The resolution of face perception varies systematically across the visual field

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Abstract

Visual abilities tend to vary predictably across the visual field – for simple low-level stimuli, visibility is better along the horizontal vs. vertical meridian and in the lower vs. upper visual field. In contrast, face-recognition abilities have been reported to show either distinct or entirely idiosyncratic visual-field variations, suggesting a dissociation between the spatial properties of low- and higher-level vision. To more clearly assess this link, we extended methods used in low-level vision to develop an acuity test for face perception, measuring the smallest size necessary to judge facial gender in peripheral vision. In 3 experiments, we demonstrate a clear advantage for gender acuity on the horizontal vs. vertical meridian and a smaller-but-consistent lower- vs. upper-field advantage. This pattern matches that of low-level vision, demonstrating that location systematically influences the resolution of face perception. Our findings support a hierarchical, feedforward process whereby face-processing systems inherit the spatial selectivity of early vision.

Keywords

face perception, spatial vision, visual field, acuity, inversion, gender

Statement of Relevance

Extensive evidence suggests that face perception relies on mechanisms that are qualitatively different from more general object recognition (e.g. with disproportionate disruptions from image inversion). This dissociation raises the question of how higher-level specialisation for faces develops within the visual system, particularly in relation to the selectivity of lower-level vision. Here, we sought to bridge a methodological gap between low- and high-level visual processing by examining the resolution of face perception across the visual field. Using a novel face acuity test, we demonstrate that the recognition of facial gender varies systematically across the visual field, with the same pattern as low-level vision. This influence of location on face perception provides a clear link between low- and high-level vision, and suggests that the spatial selectivity of higher levels of the visual system is likely to vary in the same way as earlier processing stages.

Vision varies across the visual field. For the recognition of simple low-level stimuli ranging from lines to letters, these variations are often assessed using measures of spatial resolution or acuity (e.g. the smallest size needed for accurate recognition). Our perception of these simple stimuli is systematically influenced by both eccentricity (becoming worse as distance from the fovea increases; Rosenholtz, 2016) and angular location around fixation (e.g. worse performance in the upper vs. lower visual field; Abrams et al., 2012). In contrast, the perception of high-level stimuli such as faces has been found to vary across the visual field in a unique or even idiosyncratic fashion (Afraz et al., 2010; Quek & Finkbeiner, 2016; Schmidtmann et al., 2015). These distinct variations are consistent with the view that faces are "special" in the visual system, in that they are processed by unique mechanisms which are disproportionately disrupted by inversion (Robbins & McKone, 2007; Rossion, 2008). It is difficult however to compare these low- and high-level visual abilities due to differences in the methodology used to assess them. The extent to which high-level specialised face processing systems rely on low-level perceptual variations in the visual field is therefore unclear – variations in face recognition may arise solely in high-level brain areas, independently of the variations in low-level areas. Here, we sought to align the methodology used to investigate anisotropies for low-level stimuli and faces by measuring the spatial resolution of face perception around the visual field.

As above, low-level properties such as visual acuity not only decline with eccentricity (Rosenholtz, 2016) but also vary by location, even with eccentricity held constant. Acuity is typically better along the horizontal meridian compared to the vertical (Figure 1A; Carrasco et al., 2001; Greenwood et al., 2017; Westheimer, 2005). Along the vertical meridian, acuity is better in the lower compared to the upper visual field (Carrasco et al., 2001; Greenwood et al., 2017). These two anisotropies – horizontal-vertical and upper-lower – consistently emerge for many elements of vision, including bisection acuity, contrast sensitivity and crowding (Abrams et al., 2012; Barbot et al., 2021; Himmelberg et al., 2020; Rubin et al., 1996), demonstrating that low-level visual perception is fundamentally influenced by location.

These anisotropies have been linked with the retinotopic organisation of the visual system. Multiple retinotopic maps exist throughout the visual hierarchy, with

adjacent locations in the visual field encoded by anatomically adjacent neurons (Wandell et al., 2007; Wandell & Winawer, 2011). Anatomical studies report higher densities of retinal ganglion cells along the horizontal vs. the vertical meridian (Curcio & Allen, 1990; Perry & Cowey, 1985). Similarly, in early visual cortex (V1-V3), smaller population receptive field (pRF) sizes have been found along the horizontal vs. the vertical meridian and the lower vs. the upper field, highlighting variations in sampling across the visual field (Silson et al., 2018; Silva et al., 2018). Higher cell densities and smaller pRF sizes have been linked with better acuity (Duncan & Boynton, 2003), which could explain variations in low-level information processed by early visual cortex.

Like low-level vision, face recognition declines in peripheral vision compared to the fovea (McKone, 2004). However, variations in face recognition by angular location have been reported to differ substantially from those of low-level vision. Some studies report faster recognition of face gender in the upper field relative to the lower field (Quek & Finkbeiner, 2014, 2016) – the opposite pattern to that of lower-level performance variations. Others report no significant horizontal-vertical or upper-lower differences in discriminating the identity of synthetic-contour faces, instead observing an advantage for the left (vs. right) visual field (Schmidtmann et al., 2015), consistent with the left hemifield bias for face perception (Ellis & Shepherd, 1975; Harrison & Strother, 2021). Finally, biases in the apparent gender and age of morphed faces have been found to vary across the visual field in a wholly idiosyncratic (rather than systematic) manner – where one participant perceived morphed faces as more female in the left field and more male in the right, another participant showed the opposite pattern (Afraz et al., 2010). Similar idiosyncrasies were found for biases in the perceived identity of morphed faces (Visconti di Oleggio Castello et al., 2018). These distinct and/or idiosyncratic patterns suggest a dissociation in the mechanisms driving the visual field variations in low-level vision and face perception.

This dissociation may not be surprising given evidence that faces undergo distinct forms of cognitive processing (Robbins & McKone, 2007). For instance, relative to other objects, face recognition is disproportionately impaired for upside-down vs upright faces (Yin, 1969). This *inversion effect* is driven by increased sensitivity to the spatial relationships between features (configural processing) within upright faces (Le

Grand et al., 2001; Maurer et al., 2002; Piepers & Robbins, 2012; Rossion, 2008). Functional magnetic resonance imaging (fMRI) has identified ventral occipitotemporal brain regions dedicated to face processing, such as the fusiform face area (FFA) which shows greater activation for upright vs inverted faces (Yovel & Kanwisher, 2004, 2005). Like early visual cortex, higher-level face-selective regions also show retinotopy, with smaller receptive field sizes in the fovea vs. the periphery (Kay et al., 2015; Poltoratski et al., 2021). It is unclear how the retinotopy in face-selective areas is linked to earlier regions, however. In low-level vision, neural selectivity derives from earlier stages in the visual hierarchy, with orientation selectivity in V1 simple cells arising from specific combinations of circular-symmetric LGN cells, for example (Hubel & Wiesel, 1962). The dissociations between low-level vision and face perception suggest that neuronal selectivity in face-selective regions may not have the same dependence on inputs from earlier visual cortex.

A major challenge in comparing the above variations in low- and high-level vision derives from differences in methodological approach. While measurements of low-level vision tend to focus on spatial properties such as acuity or grating resolution, face recognition experiments often measure the percent-correct recognition of facial characteristics such as gender at a fixed face size (Afraz et al., 2010; Quek & Finkbeiner, 2016; Schmidtmann et al., 2015). To align the methodology used to assess variations in low-level vision and face perception, we developed an acuity test for faces, which measures the smallest size necessary to judge gender at a given visual field location. Upright and inverted faces were included to determine whether the paradigm engaged face-specific configural mechanisms, and to assess whether visual field variations would differ according to inversion. If face processing systems inherit the spatial properties of early visual cortex, anisotropies similar to those found for low-level vision should emerge for faces. Alternatively, there could be idiosyncratic variation (Afraz et al., 2010; Visconti di Oleggio Castello et al., 2018) or a systematic but unique pattern of anisotropy (Quek & Finkbeiner, 2016; Schmidtmann et al., 2015). The latter outcomes would suggest that face perception involves distinct mechanisms that do not inherit the spatial properties of earlier brain regions, with spatial selectivity arising separately within face-selective cortices themselves.

Experiment 1

Method

Participants. 14 participants (13 female, 1 male, M_{age} = 24.9 years) took part, including authors AYM and JAG; the rest were naïve. All had normal or corrected-to-normal foveal vision of at least 20/20, assessed using a Snellen chart. 9 were right-eye dominant, determined using the Crider ring test (Crider, 1944). This sample size was derived from previous studies with similar designs (e.g. Abrams et al., 2012). All three experiments were approved by the Research Ethics Committee for Experimental Psychology at University College London and all participants gave written informed consent before testing began.

Apparatus. The experiment was programmed in MATLAB (MathWorks, Inc) and conducted on an Apple iMac running PsychToolbox (Brainard & Vision, 1997; Kleiner et al., 2007; Pelli & Vision, 1997). Stimuli were viewed binocularly on a Cambridge Research Systems Display++ monitor with 2560 x 1440 resolution and 120 Hz refresh rate. The monitor was gamma corrected and linearised through software to have a minimum luminance of 0.16 cd/m^2 and a maximum of 143 cd/m^2. Participants were seated at a 50cm viewing distance, with head movements minimised using forehead and chin rests. The experiment took place in a dark room, and responses were recorded with a keypad.

Stimuli. 8 male and 8 female faces were selected from a bank of faces (as in Laguesse et al., 2012) created by researchers at the UCLouvain, on the basis that they had received ratings of more than 8 out of 10 for either maleness or femaleness in a separate study. This screening was conducted to avoid confusion with specific faces, given that our task involved a binary gender judgement[1] to enable the fitting of psychometric functions. All faces were grayscale, front-facing, and had a neutral expression (Figure 1B). Using Adobe Photoshop CS6, each face was edited into an egg-shaped aperture measuring 657 x 877 pixels (at its widest and highest point, respectively) so that the only differences between images were due to internal features

[1] Although gender itself is not binary, we chose faces at each end of the gender spectrum to create a binary judgement suitable for psychometric function fitting.

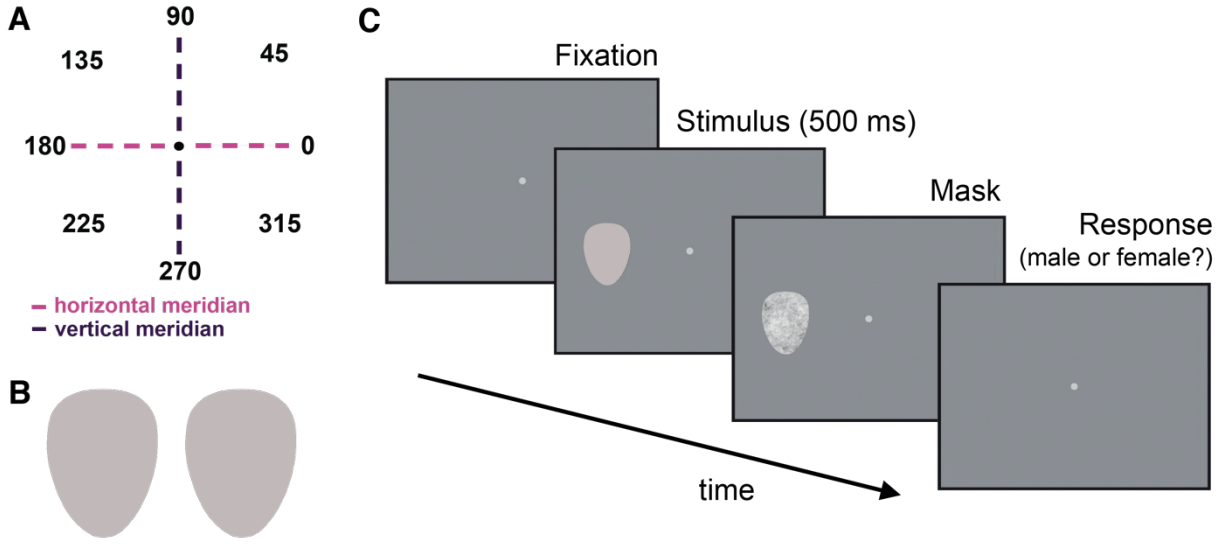

Figure 1. **(A)** The 8 polar angles tested, starting with 0° in the right visual field and preceding counterclockwise in 45° increments. The horizontal and vertical meridians are represented by pink and purple dashed lines, respectively. **(B)** Examples of female (left) and male (right) faces. **(C)** Experimental paradigm. A Gaussian fixation point first appeared, then a face was presented for 500 ms at one of the eight possible locations, selected randomly (shown here at 180°). Each face was followed by a mask which remained on screen until a keyboard response was made. Faces varied in size from trial to trial according to an adaptive QUEST procedure. *NB: Blank apertures are shown in replacement of face photographs, as journal regulations prohibit the use of identifiable faces.*

and not outer face shape (e.g. jawline). The faces were set to have the same mean luminance as the monitor, with matched root-mean square (RMS) contrast values of 0.68. This ensured that overall luminance or contrast values could not be used as cues to gender.

Procedure. Participants were instructed to fixate on a white two-dimensional Gaussian element (standard deviation of 13.8 minutes of arc) in the centre of the screen. During each trial (Figure 1C), a face was presented for 500 ms, with the image centre located at 10° eccentricity and at one of 8 possible angles (Figure 1A). The face was immediately followed by a 1/f noise egg-shaped mask, which broadly matches the spatial frequency content of faces and natural scenes (Párraga et al., 2000). The size of the mask varied trial-by-trial to match the size of the face just shown, remaining on screen until participants made their response. We used a single interval 2-alternative forced choice (2AFC) response method, with participants reporting the face as either male or female using a numeric keypad. Audio feedback was provided after each response.

Before experimental trials began, participants completed a shorter set of 72 practice trials to become accustomed to the task. For the practice trials, faces were presented at fixed sizes of 600, 400 and 200 pixels (face size refers to vertical height, with width scaled proportionately), with 9 trials at each location. Participants were required to be at least 90% correct in order to continue. During the experimental trials an adaptive QUEST procedure (Watson & Pelli, 1983) varied face sizes presented at each location according to the participant's responses, set to converge on the size at which 75% of responses were correct. Within each block of trials, QUEST estimates were computed separately for each location. Faces were presented at sizes within ±1/3 of the QUEST threshold estimate on each trial (minimum 5 and maximum 640 pixels). This "jitter" allowed us to collect data for a range of sizes, which improved the subsequent fitting of psychometric functions to the data (Tailor et al., 2021).

Each experimental block contained 50 faces shown at each of the 8 locations (with independent QUEST procedures) to give 400 trials in total. Each face was shown an equal number of times, in a randomised order, with the location it appeared at also randomised. Upright and inverted faces were presented in alternate blocks. The experiment consisted of 1-2 practice blocks, followed by 8 experimental blocks (4 repeats for both upright and inverted faces) to give 3200 trials in total. During analysis, we fit psychometric functions to the combined data from these 4 repeats (separately for each location and inversion condition).

Analyses. Responses were first sorted by face size (in pixels) and collated in 20-pixel bins (e.g. faces of 8, 15 and 18 pixels would fall in the same bin). The proportion of correct responses was then calculated for each face-size bin. Cumulative Gaussian functions (Figure 2) were fit to this data using 3 free parameters for the mean, variance and lapse rate (Greenwood, 2023). For some participants with particularly noisy data, a maximum allowable lapse rate of either 0.05 or 0.1 was also applied in order to improve curve fitting. Gender acuity thresholds for each location were taken as the size at which 75% accuracy was reached, then converted from pixels to degrees of visual angle.

Statistical analyses were carried out using a 3-way mixed effects analysis of variance (ANOVA), with participant as a between-subjects random factor and inversion (upright, inverted) and location (0, 35, 90, 135, 180, 225, 270, 315°) as within-subjects

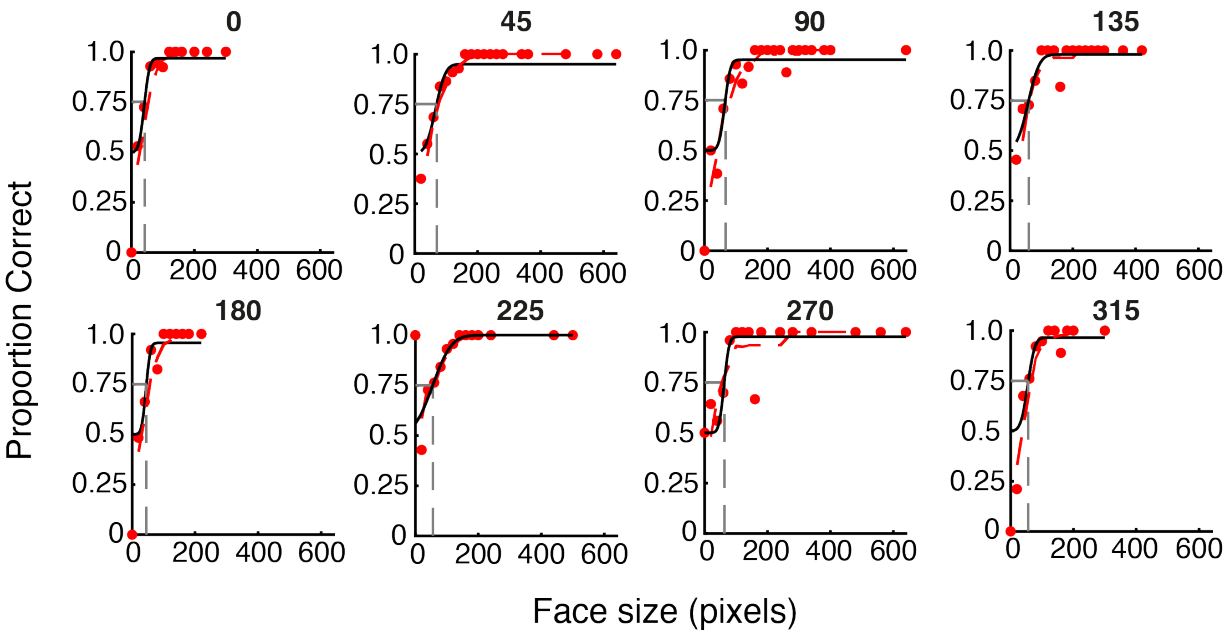

Figure 2. Psychometric functions for a single participant, showing the proportion of correct gender judgements for different sized upright faces at each of the 8 visual field locations (labelled at the top of each graph, where 0 = rightwards, 90 = upwards, etc.). Performance improves monotonically as a function of face size. Dashed grey lines plot thresholds for gender acuity (the size at which 75% accuracy was reached).

fixed factors. A priori and post-hoc comparisons took the form of repeated-measures t-tests, comparing thresholds between the horizontal (0 and 180°) vs. vertical (90 and 270°) meridians, the upper (90°) and lower (270°) field, and the left (180°) and right (0°) locations, for upright and inverted faces separately.

Results

Mean gender acuity thresholds across participants are plotted as both a bar chart and according to the polar angle of each of the 8 locations in Figure 3. Smaller values represent better gender acuity. Mean gender acuity thresholds were worse for inverted compared to upright faces overall, indicating that inversion disrupted the ability to judge gender at all locations. There was a sizeable difference in gender acuity according to location; for upright faces, there was a range of almost 2° of visual angle between the smallest threshold value in the lower field (270°) and the largest in the upper field (90°). Thresholds were smaller along the horizontal (0, 180°) as opposed to the vertical (90, 270°) meridian. Thresholds at the diagonal locations varied inconsistently, with smaller thresholds in the top left (135°) vs. top right (45°) location, but larger thresholds in the bottom left (225°) vs. bottom right (315°) location.

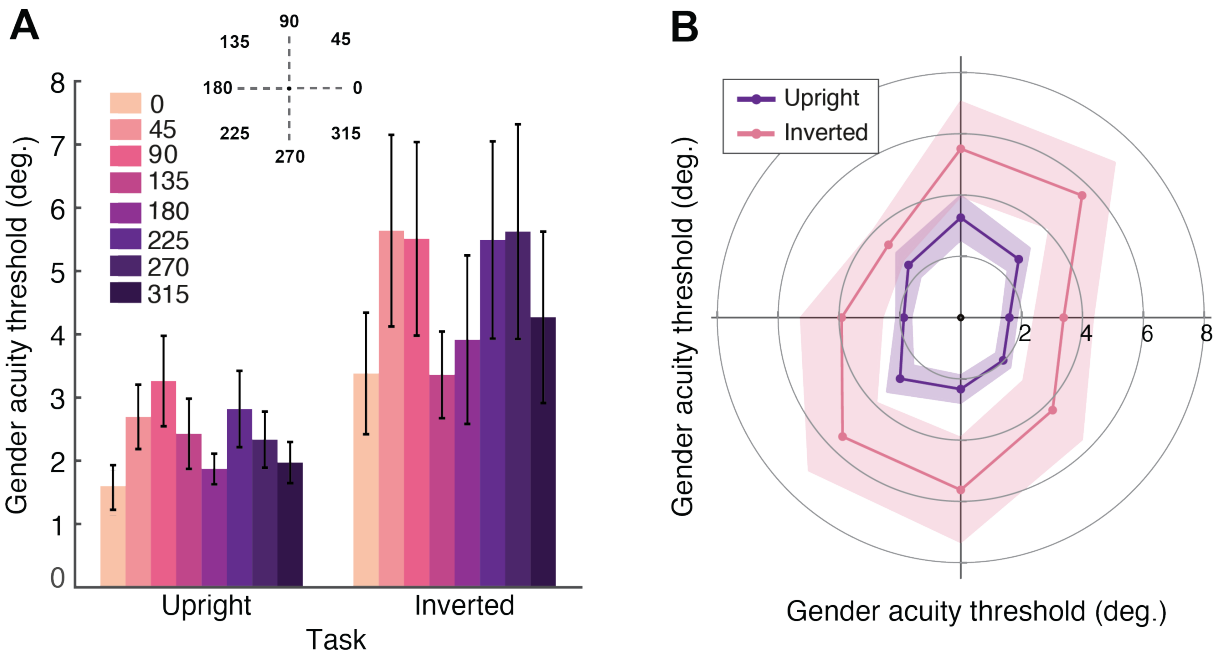

Figure 3. Mean gender acuity thresholds (in degrees of visual angle) measured in Experiment 1, plotted in two ways. Firstly, as a bar graph **(A)** with each angular location indicated via colour (see legend). Error bars represent ± 1 standard error of the mean (SEM). Secondly, as a polar angle plot **(B)**, where 0° is at the right and angles proceed counterclockwise in 45° jumps. Upright faces are shown in purple and inverted in pink. Shaded regions denote ± 1 SEM.

The ANOVA revealed a main effect of location, $F(7,91) = 3.41$, $p = .003$, $d = 0.21$, confirming that the location of faces in the visual field influenced gender perception. Planned contrasts revealed that thresholds were significantly smaller along the horizontal (0° and 180° averaged) compared to the vertical (90° and 270° averaged) meridian for both upright, $t(13) = -2.84$, $p = .014$, and inverted faces, $t(13) = -2.21$, $p = .046$. Thresholds were also smaller in the lower compared to the upper field for upright faces, $t(13) = 2.68$, $p = .019$, although not for inverted faces, $t(13) = -0.10$, $p = .923$. There was no difference between thresholds at the left and right locations for upright, $t(13) = -1.79$, $p = .096$, or inverted faces, $t(13) = -0.61$, $p = .551$. In other words, we observe both horizontal-vertical and upper-lower anisotropies for gender acuity, though performance did not differ between left and right hemifields.

The error bars in Figure 3 indicate that there was considerable between-participants variability in gender acuity thresholds, with the ANOVA showing a main effect of participant, $F(7,91) = 2.98$, $p = .029$, $d = 0.75$. However, there was no interaction between location and participant, $F(91,91) = 1.07$, $p = .383$, $d = 0.52$,

indicating that individuals varied in their overall threshold magnitude rather than exhibiting idiosyncratic variations across the 8 locations. We note in particular that a subset of participants showed thresholds that were considerably smaller (with values ~0.5°) than the rest of the group.

The presence of an inversion effect was supported by a main effect of inversion, $F(1,13) = 6.61$, $p = .023$, $d = 0.34$, showing that thresholds were significantly higher for inverted compared to upright faces. Therefore, configural information appears to have benefitted performance in our task. There was no interaction between inversion and location, $F(7,91) = 0.91$, $p = .506$, $d = 0.07$, indicating that inversion disrupted gender perception to a similar extent across the visual field. There was, however, a significant interaction between inversion and participant, $F(13,91) = 10.55$, $p = <.001$, $d = 0.60$. To investigate this interaction further, we calculated mean face inversion effect (FIE) values across participants by subtracting upright from inverted thresholds. Upon closer analysis the inversion-participant interaction appeared to be driven by two participants with very large FIEs, and indeed we found that removing their data from the analysis eliminated the interaction.

Experiment 2

Experiment 1 demonstrates that face-recognition acuity varies in the same way as low-level vision, with both horizontal-vertical and upper-lower anisotropies. Curiously, the thresholds of several participants indicated that they could correctly judge the gender of faces as low as 0.5° in size. Although it is not impossible that faces that small could be recognised at 10° eccentricity, the divergence from the group average led us to suspect that they were directly fixating the faces. Furthermore, although the upper-lower difference was significant for upright faces in Experiment 1, our face stimuli were centred on the image centre. This meant that for upright faces the eyes appeared closer to fixation in the lower vs. the upper field, and vice versa for inverted faces. This could potentially have driven the upper-lower difference, given the importance of the eye region for gender perception (Brown & Perrett, 1993; Schyns et al., 2002). In Experiment 2 we therefore sought to test the validity of our findings by adding eye-tracking and controlling for eye position by centring the locations of face stimuli on the eyes.

Method

Participants. 14 participants (12 female, 2 male, M_{age} = 23.6 years) took part, including author AYM; the rest were naïve and newly recruited. All had normal or corrected-to-normal vision. 7 were right-eye dominant.

Apparatus. In addition to the setup in Experiment 1, we used an EyeLink 1000 (SR Research, Mississauga, ON, Canada) to monitor fixation during trials.

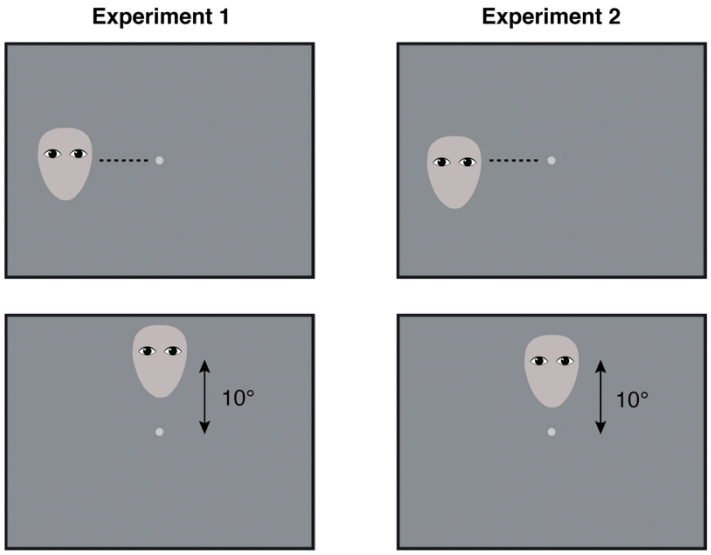

Figure 4. In Experiment 1 (left panels), faces were presented 10° from fixation according to the centre of the face. In Experiment 2 (right panels), the centre of the eyes was always 10° from fixation regardless of face size, angular location or inversion. *NB: Apertures containing cartoon eyes are shown in replacement of face photographs, as journal regulations prohibit the use of identifiable faces.*

Stimuli. The same face stimuli from Experiment 1 were used. Stimulus locations were centred on the eyes themselves, so that the centre of the eyes were always 10° from fixation regardless of face size, angular location or inversion (Figure 4). The position of each face in the egg aperture was also shifted and/or rotated slightly to ensure that the eyes fell at the same point within the aperture.

Procedure. Following calibration of the EyeLink to track their left eye, participants were required to fixate the Gaussian element (with an allowable error of 1.5° radius) in order for each trial to start. Trials in which fixation diverged from this region were cancelled and repeated at the end of the block. Participants first completed the practice block(s), as in Experiment 1. Experimental blocks were split according to whether faces were upright or inverted and locations were cardinal (0, 90, 180, 270°) or diagonal (45, 135, 225, 315°) angles, resulting in 4 blocks: upright cardinal, upright diagonal, inverted cardinal and inverted diagonal. These split blocks were introduced so that the blocks would not be too long, as the eye tracking increased the duration of data collection depending on the amount of cancelled trials

and recalibration needed. Data were collected over 4 hour-long sessions, with each of the 4 conditions repeated once per session. This gave a total of 16 blocks and 4096 trials per participant.

Results

Mean gender acuity thresholds are plotted in Figure 5. Again, smaller values represent better gender acuity. Compared to Experiment 1, thresholds in Experiment 2

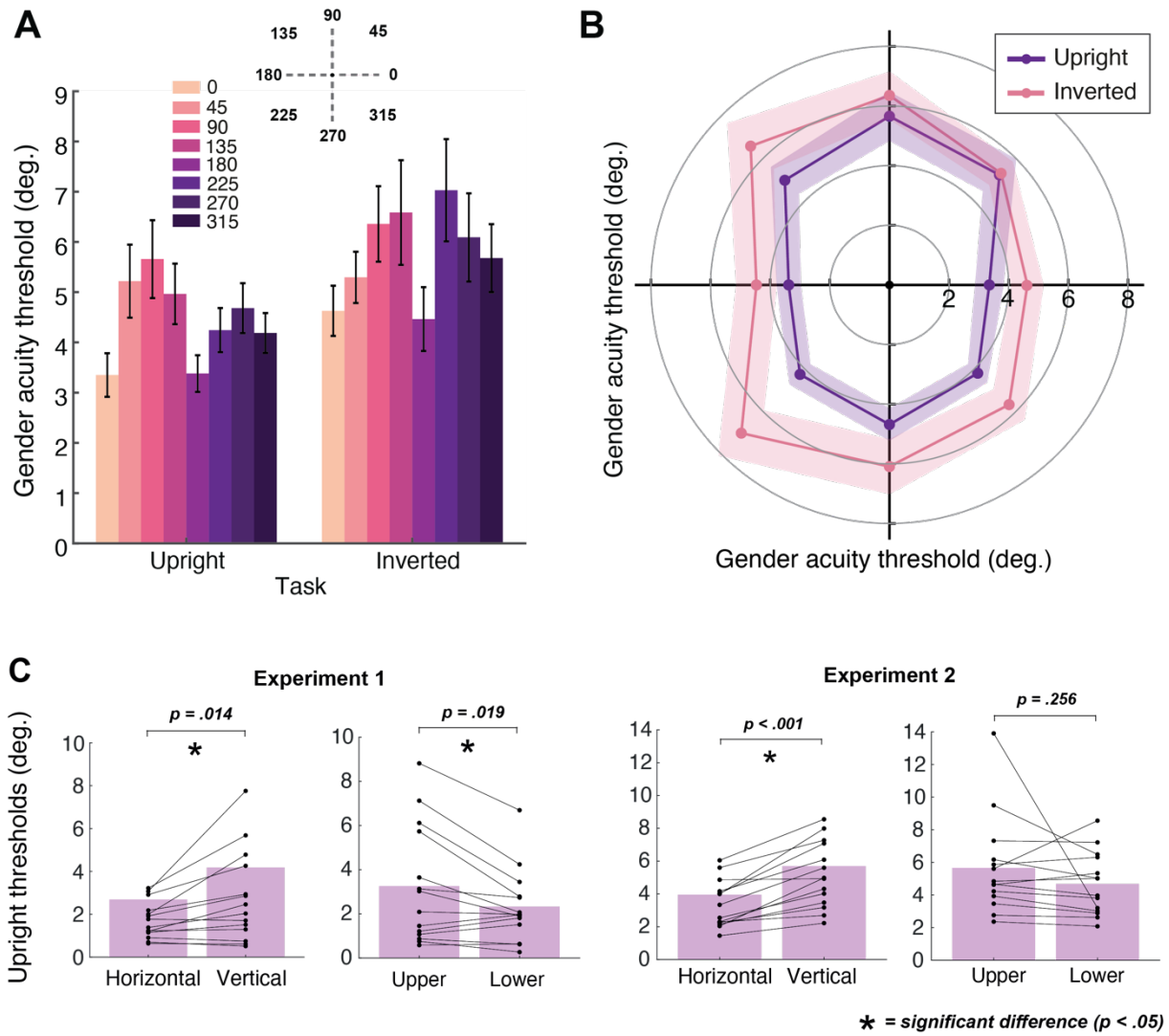

Figure 5. Mean gender acuity thresholds from Experiment 2, first shown as a bar graph **(A)** with each location indicated via colour (see legend). Error bars report ± 1 SEM. Thresholds are also visualised in a polar angle plot **(B)**, with 0° at the right and angles increasing counterclockwise by 45° each time. Upright faces are shown in purple and inverted in pink. Shaded regions represent ± 1 SEM. **(C)** Bar charts comparing the horizontal-vertical difference and upper-lower difference in Experiments 1 and 2. Data are plotted for upright faces only. Horizontal refers to thresholds averaged across 0° and 180° locations, with vertical the average of 90° and 270°. Upper represents 90° and lower 270°. Individual data points represent threshold values for a single participant. Significant differences are marked with an asterisk.

were higher overall and had reduced variability across participants (particularly in the inverted condition), suggesting that eye tracking successfully stopped participants from looking directly at faces. Indeed, the smallest-measured threshold in Experiment 2 was 1.31°, compared with 0.27° in Experiment 1.

The ANOVA revealed a main effect of location, $F(7,91) = 5.55$, $p = < .001$, $d = 0.30$, indicating that gender acuity was influenced by the location of faces. There was a clear horizontal-vertical difference, with planned comparisons revealing that thresholds were significantly smaller along the horizontal (0° and 180° averaged) compared to the vertical (90° and 270° averaged) meridian, for both upright, $t(13) = -6.16$, $p < .001$, and inverted faces, $t(13) = -3.00$, $p = .010$. However, although thresholds were smaller in the lower compared to the upper field, the difference was not significant for either upright, $t(13) = 1.19$, $p = .256$, or inverted faces, $t(13) = 0.38$, $p = .713$. Similarly, thresholds did not differ between the left and right locations for either upright, $t(13) = -0.10$, $p = .926$, or inverted faces, $t(13) = 0.39$, $p = .704$.

An overall inversion effect can be seen in the mean data (Figure 5A, B), with higher thresholds and therefore reduced ability to perceive gender (i.e. larger faces needed) for inverted compared to upright faces. This was confirmed by a significant main effect of inversion, $F(1,13) = 17.93$, $p = .001$, $d = 0.58$. There was no interaction between inversion and location, $F(7,91) = 1.29$, $p = .265$, $d = 0.09$, indicating that inversion effects did not differ significantly across the visual field.

Gender-recognition abilities again differed between individuals, which was confirmed by a main effect of participant, $F(7,91) = 11.52$, $p < .001$, $d = 0.93$. There was however no interaction between location and participant, $F(91,91) = 0.94$, $p = .623$, $d = 0.48$, indicating that location-based variations in gender perception are not specific to the individual. In other words, face perception differed across the visual field in a characteristic pattern shared across individuals.

Unlike the previous experiment there was no interaction between inversion and participant, $F(13,91) = 1.60$, $p = .100$, $d = 0.19$, indicating that individuals did not vary substantially in the inversion effect. This suggests that the significant interaction in Experiment 1 may have been caused by a subset of participants looking at the faces –

accordingly, these individuals had low thresholds for both upright and inverted faces (i.e. little to no inversion effect), likely driven by their fixating the faces in both conditions.

To compare anisotropies more clearly, bar charts displaying the horizontal-vertical difference and upper-lower difference in both experiments are shown in Figure 5C. Only data for upright faces are included. The charts on the left-hand side show that the horizontal-vertical difference was consistent across both experiments, with significantly lower thresholds (better gender acuity) for faces at horizontal compared to vertical locations. The upper-lower difference was only significant in Experiment 1, where effects could have been driven by eye movements or variations in eye position within face stimuli. Although a trend in the same direction persisted when we controlled for these factors in Experiment 2 – showing that the upper-lower difference cannot be attributed to these factors alone – the difference was no longer significant.

To summarise, gender acuity was better along the horizontal vs. vertical meridian but did not differ significantly in the lower vs. upper field. However, even in Experiment 1 the upper-lower difference was smaller than the horizontal-vertical difference, suggesting that it may simply be harder to measure. We examined this possibility in Experiment 3.

Experiment 3

Given the trend towards better gender acuity in the lower vs. upper field in Experiment 2, we next conducted further measurements at these locations to determine whether a significant difference would emerge with a greater number of trials.

Method

Participants. 14 participants (11 female, 2 male, 1 non-binary, M_{age} = 22.1 years) took part, including author AYM; the rest were naïve and newly recruited. All had normal or corrected-to-normal vision. 7 were right-eye dominant.

Stimuli. Stimuli were as in Experiment 2, with faces shown at the upper (90°) and lower (270°) locations only.

Procedure. Blocks were split according to whether faces were upright or inverted, with 128 trials in each block. Data were collected over 2 hour-long testing sessions, with each of the 2 conditions (upright/inverted) repeated 8 times per session (with an extra block completed at the start of the first session, which acted as a practice block and was not included in data analysis). This gave a total of 16 experimental blocks and 2048 trials over the experiment (doubling the number of trials per location compared to Experiment 2). Remaining parameters were as in Experiment 2.

Results

Mean gender acuity thresholds are plotted in Figure 6, with smaller values representing better gender acuity. The ANOVA revealed a main effect of location, $F(1,13) = 22.97$, $p < .001$, $d = 0.91$, indicating that gender acuity differed between the upper and lower fields. Gender acuity thresholds were significantly smaller in the lower field compared to the upper for upright faces, $t(13) = 3.82$, $p = .002$, and approached significance for inverted faces, $t(13) = 2.07$, $p = .059$. On an individual level, 12 of 14 participants showed better acuity in the lower vs. the upper field. These results highlight the presence of an upper-lower difference in face recognition, with better gender acuity in the lower half of the visual field.

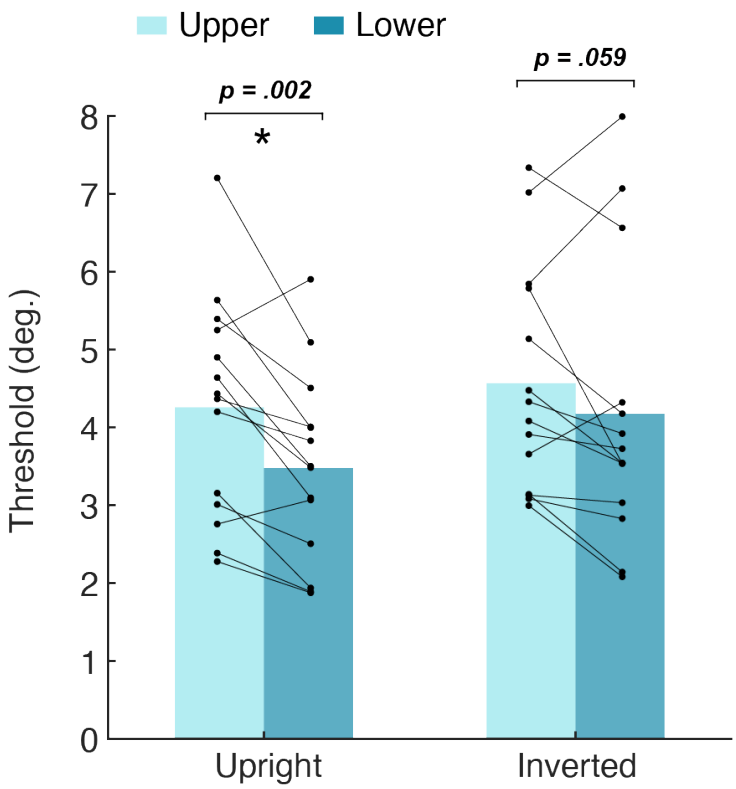

Figure 6. Mean gender acuity thresholds for the upper (90°; lighter blue) versus lower (270°; darker blue) visual field, for both upright and inverted faces. The asterisk represents a significant difference. Dots represent thresholds for each participant, with lines connecting each individual's performance between upper and lower locations.

Like the previous two experiments, there was a main effect of orientation, $F(1,13) = 8.38$, $p = .013$, $d = 0.39$, indicating an overall inversion effect whereby gender acuity thresholds were larger for inverted compared to upright faces, $t(27) = -2.92$, $p = .007$. There was also a main effect of participant, $F(1,13) = 31.12$, $p = .032$, $d = 1.00$, again highlighting overall differences in gender acuity between individuals. There was no significant interaction between location and participant, $F(1,13) = 0.58$, $p = .829$, $d = 0.37$, suggesting that there was a common pattern of gender acuity across individuals. Interactions were similarly non-significant for location and orientation, $F(1,13) = 0.91$, $p = .358$, $d = 0.07$, and orientation and participant, $F(1,13) = 1.02$, $p = .484$, $d = 0.51$, indicating that gender acuity patterns were similar for upright and inverted faces, and that inversion effects did not vary significantly between individuals.

Discussion

We demonstrate that face perception varies across the visual field in a systematic pattern, analogous to that of low-level vision. Across 3 experiments, acuity for judging facial gender showed a horizontal-vertical anisotropy – accurate recognition was possible with smaller faces on the horizontal vs. the vertical meridian. Overall, a small-but-reliable upper-lower difference was also present, with better acuity in the lower vs. the upper field. This upper-lower difference persisted when we controlled for factors such as participants' eye movements and eye position within face stimuli, though its measurement required an increase in the number of trials. The presence of both these anisotropies, and the smaller magnitude of the upper-lower than the horizontal-vertical difference, matches the patterns found in low-level vision (Barbot et al., 2021; Kurzawski et al., 2021). That is, instead of varying uniquely or idiosyncratically (Afraz et al., 2010; Quek & Finkbeiner, 2016; Schmidtmann et al., 2015), the resolution of face perception varies predictably across the visual field in the same fashion as lower-level abilities (Abrams et al., 2012; Carrasco et al., 2001). This suggests that spatial properties are preserved through the visual hierarchy and inherited by face processing systems.

Why did we find systematic variations in face recognition rather than purely idiosyncratic variations? Prior studies demonstrating these idiosyncrasies have relied on judgements of appearance (Afraz et al., 2010; Visconti di Oleggio Castello et al., 2018), which can show pronounced perceptual idiosyncrasies in low-level vision

(Moutsiana et al., 2016). Similarly, perceived object position has been shown to vary across participants due to individual differences in localised distortion across the visual field (Kosovicheva & Whitney, 2017). Using judgements of appearance to measure subtle perceptual biases in face perception may introduce similar individual-dependent distortions. Indeed, idiosyncrasies in identity judgements for specific face pairs did not correlate with other face pairs, suggesting that perceptual biases were tied to particular face stimuli (Visconti di Oleggio Castello et al., 2018). This could be driven by variations in factors like heightened contrast in face features like the eyebrows or lips, which would skew judgements towards 'female' (Russell, 2009). The use of faces morphed between one male and one female prototype (Afraz et al., 2010) could have similarly increased the susceptibility to stimulus-based and individual-based distortion effects. In contrast, we used categorical judgements with multiple unambiguously gendered faces, measuring variations in performance instead of judgments of appearance. This method would be less susceptible to smaller individual-dependent variations, allowing us to uncover the larger systematic anisotropies observed.

Our systematic variations in gender acuity also differ from the variations in face recognition found between the hemifields in prior studies. For instance, whereas judgements of the identity of synthetic-contour faces were found to be more accurate in the left visual field compared to the right (Schmidtmann et al., 2015), we found no difference between the left and right visual fields. The lack of a left hemifield advantage in our work is consistent with the broader observation that lateralisation effects are not always present for face perception. Rather, these effects may depend heavily on the task (Bourne et al., 2009; Kovacs et al., 2017; McKone, 2004; Schweinberger et al., 2003) or the stimuli involved, e.g. with the clearest effects emerging for large, chimeric faces that span fixation (Burt & Perrett, 1997; Harrison & Strother, 2021). Because synthetic faces contain only a narrow band of intermediate spatial frequencies and lack details such as skin texture (Wilson et al., 2002), their recognition may rely on sub-processes that are not representative of the full spectrum of face processing. Similarly, whereas we observe better gender acuity in the lower field than the upper, prior work has demonstrated faster recognition of face gender in the upper than the lower field (Quek & Finkbeiner, 2014, 2016). The difference here likely stems from our measurement of performance rather than reaction times, a distinction that has also been

found for lower-level stimuli – while performance measurements show a clear lower-field advantage (Abrams et al., 2012; Barbot et al., 2021; Carrasco et al., 2001), measurements of temporal processing with similar stimuli show an upper-field advantage (Abegg et al., 2015; Honda & Findlay, 1992). In other words, our findings show that when the spatial resolution of face perception is measured in the same way as more basic visual abilities, similar visual field anisotropies to low-level vision emerge.

In Experiments 2 and 3, the upper-lower difference was reduced when the position of the eyes within face stimuli was matched across locations, relative to Experiment 1 where faces were centred on the nose. This effect of eye position highlights a role for specific face features in gender perception, and confirms a particular importance of the eyes (Brown & Perrett, 1993; Schyns et al., 2002). Across all experiments, acuity thresholds were nonetheless consistently lower for upright compared to inverted faces. As in prior work (Kalpadakis-Smith et al., 2018; Kovacs et al., 2017; McKone, 2004), this inversion effect shows that the configural processing of upright faces is maintained across both foveal and peripheral vision. We conclude that our gender acuity task was sufficient to engage these face-specific mechanisms.

While inversion effects are typically measured as percent-correct performance using faces of a constant size (Yin, 1969), here we highlight a spatial component to face recognition abilities. Namely, in our study, percent-correct performance for upright and inverted faces could be matched by increasing the size of inverted faces. This may be driven by the spatial selectivity of face-selective regions, given fMRI evidence that face inversion reduces visual field coverage, in turn driven by a reduction in population receptive field (pRF) sizes (Poltoratski et al., 2021). The impaired perception of inverted faces could therefore reflect sampling by fewer neurons, with an increase in face size able to mitigate this through increased neural recruitment. Although these differences in the processing of upright vs. inverted faces appear to be *quantitative* in nature (Sekuler et al., 2004), inversion effects are often argued to represent a *qualitative* change in face processing between upright and inverted faces (Rossion, 2008). Accordingly, the requirement that inverted faces be larger than upright faces could reflect the added benefit of configural processing with upright faces (Robbins &

McKone, 2007), which may allow the gender of upright faces to be perceived at smaller sizes.

The mechanisms underlying the visual field anisotropies that we observe for face perception can be considered along similar lines. One possible explanation of these anisotropies is that they are driven by variations in *featural selectivity*. Contrast sensitivity and orientation discrimination are better for peripheral stimuli that are radially oriented – i.e. pointing towards the fovea – known as the radial bias (Rovamo et al., 1982; Westheimer, 2003). This could explain why larger inversion effects have been found for face recognition along the horizontal vs. vertical meridian (Roux-Sibilon et al., 2023), as horizontal information is particularly informative for various aspects of face perception, including identity recognition and configural processing (Dakin & Watt, 2009; Goffaux & Greenwood, 2016). Given the hierarchical nature of the visual system (Loffler et al., 2003; Riesenhuber & Poggio, 1999), anisotropies in face perception could be partly driven by the passive pooling of low-level information, with low-level featural selectivity such as the radial bias impacting the quality of information received by face processing systems. Alternatively, the process could be more active – given that horizontal spatial frequencies are especially important for face perception (Dakin & Watt, 2009; Goffaux & Greenwood, 2016) and elicit stronger responses in the FFA (Goffaux et al., 2016), a boost in the response to these orientations during higher-level processing could facilitate face recognition. However, though these factors could contribute to the horizontal-vertical anisotropy, radial variations of this kind would be matched in the upper and lower visual fields, making them unlikely to explain the upper-lower anisotropy.

Anisotropies for face recognition could also occur through variations in *spatial selectivity* around the visual field. In low-level vision, better acuity has been linked to smaller receptive field size and a larger cortical magnification factor (Benson et al., 2021; Duncan & Boynton, 2003; Silson et al., 2018; Silva et al., 2018). As above, improved acuity for faces could arise simply because higher levels *passively* inherit the enhanced low-level input from these locations (Riesenhuber & Poggio, 1999). Unlike low-level vision, however, better face perception has been linked with larger pRF sizes and the resulting increase in visual field coverage within face-selective regions

(Poltoratski et al., 2021; Witthoft et al., 2016). The anisotropies we measured for face perception could therefore stem from the way that face-selective neurons *actively* sample the visual field, with variations in coverage across different locations. Given that we found the same pattern of anisotropies for upright and inverted faces, our findings either suggest that these spatial properties vary in the same way for neurons sensitive to upright and inverted faces, or as above that these effects are driven by the quality of the information inherited from lower-level stages of processing. Either way, the similar spatial selectivity we uncover suggests that the retinotopy within face-selective regions is not entirely distinct from earlier brain areas.

In conclusion, face perception varies around the visual field with both horizontal-vertical and upper-lower anisotropies, matching patterns consistently found for low-level vision (Abrams et al., 2012; Barbot et al., 2021; Carrasco et al., 2001), and contrary to suggestions that face recognition varies in a unique or entirely idiosyncratic manner (Afraz et al., 2010; Quek & Finkbeiner, 2016; Schmidtmann et al., 2015). Our results are consistent with a hierarchical model of face processing whereby the selectivity for faces is built on the selectivity of earlier levels. The variations in face recognition that we observe are likely driven by variations in spatial selectivity, and perhaps in part by variations in the selectivity of face processing to features like orientation, both of which may be inherited passively from earlier stages or actively maintained in face-selective regions. Our finding that these face perception anisotropies match those of low-level vision, for both upright and inverted faces, points to the possibility of a common basis. Ultimately, we demonstrate that spatial variations are found throughout the visual system, causing location to influence face perception.

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References

Abegg, M., Pianezzi, D., & Barton, J. J. (2015). A vertical asymmetry in saccades. *Journal of Eye Movement Research*, *8*(5). https://doi.org/10.16910/jemr.8.5.3

Abrams, J., Nizam, A., & Carrasco, M. (2012). Isoeccentric locations are not equivalent: the extent of the vertical meridian asymmetry. *Vision Res*, *52*(1), 70-78. https://doi.org/10.1016/j.visres.2011.10.016

Afraz, A., Pashkam, M. V., & Cavanagh, P. (2010). Spatial heterogeneity in the perception of face and form attributes. *Current Biology*, *20*(23), 2112-2116. https://doi.org/10.1016/j.cub.2010.11.017

Barbot, A., Xue, S., & Carrasco, M. (2021). Asymmetries in visual acuity around the visual field. *J Vis*, *21*(1), 2. https://doi.org/10.1167/jov.21.1.2

Benson, N. C., Kupers, E. R., Barbot, A., Carrasco, M., & Winawer, J. (2021). Cortical magnification in human visual cortex parallels task performance around the visual field. *Elife*, *10*. https://doi.org/10.7554/eLife.67685

Bourne, V. J., Vladeanu, M., & Hole, G. J. (2009). Lateralised repetition priming for featurally and configurally manipulated familiar faces: evidence for differentially lateralised processing mechanisms. *Laterality*, *14*(3), 287-299. https://doi.org/10.1080/13576500802383709

Brainard, D. H., & Vision, S. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433-436.

Brown, E., & Perrett, D. I. (1993). What gives a face its gender? *Perception*, *22*(7), 829-840. https://doi.org/10.1068/p220829

Burt, D. M., & Perrett, D. I. (1997). Perceptual asymmetries in judgements of facial attractiveness, age, gender, speech and expression. *Neuropsychologia*, *35*(5), 685-693. https://doi.org/10.1016/S0028-3932(96)00111-X

Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance fields: effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spat Vis*, *15*(1), 61-75. https://doi.org/10.1163/15685680152692015

Crider, B. (1944). A battery of tests for the dominant eye. *The Journal of General Psychology*, *31*(2), 179-190. https://doi.org/10.1080/00221309.1944.10543187

Curcio, C. A., & Allen, K. A. (1990). Topography of ganglion cells in human retina. *Journal of comparative Neurology*, *300*(1), 5-25. https://doi.org/10.1002/cne.903000103

Dakin, S. C., & Watt. (2009). Biological “bar codes” in human faces. *Journal of vision*, *9*(4), 2-2. https://doi.org/10.1167/9.4.2

Duncan, R. O., & Boynton, G. M. (2003). Cortical magnification within human primary visual cortex correlates with acuity thresholds. *Neuron*, *38*(4), 659-671. https://doi.org/10.1016/S0896-6273(03)00265-4

Ellis, H. D., & Shepherd, J. W. (1975). Recognition of upright and inverted faces presented in the left and right visual fields. *Cortex*, *11*(1), 3-7. https://doi.org/10.1016/s0010-9452(75)80014-1

Goffaux, V., Duecker, F., Hausfeld, L., Schiltz, C., & Goebel, R. (2016). Horizontal tuning for faces originates in high-level Fusiform Face Area. *Neuropsychologia*, *81*, 1-11. https://doi.org/10.1016/j.neuropsychologia.2015.12.004

Goffaux, V., & Greenwood, J. A. (2016). The orientation selectivity of face identification. *Sci Rep*, *6*, 34204. https://doi.org/10.1038/srep34204

Greenwood, J. A. (2023). *Eccentric Vision Lab Github.* https://doi.org/https://www.github.com/eccentricvision

Greenwood, J. A., Szinte, M., Sayim, B., & Cavanagh, P. (2017). Variations in crowding, saccadic precision, and spatial localization reveal the shared topology of spatial vision. *Proc Natl Acad Sci U S A*, *114*(17), E3573-E3582. https://doi.org/10.1073/pnas.1615504114

Harrison, M., & Strother, L. (2021). Does face-selective cortex show a left visual field bias for centrally-viewed faces? *Neuropsychologia*, *159*(107956). https://doi.org/10.1016/j.neuropsychologia.2021.107956

Himmelberg, M. M., Winawer, J., & Carrasco, M. (2020). Stimulus-dependent contrast sensitivity asymmetries around the visual field. *J Vis*, *20*(9), 18. https://doi.org/10.1167/jov.20.9.18

Honda, H., & Findlay, J. (1992). Saccades to targets in three-dimensional space: Dependence of saccadic latency on target location. *Perception & Psychophysics*, *52*, 167-174. https://doi.org/10.3758/BF03206770

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of physiology*, *160*(1), 106. https://doi.org/10.1113/jphysiol.1962.sp006837

Kalpadakis-Smith, A. V., Goffaux, V., & Greenwood, J. A. (2018). Crowding for faces is determined by visual (not holistic) similarity: Evidence from judgements of eye position. *Sci Rep*, *8*(1), 12556. https://doi.org/10.1038/s41598-018-30900-0

Kay, K. N., Weiner, K. S., & Grill-Spector, K. (2015). Attention reduces spatial uncertainty in human ventral temporal cortex. *Curr Biol*, *25*(5), 595-600. https://doi.org/10.1016/j.cub.2014.12.050

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3?

Kosovicheva, A., & Whitney, D. (2017). Stable individual signatures in object localization. *Current Biology*, *27*(14), R700-R701. https://doi.org/10.1016/j.cub.2017.06.001

Kovacs, P., Knakker, B., Hermann, P., Kovacs, G., & Vidnyanszky, Z. (2017). Face inversion reveals holistic processing of peripheral faces. *Cortex*, *97*, 81-95. https://doi.org/10.1016/j.cortex.2017.09.020

Kurzawski, J. W., Burchell, A., Thapa, D., Majaj, N. J., Winawer, J. A., & Pelli, D. G. (2021). An enhanced Bouma model fits a hundred people's visual crowding. https://doi.org/10.1101/2021.04.12.439570

Laguesse, R., Dormal, G., Biervoye, A., Keufner, D., & Rossion, B. (2012). Extensive visual training in adulthood significantly reduces the face inversion effect. *Journal of vision*, *12*(4). https://doi.org/10.1167/12.10.14

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Early visual experience and face processing. *Nature.*, *410*(6831), 890. https://doi.org/10.1038/35073749

Loffler, G., Wilson, H. R., & Wilkinson, F. (2003). Local and global contributions to shape discrimination. *Vision Research*, *43*(5), 519-530. https://doi.org/10.1016/S0042-6989(02)00686-7

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, *6*(6), 255-260. https://doi.org/10.1016/S1364-6613(02)01903-4

McKone, E. (2004). Isolating the special component of face recognition: peripheral identification and a Mooney face. *J Exp Psychol Learn Mem Cogn*, *30*(1), 181-197. https://doi.org/10.1037/0278-7393.30.1.181

Moutsiana, C., De Haas, B., Papageorgiou, A., Van Dijk, J. A., Balraj, A., Greenwood, J. A., & Schwarzkopf, D. S. (2016). Cortical idiosyncrasies predict the perception of object size. *Nature communications*, *7*(1), 12110. https://doi.org/10.1038/ncomms12110

Pelli, D. G., & Vision, S. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437-442.

Perry, V. H., & Cowey, A. (1985). The ganglion cell and cone distributions in the monkey's retina: implications for central magnification factors. *Vision Research*, *25*(12), 1795-1810. https://doi.org/10.1016/0042-6989(85)90004-5

Piepers, D. W., & Robbins, R. A. (2012). A Review and Clarification of the Terms "holistic," "configural," and "relational" in the Face Perception Literature. *Front Psychol*, *3*, 559. https://doi.org/10.3389/fpsyg.2012.00559

Poltoratski, S., Kay, K., Finzi, D., & Grill-Spector, K. (2021). Holistic face recognition is an emergent phenomenon of spatial processing in face-selective regions. *Nat Commun*, *12*(1), 4745. https://doi.org/10.1038/s41467-021-24806-1

Párraga, C. A., Troscianko, T., & Tolhurst, D. J. (2000). The human visual system is optimised for processing the spatial information in natural visual images. *Current Biology*, *10*(1), 35-38. https://doi.org/10.1016/S0960-9822(99)00262-6

Quek, G. L., & Finkbeiner, M. (2014). Face-sex categorization is better above fixation than below: Evidence from the reach-to-touch paradigm. *Cognitive, Affective, & Behavioral Neuroscience*, *14*, 1407-1419. https://doi.org/10.3758/s13415-014-0282-y

Quek, G. L., & Finkbeiner, M. (2016). The upper-hemifield advantage for masked face processing: Not just an attentional bias. *Attention, Perception, & Psychophysics*, *78*, 52-68. https://doi.org/10.3758/s13414-015-0965-7

Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nat Neurosci*, *2*(11), 1019-1025. https://doi.org/10.1038/14819

Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, *103*(1), 34-79. https://doi.org/10.1016/j.cognition.2006.02.008

Rosenholtz, R. (2016). Capabilities and Limitations of Peripheral Vision. *Annu Rev Vis Sci*, *2*, 437-457. https://doi.org/10.1146/annurev-vision-082114-035733

Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychol (Amst)*, *128*(2), 274-289. https://doi.org/10.1016/j.actpsy.2008.02.003

Roux-Sibilon, A., Peyrin, C., Greenwood, J. A., & Goffaux, V. (2023). Radial bias in face identification. *Proceedings of the Royal Society B: Biological Sciences*, *290*(2001), 20231118. https://doi.org/doi:10.1098/rspb.2023.1118

Rovamo, J., Virsu, V., Laurinen, P., & Hyvarinen, L. (1982). Resolution of gratings oriented along and across meridians in peripheral vision. *Invest Ophthalmol Vis Sci*, *23*(5), 666-670.

Rubin, N., Nakayama, K., & Shapley, R. (1996). Enhanced perception of illusory contours in the lower versus upper visual hemifields. *Science*, *271*(5249), 651-653. https://doi.org/10.1126/science.271.5249.651

Russell, R. (2009). A sex difference in facial contrast and its exaggeration by cosmetics. *Perception*, *38*(8), 1211-1219. https://doi.org/10.1068/p6331

Schmidtmann, G., Logan, A. J., Kennedy, G. J., Gordon, G. E., & Loffler, G. (2015). Distinct lower visual field preference for object shape. *J Vis*, *15*(5), 18. https://doi.org/10.1167/15.5.18

Schweinberger, S. R., Baird, L. M., Blümler, M., Kaufmann, J. M., & Mohr, B. (2003). Interhemispheric cooperation for face recognition but not for affective facial expressions. *Neuropsychologia*, *41*(4), 407-414. https://doi.org/10.1016/S0028-3932(02)00173-2

Schyns, P. G., Bonnar, L., & Gosselin, F. (2002). Show me the features! Understanding recognition from the use of visual information. *Psychological science*, *13*(5), 402-409. https://doi.org/10.1111/1467-9280.00472

Sekuler, A. B., Gaspar, C. M., Gold, J. M., & Bennett, P. J. (2004). Inversion leads to quantitative, not qualitative, changes in face processing. *Curr Biol*, *14*(5), 391-396. https://doi.org/10.1016/j.cub.2004.02.028

Silson, E. H., Reynolds, R. C., Kravitz, D. J., & Baker, C. I. (2018). Differential sampling of visual space in ventral and dorsal early visual cortex. *Journal of Neuroscience*, *38*(9), 2294-2303. https://doi.org/10.1523/JNEUROSCI.2717-17.2018

Silva, M. F., Brascamp, J. W., Ferreira, S., Castelo-Branco, M., Dumoulin, S. O., & Harvey, B. M. (2018). Radial asymmetries in population receptive field size and

cortical magnification factor in early visual cortex. *Neuroimage*, *167*, 41-52. https://doi.org/10.1016/j.neuroimage.2017.11.021

Tailor, V. K., Theodorou, M., Dahlmann-Noor, A. H., Dekker, T. M., & Greenwood, J. A. (2021). Eye movements elevate crowding in idiopathic infantile nystagmus syndrome. *Journal of vision*, *21*(13), 9-9. https://doi.org/10.1167/jov.21.13.9

Visconti di Oleggio Castello, M., Taylor, M., Cavanagh, P., & Gobbini, M. I. (2018). Idiosyncratic, Retinotopic Bias in Face Identification Modulated by Familiarity. *eNeuro*, *5*(5). https://doi.org/10.1523/ENEURO.0054-18.2018

Wandell, B. A., Dumoulin, S. O., & Brewer, A. A. (2007). Visual field maps in human cortex. *Neuron*, *56*(2), 366-383. https://doi.org/10.1016/j.neuron.2007.10.012

Wandell, B. A., & Winawer, J. (2011). Imaging retinotopic maps in the human brain. *Vision Res*, *51*(7), 718-737. https://doi.org/10.1016/j.visres.2010.08.004

Watson, A. B., & Pelli, D. G. (1983). QUEST: a Bayesian adaptive psychometric method. *Percept Psychophys*, *33*(2), 113-120. https://doi.org/10.3758/bf03202828

Westheimer, G. (2003). The distribution of preferred orientations in the peripheral visual field. *Vision Res*, *43*(1), 53-57. https://doi.org/10.1016/s0042-6989(02)00398-x

Westheimer, G. (2005). Anisotropies in peripheral vernier acuity. *Spat Vis*, *18*(2), 159-167. https://doi.org/10.1163/1568568053320611

Wilson, H. R., Loffler, G., & Wilkinson, F. (2002). Synthetic faces, face cubes, and the geometry of face space. *Vision Research*, *42*(27), 2909-2923. https://doi.org/10.1016/S0042-6989(02)00362-0

Witthoft, N., Poltoratski, S., Nguyen, M., Golarai, G., Liberman, A., LaRocque, K. F., . . . Grill-Spector, K. (2016). Reduced spatial integration in the ventral visual cortex underlies face recognition deficits in developmental prosopagnosia. *BioRxiv*, *051102*. https://doi.org/10.1101/051102

Yin, R. K. (1969). Looking at upside-down faces. *Journal of experimental psychology*, *81*(1), 141. https://doi.org/10.1037/h0027474

Yovel, G., & Kanwisher, N. (2004). Face perception: domain specific, not process specific. *Neuron*, *44*(5), 889-898. https://doi.org/10.1016/j.neuron.2004.11.018

Yovel, G., & Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology*, *15*(24), 2256-2262. https://doi.org/10.1016/j.cub.2005.10.072