement value of 24° when comparing head upright to head tilt in world-referenced coordinates ($t_{(13)} = 17.63$, $p < 0.001$). There was a systematic offset of 2.6° in saccade directions, likely reflecting ocular counter roll (OCR; $t_{(13)} = 3.13$, $p = 0.008$). When participants viewed an Earth upright natural scene during head tilt, we found that the orientation of the head still influenced saccade directions ($t_{(13)} = 3.7$, $p = 0.001$). These results suggest that nonvisual information about head orientation, such as that acquired by vestibular sensors, likely plays a role in saccade generation.

Key words: direction bias; eye movements; head tilt; saccades; vestibular; virtual reality

Significance Statement

We show that the statistics of saccade directions, from data collected during free viewing of fractal (radially symmetric) and natural scene images, are influenced by head orientation. During fractal viewing, saccade directions largely followed the orientation of the head with systematic offsets likely explained by ocular counter roll (OCR). During natural scene viewing of an Earth upright image, saccade directions were still influenced by head orientation. These results suggest that head and retinal orientation relative to gravity play a key role in saccade generation. Future work should consider the influence of head orientation when predicting saccade landing points or when using existing saccade generation models.

Introduction

While saccades can be made in any direction, saccades in the cardinal directions are more prevalent than the oblique directions, and saccades in the horizontal direction are more prevalent than the vertical direction. This

saccade direction bias is well documented and has been observed in tasks such as visual search (Gilchrist and Harvey, 2006; Najemnik and Geisler, 2008), movie watching (Costela and Woods, 2019), fixation (Otero-Millan et al., 2013), and free viewing (Foulsham et al., 2008; Tatler

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and Vincent, 2009; Otero-Millan et al., 2013; Anderson et al., 2020; Bischof et al., 2020).

There are many factors that likely contribute to the saccade direction bias, with oculomotor, neural, environmental, and behavioral origins. For example, purely horizontal saccades require the activation of fewer extraocular muscles and brain regions than saccades in other directions (Leigh and Zee, 2015); scenes have prevalent cardinal (especially horizontal) contour orientation biases that influence perception and saccade directions (Foulsham et al., 2008; Girshick et al., 2011; Raman and Sarkar, 2017; Rolfs and Schweitzer, 2022); and learned, directionally-biased behaviors such as reading may reinforce motor biases throughout the lifespan (Abed, 1991; Van Renswoude et al., 2016).

An additional contributor to the saccade direction bias that has not yet been systematically examined is the influence of gravitational signals indicating head orientation. Head tilt is a powerful tool to determine the relative contribution of gravitational signals because tilting the head disrupts the alignment between the direction of gravity and the head. When humans are upright, the visual world, gravity, head, and eyes are all in alignment, but during head tilt in the roll direction, the head is no longer aligned with the visual world or gravity. Moreover, ocular counter roll (OCR), occurring in response to head tilt, rotates the eye in the opposite direction of the head and breaks the alignment between the head and the retina.

There are many reasons why gravitational signals indicating head tilt may play a role in saccade generation. Previous studies have found that the perception of upright changes following head tilt (De Vrijer et al., 2009). This change in the perception of upright can be independent of changes in OCR (Otero-Millan and Kheradmand, 2016). The oblique effect, a perceptual effect characterized by enhanced discrimination for horizontal and vertical orientations, is also influenced by gravity and weakens when lying supine (Mikellidou et al., 2015). Other studies have used changes in head orientation to understand the underlying reference frame of perceptual and motor biases seen in tasks measuring visual acuity and stereoacuity (Ebenholtz and Walchli, 1965; Banks and Stolarz, 1975; Lam et al., 2008). Whether the effects of head orientation on vision can be completely explained by OCR is an active area of research (Banks and Stolarz, 1975; Medendorp et al., 2002; Klier et al., 2005). Given the influence of head orientation on visual perception and performance, it is likely that

head orientation similarly influences saccade generation and saccade execution.

In the present study, we examined whether roll tilting the head influences saccade direction distributions during free viewing. For clarity, we focus on the primary horizontal bias of saccade directions, but we expect the weaker vertical bias to also be present. Figure 1 shows the two alternative hypotheses for the effect of head tilt on saccade direction biases. First, according to the “world orientation hypothesis” (blue), saccade directions will remain primarily horizontal with respect to the world despite intervening head tilt. Second, according to the “head orientation hypothesis” (orange), the saccade bias will rotate with the head and remain horizontal with respect to the head. We first test the impact of head orientation on saccade directions when people visually explore images absent of visual cues of upright (fractal images), and ask which hypothesis is supported. Next, we examine the impact of head orientation during the viewing of Earth upright natural scenes. Finally, we show that our paradigm replicates previous work showing the effect of natural scene tilt by itself.

Materials and Methods

Participants

Fourteen adults (ages 22–38 with mean of 27 years; seven female, six male, and one nonbinary individual) from the community in and around Berkeley, CA participated in the study. All participants provided informed consent before data collection. The research followed the tenets of the Declaration of Helsinki, and the Institutional Review Board of the university approved the study.

Before conducting the study, we implemented an a priori one-tailed *t* test power analysis using G*Power (Faul et al., 2007), which revealed that at least 12 participants were required for the study based on an effect size of 0.8 (supported by pilot data that showed 7.7° of effect and 9.7° SD), an α of 0.05, and a power of 0.8.

Apparatus

Stimuli were presented on a FOVE 0 Virtual Reality headset, controlled with a desktop computer. The FOVE (FOVE Inc) has a display resolution of 2560 × 1440 pixels, a field of view up to 100°, a weight of 520 g, and a frame rate of 70 Hz. The built-in binocular eye tracker uses a stereo infrared system that runs at 120 Hz. The FOVE measures head position and head rotation with an external infrared camera and a built-in inertial measurement unit (IMU), respectively.

The virtual space for stimulus presentation was created in Unity (version 2019.4.18f; Unity Technologies) and experimental structure was created with the Unity Experiment Framework, UXF version 2.1.1 (Brookes et al., 2020), which allows for the automation of data collection and data output. Eye movements were recorded using the Unity FOVE plugin (version 4.1.0). Custom scripts were written in C# to run the experiment.

The head stabilizing system consisted of adjustable pads that gently held and compressed the temporal sides

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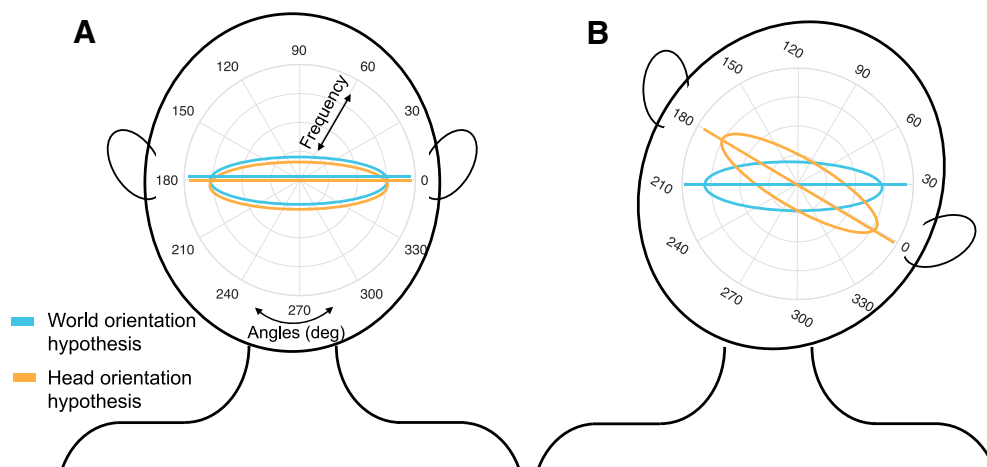


Figure 1. Predictions for the horizontal saccade direction bias as a function of head tilt. Polar histograms indicate the frequency of each saccade direction as a function of angle in degrees. **A**, When the head is upright, the horizontal saccade bias looks the same for both the world orientation hypothesis and the head orientation hypothesis. **B**, When the head is tilted, it is possible that the saccade bias will either rotate with the head (head orientation hypothesis) or stay consistent with the world and Earth upright (world orientation hypothesis). Blue and orange lines indicate reference lines (i.e., the horizontal axis) for the world and head orientation hypotheses, respectively.

of the head (Fig. 2A). These pads were mounted to a rotating device that was able to roll tilt 360° and lock in place. Participants were held in place with the system and were released from the head stabilizers after every head tilt block (~20 min).

Stimuli

The stimuli consisted of 30 abstract fractals (Fig. 2B) and 30 natural scenes (indoor and outdoor scenes; Fig. 2C). The natural scenes were downloaded from Flickr and had CC-BY-2.0 licenses at minimum. The fractals were created with Procreate (Savage Interactive Ltd, Tasmania) on an iPad Pro (second generation, 11-inch). The fractals

had 30° of radial symmetry and appeared in an amalgam of patterns and colors. Both scenes and fractal images were converted into equirectangular projection and then projected onto the inside of a sphere so that participants were completely immersed in the scene (i.e., the stimulus took up the entire field of view of the FOVE). The sphere had a diameter of 20 virtual meters. Although the FOVE allows for stereoscopic displays, the stimuli used in this study did not contain binocular or motion depth cues.

Procedure

The experiment consisted of one session broken up into three blocks, one for each head tilt. At the beginning

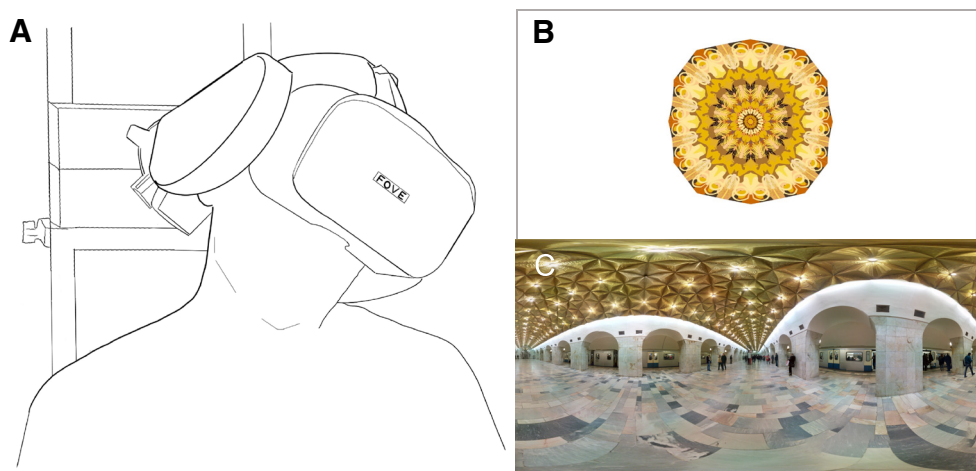


Figure 2. **A**, Head stabilization system for the FOVE virtual reality headset. **B**, Example fractal photosphere image. **C**, Example scene photosphere image licensed by Artem Svetlov and obtained from Flickr. The Flickr image was released with a CC-BY-2.0 license.

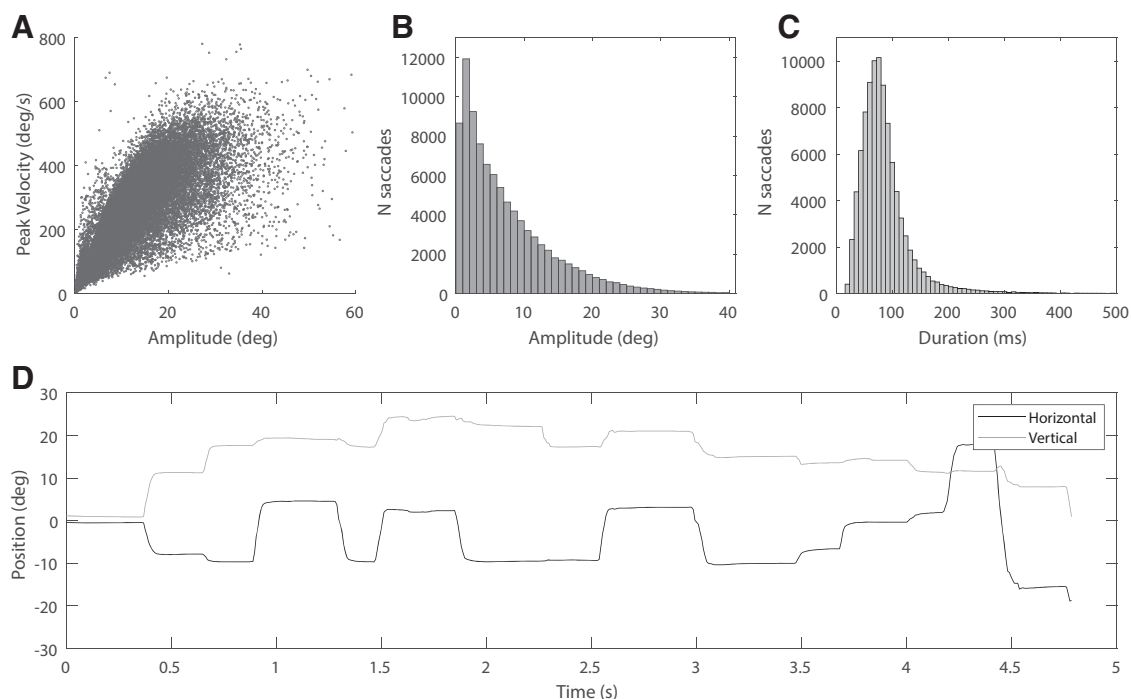


Figure 3. **A**, Main sequence of all saccades showing the stereotyped relationship between peak velocity and amplitude. **B**, Histogram showing the number of saccades as a function of amplitude. **C**, Histogram showing the number of saccades as a function of duration. **D**, Horizontal and vertical eye traces for one subject during one trial.

of each block and after eye movement calibration, the participant's head was tilted and constrained at -30° (head tilt), 0° (head upright), or 30° (head right) rotation. Within each block, there were 60 free viewing trials that displayed a different image (30 natural scenes and 30 fractals) at -30° , 0° , or 30° relative to the head for a total of 180 trials in the session. Relative to the world, images could be tilted up to 60° or -60° for conditions where the image tilt and the head tilt were in the same direction. The image type and image tilt for each trial were presented in a random order within each head tilt block. Thus, within each head tilt block the images presented at different image tilts were all different. The head tilt block order was preset and balanced across participants.

At the start of the session, participants were prompted to complete a FOVE calibration consisting of a moving dot following an expanding spiral path. After successful calibration, the experimenter tilted the participant's head the desired amount (-30° , 0° , or 30° , block dependent). Participant head tilt was monitored with an external digital angle gauge and an internal head rotation measurement exported by the FOVE while the experiment took place. Subjects maintained an average head tilt of $27.14 \pm 3.66^\circ$ (mean \pm SD) to the right, $0.19 \pm 2.24^\circ$ upright, and $-26.68 \pm 2.37^\circ$ to the left. The FOVE was configured so that the scene remained static in the head mounted display regardless of head movements.

Participants fixated a central dot and initiated each trial with a key press. After the button press, the fixation dot disappeared and was replaced with a natural scene or fractal. Participants had 15 s to explore the scene with their eyes without moving their head. After the allotted

time, the image disappeared and was replaced with the central fixation dot. Every 20 trials, a white screen appeared, and participants initiated a calibration sequence with a space bar press. A blue dot appeared for 2 s at five different locations, and participants were instructed to follow the dot with their eyes.

Data analyses and statistics

Binocular eye movement data were exported from the FOVE and analyzed in MATLAB. Saccade detection was implemented using custom-built MATLAB functions that were based on the method described by Engbert and Kliegl (2003). Instantaneous velocity was calculated with a differential smoothing filter for each eye. Velocity thresholds for saccade detection were determined based on the robust standard deviation of the data using a λ of 8 (λ is a parameter in the Engbert algorithm that represents a multiplier of the standard deviation). We confirmed that detected saccades followed the main sequence (Fig. 3A) and other known characteristics such as the bias toward smaller (Fig. 3B) and shorter duration (Fig. 3C) saccades during free viewing. Eye movement traces were visually inspected for any abnormalities (Fig. 3D).

We calculated polar distributions of saccade directions by applying a circular kernel density estimate (KDE) to the data (Muir, 2022). The kernel, a wrapped Gaussian 0.1 radians in width, was applied from 0° to 360° in steps of 0.1° . To quantify the differences among subsets of polar distributions, for each subject, we obtained circular cross-correlation values between pairs of polar distributions (see Results) and found the direction distribution displacement

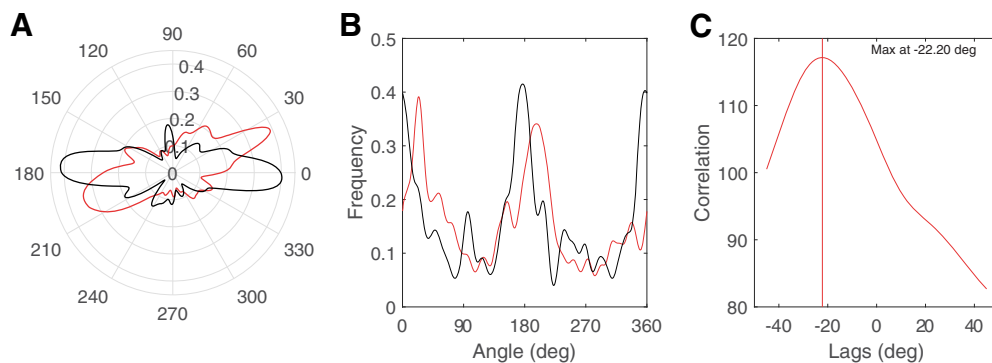


Figure 4. **A**, Polar distributions for a single subject during free viewing of fractal images for head tilt right (red) and head upright (black). The angles of the polar plots represent degrees while the radius indicates normalized frequency. **B**, The unwrapped polar distributions from **A**. **C**, The output of the circular cross-correlation that identifies the lag (in degrees) that results in the maximum correlation.

in degrees (Δ) that resulted in the maximum correlation (Fig. 4). To avoid edge effects, the circular cross-correlation, was implemented by repeating and concatenating the kernel density estimate three times so as to cover the range from -360° to 720° instead of only 0° to 360° and searching for a maximum correlation within a $\pm 45^\circ$ range to avoid finding spurious peaks given the 180° or 90° symmetry of the distributions. Implementing the circular cross-correlation was made possible by the fact that individual subjects had saccade direction distributions that were anisotropic; thus, the lag that resulted in the maximum correlation was indeed the highest (Fig. 4). These direction distribution displacements for individual subjects were bootstrapped to determine 95% confidence intervals (CIs). A positive direction distribution displacement value indicates a clockwise rotation of the saccade bias while a negative value indicates a counterclockwise rotation of the bias.

The reference frame index (RFindex) was calculated for each subject according to the equation $RFindex = \frac{\Delta_{30} + (-\Delta_{-30})/2}{T}$ where Δ represents the direction distribution displacement between 30° and 0° tilt (Δ_{30}) and between -30° and 0° tilt (Δ_{-30}), and T indicates the absolute average tilt of either the head or image tilt in degrees associated with a given condition. That is, for each subject, we sign-reversed the direction distribution displacement values corresponding to head or image tilt towards the left, calculated the mean direction distribution displacement for left and right tilt, and then scaled the values by the absolute average tilt associated with the experimental condition. A RFindex of 0 corresponds with a saccade bias that is oriented to a head reference frame while a RFindex of 1 corresponds with a world or gravity fixed reference frame (see Results for exceptions). The RFindex allows us to combine the data from left and right tilts and summarize it into a single number to test the overall significance of our effects.

We were able to obtain the torsional component of recorded eye movements for 11 of the 14 subjects. We analyzed OCR during our study by calculating the median OCR over time for each trial to reduce the effect of outliers, and then calculating the average OCR for each subject, head tilt, and image type. We calculated the change

in OCR between head tilts for fractal viewing by subtracting the OCR during head tilt right from the OCR during head upright and by subtracting the OCR during head tilt left from the OCR during head upright.

Results

Effect of head tilt on saccade direction distributions while free viewing fractal images

Our main research question was whether saccade direction distributions would rotate as a function of head tilt (head orientation hypothesis) or stay consistent with the environmental upright (world orientation hypothesis; Fig. 1). For this question, we examined eye movements during trials showing radially symmetric fractal images since these fractals do not contain directional cues or other semantic content.

Figure 5 displays the three polar distributions (one for each head tilt) in both world-referenced coordinates (top row) and head-referenced coordinates (bottom row). The saccade distributions plotted in Figure 5 clearly rotate with the orientation of the head and are not world-fixed. In world coordinates (top row), the average direction distribution displacement (obtained from the cross-correlation technique described in Materials and Methods) across all subjects was 24.13° (95% CI [20.75, 27.51]) between head upright and head right, which was significantly different from the average -24.22° (95% CI [-27.87, -20.56]) displacement between head upright and head left ($t_{(13)} = -21.13$, $p < 0.001$; Cohen's $d = 5.65$). This result indicates that saccade directions during free viewing of fractal images are influenced by head orientation and do not follow the world orientation hypothesis.

After rejecting the world-orientation hypothesis, we next asked to what extent saccade directions follow the head orientation hypothesis. In head coordinates (Figs. 5, 6A,B, bottom row), the average angular direction distribution displacement across all subjects was -3.02° (95% CI [-5.70, -0.33]) between head upright and head right and 2.47° (95% CI [-0.52, 5.48]) between head upright and head left. The average RFindex for these data were 0.10 (Fig. 6D), which was significantly different from zero ($t_{(13)} = 3.12$, $p = 0.008$, Cohen's $d = 0.84$) and confirms that

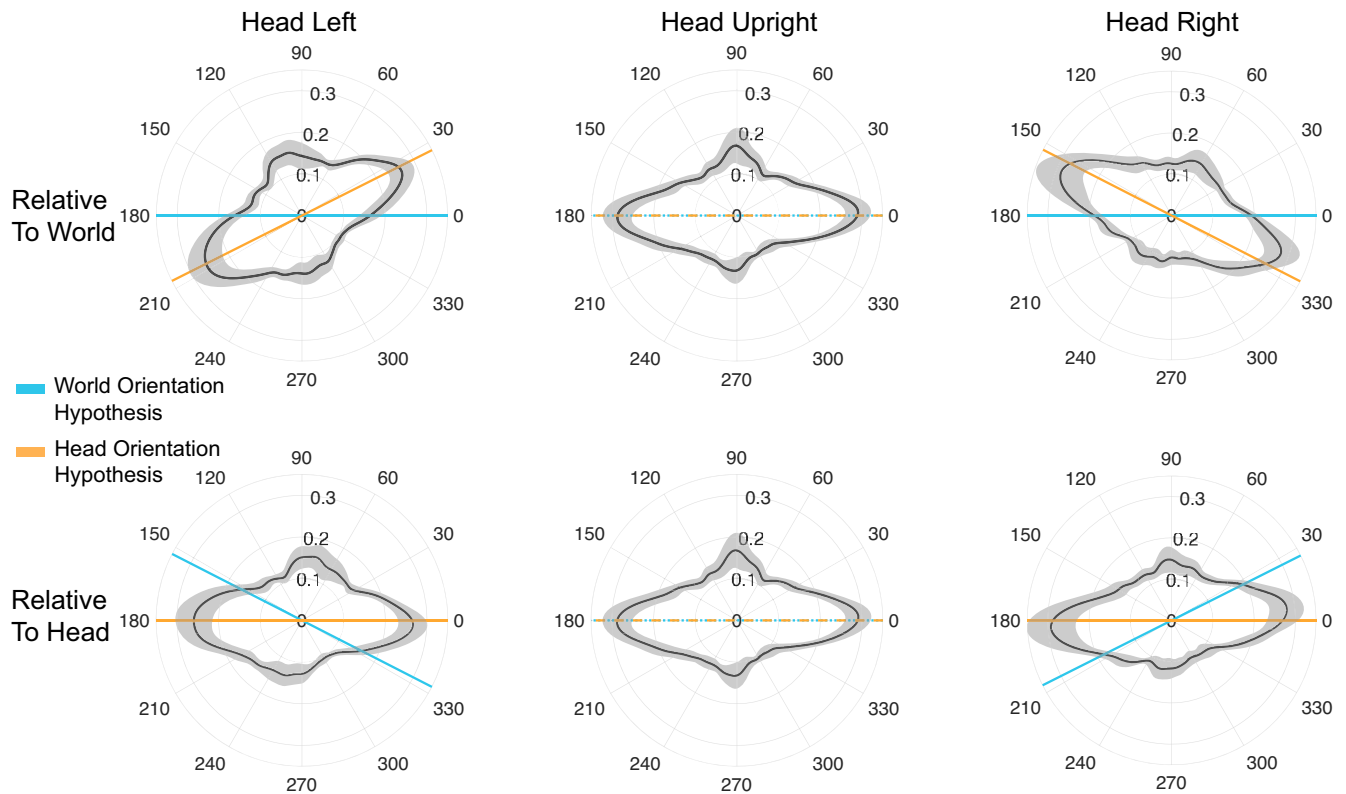


Figure 5. Saccade direction distributions during free viewing of fractal images for head tilt left, head upright, and head tilt right. The top row shows the data relative to the world (i.e., accounting for subject head tilt), while the bottom row shows the data relative to the head. Each polar plot is calculated by applying a circular kernel density estimate on saccade direction data. The angles of the polar plots represent degrees while the radius indicates normalized frequency. The black histogram line indicates the mean across subjects while the shaded gray indicates 95% CIs. The blue and orange lines indicate the orientation of the world and head hypotheses, respectively, showing the average measured head tilt.

the head orientation hypothesis can be rejected. This indicates that saccade directions do not perfectly follow the head orientation and that there is some degree of offset that may originate from ocular counter roll.

These results suggest an alternative to the world-orientation or head-orientation hypothesis. During head tilt, ocular counter roll (OCR) brings the eye in the opposite direction of the head toward Earth upright. OCR only partially compensates for head tilt in humans, and asymptotes at around 8° – 10° . It is thus possible that the saccade bias is generated with respect to a retinal or eye reference frame instead of a head reference frame. Indeed, the deviations observed relative to the head-orientation hypothesis for both tilt directions are qualitatively consistent with this hypothesis, so we explored it further. We aimed to analyze the eye tracking torsion data for all subjects to determine whether a retinal reference frame is the best explanation for the saccadic eye movements during free viewing of fractals. Figure 7A shows OCR traces for one subject while Figure 7B shows the change in median OCR values for all subjects where torsion was successfully measured (11 of 14 subjects). On average, the change in median OCR between head tilt right and upright was -2.57° (95% CI [-3.9 , -1.2]) while the change in median OCR between head tilt left and upright was 5.49° (95% CI

[4.2 , 6.8]; Fig. 7B). The direction distribution displacement values, obtained with the cross-correlation technique described in Materials and Methods, and the median OCR values are roughly on the same order of magnitude (Fig. 7C). Although there is not a direct correlation ($\rho = 0.21$, $p = 0.36$), the study was not designed to have sufficient power to detect a correlation. To determine whether saccades are generated with a retinal reference frame, we calculated an additional reference frame index by scaling direction distribution displacement values by the change in median OCR. The average reference frame index for these data were 0.78 (Fig. 7D), which was significantly different from zero (indicating a head reference frame; $t_{(13)} = 3.63$, $p = 0.005$, Cohen's $d = 1.09$) and not significantly different from one (indicating a retinal reference frame; $t_{(10)} = 1.00$, $p = 0.34$). This suggests that the orientation of the saccade direction bias during fractal viewing as a result of head tilt may be explained by OCR.

Effect of head tilt on saccade direction distributions while free viewing a scene

We next asked whether saccade directions are influenced by head tilt when viewing an Earth upright scene. If the content of the scene is strong enough to change the orientation of the horizontal bias in response to scene tilt

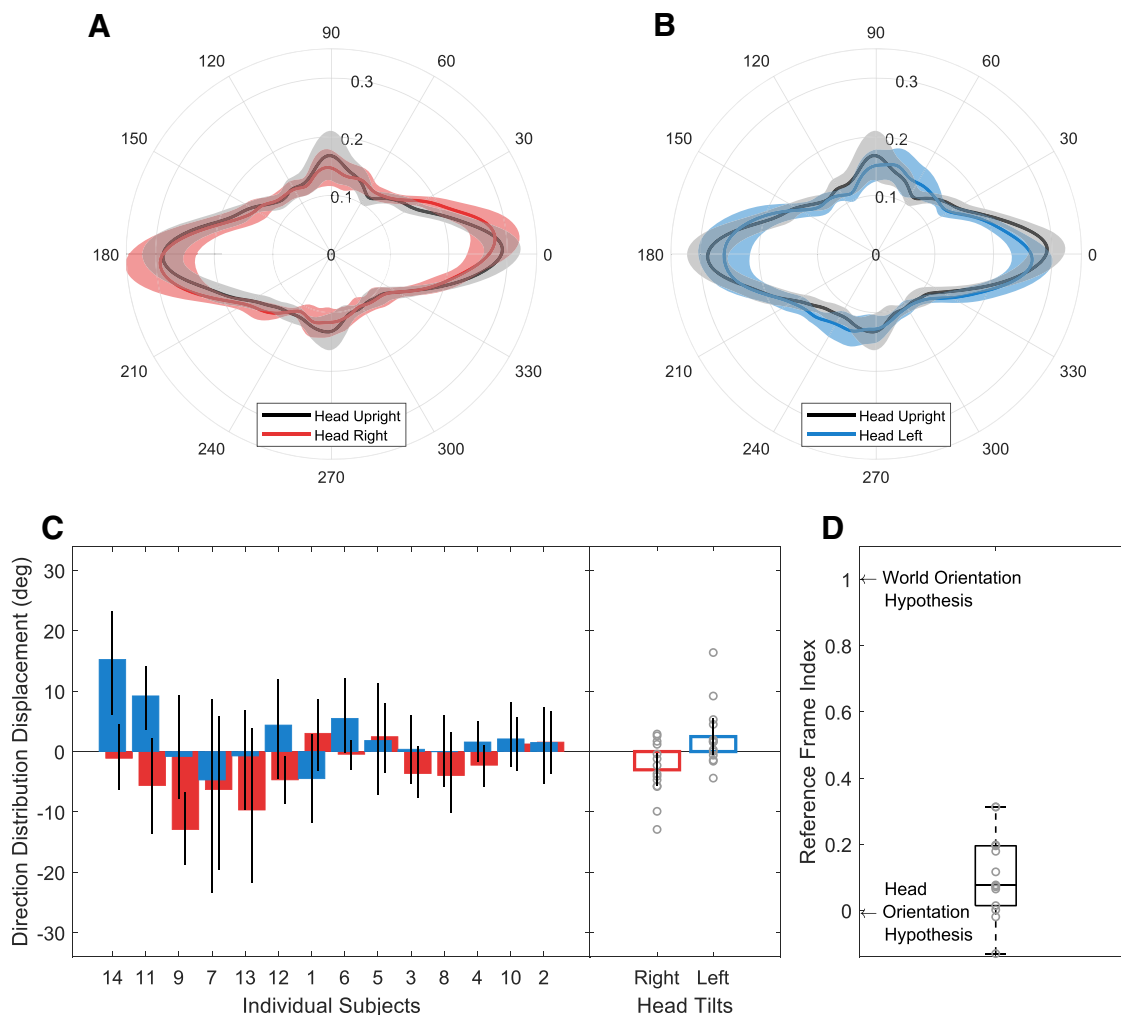


Figure 6. Saccade polar histograms for all subjects during fractal viewing, shown in head coordinates, for (A) head upright and head tilt right distributions and (B) head upright and head tilt left distributions. C, Left, Bootstrapped average displacements for individual subjects with 95% CI error bars. Right, Bar plots showing the direction distribution displacement for all subjects. Circles represent individual data and error bar represents 95% CIs. D, Box and whisker plot showing the reference frame index derived by scaling the direction distribution displacement values for each subject by their head tilt amount in degrees.

(Foulsham et al., 2008; Bischof et al., 2020), then one possibility is that the saccade distributions for all Earth upright scenes will look the same regardless of head orientation (we call this the “image orientation hypothesis”). However, if head or retinal orientation play a key role in saccade generation, then we would expect different distributions among head tilts. For this analysis, we calculated polar histograms in world coordinates (i.e., accounting for head tilt; Fig. 8A,B) and then implemented the cross-correlation procedure (see Materials and Methods) for each subject to obtain direction distribution displacements. We used the subset of conditions with Earth upright scenes for this analysis: namely, 30° natural scenes during head tilt left, 0° natural scenes during head upright, and −30° natural scenes during head tilt right. We found an average direction distribution displacement of 12.01° (95% CI [8.36, 15.66]) when comparing head tilt right and upright and −8.32° (95% CI [−11.35, −5.30]) when comparing head tilt left and

upright (Fig. 8C). The average reference frame index was 0.38, which was significantly different from zero (indicating an image reference frame; $t_{(13)}=8.16$, $p < 0.001$, Cohen’s $d=2.18$) and one (indicating a head reference frame; $t_{(13)}=13.38$, $p < 0.001$, Cohen’s $d=3.58$). This result indicates that when individuals view an upright natural scene while their head is tilted, saccades do not precisely follow the orientation of the image or the orientation of the head. Instead, saccade directions fall somewhere in the middle, which suggests that head orientation matters even when viewing an Earth upright scene.

Effect of scene tilt on saccade direction distributions

Previous work has shown that saccade directions follow the orientation of a natural scene. To confirm the influence of natural scene tilt on saccade directions while the head is upright, we calculated polar histograms (Fig. 9A, B) and measured the direction distribution displacements

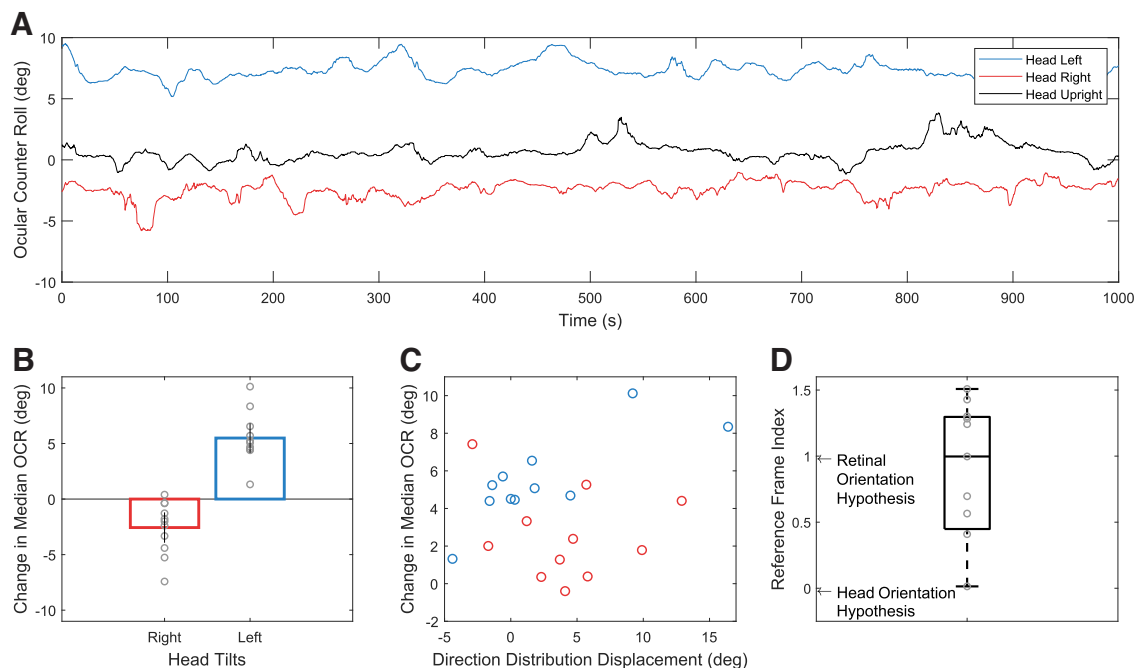


Figure 7. **A**, Ocular counter roll traces from one subject from head tilt left, head upright, and head tilt right conditions. **B**, Change in median OCR values for each subject derived by subtracting the median OCR value of head tilt left (or right) from the median OCR value of head upright. Circles represent individual subjects. Error bars indicate 95% CIs. **C**, Change in median OCR as a function of the cross-correlation displacement values for each subject (negative values were reversed). **D**, Reference frame index found by scaling the direction distribution displacement values for each subject by their change in median OCR amount in degrees.

(Fig. 9C) between -30° and 0° scene tilts as well as 30° and 0° scene tilts. In our sample, we found that some subjects were very likely to make saccades following the orientation of the image while others were less likely. There was a mean direction distribution displacement of 14.02° (95% CI [9.33, 18.70]) when comparing 0° and 30° scene tilts and -10.71° (95% CI [15.09, -6.33]) when comparing 0° and -30° scene tilts (Fig. 9C). The reference frame index was 0.41 (Fig. 9D), which was significantly different from zero (indicating a head reference frame; $t_{(13)} = 7.35$, $p < 0.001$, Cohen's $d = 1.97$) and significantly different from one (indicating an image reference frame; $t_{(13)} = 10.48$, $p < 0.001$, Cohen's $d = 2.80$). This result suggests that saccade directions were made neither in direct alignment with the scene (that was Earth upright) nor the head (that was tilted). The exact reference frame here is somewhat ambiguous, perhaps in part because of the high variability across subjects in our data (Fig. 9C). We also compared the effect of image tilt relative to the head for all three head tilts and observed a comparable effect ($F_{(2,39)} = 2.96$, $p = 0.06$).

Discussion

When humans free view scenes, saccades are more likely to occur in the cardinal directions and especially in the horizontal direction. It is unclear what happens to saccade direction biases in response to head tilt. We asked whether saccade biases remain fixed to a world reference frame, a head reference frame, or some other reference frame. To answer this research question, we used the saccade direction anisotropy to study the impact of head orientation on

saccade generation by recruiting individuals to view fractal and natural scene images at three head orientations and measuring changes in the distribution of saccade directions.

When participants viewed fractals that contained radially-symmetric orientation cues, we found that saccade direction distributions remained largely fixed relative to head orientation. However, we found that saccade distributions were systematically offset from exact alignment with the head. This slight offset was of the same order of magnitude and direction as predicted by ocular counter roll (OCR). These results suggest that when strong orientation information is unavailable (such as when free viewing fractal images), saccades are generated with respect to an egocentric reference frame that is likely in retinal coordinates. Additionally, when participants viewed Earth upright natural scenes while tilting the head, we found that head orientation had a significant effect on saccade directions with saccade distributions falling in between a head reference frame and a world reference frame. Given previous work showing that the orientation of a scene influences the way we look at it (Foulsham et al., 2008; Anderson et al., 2020; Bischof et al., 2020), this finding clarifies that it is not just the orientation of the scene that matters, but also the orientation of the head and retina with respect to the gravity-driven world. From this analysis, we conclude that head orientation has an impact on saccade directions even when viewing an Earth upright scene.

As a confirmation of previous work, we also set out to examine the effect of scene tilt on saccade directions when the head is upright. In general, we found agreement

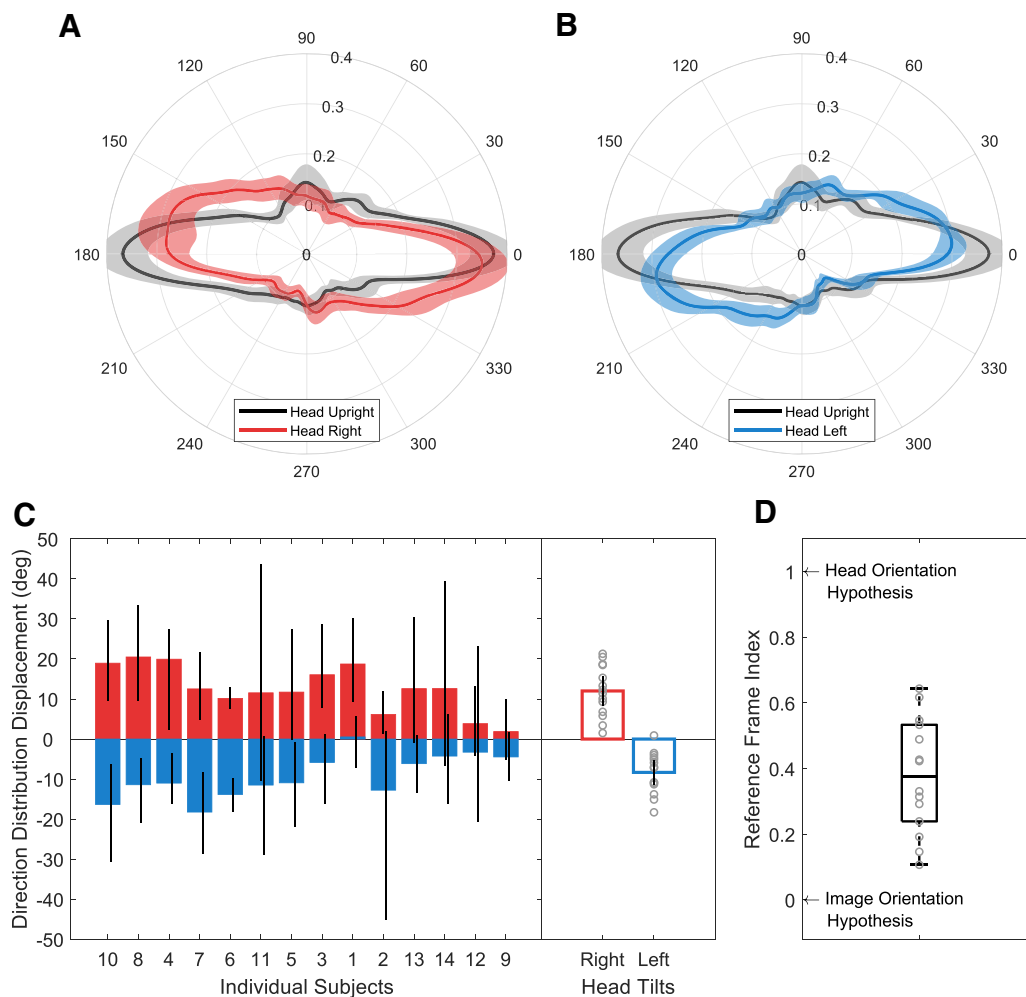


Figure 8. Saccade polar histograms for all subjects during Earth upright scene viewing, shown in world coordinates, for (A) head upright and head tilt right distributions and (B) head upright and head tilt left distributions. C, Left, Bootstrapped average displacements for individual subjects with 95% CI bars. Right, Bar plots showing the direction distribution displacement for all subjects. Circles represent individual data and error bar represents 95% CIs. D, Box and whisker plot showing the reference frame index derived by scaling the direction distribution displacement values for each subject by their head tilt amount in degrees.

with previous literature showing that saccade directions follow the orientation of the scene (Foulsham et al., 2008; Anderson et al., 2020; Bischof et al., 2020). However, while previous work appeared to show almost perfect alignment between saccade directions and scene orientation as shown qualitatively by polar histograms, our data revealed high subject variability such that some subjects made saccades that were closely aligned with the scene while others made saccades that were not aligned with the scene. It is currently unclear why this discrepancy occurs. One difference among studies is the angles of image tilt tested. While we only focused on a 30° tilt, previous studies used 45° and 90° tilts.

There are known biases in visual perception and scene statistics that might be related to the biases observed in saccade direction. In perception, the oblique effect corresponds with enhanced performance of the discrimination of horizontally and vertically oriented stimuli (Appelle, 1972; B Li et al., 2003), while the visual field effect shows biases in performance for stimuli located along the vertical

and horizontal meridians (Carrasco et al., 2001). It could be that these perceptual biases are related to saccade motor biases in one of two ways: (1) the visual system could compensate for worse perception in the oblique directions, such as in the visual field effect, by generating more saccades in those directions, or (2) enhanced perception in horizontal and vertical directions may increase the likelihood of selecting a target and prompting a saccade in those directions. There is evidence for this second possibility in studies using gaze-contingent displays that shows that humans make more saccades in the direction where their vision is best (Foulsham et al., 2011). Researchers have hypothesized that these perceptual biases result from an optimal adaptation to scene statistics (Girshick et al., 2011). Indeed, orientation contours in natural scenes are strongest for the horizontal and vertical directions (Switkes et al., 1978). The saccade biases may be related directly to the statistics of natural scenes by increasing the power of parallel orientations in scenes during saccades (Rolfs and Schweitzer, 2022). Others have

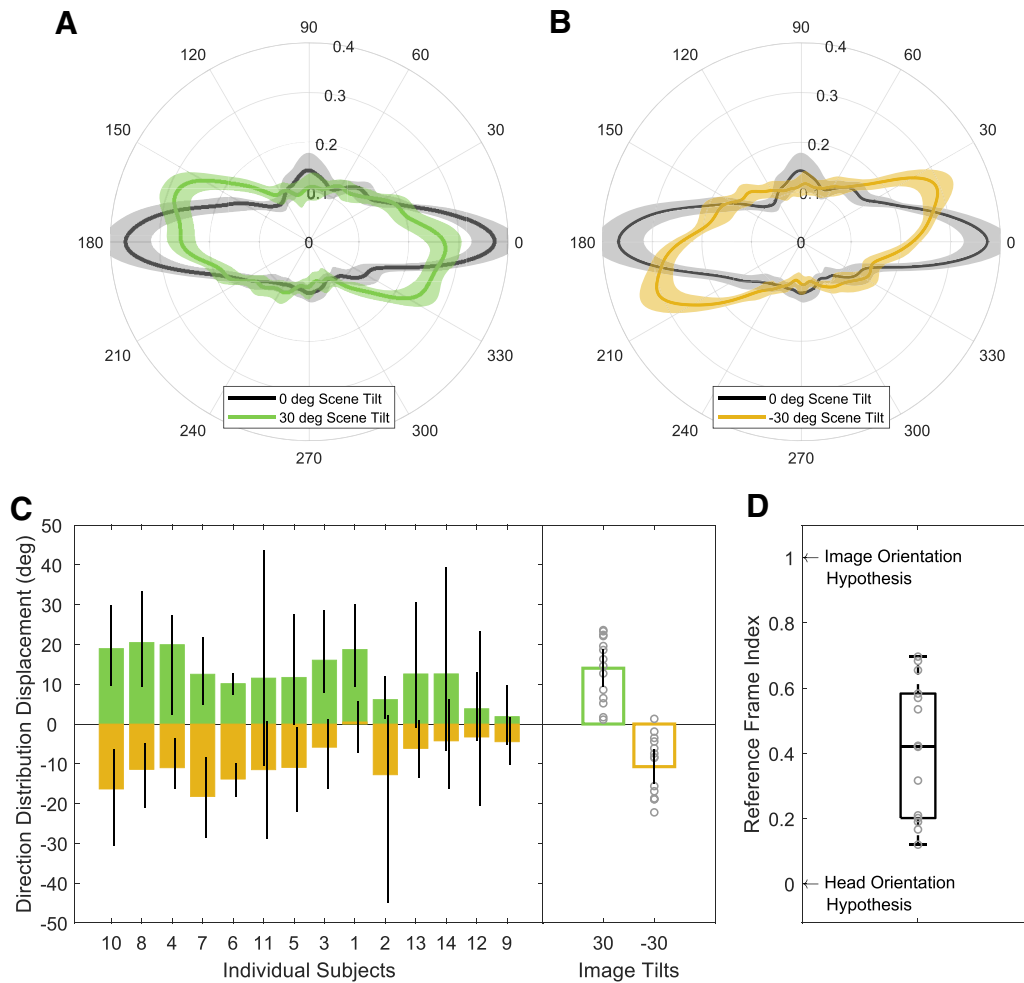


Figure 9. Saccade direction polar histograms during head upright for scenes with (A) 0° and 30° tilt and (B) 0° and -30° tilt. C, Left, Bootstrapped average displacements for individual subjects with 95% CI bars. Right, Bar plots showing the direction distribution displacement for all subjects. Circles represent individual data and error bar represents 95% CIs. D, Box and whisker plot showing the reference frame index derived by scaling the direction distribution displacement values for each subject by the scene tilt amount in degrees.

found that natural scene statistics and neural representations of natural images are critical factors in guiding saccades and saccade amplitudes across species (Samonds et al., 2018). Our analysis confirms previous work showing that scene orientation influences saccade directions, although it is unlikely that scene statistics are entirely responsible for the bias in saccade directions since the saccade bias is present even in the absence of a scene (Otero-Millan et al., 2013).

Previous studies have looked at the effect of head tilt on some of these perceptual biases and on how the brain encodes visual stimuli during head tilt. For example, Mikellidou (2015) examined whether the oblique effect is anchored to an allocentric or egocentric reference frame and found that the effect was allocentric when sitting upright (regardless of head tilt) but egocentric when lying supine. Banks and Stolarz (1975) also examined whether visual sensitivity (acuity) was grounded in allocentric or egocentric coordinates and found that the decrease in visual performance with head tilt was likely

explained by OCR, which indicates that meridional visual acuity differences correspond to the retinal and not spatial orientation of the stimulus. Clearly the brain has access to multiple frames of reference, but it is unclear how this information is combined and used. While it is possible that saccades are generated retinotopically since cortical areas of the brain are retinotopically organized and receive retinotopic visual information, it is also possible that neurons store sensory and motor events in multiple reference frames simultaneously. For example, even when accounting for ocular torsion, neuronal receptive fields shift in early visual areas (Pouget et al., 2002; Daddaoua et al., 2014; Khazali et al., 2020). In this view, there is not a single reference frame that is or is not transformed, but rather multiple flexible reference frames that can be accessed in a variety of ways.

Determining the reference frame of saccade planning and execution has been a major subject of research for decades, and yet, to this day, we are still puzzled by the ways in which the brain encodes complex

visual information and interprets it into a well-coordinated motor command. From animal, human, and computational studies, five general brain regions have been identified as contributing in a significant way to saccade generation: brain stem reticular formation saccadic burst generators, superior colliculus, cerebellum, basal ganglia, and premotor cortical areas (Girard and Berthoz, 2005). The overall task of all these brain areas is to select what saccade must be executed by integrating information from visual, vestibular, auditory, and proprioceptive sensory modalities that are encoded in different frames of reference. Whichever brain area or areas are the source of the biases in saccade generation must encode saccades with a mixture of egocentric (eye or head) and allocentric reference frames. Indeed, most studies of goal-related activity in the superior colliculus (SC), frontal cortex, and posterior parietal cortex (PPC) have shown that a gaze-centered retinal frame of reference is likely (Klier et al., 2001; Andersen and Buneo, 2002; Crawford et al., 2011), in alignment with the work presented here. However, allocentric maps must also be created and used in saccade generation since we know that saccade directions are influenced by the orientation of natural scenes and allocentric cues are important for gaze precision (J Li et al., 2017). Such allocentric maps could influence saccade direction biases through the alignment of salient or semantically important objects, through low-level visual statistics such as orientation energy, or even from high-level perception of gravitational upright. Recently, research has suggested that allocentric and egocentric maps are combined in the frontal eye fields (FEFs; Bharmauria et al., 2020), although other brain areas are likely involved as well.

In conclusion, we show that signals indicating head orientation can influence known statistics of saccade directions. These results suggest that head and retinal orientation relative to gravity play a key role in saccade generation. Head tilt is a valid tool that can be used to disambiguate the reference frame of saccade generation mechanisms by comparing retinal, head, and world coordinates. Moving forward, integrating head orientation information into models of saccade generation and target selection may improve our ability to understand and predict saccade patterns under natural viewing conditions.

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