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The Upper Eye Bias: Rotated Faces Draw Fixations to the Upper Eye

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Abstract
There is a consistent left-gaze bias when observers fixate upright faces, but it is unknown how this bias manifests in *rotated faces*, where the two eyes appear at different heights on the face. In two eye-tracking experiments, we measured participants' first and second fixations, while they judged the expressions of upright and rotated faces. We hypothesized that rotated faces might elicit a bias to fixate the *upper eye*. Our results strongly confirmed this hypothesis, with the *upper eye bias* completely dominating the left-gaze bias in ±45° faces in Experiment 1, and across a range of face orientations (±11.25°, ±22.5°, ±33.75°, ±45°, and ±90°) in Experiment 2. In addition, rotated faces elicited more overall eye-directed fixations than upright faces. We consider potential mechanisms of the upper eye bias in rotated faces and discuss some implications for research in social cognition.

Keywords
attention, eye movements, face perception, features/parts

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Introduction

Faces are like visual magnets, drawing our visual attention quickly, automatically, even if we attempt to avoid them (Crouzet, Kirchner, & Thorpe, 2010). Gazing at a face allows us to extract socially relevant information about the person, including identity, gender, age, race, expression, and the direction of gaze. In turn, the type of information we seek to gather from a face influences how we scan the face and what facial features we are most likely to fixate (Boutet, Lemieux, Goulet, & Collin, 2017; Vaidya, Jin, & Fellows, 2014). Although the task, context, individual differences, and social and cultural factors can all affect our gaze behavior toward faces, there are also consistent biases found across most observers.

One of the most well-studied biases in face processing is the *left-gaze bias* in which most right-handed observers tend to fixate and attend more to the left side of the face (i.e., left from the observer's perspective). A left perceptual bias in face perception was first reported by Gilbert and Bakan (1973) using *chimeric* faces that were constructed by combining two face halves. They found that most observers judged *left/left* chimeric faces to be more similar to the original face than *right/right* chimeric faces. This bias did not depend on any particular asymmetries of the face but rather on which side of the visual field the face half appeared. Campbell (1978) later found a similar perceptual bias when people judge emotional expressions: Chimeric faces with different expressions on each half were more likely to be judged based on the expression on the left half. These behavioral findings have been corroborated by a large body of eye-tracking research showing that across a variety of tasks and contexts, most right-handed observers fixate more often and longer on the left side of faces (Butler et al., 2005; Guo, Meints, Hall, Hall, & Mills, 2009; Guo, Smith, Powell, & Nicholls, 2012; Hsiao & Cottrell, 2008; Mertens, Siegmund, & Grüsser, 1993; Van Belle, Ramon, Lefèvre, & Rossion, 2010).

An advantage for processing the left side of the face is likely related to the right-hemisphere lateralization of the face-processing network (Yovel, Tambini, & Brandman, 2008). Early patient studies showed that damage to the right temporal and occipital lobes caused impairments in face perception (Benton, 1980; Damasio & Damasio, 1989). More recent electrophysiological and neuroimaging studies of healthy, right-handed observers consistently show stronger responses to faces in the right-hemisphere face-processing regions, including the fusiform gyrus, right inferior occipital gyrus, and right superior temporal gyrus, compared with their left-hemisphere counterparts (Davidenko, Remus, & Grill-Spector, 2012; Kanwisher, McDermott, & Chun, 1997; Rossion, Joyce, Cottrell, & Tarr, 2003; Yovel et al., 2008). For example, Yovel et al. (2008) found that the lateral asymmetry of the fusiform face area was correlated with individuals' left visual field advantage in face processing. Nevertheless, the relationship between a right-lateralized face-processing network and the tendency to *gaze* at the left half of the face is less well understood. Gazing at the left half of the face places the majority of the face in the right visual field, which is not optimal for right-hemisphere processing. One possibility is that the right face-processing regions can process faces with less visual information, so a left-gaze bias might allow for more efficient division of labor between the two hemispheres.

The vast majority of research examining the left-gaze bias in face processing has been conducted using upright face stimuli; however, the in-plane orientation of a face is known to dramatically affect face perception and recognition. Early behavioral work by Yin (1969) and Thompson (1980) showed that there are disproportionate impairments in face perception and recognition when faces are rotated by 180° or vertically inverted. This phenomenon, known as the *face inversion effect*, is so prominent that it is often used as a behavioral marker of holistic processing. When a face is inverted or rotated by 180°, the typical configuration of its features (two eyes on top, a nose in the middle, and a mouth on the bottom) is disrupted, and so are the holistic behavioral and neural face-processing mechanisms that depend on that spatial configuration (Marinkovic, Courtney, Witzel, Dale, & Halgren, 2014; Zhang, Li, Song, & Liu, 2012; Zhao et al., 2014). But the disruption of holistic face processing is not limited to inverted faces; impairments are evident in processing sideways faces (Stürzel & Spillmann, 2000; Rossion, 2008), $\pm 45°$-rotated faces (Valentine & Bruce, 1988), and even $\pm 15°$-rotated faces (Rosenthal, Levakov, & Avidan, 2017).

Although it is clear that the in-plane orientation of a face has a profound influence on perception, the effect of in-plane orientation on fixation patterns to faces is largely unknown. A few past studies have reported differences in how we fixate upright compared with inverted faces (Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006; Xu & Tanaka, 2013). Whereas upright faces elicit most fixations to the eyes and nose, inverted faces draw most fixations to the nose and mouth. However, no study to our knowledge has systematically examined gaze behavior to faces at intermediate in-plane orientations and in particularly how the left-gaze bias manifests (or fails to manifest) in rotated faces. This article aims to address this question.

Geometrically, rotating a face clockwise or counterclockwise disrupts its horizontal symmetry and creates vertical asymmetries in the placement of features. In particular, when a face image is rotated counterclockwise, the right eye (from the observer's perspective) ends up higher in the observer's visual field than the left eye. Based on previous research showing upper field advantages in visual processing (Najemnik & Geisler, 2005; Paulun, Schütz, Michel, Geisler, & Gegenfurtner, 2015), we hypothesized that rotated faces would elicit an *upper eye bias* that would compete with (and possibly override) the left-gaze bias in counterclockwise-rotated faces.

Here, we present data from two eye-tracking experiments designed to test this hypothesis. In Experiment 1, participants completed an expression judgment task with faces presented upright, rotated by $+45°$ (clockwise), or rotated by $-45°$ (counterclockwise). We analyzed the distribution of first and second fixations as a function of face orientation. Based on the results, we designed Experiment 2 to measure fixations to faces at a broader range of in-plane orientations. Our findings across the two experiments provide novel evidence of a strong *upper eye bias* when observers gaze at rotated faces.

Methods and Results

Experiment 1: Do Rotated Faces Elicit an Upper Eye Bias?

The goal of Experiment 1 was to determine whether rotating a face image by $\pm 45°$ (thereby introducing a discrepancy in the height of the two eyes) leads observers to fixate more on the upper eye. If the left-gaze bias is robust to changes in orientation, observers should be biased to fixate the left eye over the right eye across upright and rotated faces alike. Alternatively, if there is a fixation bias favoring the upper eye in rotated faces, observers' left-gaze bias should be attenuated in counterclockwise-rotated faces in which the right eye appears higher in the observer's visual field than the left eye.

Stimuli. We selected 42 front-view faces (21 females, 21 males) from the FERET face database (Phillips, Moon, Rizvi, & Rauss, 2000; Phillips, Wechsler, Huang, & Rauss, 1998) lacking any distinguishing characteristics (such as moles or scars) that might bias observers to look more to one side of the face over the other. Images were cropped with an oval region preserving only the face. For the eye-tracking experiment, we presented both intact and mirror-reversed versions of each face image, to eliminate stimulus-level factors. However, to confirm that mirror-reversing the faces would not produce unusual asymmetries (e.g., by reversing typical hair styles), we conducted a pilot study to test whether observers could distinguish between intact and mirror-reversed faces. For the pilot study, 23 undergraduates (18 females) from the University of California (UC), Santa Cruz were asked to report whether they thought each of the 42 face images was original or mirror-reversed by pressing one of the two buttons. Performance was at chance: The mean proportion correct across the 23 participants was .51 (95% confidence interval [.48, .54]) which did not differ from chance, $t(22) = 0.70$, $p = .5$. Similarly, the mean proportion correct across the 42 face images was .51 (95% confidence interval [.47, .54]), which did not differ from chance, $t(41) = 0.61$, $p = .5$. These pilot data indicate that observers are not able to determine whether or not a face image has been mirror-reversed. In the eye-tracking experiment, face images were shown on a 21″ computer screen placed 18″ away from the observer. The computer screen subtended approximately 53° (width) by 32° (height), and faces subtended approximately 11° by 14° when presented upright.

Participants. For the eye-tracking experiment, we recruited 15 participants (10 females) from UC Santa Cruz who were compensated with course credit. Based on previous studies of the left-gaze bias, we believed this would be an appropriate sample size. The study was approved by UC Santa Cruz's Institutional Review Board, and participants gave informed consent before participating. Participants were all right-handed, had normal or corrected-to-normal vision with contact lenses, and were naive to the purpose of the experiment.

Procedure. Participants sat upright using a chin and forehead rest to stabilize their heads. Before the study began, participants' eyes were calibrated with nine fixations points on the screen. In each trial, participants were first prompted to fixate a central cross. After 2 seconds, the fixation cross disappeared, and a face was displayed such that the tip of the nose appeared in the location where the fixation cross had been. Participants were instructed to judge the expression of the face as smiling or neutral and wait for an audible beep (which occurred 1.5 seconds after the face appeared) before entering their response by pressing one of the two keys. Across trials, faces appeared randomly in one of the three possible orientations: 0° (upright), +45° (clockwise), or −45° (counterclockwise), with 14 faces shown at each orientation. Across participants, we counterbalanced which faces were shown in the original or mirror-reversed format to eliminate potential stimulus asymmetry effects. The study took approximately 8 minutes to complete.

Eye tracking. We used a GazePoint Eye Tracker with 60 Hz sampling frequency and 0.5° accuracy. Screen recordings superimposed with the interpolated fixation positions were analyzed during the 1.5 seconds (90 frames) face-exploration phase of face exploration in each trial. Because the position of face features differed widely across different face stimuli and orientations, analysis of fixations was done manually by trained research assistants who were unaware of the purpose of the experiment. First and second fixations in each trial were coded by three independent research assistants as fixations lasting 150 milliseconds or more, falling on one of the following locations: left eye (including eyebrow), right eye (including eyebrow), nose (including bridge of the nose), mouth, forehead, or other. To ensure reliability of results, the analyses below are based on trials in which there was agreement between at least two of the three coders, which resulted in an average of 82% usable trials per participant.

Results of Experiment 1

The distribution of first and second fixations to upright and rotated faces is shown in Figure 1. Analysis of first fixations revealed a significant left-gaze bias in upright faces, manifesting as a higher proportion of first fixations to the left eye ($M = .19$, standard error [SE] = .04) compared with the right eye $M = .02$, $SE = .02$, $t(14) = 2.16$, $p = .05$. The left-gaze bias was even more apparent in second fixations, with many more second fixations landing on the left eye ($M = .32$, $SE = .07$) compared with the right eye, $M = .08$, $SE = .04$, $t(14) = 2.87$, $p = .01$. Critically, the orientation of the face had a strong effect on the distribution of first and second fixations. Clockwise-rotated (+45°) faces elicited an even larger left-gaze bias than upright faces, with a higher proportion of first fixations to the left eye ($M = .34$, $SE = .09$) compared with the right eye, $M = .01$, $SE = .01$, $t(14) = 3.68$, $p = .002$. In contrast, counterclockwise-rotated (−45°) faces showed the opposite: a strong *right eye bias*, with significantly more fixations to the right eye ($M = .27$, $SE = .09$) compared with the left eye ($M = .02$, $SE = .01$). In other words, the *upper eye* elicited a plurality of first fixations in 45°-rotated faces, regardless of whether it was the left or right eye.

This upper eye bias remained just as strong in second fixations, with second fixations to the upper eye surpassing second fixations to the lower eye in clockwise-rotated faces, M_{Upper}

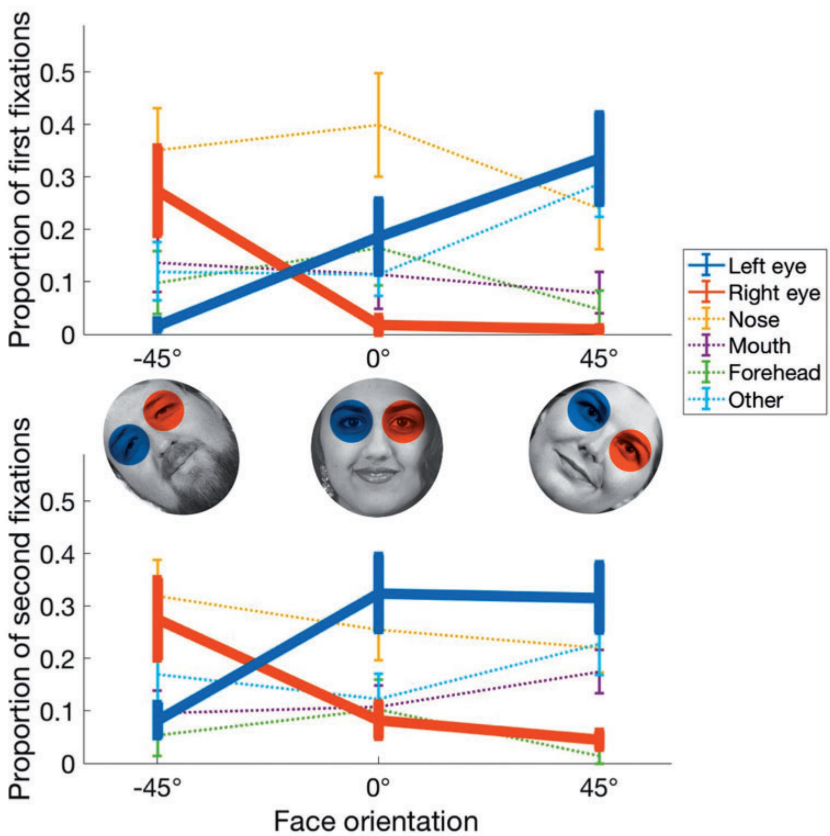

Figure 1. Results of Experiment 1. The average distribution of first (top panel) and second (bottom panel) fixations across 15 participants to the left eye (blue), right eye (red), and other features in upright and rotated faces. Error bars denote the standard error of the mean.

$_{\text{Eye}} = .31$, $SE = .07$ versus $M_{\text{Lower Eye}} = .04$, $SE = .02$, $t(14) = 3.56$, $p = .003$, as well as in counterclockwise-rotated faces, $M_{\text{Upper Eye}} = .28$, $SE = .08$ versus $M_{\text{Lower Eye}} = .08$, $SE = .03$, $t(14) = 2.20$, $p = .05$ (see Figure 1, lower panel). Overall, these results clearly indicate the existence of a robust *upper eye bias* in ±45°-rotated faces that not only competes with but also dominates the left-gaze bias.

Experiment 2: At What Orientation Does the Upper Eye Bias Emerge?

It is clear from the results of Experiment 1 that a ±45° rotation is sufficient to override participants' left-gaze bias in favor of an upper eye bias. The goal of Experiment 2 was to determine more precisely at what angle the upper eye bias emerges and how fixation patterns change across a broader range of face orientations.

Stimuli. For this experiment, we selected 196 faces from the Chicago Face Database (Ma, Correll, & Wittenbrink, 2015); half smiling and half neutral, half female and half male, and half White and half Black. Faces were shown in gray-scale, cropped below the neck, and subtended approximately 10° by 13° of visual angle when upright. Each face was shown at one of the 14 orientations (0°, ±11.25°, ±22.5°, ±37.75°, ±45°, ±90°, ±135°, and 180°), with 14 unique faces shown at each orientation. As in Experiment 1, we used half intact and half mirror-reversed images to avoid potential stimulus asymmetry effects. The orientation at which each face image was shown, and its presentation as intact or mirror-reversed, was randomized across participants.

Participants. We recruited a new group of 13 participants (9 females) from UC Santa Cruz who were compensated with course credit. The study was approved by UC Santa Cruz's Institutional Review Board, and participants gave informed consent before participating. All participants were naive to the hypothesis of the experiment, and none had participated in Experiment 1. Participants were all right-handed and had normal or corrected-to-normal vision with contact lenses.

Procedure. The procedure was identical to that in Experiment 1, except that there were 196 trials, and the study took approximately 15 minutes to complete.

Eye tracking. We used the same GazePoint eye tracker as in Experiment 1 and the same coding paradigm for classifying first and second fixations, with three independent research assistants coding each participant's data. The analyses below are based on trials in which there was agreement between at least two of the three coders, which resulted in an average of 88% usable trials per participant.

Results of Experiment 2

The distribution of first and second fixations to faces at different orientations is shown in Figure 2 (top and bottom panels, respectively). Although there was a slight tendency for participants to fixate the left eye (0.11 first fixations and 0.13 second fixations) over the right eye (0.06 first fixations and 0.10 second fixations) in upright faces, this difference did not reach statistical significance ($|T\text{s}| < 0.8$, $p\text{s} > .4$). Of the 13 participants, 6 showed a consistent left-gaze bias, 2 showed a consistent right-gaze bias, and 5 showed no significant lateral bias.

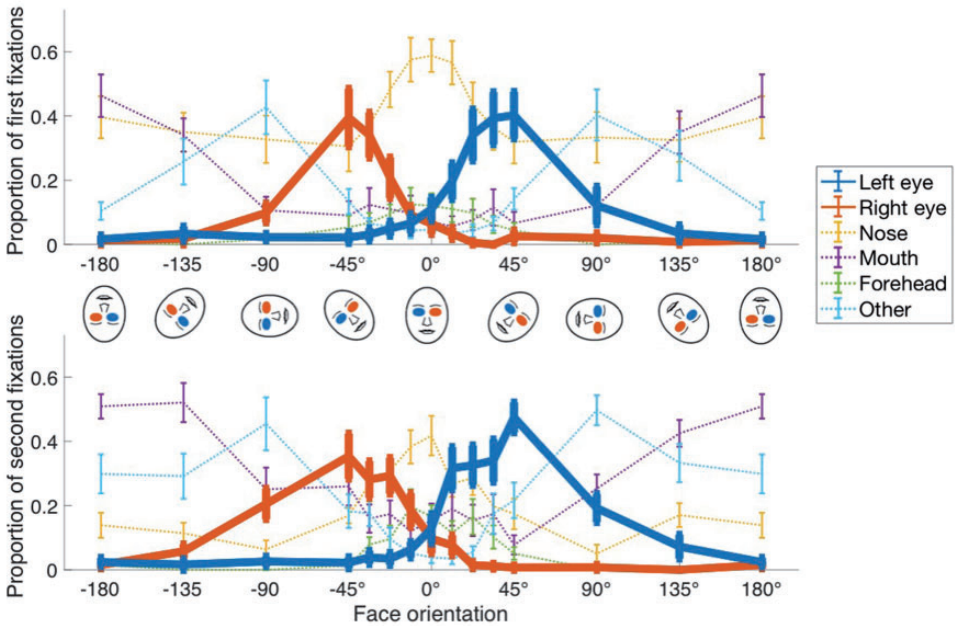

Figure 2. Results of Experiment 2. The average distribution of first (top) and second (bottom) fixations across 13 participants to the left eye (blue), right eye (red), and other features in upright and rotated faces. Error bars denote the standard error of the mean. Data at $-180°$ and $180°$ are the same and shown for symmetry.

Despite a weak left-gaze bias to upright faces, rotated faces once again elicited a robust *upper eye bias* not only at $-45°$ and $+45°$ (replicating Experiment 1) but also across a wide range of face orientations (see Figure 2, red and blue curves). We found a significantly larger proportion of first fixations to the upper eye compared with the *lower eye* for faces at $\pm 90°$, $t(9) = 2.3$, $p = .05$, $\pm 45°$, $t(9) = 4.7$, $p = .001$, $\pm 33.75°$, $t(9) = 5.1$, $p = .0007$, $\pm 22.5°$, $t(9) = 4.36$, $p = .002$, and even $\pm 11.25°$, $t(9) = 2.38$, $p = .04$. That is, with as little as a $\pm 11.25°$ rotation of the face, participants showed a consistent tendency to fixate the upper eye more than the lower eye in their first fixations. The results are nearly identical for second fixations (see Figure 2, bottom panel).

Our data revealed several other interesting gaze patterns for face orientations beyond $\pm 45°$. First, sideways faces (at $+90°$ or $-90°$) elicited significantly fewer first fixations to the upper eye (0.12 and 0.10, respectively) compared with 45° or $-45°$ faces (0.40 and 0.39, respectively; $|Ts| > 3.6$, $ps < .004$), suggesting that the upper eye bias may peak closer to $\pm 45°$ rather than $\pm 90°$, where the two eyes have maximum vertical distance. Second, upside-down faces (180°) elicited a majority of fixations to the mouth region, corroborating past findings (Barton et al., 2006; Xu & Tanaka, 2013). Considering the pattern of fixations across all face orientations suggests there may be a general *upper feature bias* when looking at rotated faces: The upper-most feature (whether it is the left eye, right eye, or the mouth) draws observers' gaze.

Overall Fixations to the Eyes

We also found that *overall fixations to the eyes* (defined as the proportion of combined fixations to the left and right eyes) were more frequent in rotated compared with upright faces (which in turn drew most fixations to the nose; see Figure 2, yellow curve). For example, the average proportion of fixations to the eyes in $\pm 45^\circ$ faces was 0.42 compared with 0.17 for upright faces, which is a significant difference, $t(12) = 3.20$, $p = .008$. The proportion of fixations to the eyes was also higher in faces at $\pm 37.75^\circ$, $M = .38$, $t(12) = 3.35$, $p = .006$, and $\pm 22.5^\circ$, $M = .30$, $t(12) = 2.31$, $p = .04$, compared with upright faces ($M = .17$). Thus, our data show not only that rotated faces elicit a plurality of fixations to the upper eye, but also they draw more overall fixations to the eyes than upright faces.

Performance in the Expression Judgment Tasks

In Experiment 1, we used face images that were classified as having a neutral expression in the FERET database; nevertheless, participants did not consider most of these faces as neutral and responded that they were smiling on 65% of trials. Because we did not include truly smiling faces, we could not distinguish between performance and a smiling bias in this task. In Experiment 2, half of the faces were truly smiling, and half were neutral. However, behavioral performance on the expression judgment task was near ceiling (94.4% on average) and did not vary significantly across orientations, $F(13,181) = 1.3$, $p = .2$. This is not surprising, as the expressions were obvious and participants had at least 1,500 milliseconds to observe each face before responding. Thus, our tasks in Experiments 1 and 2 were not ideally designed to examine potential relationships between fixation behavior and performance in judging expressions across orientations.

Robustness of the Upper Eye Bias Across Experiments

In Experiments 1 and 2, we found a robust upper eye bias across a range of face orientations, and in particular at $\pm 45^\circ$. Although participants across the two experiments observed different sets of faces, we conducted a cross-experiment analysis by defining an *upper eye bias index* for each participant, as the mean proportion of upper eye fixations minus lower eye fixations across -45° and $+45^\circ$ faces, collapsed across first and second fixations. This index ranges from -1 to $+1$, with negative values indicating a lower eye bias and positive values indicating an upper eye bias. Of the 28 total participants, 26 showed an upper eye bias, 1 showed a lower eye bias, and 1 showed no bias (see Figure 3).

General Discussion

We have shown for the first time that *rotated faces* elicit a strong upper eye bias, manifesting as a tendency to fixate the upper eye compared with the lower eye. This bias is evident in first and second fixations, and it is strong enough to override the left-gaze bias for faces at a broad range of rotations. In fact, the tendency to look at the upper eye in rotated faces actually increased the total number of fixations to the eyes compared with upright faces. Here, we consider potential mechanisms of the upper eye bias and discuss implications for research in social perception and cognition.

Mechanisms: General or Face-Specific?

What are possible mechanisms for the *upper eye bias* when participants look at rotated faces? One possibility is that the upper eye bias arises from a general (not face-specific) tendency to attend to stimuli in the upper visual field (Najemnik & Geisler, 2005; Paulun et al., 2015). Our face stimuli were always presented centrally, such that the initial fixation was on the tip of the nose. Therefore, our experiments do not allow us to distinguish

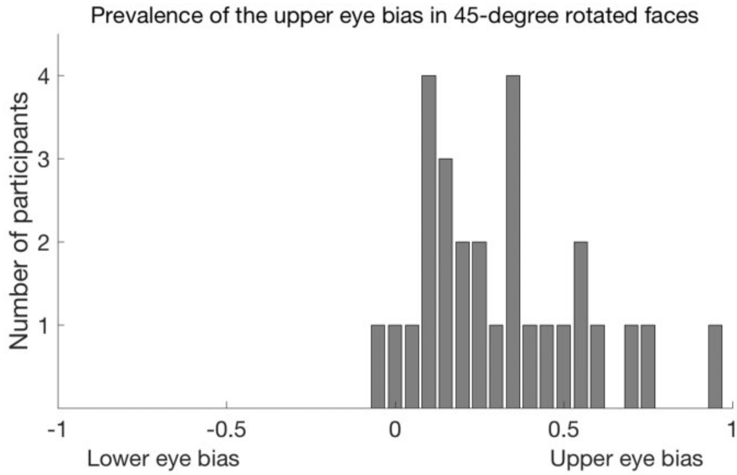

Figure 3. Distribution of the *upper eye bias index* in -45° and $+45^{\circ}$ rotated faces across 28 participants from Experiments 1 and 2. Positive values indicate more fixations to the upper than lower eye.

whether the upper eye bias reflects a bias to fixate the eye that is higher up on the face or simply to fixate the eye that is more directly above fixation. Future experiments may dissociate these possibilities by presenting rotated faces in different positions in the visual field, which may influence first fixations (see Luke & Pollux, 2016). Research showing that infants and adults tend to tilt their heads slightly to the right suggests another possible mechanism for the left eye and upper eye biases (see Güntürkün, 2003). If people typically tilt their heads to the right, it might produce a subtle shift in people's *perceptual upright* consistent with a slight counterclockwise rotation of stimuli (see Dyde, Jenkin, & Harris, 2006). If this is the case, then forcing participants' heads to be upright during eye-tracking experiments may lead to an apparent clockwise rotation of visual stimuli, which could cause the left eye of an upright face to appear slightly higher (closer to the perceptual upright) than the right eye.

It is also possible that the upper eye bias in rotated faces reflects a face-specific fixation strategy. Previous research indicates that there is an optimal viewing position when processing faces: just below the eyes and slightly the left of center (although the exact position varies across tasks and individuals; Arizpe, Walsh, Yovel, & Baker, 2016; Hsiao & Liu, 2012; Peterson & Eckstein, 2012, 2013; Peterson, Lin, Zaun, & Kanwisher, 2016). From this fixation position, the eyes are slightly above and lateral to fixation, and nose and the mouth are below fixation. Recent neuroimaging evidence suggests that responses in face-selective cortex may be tuned to these typical feature positions in the visual field. de Haas et al. (2016) presented observers with isolated face features in different positions in the visual field and measured recognition performance and functional magnetic resonance imaging responses in face-selective cortical regions. When isolated eyes were presented above fixation, they elicited better performance and more consistent face-selective activations than when they were presented below fixation; conversely, an isolated mouth presented below fixation was better recognized and elicited more consistent face-selective activations than when it appeared above fixation (de Haas et al., 2016). Thus, the tendency to fixate just below the eyes in upright faces may serve to optimize the positions of the remaining face features within the visual field for perceptual and neural processing.

When an observer is presented with a *rotated* face, the upper eye might represent a more optimal fixation position than the lower eye because fixating the upper eye places the remaining face features in more typical positions within the observer's visual field. For example, if an observer fixates the upper (right) eye of a -45° (counterclockwise) face, the nose and mouth fall directly below fixation, which is optimal (see Figure 1). In contrast, if the observer fixates the *lower* (left) eye, the nose and mouth fall lateral to fixation, which is not optimal. Thus, the upper eye bias in rotated faces may arise, at least in part, as a strategy to place the remaining rotated face features closer to their optimal positions within the visual field. This hypothesis could be examined by testing whether the upper eye bias is attenuated when eyes are presented in the absence of other facial features or when upright faces are presented that have one eye slightly elevated relative to the other.

Open Questions

Our results leave open the important question of how the upper eye bias might depend on the task and the social context in which rotated faces appear. Here, we employed a simple expression judgment task with static face images, but we posit that the upper eye bias is likely to show up in other tasks (gender discrimination, identity recognition, speech perception, etc.) that use rotated faces. Because our expression judgment tasks either had no truly smiling faces (Experiment 1) or elicited ceiling-level performance (Experiment 2), we were not able to determine whether fixating the upper eye aids or hinders performance in expression judgments. Future studies can employ different (and in particular, more difficult) face perception tasks to examine how performance and gaze patterns vary as a function of face orientation. In particular, it would be possible to test whether fixating the upper eye leads to advantages in face recognition by briefly presenting faces with forced fixation to the upper eye versus lower eye across different face tasks. Such methods have been previously used to determine optimal fixation positions for identity, gender, and emotion processing and for detecting *Thatcherized* features in upright faces (see de Haas & Schwarzkopf, 2018; Peterson & Eckstein, 2012).

Another open question is how the upper eye bias may manifest outside of the lab, where individual differences and social factors play a large role in gaze behavior (see Peterson et al., 2016). Although there is research showing that the left-gaze bias is present during audiovisual speech perception with dynamic faces (Everdell, Marsh, Yurick, Munhall, & Paré, 2007), it is unknown how these findings extend to rotated faces. In real-life, face-to-face conversations, our heads do not always remain upright. Conversational partners often tilt their heads as part of nonverbal communication, sometimes in parallel and sometimes in opposite directions of one another (Ishi, Ishiguro, & Hagita, 2014). It is likely, then, that the angular disparity between partners' faces will often be large enough to influence their mutual gaze behavior. Our data would predict that the more the two partners' faces deviate in their relative orientations, the more each partner will fixate the other's upper eye. Pertinent to this question is the role different reference frames may have in determining which eye is the upper eye. Research has shown that orientation effects in face processing are sensitive not only to the retinal (or egocentric) orientation of face stimuli but also to faces' orientation relative to the environmental reference frame (Davidenko & Flusberg, 2012). To dissociate the influence of these different reference frames, a future study could compare the effect of rotating the face image (as in our experiments) to the effect of rotating the observer's head. If the environmental reference frame plays a significant role, the upper eye bias should be diminished when it is the observer's head rather than the face image that is rotated.

Finally, our finding that rotated faces led to more *overall fixations to the eyes* than upright faces may have intriguing implications for research in social cognition. For example, individuals diagnosed with autism spectrum disorder often show impairments in face processing and display atypical gaze patterns to faces, tending to avoid looking at the eyes (Behrmann, Thomas, & Humphreys, 2006; Dalton et al., 2005). These gaze patterns are not just diagnostic of impairments in social cognition, but they can perpetuate these impairments by providing their visual system with suboptimal information for processing faces (Tanaka & Sung, 2016). Although our studies were conducted on a neurotypical population of undergraduate students, it would be intriguing to examine whether rotated faces also elicit more fixations to the eyes in autism spectrum disorder individuals and whether this behavior could lead to improved face perception.

Conclusion

We have shown for the first time that rotated faces elicit an *upper eye bias*—a strong tendency to fixate the upper eye. This upper eye bias can be detected with as little as an $\pm 11.25^\circ$ rotation and appears to peak with a $\pm 45^\circ$ rotation of the face. The upper eye bias dominated the more well-documented left-gaze bias and thus warrants further investigation. The fact that rotated faces drew more overall fixations to the eyes than upright faces has potential implications for research in social cognition.

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References

Arizpe, J., Walsh, V., Yovel, G., & Baker, C. I. (2016). The categories, frequencies, and stability of idiosyncratic eye-movement patterns to faces. *Vision Research*, *141*, 191–203.

Barton, J. J., Radcliffe, N., Cherkasova, M. V., Edelman, J., & Intriligator, J. M. (2006). Information processing during face recognition: The effects of familiarity, inversion, and morphing on scanning fixations. *Perception*, *35*, 1089–1105.

Behrmann, M., Thomas, C., & Humphreys, K. (2006). Seeing it differently: Visual processing in autism. *Trends in Cognitive Sciences*, *10*, 258–264.

Benton, A. L. (1980). The neuropsychology of facial recognition. *American Psychologist*, *35*, 176–186.

Boutet, I., Lemieux, C. L., Goulet, M. A., & Collin, C. A. (2017). Faces elicit different scanning patterns depending on task demands. *Attention, Perception, & Psychophysics*, *79*, 1050–1063.

Butler, S., Gilchrist, I. D., Burt, D. M., Perrett, D. I., Jones, E., & Harvey, M. (2005). Are the perceptual biases found in chimeric face processing reflected in eye-movement patterns? *Neuropsychologia*, *43*, 52–59.

Campbell, R. (1978). Asymmetries in interpreting and expressing a posed facial expression. *Cortex*, *14*, 327–332.

Crouzet, S. M., Kirchner, H., & Thorpe, S. J. (2010). Fast saccades toward faces: Face detection in just 100 ms. *Journal of Vision*, *10*, 1–17.

Dalton, K. M., Nacewicz, B. M., Johnstone, T., Schaefer, H. S., Gernsbacher, M. A., Goldsmith, H. H., . . . Davidson, R. J. (2005). Gaze fixation and the neural circuitry of face processing in autism. *Nature Neuroscience*, *8*, 519–526.

Damasio, H., & Damasio, A. R. (1989). *Lesion analysis in neuropsychology*. New York, NY: Oxford University Press.

Davidenko, N., & Flusberg, S. (2012). Environmental inversion effects in face perception. *Cognition*, *123*, 442–447.

Davidenko, N., Remus, D. A., & Grill-Spector, K. (2012). Face-likeness and image variability drive responses in human face-selective ventral regions. *Human Brain Mapping*, *33*, 2334–2349.

de Haas, B., & Schwarzkopf, D. S. (2018). Feature–location effects in the Thatcher illusion. *Journal of Vision*, *18*, 16, 1–12.

de Haas, B., Schwarzkopf, D. S., Alvarez, I., Lawson, R. P., Henriksson, L., Kriegeskorte, N., & Rees, G. (2016). Perception and processing of faces in the human brain is tuned to typical feature locations. *Journal of Neuroscience*, *36*, 9289–9302.

Dyde, R. T., Jenkin, M. R., & Harris, L. R. (2006). The subjective visual vertical and the perceptual upright. *Experimental Brain Research*, *173*, 612–622.

Everdell, I. T., Marsh, H. O., Yurick, M. D., Munhall, K. G., & Paré, M. (2007). Gaze behaviour in audiovisual speech perception: Asymmetrical distribution of face-directed fixations. *Perception*, *36*, 1535–1545.

Gilbert, C., & Bakan, P. (1973). Visual asymmetry in perception of faces. *Neuropsychologia*, *11*, 355–362.

Güntürkün, O. (2003). Human behaviour: Adult persistence of head-turning asymmetry. *Nature*, *421*(6924), 711.

Guo, K., Meints, K., Hall, C., Hall, S., & Mills, D. (2009). Left gaze bias in humans, rhesus monkeys and domestic dogs. *Animal Cognition*, *12*, 409–418.

Guo, K., Smith, C., Powell, K., & Nicholls, K. (2012). Consistent left gaze bias in processing different facial cues. *Psychological Research*, *76*, 263–269.

Hsiao, J. H., & Cottrell, G. (2008). Two fixations suffice in face recognition. *Psychological Science*, *19*, 998–1006.

Hsiao, J. H., & Liu, T. T. (2012). The optimal viewing position in face recognition. *Journal of Vision*, *12*, 22–22.

Ishi, C. T., Ishiguro, H., & Hagita, N. (2014). Analysis of relationship between head motion events and speech in dialogue conversations. *Speech Communication*, *57*, 233–243.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.

Luke, C. J., & Pollux, P. M. (2016). Lateral presentation of faces alters overall viewing strategy. *PeerJ*, *4*, e2241.

Ma, D. S., Correll, J., & Wittenbrink, B. (2015). The Chicago face database: A free stimulus set of faces and norming data. *Behavior Research Methods*, *47*, 1122–1135.

Marinkovic, K., Courtney, M. G., Witzel, T., Dale, A. M., & Halgren, E. (2014). Spatio-temporal dynamics and laterality effects of face inversion, feature presence and configuration, and face outline. *Frontiers in Human Neuroscience*, *8*, 8681–8612.

Mertens, I., Siegmund, H., & Grüsser, O. J. (1993). Gaze motor asymmetries in the perception of faces during a memory task. *Neuropsychologia*, *31*, 989–998.

Najemnik, J., & Geisler, W. S. (2005). Optimal eye movement strategies in visual search. *Nature*, *434*, 387–391.

Paulun, V. C., Schütz, A. C., Michel, M. M., Geisler, W. S., & Gegenfurtner, K. R. (2015). Visual search under scotopic lighting conditions. *Vision Research*, *113*, 155–168.

Peterson, M. F., & Eckstein, M. P. (2012). Looking just below the eyes is optimal across face recognition tasks. *Proceedings of the National Academy of Sciences*, *109*, E3314–E3323.

Peterson, M. F., & Eckstein, M. P. (2013). Individual differences in eye movements during face identification reflect observer-specific optimal points of fixation. *Psychological Science*, *24*, 1216–1225.

Peterson, M. F., Lin, J., Zaun, I., & Kanwisher, N. (2016). Individual differences in face-looking behavior generalize from the lab to the world. *Journal of Vision*, *16*, 12.

Phillips, P. J., Moon, H., Rizvi, S. A., & Rauss, P. J. (2000). The FERET evaluation methodology for face recognition algorithms. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, *22*, 1090–1104.

Phillips, P. J., Wechsler, H., Huang, J., & Rauss, P. (1998). The FERET database and evaluation procedure for face recognition algorithms. *Image and Vision Computing Journal*, *16*, 295–306.

Rosenthal, G., Levakov, G., & Avidan, G. (2017). Holistic face representation is highly orientation-specific. *Psychonomic Bulletin & Review*, *25*, 1–7. doi:10.3758/s13423-017-1381-x

Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychologica*, *128*, 274–289.

Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *Neuroimage*, *20*, 1609–1624.

Stürzel, F., & Spillmann, L. (2000). Thatcher illusion: Dependence on angle of rotation. *Perception*, *29*, 937–942.

Tanaka, J. W., & Sung, A. (2016). The "eye avoidance" hypothesis of autism face processing. *Journal of Autism and Developmental Disorders*, *46*, 1538–1552.

Thompson, P. (1980). Margaret Thatcher: A new illusion. *Perception*, *9*, 483–484.

Vaidya, A. R., Jin, C., & Fellows, L. K. (2014). Eye spy: The predictive value of fixation patterns in detecting subtle and extreme emotions from faces. *Cognition*, *133*, 443–456.

Valentine, T., & Bruce, V. (1988). Mental rotation of faces. *Memory & Cognition*, *16*, 556–566.

Van Belle, G., Ramon, M., Lefèvre, P., & Rossion, B. (2010). Fixation patterns during recognition of personally familiar and unfamiliar faces. *Frontiers in Psychology*, *1*, 201–208.

Xu, B., & Tanaka, J. W. (2013). Does face inversion qualitatively change face processing: An eye movement study using a face change detection task. *Journal of Vision*, *13*, 22.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*, 141–145.

Yovel, G., Tambini, A., & Brandman, T. (2008). The asymmetry of the fusiform face area is a stable individual characteristic that underlies the left-visual-field superiority for faces. *Neuropsychologia*, *46*, 3061–3068.

Zhang, J., Li, X., Song, Y., & Liu, J. (2012). The fusiform face area is engaged in holistic, not parts-based, representation of faces. *PLoS One*, *7*, e40390.

Zhao, M., Cheung, S. H., Wong, A. C. N., Rhodes, G., Chan, E. K., Chan, W. W., & Hayward, W. G. (2014). Processing of configural and componential information in face-selective cortical areas. *Cognitive Neuroscience*, *5*, 160–167.