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Report

# Spatial Heterogeneity in the Perception of Face and Form Attributes

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## Summary

**The identity of an object is a fixed property, independent of where it appears, and an effective visual system should capture this invariance [1–3]. However, we now report that the perceived gender of a face is strongly biased toward male or female at different locations in the visual field. The spatial pattern of these biases was distinctive and stable for each individual. Identical neutral faces looked different when they were presented simultaneously at locations maximally biased to opposite genders. A similar effect was observed for perceived age of faces. We measured the magnitude of this perceptual heterogeneity for four other visual judgments: perceived aspect ratio, orientation discrimination, spatial-frequency discrimination, and color discrimination. The effect was sizeable for the aspect ratio task but substantially smaller for the other three tasks. We also evaluated perceptual heterogeneity for facial gender and orientation tasks at different spatial scales. Strong heterogeneity was observed even for the orientation task when tested at small scales. We suggest that perceptual heterogeneity is a general property of visual perception and results from undersampling of the visual signal at spatial scales that are small relative to the size of the receptive fields associated with each visual attribute.**

## Results

We have measured the effect of retinal position on the perceptual appearance of objects for a number of object dimensions and find substantial departures from invariance. The perceived identity of an object should remain the same at different locations, but our first experiment showed a remarkable variation in biases for male or female percepts as a function of location, a local variation that offers insights into the scale and nature of the underlying analyses. In this first experiment, subjects were asked to identify the gender of faces that were chosen randomly from a morphing spectrum between male and female prototypes (FaceGen) based on 3D scans of real faces. The stimuli (in all of the experiments) were flashed in one of the eight possible locations at 3° eccentricity around a central fixation point (see Supplemental Experimental Procedures available online). The results were plotted separately for each of the 11 subjects as the proportion of "female" response (Figure 1). Data points were fitted with a logistic function to calculate the point of subjective equality (PSE, "androgyny" in this case) where the face looked equally male and female for each of the eight tested positions on the display circle. Figure 1 shows the results for one of the subjects. We found that the PSE for facial gender varied dramatically across different locations with the same eccentricity. The average range of PSEs for individual subjects was 0.42 on a scale of 0 to 1 (0 representing the 100% male stimulus, and 1 standing for the 100% female stimulus), a location-specific bias that spans almost half of the gender spectrum. The variation of PSE across space was significant in all subjects (logistic regression, $p < 0.0001$). The color map of Figure 1 shows the spatial distribution of local perceptual biases for one of the subjects (see Figure S1 for additional subjects and information). The shape of the PSE mosaic was unique for each individual, whereas the PSEs averaged across subjects showed not only no systematic pattern (Figure S1A) but also no significant bias (deviation from midpoint on gender scale) at any location ($p > 0.1$ for all locations). Also, we have not identified any source for these individual biases in variables we have examined so far: a four-way repeated-measures analysis of variance (ANOVA) was performed with location as the within-subjects factor and with subject gender, height, and handedness as the between-subjects factors against PSE as the dependent variable. Results showed no significant effect of location ($F(7,35) = 0.96$, $p = 0.47$) in these group data. The results also showed no main effects of subject gender ($F(1,5) = 0.5$, $p = 0.51$), subject height (to see whether the higher average height for males compared to females can possibly influence statistics of male and female faces in upper and lower visual fields across lifetime experience of the subjects; taller versus shorter, $F(1,5) = 0.54$, $p = 0.49$), or subject handedness ($F(1,5) = 0.35$, $p = 0.58$). None of the interactions were significant ($p > 0.3$ for all). A contrast analysis was also performed to compare the averaged PSEs for the three upper visual field locations versus the three lower visual field ones. No significant difference was observed ($t(10) = 0.3$, $p = 0.76$). The same contrast was made for the left three versus the right three locations (to check for the possible effect of lateralization on local biases). Again, no significant hemifield effect was observed ($t(10) = 1.1$, $p = 0.28$). Finally, to investigate the possible effect of visual field quarters, we performed a one-way ANOVA only including the four corner locations. Here as well, no significant effect was observed ($F(3, 30) = 0.37$, $p = 0.78$).

### Perceptual Fingerprint: Specificity and Stability of the Bias Pattern over Time

To measure the specificity and stability of the effect, we repeated the experiment after 3 to 5 weeks for eight of the subjects. For each subject, the mosaic of gender bias remained quite similar across the test-retest interval. The correlation between the PSE patterns obtained from the two measurements was above 0.7 for all of the individual subjects (Pearson $r > 0.7$ and $p < 0.05$ for all subjects; see Figure 2A and Figures S2B and S2C). This confirms that although the spatial

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pattern of the gender bias mosaic does not follow any noticeable order across subjects, it is highly stable within each individual.

To rule out possible contribution of monocular mechanisms such as higher-order optical aberrations or random variation of retinal cone mosaic in the observed effect, we had three subjects take the test monocularly, once with the left eye and once with the right eye (randomly intermingled blocks). PSE mosaics obtained from a subject's two eyes were highly similar, and this held for all three subjects ($r > 0.9$ and $p < 0.0001$ in all cases). The faces used in this study are asymmetrically illuminated, so we flipped the original face stimuli horizontally and tested four of the subjects with the flipped stimuli to rule out the effect of lighting direction. The pattern of perceptual heterogeneity was unaffected by flipping ($r > 0.8$ and $p < 0.01$ in all cases).

## Two Identical Faces May Look Different

The shifts of the psychometric function (and its PSE) across locations might reflect an actual perceptual bias or a motor response bias. Although it is unlikely that subjects have motor choice biases for different parts of their visual field, we ran a second experiment to rule out this possibility and to confirm the original effect with an independent method. Two faces were flashed simultaneously for 50 ms, and the subjects reported with a key press whether the faces looked the same or different. The pair of locations where the two faces were shown was selected based on the PSE mosaic of each individual. Two different pairs of locations were used: (1) biased pair with maximum bias to opposite gender directions and (2) unbiased pair with similar PSEs (near neutral) for facial gender (see Figure S3). The two faces were identical in half of the trials (randomly interleaved) and were slightly different (one female and the other male) in the other half (see Supplemental Experimental Procedures for more details). Subjects perceived two identical faces as different more frequently if they were presented at the biased pair of locations (paired sample t test, $t(3) = 9.9$, $p < 0.01$). For the trials in which the two faces were different, there was a significant interaction between the pair location and stimulus congruency ($F(1,3) = 17.6$, $p < 0.05$; see Figure S3). Specifically, in the case of biased location pair, when the stimulus genders were consistent with the bias, the proportion of seeing the pair as dissimilar was maximal, whereas when the stimulus genders were the opposite of the PSE bias, the two faces were perceived as "the same" more frequently (paired sample t test, $t(3) = 5.3$, $p < 0.01$). There was no effect of stimulus congruency (with

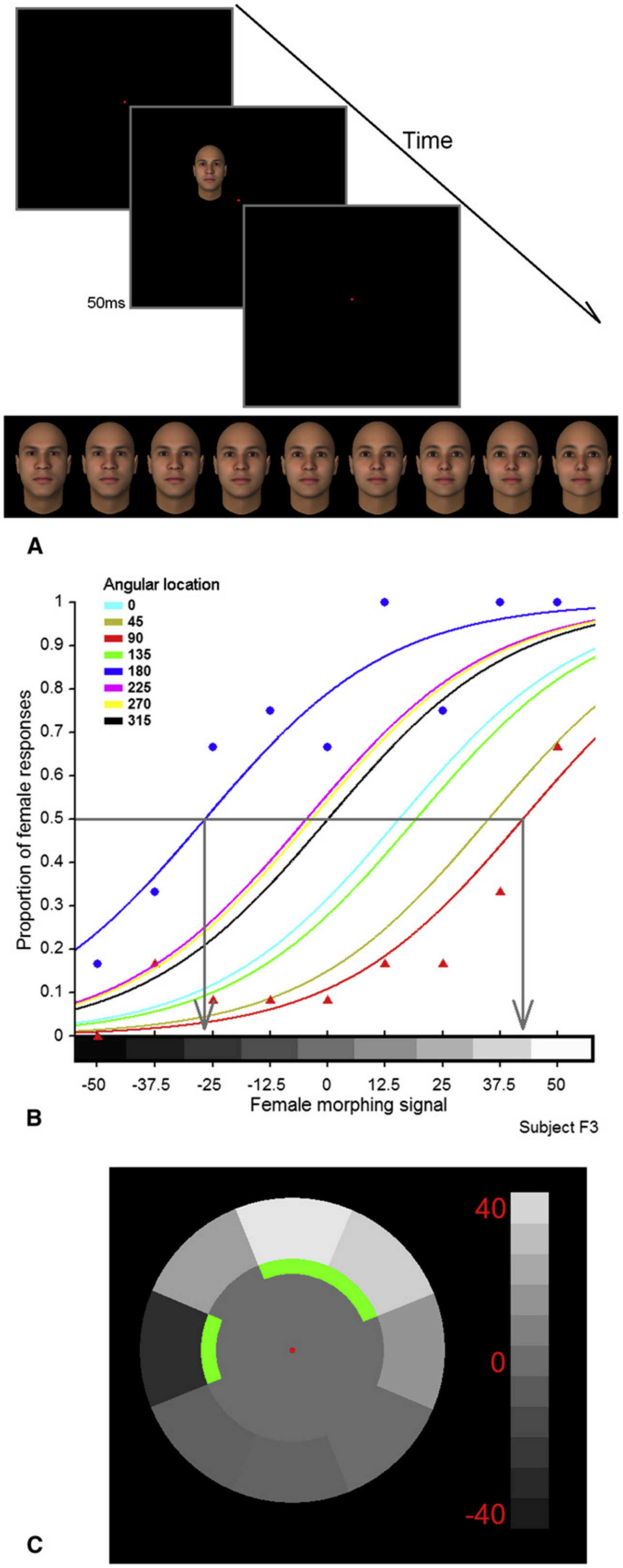

Figure 1. Heterogeneity of Facial Gender Perception across the Visual Field

(A) Experimental paradigm. The stimuli (faces selected from a morphing spectrum between male and female prototypes) were shown for 50 ms in one of the eight possible locations around the fixation point. Subjects had to indicate the stimuli's gender by pressing a key.

(B) Psychometric functions. The horizontal axis shows the face morphing level. Positive values indicate female faces (lighter shades), and negative values stand for male faces (dark shades). The vertical axis indicates the proportion of female responses. Colored curves show the logistic fits to the psychometric results for the eight tested locations separately. The angular location of the eight locations are color coded (angles begin at 0° to the right of the fixation and increase in the counterclockwise direction). Actual data points are shown only for the leftmost and rightmost curves to avoid visual clutter. The two gray arrows indicate points of subjective equality (PSEs) of the most female-biased (left) and the most male-biased (right) curves.

(C) Gender PSE mosaic. The same results are shown as a shaded radial mosaic. Each location on the mosaic corresponds to the same tested location around the fixation point. The gray level shade indicates the PSE at each spot. The green arcs indicate statistical significance of the deviation of the PSE from the average (logistic regression $\alpha = 0.001$, Bonferroni corrected).

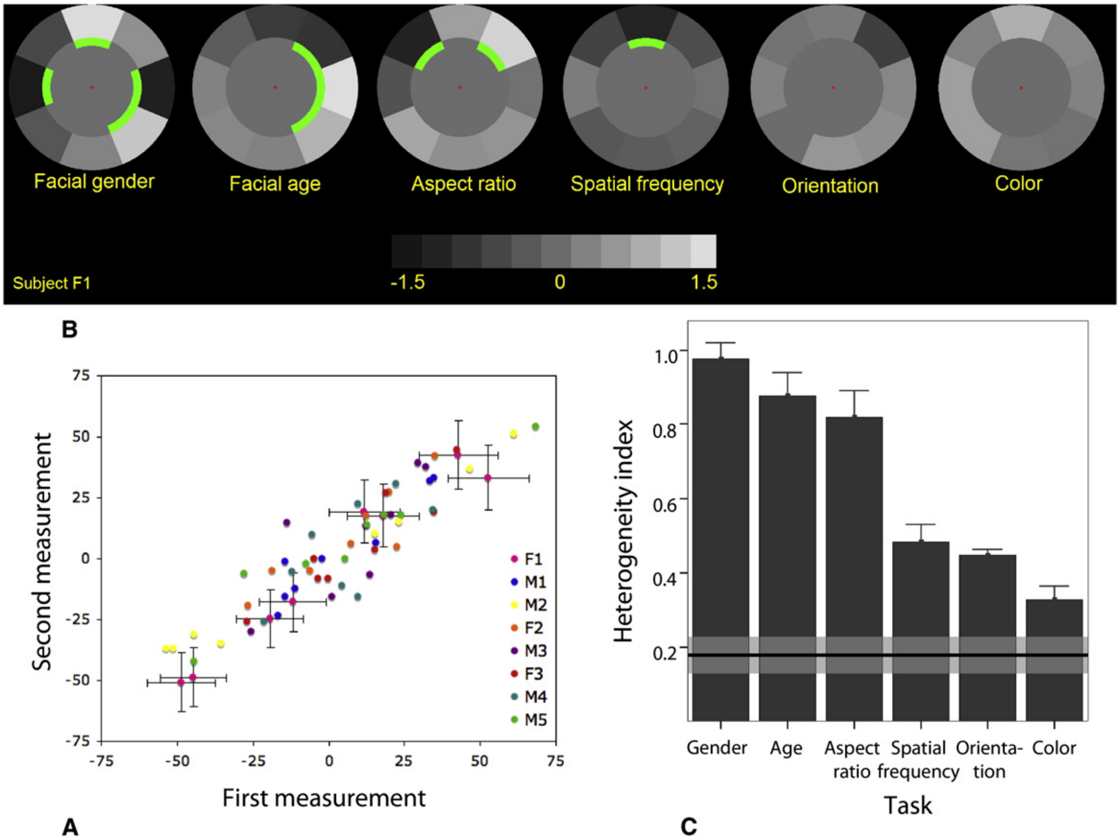

Figure 2. Stability of the Original Effect across Time and the Perceptual Heterogeneity for Six Visual Tasks

(A) Scatter plot comparing the first and second measurements of PSEs for eight subjects at each of the eight locations.

(B) PSE mosaics for the five visual tasks for one of the subjects. To make it possible to compare the heterogeneity magnitude across five different tasks, we normalized PSEs of each task to the corresponding just noticeable difference (JND). The color map indicates PSE/JND.

(C) Heterogeneity indices. The bar plot demonstrates the perceptual heterogeneity index (see Results) for the five investigated visual tasks. The horizontal black line and gray band indicate the mean ± 1 standard error (SE) of the heterogeneity index expected with local biases due only to noise (based on Monte Carlo simulation). Error bars show ±1 SE of mean.

the much smaller PSE difference) at the unbiased pair of loci (paired sample t test, $t(3) = -0.7$, $p = 0.53$).

These results confirm that the observed PSE shifts of the first experiment indicate intrinsic heterogeneity of visual object perception. Two identical faces look dissimilar if they fall at oppositely biased locations, and, more interestingly, two physically different faces can look perceptually similar if they fall in oppositely biased spots, clear counterexamples to translation invariance.

### Perceptual Heterogeneity for Other Visual Tasks

We next measured the perceptual heterogeneity for five additional visual tasks: perceived facial age, perceived aspect ratio of an ellipse, orientation of a grating, spatial frequency discrimination of a grating, and color discrimination of a uniform color patch. Stimulus setting and timing and the eight test locations were the same as in the first experiment. See the Supplemental Experimental Procedures for details of the tasks. The ellipse task, the spatial frequency task, and the color task could reveal underlying factors contributing to the gender bias: female faces are wider than male faces [4, 5], male skin tone tends to be slightly reddish and female skin tone tends to be slightly greenish [6], and spatial frequency (especially in the horizontal orientation) is claimed to carry information about face category [7].

Six subjects (from the group of 11 subjects of experiment 1) participated in these new experiments. The PSEs were calculated for each of the eight tested locations, and the standard deviation of the PSEs across the eight locations was used as the measure of heterogeneity for each task. To normalize these values, we divided them by the just noticeable difference (JND) for each task and subject separately to get a "heterogeneity index" (see Supplemental Experimental Procedures for details). The "heterogeneity index" is defined in JND units to provide a standard psychometric measure for cross-task comparisons.

Figure 2B shows the normalized PSE mosaics for all of the five tasks (including the original gender task) for one of the subjects (see Figure S1 for others). The heterogeneity index for the facial age task was almost as large as for the gender task in all subjects. The heterogeneity was slightly smaller, but still substantial, for the aspect ratio task; heterogeneity was smallest for the spatial frequency, orientation, and color tasks in all subjects (Figure 2C). A one-way ANOVA (with subject as the random factor) showed a significant effect of the task type on the heterogeneity index ($F(5,18) = 46.15$, $p < 0.001$). Also, a separate repeated-measures ANOVA on the four subjects who participated in all of the control experiments showed again the significant effect of task type on the heterogeneity index ($F(5,15) = 51.02$, $p < 0.001$). Critically, there was no significant within-subject correlation between the individual patterns of any of the five tasks, ruling out local variations in color, spatial frequency, or geometry as the source of the gender biases.

To further analyze the spatial scale of the perceptual heterogeneity effect, we autocorrelated the PSE mosaics for each subject-task combination (see Figure S2A for details). The results indicate that the spatial scale of analysis for the gender, age, and aspect ratio tasks was larger than that for color, spatial frequency, and orientation.

### Neural Undersampling and Perceptual Heterogeneity

We suggest that the perceptual heterogeneity we have observed is a simple consequence of sparse neural sampling. We note first that stimuli even at the highest levels of the visual system are analyzed by cells with receptive fields that have a limited spatial extent that does not cover the entire visual field [8]. Second, we suggest that individual units or groups of units that analyze the same attribute over different regions are only coarsely calibrated with each other. As a result, when a stimulus is small relative to the analysis area, it activates only a few cells or groups of cells, and the responses will reveal any underlying local bias. A larger stimulus will activate a broader group of cells, and the variations should average out.

A clear example of this "undersampling" effect is seen in color perception. When the retina is stimulated with an extremely narrow beam that activates only a few retinal cones, the color percepts vary widely for the same stimulus as each location of the beam on the retina samples different ratios of cone classes [9]. With larger color patches (like the ones used in our experiment here), judgments become much more stable across locations as many more cones are activated and the mean responses converge to the population values.

We evaluated the undersampling hypothesis in the next experiment by systematically varying the size of the visual stimulus, either a face or an oriented Gabor, at 5° eccentricity. We evaluated the perceptual heterogeneity for facial gender and orientation discrimination tasks across different locations using the same method as the original experiment but now with four stimulus sizes (only three sizes for faces, because they were not identifiable at the smallest size). If local biases are inherent to neural populations of smaller size (small n), we expect to observe significant spatial heterogeneity even for orientation judgments when tested with smaller Gabor patches. Conversely, the heterogeneity for faces should be reduced for faces of larger size. The results (Figure 3) indicate that perceptual heterogeneity decreases in a similar way for both orientation and gender with increased size of the visual stimulus. The effect of stimulus size on the heterogeneity index was significant for the orientation discrimination task (repeated-measures ANOVA, $F(3,9) = 32.2$, $p < 0.001$) and the facial gender discrimination task (repeated-measures ANOVA, $F(2,6) = 63.6$, $p < 0.001$). The perceptual heterogeneity of orientation task almost reaches that of the face task for the smallest Gabor patch we used. Note that the increase in the heterogeneity for smaller stimuli is not the result of increase in the task difficulty, because the results are normalized to the psychometric slope (reported in JND units) and the effect of task difficulty is taken out. Although perceptual heterogeneity is substantial for Gabor patches at small spatial scales, similar in magnitude to that for faces, the pattern of heterogeneity seems to be idiosyncratic. There is no systematic effect of location on PSE for the population of subjects (one-way ANOVA, $F < 2$ and $p > 0.1$ in all of the four tested scales), but for each subject and stimulus type, the patterns of PSE bias for the two patch sizes (1.38° and 0.8°) are significantly correlated ($p < 0.05$ for all of the subjects).

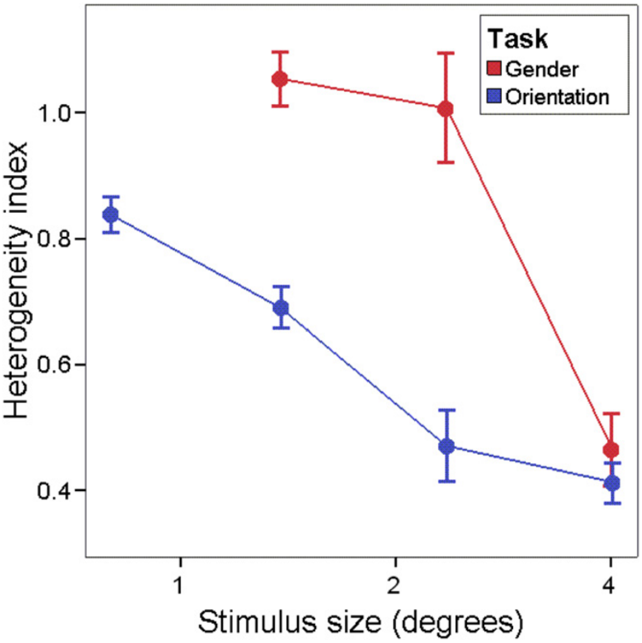

Figure 3. The Effect of Stimulus Size on Perceptual Heterogeneity
Heterogeneity indices are reported for facial gender and orientation discrimination tasks with various sizes of the visual stimulus. The face stimuli were not tested for the 0.8° stimulus size because gender recognition in the periphery at that size is impossible. Heterogeneity index systematically and significantly increases for both tasks at the stimulus size drops. See Figure S5 for examples of the psychometric functions underlying this figure. Error bars show ±1 SE of mean.

## Discussion

Our results suggest that perceptual heterogeneity is a general phenomenon of visual perception and that its magnitude depends on the neural undersampling that is a consequence of the size of the stimulus relative to the size and spacing of the receptive fields that analyze it. This effect exists at a very fine grain for cones of the retina and the variations of perceived color for identical small stimuli as a function of location [10]. Here we show that the same phenomenon holds at a range of much larger spatial scales up to high levels of visual processing. The scale at which heterogeneity of a particular attribute becomes evident reveals the scale of the underlying regions of analysis. For example, object-selective cells are organized retinotopically [11] with moderate size (nonglobal) receptive fields that are clearly not large enough to provide complete translation invariance [8, 12–15]. Electrical microstimulation of a small group of these cells directly affects face perception [16]. We speculate that perceptual decisions about shape and gender or age of faces might be based on the responses of relatively independent, small groups of cells that analyze stimuli in a moderately sized region and that have a fair amount of natural variation in their responses from location to location. Such cells probably inherit and accumulate the response biases of upstream neurons, in addition to reflecting their own biases onto their output. A moderately sized face stimulus will therefore reveal these local variations across groups of cells, whereas a larger face stimulus would engage many more groups, and the variations should average out (Figure 3). In contrast, our color, spatial frequency, and orientation stimuli are analyzed by neurons with much smaller receptive fields, so the same size stimulus activates many more cells, and the average of these responses will be more stable across locations. Again, testing with the orientation judgments with smaller stimuli revealed the local biases (Figure 3) that were averaged out with the larger stimuli.

To conclude, the finding that perceived gender, age, or shape of a given object varies significantly across retinal location questions one of the oldest tenets of vision science: the independence of object identity and location. Our results suggest that the perceptual heterogeneity is not specific to facial gender recognition and reflects a general property of object representation.

The fine-grain anisotropy of visual cortex in representing various orientations has been used by fMRI studies to decode the visual stimulus from the voxel activation pattern in early visual areas [17, 18]. This cortical anisotropy is coherent with our finding of perceptual heterogeneity for orientation at smaller spatial scales. Our results suggest that the same cortical anisotropy exists in higher cortical areas as well, opening the door for finer reconstruction of the experienced world by reading out patterns of cortical activation.

## Supplemental Information

Supplemental Information includes four figures and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2010.11.017.

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