Dissociating retina- and face-centered reference frames of human face recognition.

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Abstract

Face identity recognition is a core function of the human brain, predominantly driven by horizontally-oriented facial cues. The reference frame of the (horizontal) information driving human face identification has not been systematically addressed. Therefore, a core characteristic of human face identity recognition remains undefined.

The reference frame of the horizontal information driving face identification may be centered either on the observer's retina (i.e. retina-centered), or the face stimulus (i.e. face-centered). To disentangle these alternatives, 42 young adults performed identity recognition of famous faces. Stimuli were filtered to restrict content to narrow orientation bands (i.e., from 0° to 150°, in 30°-steps), and presented either upright, rotated by ±45°, or by ±90° away from upright. If the horizontal face identity information is defined along retinal coordinates, the peak of identification performance should shift away from horizontal (90°) as a function of rotation angle (peak shift from 90° to 135° for a +45° rotation). In contrast, a reference frame centered on the face identity recognition performance should stay tuned to the horizontal irrespective of rotation angle.

Overall performance significantly decreased when faces were rotated by ±90° compared to other rotation angles. Recognition performance peaked in the horizontal range of the face stimulus regardless of rotation angle. However, the advantage of the horizontal over the vertical range decreased significantly for ±90° compared to upright and ±45° rotations suggesting partial dependence on the retina-centered reference frame. These results indicate that the horizontal information driving human face-specialized identity recognition is defined within the reference frame of the face-image.

Keywords: identity recognition; human face; reference frame; horizontal tuning; orientation selectivity; rotation.

Introduction

Faces abound in our visual environment and their visual processing is a pillar of human social communication (Holler, 2025). The human brain has developed visual mechanisms specialized for the perception of the rich and complex social cues conveyed by faces (e.g., gaze direction, age, identity, emotional expression, etc). In particular, visual mechanisms for identity recognition have consistently been shown to be selectively tuned to the horizontally-structured input of the face stimulus. For example, when humans are asked to recognize the identity of face images filtered to restrict content to a narrow band of orientation, recognition performance typically draws a Gaussian, peaking in the horizontal range, and reaching its minimum for vertically-filtered faces. This horizontal tuning of face processing is robust, as it has been found using diverse manipulations of image oriented content such as orientation filtering (Dakin & Watt, 2009; Dumont et al., 2024; Duncan et al., 2017a, 2019; Goffaux et al., 2015, 2016; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016), noise masking (Goffaux & Dakin, 2010; Pachai et al., 2013, 2017), and phase randomization (Jacques et al., 2014) as well as across various cognitive tasks such as identity recognition (Dakin & Watt, 2009; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Pachai et al., 2017), detection (Balas, Schmidt, et al., 2015), and emotional expression recognition (Balas, Huynh, et al., 2015; Duncan et al., 2017b; Huynh & Balas, 2014; Yu et al., 2018).

Altogether, this past evidence suggests that the specialization and efficiency of face identity processing by the human brain relies on orientation-dependent visual mechanisms and, more specifically, resides in the selective processing of horizontally-oriented face cues. Yet, this characterization of the visual information supporting the essential function of face identity recognition is missing one key insight: its reference frame. It is elusive whether the horizontal information driving human face identification is best defined in egocentric coordinates, namely with respect to the observer's retina, or in allocentric coordinates, with respect to the vertical elongation axis of the face stimulus. Indeed, retina and face-centered reference frames have been confounded in past investigations of the horizontal tuning of face recognition as face stimuli were typically presented upright (or inverted) to observers sitting head-straight in front of the computer screen (See Figure 1 top).

A reference frame fully centered on the retina would imply that the horizontal face identity information is determined in retinotopic visual areas like V1. However, such a purely retinotopic code is unlikely (Duncan et al., 2019; Jacobs et al., 2020). Indeed, face inversion in the image plane and contrast negation (Dumont et al., 2024 for inversion and negation; Goffaux & Dakin, 2010; Goffaux & Greenwood, 2016; Pachai et al., 2017 for inversion alone) severely disrupt the horizontal tuning of human face recognition despite maintaining the alignment of face- and retina-centered coordinates. Moreover, past evidence indicates that the horizontal tuning of face perception emerges in high-level regions in the ventral visual pathway (Goffaux et al., 2016; Jacques et al., 2014), which are only broadly tuned to retinal position (Henderson et al., 2023; Poltoratski et al., 2021). Altogether, this evidence indicates that the reliance on face horizontal information predominantly arises in high-level mechanisms tuned to the statistical properties of the *upright* human face and is not primarily driven by retinotopic mechanisms. Yet, a systematic investigation of the respective contribution of retina- and face-centered frames of reference is timely in order to quantify the retinotopic influence, if any, on the specialized and horizontally-tuned mechanisms recruited during face identity recognition.

To investigate the contribution of retina- and face-centered reference frames to identity recognition, we filtered face images in the orientation domain and presented these images rotated in space to upright-sitting observers. In these conditions, upright (0° rotation) face images had both cardinal axes aligned with those of the observer retina's while rotating the face image (by 45° or 90°) misaligned image and retina axes proportionally to rotation angle. By comparing the orientation tuning profile of identity recognition performance of orientation-filtered faces at different rotation angles, we were able to determine the reference frame(s) contributing to the advantage of horizontal information for face recognition. If the reference frame is strictly face-centered, we expect that recognition performance remains tuned to the horizontal range, no matter the rotation angle of the face stimulus. A strict retinotopic reference frame instead implies a shift of the orientation tuning peak equal to the face rotation angle. For instance, with faces rotated by 45°, recognition performance would be best for faces filtered with a filter centered on 135° (i.e., 90° (horizontal filter) + 45° (rotation) = 135°; Figure 1 bottom). However, considering the evidence reviewed above, a more nuanced pattern where the peak of the tuning curve deviates only slightly from the horizontal according to rotation angle seems more plausible. The amount of deviation would enable quantifying the extent of the retinal contribution to face identity recognition.

[Insert Figure 1]

Figure 1: Left. In upright faces (0° rotation), the orientation-filtered stimulus content is aligned across the face- and retina-centered reference frames. Rotating the face stimulus away from upright misaligns the face- and retina-centered frames of reference. **Right.** Predictions of the orientation tuning profile of face recognition are presented, in the case of a strictly face-centered reference frame top) and in the case of a strictly retina-centered reference frame.

Material and Methods

Our goal was to characterize the coordinate system of the (horizontal) information driving human face recognition. To this end, we filtered faces in orientation ranging from 0° to 150° in steps of 30° (in face-centered coordinates; 0° being vertical and 90° horizontal). These images were then presented either upright or rotated by 45° and 90° (counter) clockwise, relative to the observer. Not exceeding a 90° rotation ensured the engagement of face-specialized mechanisms in all conditions (e.g., Carbon et al., 2007; Stürzel & Spillmann, 2000).

Participants

A total of 46 participants were recruited via ads on Facebook groups from 02/11/23 to 10/05/24. A total of 42, nine males, two non-binary participants, aged 25.38 ± 3.7 completed the experiment, divided into two groups, one for each rotation side: 17 for clockwise and 25 for counter clockwise. Before the start of the experiment participants gave their written informed consent, based on a short descriptive of the study and its goal. They were informed that they could withdraw their consent at any time. The experiments lasted for 3 sessions of approximately 1h, participants were compensated 10 euros per session. At the end of their last session participants had the opportunity to ask any question they wished.

All participants had normal or corrected to normal vision (FrACT scores < 0 for all enrolled participants), as well as normal face recognition abilities (Benton recognition task scores; 48.56 ± 2.86). The experimental protocol was approved by the local ethical committee (Psychological Sciences Research Institute, UCLouvain).

Stimuli

Orientation-filtered images of famous actors' faces were presented upright, rotated by 45° or 90° degrees (counter)clockwise. We used the FameSet image set as in Dumont et al., (2024). The set consists of images of famous male actors, selected through an online piloting phase on Pavlovia (Open Science Tools, Nottingham, UK), to ensure recognition from the greatest numbers of participants (see Dumont et al. (2024) Supporting information S1). The image set was composed of a total of 72 full front (or close to full front) pictures, 4 images for each identity, deprived of any distinctive accessory (such a glasses, tattoos or piercings). All actors were white American or English males. Images were greyscaled and rotated to align the eyes with the horizontal meridian when necessary. Images were cropped to encompass the face from forehead to chin and resized to 302 x 339 pixels. Pixel values were normalized to vary between 0 and 1. We set each image mean luminance to 0.5, and RMS contrast to 0.1, all the while insuring a clipping proportion (proportion of pixel below zero or above 1) under 3%. Images were symmetrically padded to thrice their size to avoid border effect during filtering. Images were fast Fourier Transformed, and their amplitude spectra were multiplied with wrapped Gaussian filters designed to restrict image energy to narrow orientation bands. The center of the Gaussian filters ranged from 0° to 150° in steps of 30°, with a standard deviation of 20° (see Figure 2). Compared to our previous study (Dumont et al., 2024), the filter's standard deviation was reduced (from 25° to 20°) to avoid ceiling performance for upright images. After the inverse Fourier Transform, the mean luminance and RMS contrast of all filtered images was again equalized to match 0.5 and 0.1. An aperture designed to broadly match the contours of the average of the face images was alpha-blended with each filtered and full spectrum image. Finally, pink noise masks (1/f) were designed to match the mean luminance and RMS contrast values of the face images (as in Dumont et al., 2024). MatlabR2014a and Python3.11 were used for image processing.

All of the stimuli (faces images and masks) were displayed on an isoluminant uniform grey background ([127.5, 127.5, 127.5] in RGB).

Procedure

Before starting the experiment, participants selected actors whose faces were familiar to them (See Supplementary Information). The actor selection process consisted of each of the 72 images (4 images for each of the 18 identities) presented in the middle of the screen for 500 ms, followed by 5 actors names (the name of the actor just presented and 4 other names, randomly selected among the 17 remaining actors). Participants had to click on the name of the actor that was just presented or on the "I don't know" button. An actor was only considered familiar if the participant recognized him in at least 3 out of the 4 images. Each participant had to recognize and select 10 actors to move on to the main experiment.

The main experimental task consisted in a delayed face identity matching task, similar to the one used in Dumont et al., (2024). A trial started with a white fixation point lasting randomly between 750 ms to 1350 ms, followed by a face image for 200 ms, a mask during 200 ms and the second face image during 200ms, all displayed at screen center. Participants had to press the letter “S” for same identity and “L” for different identity on the keyboard placed in front of them. Whether the pair similarity was “same” or “different” identities, the displayed images were different, to avoid reliance on image matching strategies. Answers were recorded from stimulus onset and up to 4000ms after stimulus offset. The fixation point turned to green after a correct answer and red for an incorrect answer, then back to white, after which a new trial began.

Trials were blocked per rotation condition (either upright, at 45° or at 90°). Each block was made of 14 trials, two for each filter condition (including full spectrum). Each block was followed by a three-second break, after which a tone indicated the start of the new block. Blocks were grouped by three, one for each rotation condition, in a randomized order. After each block triplet, the accuracy score, calculated over the last block triplet, appeared as well as the block number. This screen lasted for at least 10 seconds and required participants to press the “space” bar to continue the experiment.

Before the main experiment, participants were trained to the task (42 trials), first with- full spectrum upright and rotated images (rotation angle at 45° or 90°; clockwise for 17 participants, counter clockwise for the 25 others), and next with upright and rotated full spectrum as well as orientation-filtered. In order to move to the main experiment, accuracy had to be of at least 80% for full-spectrum trials and 75% for orientation-filtered trials.

The main experiment consisted of a total of 90 blocks (30 blocks per rotation condition), giving a total of 1260 trials, 30 trials per condition combination: three rotation angles (0°, 45°, 90°) as each participant saw either clockwise or counterclockwise rotations, seven orientation content (full spectrum, 0°, 30°, 60°, 90°, 120°, 150°), and two levels of pair similarity (same/different).

Stimuli were presented on a Viewpixx monitor (VPixx Technologies Inc., Saint-Bruno, Canada) with a 1920 × 1080 pixels resolution and a 70Hz refresh rate. Participants used a head-and-chin-rest to maintain head position and a viewing distance of 60 cm. Face images presented at this distance subtended a visual angle of 9° by 10.4°, which simulates face viewing at conversational distance; the masks had a diameter of 11°. The experiment lasted for three hours split into three one-hour sessions. We used Psychopy2021.2.3 to code and run the experiment.

[Insert Figure 2]

Figure 2: **Top**. Illustration of experimental conditions (filter x counter-clockwise rotation angle) with one of the images of Leonardo DiCaprio. Images are filtered from 0° to 150° in steps of 30°. The filter standard deviation is 20°. The clockwise 45° and 90° rotations are not represented. **Bottom**. Example trial with a pair of 120°-filtered face images rotated by -45° rotation. It is a *same* trial, using two different images of the same identity, here, Daniel Radcliffe.

Data analysis

To determine the reference frame of the horizontal cues to face identity, we compared the orientation tuning profile of recognition performance across stimulus rotation angles. Our analyses are similar to Dumont et al., (2024).

For each participant, we analyzed response accuracy and latency. First, we removed all participants who did not complete the full experiment in 3 sessions; this brought the final number of participants from 46 to 42. We checked that all participants scored above chance level in all conditions. Finally, to exclude outlier response, we 10log transformed the response time (Log_{10}(RT))), calculated its mean and standard deviation (sd) for each subject and kept only the trials which Log_{10}(RT) were included in [mean – 2.5*sd, mean + 2.5*sd], resulting in a removal of 2% of the trials overall.

We analyzed sensitivity d' to control for potential response bias (for accuracy analysis, see Supplementary Information S1). For d' calculation, we designated *same* answers for same identity as ***hits***, *same* answers for different identity as ***false alarms***, *different* answers for different identity as ***correct rejections*** and *different* answers for same identity as ***misses***. Hit and false alarm rates were corrected following Hautus (1995). To increase intersubject comparison across conditions and facilitate data modelling the resulting d' values were normalized (*normd')* with a z transform using the grand (i.e. across conditions and subjects) mean and standard deviation. Finally, we duplicated the 0°-filter *normd'* to make the 180°-filter to center the orientation tuning profiles on the horizontal.

First, we investigated the effect of stimulus rotation angle on identity recognition irrespective of orientation content using a Bayesian General Linear Mixed Model

(GLMM) on *normd'* with subjects as a random effect and with *brms* automatic priors. The model followed this formula:

normd' ~ Rotation Angle + (Rotation Angle | Subject)

Second, we examined the orientation tuning profile of identity recognition across face rotations. Performance as a function of the orientation filter followed a Gaussian distribution in each rotation angle. To compare the orientation of face recognition tuning across rotation angles, we modelled each tuning curve with a Bayesian non-linear, Gaussian, model. The Gaussian formula is the same as used in Dumont et al. (2024) and Goffaux & Greenwood (2016):

$$Normd' \sim Base\ Amplitude + Peak\ Amplitude * e^{\frac{(Orientation\ filter - Peak\ Location)^2}{2 Standard\ Deviation^2}}$$

Peak location is the orientation filter at which recognition performance is best; standard deviation measures the sharpness of the performance's orientation tuning around the peak location; base amplitude is the minimum performance; and peak amplitude indicates the difference between minimum and maximum (i.e., peak) performance. The estimated parameters were compared between rotation angles using their 89% credible intervals (CrI) to test for a "significant" difference.

With all 4 parameters estimated defined along these linear regressions:

Peak Location ~ 1 + Rotation Angle + (1 + Rotation Angle | Subject)

Standard Deviation ~ 1 + Rotation Angle + (1 + Rotation Angle | Subject)

Base Amplitude ~ 1 + Rotation Angle + (1 + Rotation Angle | Subject)

Peak Amplitude ~ 1 + Rotation Angle + (1 + Rotation Angle | Subject)

For each of these regression models, prior distributions were defined for intercept (i.e., 1), slope (i.e. the effect of Rotation Angle), and random effect of Subjects. Priors for the intercepts of the linear regression models were normal distributions, whose means were chosen based on theoretical expectations and previous results. For example, the prior for Standard deviation was set at 50°, halfway between previous results from our team (Dumont et al., 2024; Goffaux & Greenwood, 2016). Priors for slopes of the linear regression models were also normal distributions centered on 0 (i.e., the most probable *a priori* was that there would be no difference between the tuning curves of each rotation angle). Precise values of the standard deviations of prior normal distributions were chosen in a compromise between allowing Monte Carlo Markov chains (MCMC) to converge and keeping priors as broad, thus uninformative, as possible, to not influence the model toward a specific estimation. Since the model had to fit five Gaussians compared to two, which complicated the convergence of MCMC, the priors used here were slightly more limited than in (Dumont et al., 2024). Finally, priors for random effects were exponential distributions (i.e. positive values only, to specify that there cannot be less than zero variance between subjects; see Table 1 for details about the prior distributions used in the model).

Table 1. Priors of Bayesian non-linear Gaussian models. Normal prior distributions were set on parameters of linear regressions (intercept and slope) and exponential distributions were set on parameters estimating random effects.

Parameter of non-linear Gaussian model	Peak Location	Standard Deviation	Peak Amplitude	Base Amplitude
Prior for Intercept	normal(90, 5)	normal(50, 10)	normal(1.5, 1)	normal(-1.5, 1)
Prior for slope (effect of Stimulus Type)	normal(0, 5)	normal(0, 10)	normal(0, 1)	normal(0, 1)
Prior for random effects	exponential(0.1)	exponential(0.1)	exponential(0.1)	exponential(0.1)

All models were fitted with four MCMC with 12,000 iterations each (4,000 warm up, resulting in 32,000 iterations after warmup). The fit of each model was evaluated with convergence of MCMC chains thanks to diagnostic values such as the number of divergent chains post warmup, Rhat statistics, effective sample size and number of divergent chains.

For sake of comprehensibility, it is important to remind the reader that, in Bayesian mixed-effects analysis, “population-level” includes all participants (fixed effects), and “group-level” is used to describe the sub-categories of the multilevel analysis (random effects), here the participant level.

The analysis was done using R 4.2.2. We used the *brms* package (Bürkner, 2017, 2018) to fit all Bayesian models. Data and analysis codes can be found at https://osf.io/zyv7b/?view_only=9dd0672a866748e5b2d489b9ec625db0.

Results

As expected, overall recognition performance (*normd’*) was best for upright images and decreased progressively as a function of stimulus rotation angle (see Figure 3). The 89%

Credible Intervals reported in Table 2 show a significant difference between upright (i.e., 0° rotation) and all other rotation angles, as well as between the +45° and -45° rotations and the rest of the rotation angles. The clockwise or counter-clockwise direction of rotation did not influence *normd'*. Similar results were found for full spectrum images with decreasing performance as a function of face rotation (Supplementary S3).

[Insert Figure 3]

Figure 3: Predictions from the Bayesian GLMM comparison of the rotation condition. The non-overlapping 89% credible intervals (CrI) of model predictions indicate a substantive difference between each rotation angle. Triangles and error bars represent the means and standard errors. Squares are the model predicted means, and the shaded regions represent the 89% CrI.

Besides these overall influences of stimulus rotation on recognition performance, we examined the orientation tuning profile of identity recognition performance at each rotation angle. Across rotation angles, human sensitivity to identity described a Gaussian peaking at 90° (i.e., horizontal) progressively decreasing towards 0° (i.e., vertical) (Figure 4 Top; see Supplementary S1 for analyses of accuracy). The Gaussian models we obtained with the Bayesian non-linear mixed modelling confirmed these observations (Figure 4 Bottom).

[Insert Figure 4]

Figure 4: **A**. Group-level normalized sensitivity (*normd'*) for identity recognition as a function of orientation filters and stimulus rotation. The black diamonds represent the mean performance for each condition and the boxplots represent the 25%, 50% (median) and 75% quantiles. Each point is one participant's recognition performance for an Orientation filter and Stimulus rotation. The half violins represent data distribution in each condition. The straight lines on top are the *normd'*, with standard deviation in lighter lines for full-spectrum images for each stimulus rotation. **B.** Bayesian non-linear Gaussian mixed model predictions of *normd'* for each rotation condition. Dots represent population-level mean recognition sensitivity and error bars are 95% confidence intervals (CI). The model mean posterior predictions for each Stimulus rotation are drawn in black (line) and the 89% credible intervals (CrI) of predictions are represented as the faded ribbons. *Normd'* peaked in the horizontal range and decreased towards the vertical orientation at all stimulus rotation angles.

To compare the orientation tuning of face recognition across stimulus rotation angles, we analyzed the posterior parameters estimates from the Gaussian model (see Figure 5). Peak location estimates did not differ across rotation angles. The 89% CrI were all tightly centered on the 90° filter and overlapped in-between rotation angles. Indeed, they ranged from CrI =

[84.29, 91.98] for +90° rotation to [87.52, 94.68] for -90° rotation (see Table 3). The stability of peak location against face rotation indicates that the horizontal information to which face recognition attunes is defined in a face-centered reference frame. Tuning sharpness (standard deviation parameter) varied slightly, yet not significantly, across rotation angles. The selectivity of the horizontal tuning tended to be broader for upright than rotated faces. Base amplitude estimates progressively increased, although not significantly (i.e., better recognition for vertically-filtered faces) as rotation angle approached 0°. Finally, peak amplitude estimates 89% CrI were significantly larger for upright faces (0°-rotation, upright: CrI = [1.87, 2.53]), and moderately rotated faces (+45° rotation: CrI = [1.88, 2.73]; -45° rotation: CrI = [1.77, 2.45]) compared to the most extreme rotation angles (+90° rotation: CrI = [1.14, 1.83], -90° rotation: CrI = [1.24, 1.76]). However peak amplitude at +90° rotation was not significantly different -45° rotation.

Altogether, while these results indicate that rotating faces away from upright does not influence the preferred (horizontal) orientation of face identity recognition, performance in the horizontal range selectively decreased at extreme rotations.

[Insert Figure 5]

Figure 5: 89% Credible Intervals (CrI) of the Bayesian Gaussian model posterior parameter estimates across stimulus rotation angles. The only significant difference is found for the peak amplitude estimate, where the amplitude for the orientation tuning of face recognition is significantly lower for 90° and -90° rotations than for other rotation angles (dashed grey lines).

Table 3: Gaussian parameter estimates mean, median and 89% credible intervals (CrI) for each face rotation angle.

	Peak Location (°)				Standard Deviation(°)			
	Mean	Median	CI_low	CI_high	Mean	Median	CI_low	CI_high
R -90°	91.13	91.12	87.52	94.68	52.10	52.65	41.93	63.54
R -45°	89.99	89.99	87.77	92.15	57.16	57.25	51.01	64.02
R 0°	90.19	90.19	88.06	92.34	65.02	65.31	56.57	73.82
R 45°	88.07	88.07	84.99	91.26	60.54	60.87	50.49	70.47
R 90°	88.15	88.15	84.29	91.98	53.38	53.91	42.08	65.16
	Base Amplitude				Peak Amplitude			
	Mean	Median	CI_low	CI_high	Mean	Median	CI_low	CI_high
R -90°	-1.61	-1.63	-1.89	-1.37	1.41	1.43	1.14	1.69
R -45°	-1.45	-1.46	-1.70	-1.21	2.09	2.09	1.82	2.37
R 0°	-1.27	-1.29	-1.61	-0.95	2.22	2.24	1.89	2.57
R 45°	-1.62	-1.65	-2.07	-1.20	2.33	2.35	1.91	2.79
R 90°	-1.68	-1.70	-2.03	-1.37	1.50	1.52	1.16	1.85

Discussion

In order to define the reference frame of the horizontal information driving face identity recognition, this experiment compared the orientation tuning profile of identity recognition performance with orientation-filtered faces, rotated at different angles.

Overall human sensitivity to face identity was best for upright faces and decreased as a function of face rotation angle in agreement with previous studies (Jacques & Rossion, 2007; Rossion, 2008; see Rossion & Boremanse, 2008 for review).

Despite this overall downward shift in recognition sensitivity, the relative orientation tuning profile was largely stable, with comparable peak location, base amplitude and standard deviation across rotation angles. In other words, identity recognition kept tuned to the horizontal range with comparable sharpness and comparable floor performance in the vertical range. Whereas identity recognition performance invariably peaked in the horizontal range (see also Huynh & Balas, (2014) for a similar finding for emotional expression perception), peak amplitude, i.e., the recognition advantage of horizontal over vertical information, was significantly smaller for 90° and -90° than for 45°, 0° and -45° rotation angles. This indicates that the overall drop of sensitivity with stimulus rotation found here and in past studies (e.g., (Dumont et al., 2024; Goffaux & Greenwood, 2016; Jacques & Rossion, 2007; Pachai et al., 2017; Rossion, 2008; Rossion & Boremanse, 2008) is due to the impaired processing of horizontal face cues.

The stability of the horizontal preference for identity recognition despite face rotation (up to ±90°) confirms that the horizontal information primarily driving human face identity recognition is best defined in a face-centered reference frame. The orientation tuning of face recognition thus reflects the diagnosticity of the information oriented orthogonally to the vertical elongation axis of the human face, irrespective of its orientation when imprinting the observer's retina. The functional importance of the horizontal face information is thus linked to the natural statistics of the upright human face more than to its retinotopic projection (see Dakin and Watt, 2009).

While our results demonstrate its non-retinotopic, high-level and face-centered nature, they do not exclude the possibility that the horizontal tuning of face identity recognition emerges based on functional interactions across visual processing levels, including the primary visual cortex (V1) (de-Wit et al., 2012; Goffaux et al., 2016). The observation of a selective reduction of sensitivity to identity cues in the horizontal range with stimulus rotation may still suggest some retinotopic influence on the encoding of face identity information. Orientation selectivity is a core functional property of V1 and past evidence suggests this function is not limited to the early and static orientation filtering of visual input; instead V1 orientation-selective encoding is a dynamic and protracted process (Ringach et al., 1997, 2002, 2003) operating under the top-down influence of internal representations (e.g., Bullier, 2001; Goffaux et al., 2016; Kok et al., 2012; Muckli, 2010; Schuurmans et al., 2023), unconstrained by retinotopy (de-Wit et al., 2012; Hsieh et al., 2010; Williams et al., 2008).

Our study focused on disentangling the retino- and face-centered coordinate systems of face identity information and discarded another fundamental reference frame: the one relative to the space in which the stimulus is viewed and/or to the directional pull of gravity, i.e. the environmental reference frame. Few studies rotated both the observer and the stimulus to address whether human face perception operates in an environmental coordinate system. Findings are mixed (Davidenko & Flusberg, 2012; de Schonen et al., 1998; Lobmaier & Mast, 2007; Troje, 2003). If the horizontal tuning of face identity recognition operates in line with environmental coordinates, we would expect it to be stronger when faces are upright with respect to the environment alone (e.g., when the observer is rotated by 90° but the stimulus is projected upright on the screen) than with respect to the observer alone (e.g. when both observer and stimulus are rotated by 90°). However, since past evidence for the environmental influence on human face perception is scarce and small (Davidenko & Flusberg, 2012), we think that this frame of reference is unlikely to contribute to our results.

Although identity recognition peaked in the horizontal range irrespective of face rotation, the magnitude of the horizontal advantage over vertical (i.e., peak amplitude) decreased for extreme ±90° rotations. It is unlikely that such reduction in horizontal peak amplitude resulted from a floor effect in the vertical range preventing the downward shifting of the psychometric curve. Indeed, accuracy in the vertical range was well above chance level for ± 90° rotations (See Supplementary S1). Instead, we believe that the reduced horizontal peak amplitude of face identity recognition at ±90° observed here results at least in part from the disruption of face-specialized holistic processing, namely the perceptual integration of local facial features into a global representation of face identity (Farah et al., 1995; Rossion, 2008). Past evidence of face recognition deficit at ±90° of rotation (Edmonds & Lewis, 2007; Jacques & Rossion, 2007; McKone, 2004; McKone et al., 2001) has been attributed to the disruption of specialized holistic processing (Bozana Meinhardt-Injac, Malte Persike, Günter Meinhardt, 2013; Jiang et al., 2011; Rossion, 2008; Rossion & Boremanse, 2008; Schwaninger & Mast, 2005). Our past work indicates that the holistic processing of faces is mainly driven by horizontal face cues (Goffaux & Dakin, 2010). The selectivity of the recognition impairment to the horizontal range for ±90° face rotations may alternatively reflect a more fundamental contribution of the horizontal face information namely the carriage of the natural statistics of the upright human face that are essential at triggering the visual (e.g., holistic among others) mechanisms that are specialized to this category (Dakin & Watt, 2009; Dumont et al., 2024; Goffaux et al., 2016; Goffaux & Greenwood, 2016; Jacques et al., 2014).

To summarize, our results demonstrate that human face identification stays horizontally-tuned irrespective of face rotation therefore suggesting that the horizontal cues to face identity are defined in a face-centered reference frame. This agrees with the notion that the horizontally-driven visual mechanisms supporting face-specialized identity recognition are tuned to the natural statistics of the upright face.

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