Face discrimination does not outperform house discrimination at foveal to parafoveal locations

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Abstract

Since perceptual and neural face sensitivity is associated with a foveal bias, and neural place sensitivity is associated with a peripheral bias (integration over space), we hypothesized that face perception ability will decline more with eccentricity than place perception ability. We also hypothesized that face perception ability may show an upper visual field (UVF) bias due to the proximity of face-related regions to UVF retinotopic representations, and a left visual field (LeVF) bias due to earlier reports suggesting right hemisphere dominance for faces. Participants performed fovea and parafoveal face discrimination tasks (≤ 4°) while their eye movements were monitored. Additional within-category discrimination performance was measured for houses, inverted faces, shapes and low-level visual acuity. While, as expected, eccentricity-related accuracy reductions were evident for all categories, in contrast to our hypothesis, there was no significant difference between face and house-related accuracy. Furthermore, RTs for houses were significantly faster than for faces at all locations including the fovea. Significant LeVF bias was evident for upright and inverted faces, and face inversion effect was found at all parafoveal eccentricities. Our results suggest that low-level and possibly top-down factors, and not only the face-fovea place-peripheral associations found in high-level visual cortex, influence perceptual performance.

Keyword: face, house, parafovea, face inversion effect, eccentricity, upper visual field, lower visual field, right visual field, left visual field

Introduction

One of the main coding principles in the visual cortex is eccentricity, where the foveal representation is significantly magnified in the visual cortex relative to its size on the retina, and as distance from the fovea grows, the cortical representation is reduced [1–3]. This foveal magnification is assumed to be the main factor contributing to reduced performance with growing eccentricity for multiple (but not all) visual tasks [4–6]. It has also been shown that this foveal enhancement can be overcome if peripheral information is scaled to match the cortical representation (aka M-scaling [7]).

Another coding principle is hierarchical processing, where visual information is initially processed according to the physical aspects in early visual areas (e.g. in V1, V2) and as information progresses in the visual hierarchy it is integrated and becomes associated with perceptual aspects (specialization) rather than the physical aspects of the stimulus in higher visual areas (e.g. in LOC, FFA, PPA) [8–14]. This high-level visual specialization is predominantly manifested in two anatomically distinct visual processing pathways, the ventral perception visual pathway processing aspects related to shape and form, and the dorsal spatial visual pathway processing aspects related to action preparation and location in space [15–19].

Multiple neuroimaging and electrophysiological studies investigating the ventral perception visual pathway have revealed that face processing is associated with foveally biased regions while place and house related processing are associated with peripherally biased regions [20–30] sensitive to integration over space [20,31]. Recent studies further suggest that the structure of these category selective regions is also distinct [25,26].

Reasoning that neural coding preferences likely reflect behavioural performance, and based on earlier studies and on reduced visual performance at peripheral locations [6], we hypothesized that face related tasks, that are associated with a cortical foveal bias would show reduced performance in more peripheral locations relative to the control category of houses which is associated with a cortical peripheral bias. This entails that we expected that place related tasks would be less affected by eccentricity and would show, on top of the expected eccentricity reductions [6], higher performance than faces as eccentricity increases (as presented in the middle and left models in Fig. 1a) while faces may outperform houses at the centre due to their foveal bias (cf. Fig. 1a middle and left panels). However, we cannot rule out the possibility that despite differences in neural representations, face and house performance will not show significant differences across foveal to parafoveal locations (see Fig. 1a right model). Furthermore, we also hypothesized that due to the proximity of face-related regions to upper visual field (UVF) retinotopic representations, face perception ability may show an UVF bias, or a left visual field (LeVF) bias due to earlier reports suggesting right hemisphere dominance for faces [32–40].

To test these hypotheses we measured face discrimination performance at foveal to parafoveal locations (up to 4°, see Figure 1b-e) in each of the four visual field quadrants in a group of normally sighted individuals while participants held fixation and their eye movements were being monitored. Their face-related performance was compared to their performance for control categories (houses, inverted faces, shapes and visual acuity) in the same visual field locations.

Results

In line with our hypothesis that face related tasks would show a foveal bias relative to performance in more peripheral locations, as well as the known effect of eccentricity on visual performance, we found that face discrimination accuracy and d-prime were highest at the centre of the visual field and dropped significantly as eccentricity increased (see Figure 2a and b, Table 1 for detailed results and Table 2 for statistical results). The superior performance for face discrimination at the centre of the visual field was also evident in longer RTs for growing eccentricities (see Figure 2e and Table 2 for statistics). Similar eccentricity effects for accuracy, d-prime and RTs were also evident for all other within-category discrimination tasks (see Figure 2a, b and e, and Table 2). Since we hypothesized that despite the eccentricity expected reductions for peripheral stimuli, place related tasks would be less affected by eccentricity than faces and would show better performance than faces as eccentricity increases, we directly compared between-category performances. A 2-way ANOVA with eccentricity and category (faces, inverted faces, houses and shapes) on accuracy confirmed significant effects for eccentricity and category but no interaction (see Table 2 accuracy results). Post-hoc analysis revealed that, as expected [41–43], inverted faces accuracy was lower than that of faces, and was also lower than that of houses. Furthermore, in contrast to our prediction, there was no significant difference between faces and houses, and average accuracy and d-prime for houses were higher than that of faces at all eccentricities including at the fovea (see Figure 2a and b). As can be seen in Figure 2e, this was not a result of a speed accuracy trade-off, as house discrimination RTs were faster on average than face discrimination RTs at each eccentricity. To test whether this was statistically significant we ran a 2-way ANOVA with eccentricity and category (faces, inverted faces, houses and shapes) on RTs and found again significant effects for eccentricity and category but no interaction (see Table 2 RT section). Upright faces' RTs were slowest, significantly slower than houses, even at the centre.

VA related measurements were also estimated by the 'VA' tumbling E experiment at different locations to assess whether performance decline with eccentricity can be attributed to the decline in VA. As can be seen in Figure 2c, at 2° visual acuity seems to decline relative to the centre by an average of 0.2 LogMAR units which correspond to 2 lines on the ETDRS chart, and an additional decline of another line on the ETDRS chart for 4°. Typically, a value of 0 LogMAR corresponds to static VA of 6/6, and a 0.1 difference reflects one line in the static chart. While there is a clear and significant decline in dynamic VA as eccentricity grows as is expected for visual processing in general, this is unlikely to be the sole cause of performance reduction for the perceptual categories, as we can see a clear difference between the different categories (see Table 2 between category differences as evident for accuracy, d-prime, RTs and performance index (PI)).

Performance index

Assuming that faces' performance would be best at the centre, we calculated a performance index relative to central performance (see Methods). We were interested to test whether performance was modulated by eccentricity in a different manner for each of the visual categories (see Figure 2d). However, results for faces and for houses were surprisingly similar with no significant differences (see Table 2 performance index results). Interestingly, significantly faster decline of performance was found for inverted faces relative to upright faces; inverted faces declined faster than houses, although this did not reach significance.

Visual field comparisons

As can be seen in Figure 3 and in Table 3, no significant differences between upper visual field (UVF, in blue) and lower visual field (LoVF, in green) were found for upright faces despite better average performance in the upper visual field, and no UVF-LoVF differences were found for the other categories.

Further exploration for possible differences between left visual field (LeVF, in red) and right visual field (RVF, in yellow) revealed significantly higher LeVF performance (relative to RVF) for upright and for inverted faces (see Table 3 for detailed results and Table 4 for statistics). No such differences were found for the other categories.

Estimating physical differences' contribution to performance

Since we did not anticipate finding reductions in performance for houses as those found for faces, we calculated the physical differences between sets of images used in our experiments to examine whether these could possibly account for the similar behavioural performance. To that end, we estimated for each pair of different images used in the discrimination house or face experiments the physical difference between them (Euclidean distance) and examined whether bigger physical differences would be associated with higher performance (see Methods for more details). We reasoned that a bigger physical difference would facilitate distinguishing between different images (and thus improving accuracy on the 'different' condition). Figure 4 shows accuracy performance (Fig. 4a) and RTs (Fig. 4b) for faces and houses for the different house discrimination experimental versions as a function of eccentricity, and the physical difference between pairs of images for each experiment (Fig. 4c). As can be seen, the category showing the smallest difference (faces) also showed the lowest performance in accuracies and in RTs. Similarly, the category showing the biggest difference (houses, version 1, see Methods) showed the best performance. There was a small but significant performance difference between the two house versions (2-way ANOVA with version and eccentricity as main effects revealed as expected a significant effect of eccentricity $F(3,30) = 19.657$, $p<0.0001$, and a significant effect of version $F(1,10) = 5.134$, $p=0.047$, with no interaction). However, since the physical difference for the inverted faces is the same as that of the upright faces but their performance is significantly different, it seems that physical difference on its own is not likely to fully account for the behavioural performance. The same analysis for RTs yielded similar results, where slower RTs were found for the category with the smallest physical difference (faces) and the two house versions showing a significant physical difference between them showed no difference in RTs. Again, the inverted faces with identical physical difference do not perfectly fit with the account that low level physical differences account for the behavioural (RTs) effects. Thus, these analyses indicate that physical aspects may account only partially for the similar behavioural performance we found for houses and faces.

Methods

Participants

A group of 30 neurotypical participants aged 19–47 (mean age 28 years ± 6.4(SD)) with normal or corrected-to-normal vision participated in this study. 24 participants took part in the upright face discrimination experiment, 12 of them participated in the inverted face discrimination experiment, 22 of them and an additional participant (altogether 23 participants) participated in the tumbling E experiment [44], 7 of them and 4 additional participants (altogether 11 participants) participated in the house discrimination experiment, 4 of them and additional 4 participants (altogether 8 participants) participated in the shape discrimination experiment. All participants signed an informed consent form before their participation. The Bar Ilan University ethics committee approved the experimental protocol.

Apparatus

All experiments were conducted on an Eizo FG2421 24" HD LCD monitor (1920×1080 pixels resolution) running at 100 Hz, using an in-house developed platform for psychophysical and eye-tracking experiments (PSY) developed by Yoram S. Bonneh [45] running on a Windows PC.

Eye tracking

In order to ensure fixation during all experimental sessions, eye movements were recorded with an EyeLink infrared system (SR Research, Ontario, Canada) with a sampling rate of 500Hz, equipped with a 35mm lens while head movements were limited by a chin rest. Eye movements were recorded binocularly, only left eye data were analyzed. A standard 5-point calibration was performed before each session. In addition, in-session calibration trials were incorporated into the beginning and end of each session to estimate the deviation from fixation for each session. This was computed as the difference between the eye position during the in-session position calibration (baseline) and the average eye position during that session. Trials with a deviation from fixation greater than $0.85°$ during a time window around the onset of the target stimulus were excluded from the analysis.

General procedure

Participants were instructed to look at the fixation point and be alert to and aware of the surrounding area in which the target could appear. Each experimental session included eye position calibration trials before and after the main experiment (see more details below). Throughout all experimental sessions participants started each trial at their own pace by pressing a key after fixation appeared at the centre of the screen. Experiments were performed in a dark room, no feedback was given, and the viewing distance was 60 cm.

Main experiments:

1. Upright faces discrimination experiment

In each trial, participants were asked to judge whether two faces presented sequentially were the same or different. A study face always appeared at the centre of the screen for 200ms, and after an ISI of 250ms, a target face (either same or different than the study face) appeared for 200ms (to eliminate the possibility of succeeding in the task if performing a saccade towards the target) at a location chosen randomly from 13 possible locations in the visual field (centre or one of 4 locations at 2°, 3° or at 4°, as depicted in Figure 1e). The face images for the same condition (same image served as the study and the target face) were chosen randomly from a set of 5 different faces, each appeared once in each location per session. For the different condition, each of the two face images was chosen randomly from two different sets of 5 face images each, 5 of the face images used for the different condition were the images used in the same condition. All face images were full-front colored photographs of real men with a neutral expression cropped and aligned to each other (see full details at [46,47] with the original images taken from 2 databases (CVL Face Database [http://www.lrv.fri.uni-lj.si/facedb.html]; AR Face Database [Martinez and Benavente 1998]). The faces were presented on a black background and subtended 1.6° x 2.2° (width x height). Trials were mixed randomly in terms of condition (same/different) and location in the visual field. Each participant underwent 5 runs of the experiment with each condition (same/different) repeated 5 times in each of the 13 locations. Overall, there were 25 'same' face trials and 25 'different' face trials for each of the 13 locations for each participant. Face discrimination performance was measured as accuracy (percent correct) per location. Experimental procedures are illustrated in Figure 1.

2. Houses discrimination experiment

The experimental design was identical to that used in the face discrimination paradigm except for the use of gray house images rather than face images. We ran two versions of the experiment, each using a different set of house images. Each participant performed the first version (V1) twice and the second version (V2) 3 times; order of sessions was V1-V2-V2-V1-V2. Houses subtended 2.4° x 2° (width x height). Experimental procedures are illustrated in Figure 1.

3. Inverted faces discrimination experiment

The experimental design was identical to that used in the face discrimination paradigm except that faces were inverted (both study and target faces). Experimental procedures are illustrated in Figure 1.

4. Shape discrimination experiment

The experimental design was identical to that used in the face discrimination paradigm except the first and second stimulus in each trial were a gray E on a gray background facing one of 2 directions (up or down) randomly. The participants’ task was to determine whether the two consequently presented E's faced the same direction or not. The E stimuli were black on a gray background and subtended 0.38° x 0.38° (width x height). The size of the E’s was determined after preliminary psychophysical assessments revealed that larger E’s (sized similarly to the face or house images) led to ceiling performance at all eccentricities.

5. VA tumbling 'E' experiment

A tumbling E test was used to measure visual acuity (VA) threshold [44] at 9 different visual field locations (centre, 2° and 4°, 4 locations at each eccentricity). Separate staircase procedures were applied for each of the 9 locations; trials of all locations were mixed randomly in each session. The stimuli were a black E on gray background that in each location subtended initially 0.5° and faced 1 of 4 optional directions. Participants' task was to determine the E’s facing direction (4AFC), while the E’s size was reduced in a 3:1 staircase procedure with 0.1 log unit steps according to performance

(stopping after 6 reversals) . Experimental procedure is illustrated in Figure 1d and e. Results are reported in log MAR units (minimum angle of resolution (MAR) needed to correctly discriminate (at 79% accuracy performance) the E's facing direction, values closer to 0 indicate better VA).
Note that our measurements of dynamic VA are not precisely comparable to the standard static ETDRS measurements since (i) our viewing distance (60 cm) was not standard (for near 40 cm or for far 3 m), (ii) exposure time was limited (vs. unlimited exposure in static VA examinations), (iii) divided attention across the VF (vs. focusing all attention on the centre of VF), (iv) contrast was lower than used in standard VA tests. However, the dynamic tumbling E measurements have been shown to correspond to VA standard measures [50,51].

Analysis

All analyses reported were calculated individually and then the average over participants and SE are reported.

For each of the discrimination experiments performance was measured as accuracy (percent correct) per location and for the VA experiment performance was reported in log MAR units per location (as presented in Figure 2). For each location we calculated individual performance and we present the average results over all participants. For each experiment and each eccentricity, we averaged the performance of all 4 locations (upper/lower left/right locations) of that eccentricity. To compare upper vs. lower VF and the right vs. the left VF performances, the two locations at each eccentricity and each hemifield were averaged (e.g. to compare UVF vs. LoVF, for the 2°, 2° right UVF and left UVF were averaged and compared to the average of 2° right LoVF and left LoVF), see Figure 3.

Error bars represent standard errors across participants calculated using the Cousineau method (see [52] for details).

In order to assess the eccentricity effect (i.e. the drop in visual performance with eccentricity) and compare it across all discrimination tasks, we computed a performance index (PI), see Figure 2d. PI was calculated as the performance (accuracy) at each eccentricity divided by the performance at the centre.

Statistical analyses (ANOVA and post-hoc) were performed with StatView5.0 software for Windows (SAS Institute Inc, Cary, NC) and presented in Tables 2 and 4.

To estimate physical distances that may account for differences in performance, we calculated the Euclidean distance between 2 different face images (for faces) or 2 different house images (for houses). Euclidean distance between 2 images was estimated as the mean luminance level absolute difference over all pixels in these images.

Discussion

Our investigations into face-related processing in central to parafoveal locations (up to 4°) revealed that, as expected, faces, as well as all tested categories, show an eccentricity effect (i.e. reduced accuracy and d-prime and slower RTs with growing eccentricity [6]. While we anticipated finding that face related processing may outperform other categories at the central visual field (see model in Fig. 1a on left) and that place-related processing would be less affected by eccentricity than face related processing (as proposed in both left and middle models in Fig. 1a), we found that face discrimination was not superior to house discrimination at any locations and in any measure, supporting the model presented in Fig. 1a on the right. Accuracy for inverted faces was worse than for upright faces at all eccentricities, as expected [41–43]. In addition, we found a small but significant performance bias for faces (upright and inverted) in the LeVF over the RVF, but no performance differences between the upper and lower visual fields.

The study predictions are based on multiple neuroimaging and electrophysiological studies [20,23–26,30] showing that faces are associated with foveal processing and houses and places with peripheral processing and integration over space [31]. Our first prediction (see Figure 1a on the left) suggests that since faces are known to have a foveal bias and houses a peripheral bias, then faces may be processed more efficiently than houses at the fovea (in terms of accuracy and speed). However, our results are not in line with this prediction. One explanation could be that the foveal bias faces show is merely the common eccentricity bias evident for multiple visual functions [6] reflecting a within-category processing preference (such that faces would be processed better at the fovea relative to peripheral locations), and not a bias relative to other visual categories (see more below). Our results are also not in line with the second study prediction (see Figure 1a, middle model), as house performance at the periphery is not significantly better than faces and actually declines with eccentricity in a similar manner to faces. Interestingly, our results are in line with the third study prediction (Fig. 1a on the right), that house related processing would show similar eccentricity reductions in performance as seen for faces. There are a few possibilities that could underlie the unexpected similar reductions in performance with growing eccentricity we found for houses and faces. One possibility is that at the parafoveal eccentricities we investigated (up to 4°) the house-related periphery effects are not as evident as they would be in further periphery, when peripheral mechanisms start to kick in. Thus, for the parafoveal eccentricities we used, house related discrimination may still rely, to some extent (regardless of stimulus size), on foveal mechanisms. In such a case, the behavioural judgements may be a consequence of combined processing of foveal mechanisms and those of periphery related mechanisms. A second possibility relates to the small size of the house stimuli. Houses and places in our daily life are typically big and take up a bigger portion of the visual field [27]. The small houses used in our experiment may have forced the system to rely on additional mechanisms that are non-typical to house related processes, and these non-typical mechanisms contributed to the performance reductions we found for houses. A third possibility is that low-level aspects of the stimuli could underlie the similar effects we found for faces and houses. For example, when low-level aspects of the stimuli induce higher demands on the visual system, performance is expected to be lower. Indeed, the analysis we carried out examining whether physical differences may account for the performances we observed (see Figure 4) indicates that physical differences may explain performance up to some extent. A fourth possibility is that top-down attentional mechanisms influence performance according to visual field location and visual category [5,53–55]. In fact, the face pop out effect [56,57] seems to point to enhanced top down influences for faces at peripheral locations relative to other visual categories (but see [58]). According to this, at parafoveal locations face performance may have benefitted from enhanced attention elevating it to reach house related performance levels. Hence the similar effects of eccentricity on face and house discrimination could be partially due to the demands imposed on the system by low-level aspects or by top-down attentional mechanisms rather than being attributed solely to face or house related perceptual mechanisms.

The fact that house related performance was faster than that of faces, even at the fovea, may seem counterintuitive. However, in addition to house/place related processing relying on different cortical mechanisms and different computations than those of faces [25,26,59,60], house/place related mechanisms also show a tendency for transient rather than sustained activity [59,61]. One study shows that house related areas as the house related ventral PPA and dorsal TOS areas also exhibit transient BOLD responses while the face related areas (ventral FFA and also OFA) show sustained BOLD activity and this is independent of the preferred or non-preferred category [59]. Another recent study shows that different areas in the ventral stream receive different contributions of transient and sustained inputs [62]. If transient related activity is associated with faster processing than that associated with sustained activity, then these differences could contribute to differences in response timing. Another possibility is that the differences in physical low level aspects could contribute to the speed of processing. As we discussed above (and see also Fig. 4c), there were bigger physical differences between pairs of house images than between pairs of face images. Thus, the house task may have been easier and thus a decision may have been reached sooner.

Since face-related regions are contiguous to UVF retinotopic representations we hypothesized that face perception ability may show an UVF bias relative to the LoVF. We employed a face discrimination task where a central study face was compared to peripheral (up to 4° in either UVF or LoVF) target face. However, we did not find any such difference between UVF and LoVF performance for the upright faces, or for the other control categories. One possible explanation is that if visual field differences exist for upright faces, they would be evident in more peripheral locations in the VF (> 4°). Another possibility is that VF differences exist for specific perceptual face tasks but not for the face discrimination task we employed.

We also hypothesized that we may find LeVF vs RVF differences for upright faces, given that several earlier studies reported finding a LeVF preference for upright faces [32,33,37,63–66]. Indeed, we found that LeVF was better than RVF performance with a small but significant difference, and this was also true for inverted faces. As shown by Maurer and Lewis [67], at earlier stages of development, visual inputs from each hemifield (R/Le) cross over to the contralateral visual retinotopic cortex. Thus, at early age (e.g. before 4 months of age), LeVF inputs probably predominate in right visual cortex processing [67]. These may strengthen the reliance of right hemisphere face processing on LeVF inputs and strengthen the connections between them. This is also in line with findings suggesting right hemisphere dominance for face perception [22,32,33,37–39,68,69]. Although we did not find the LeVF bias for all categories, we cannot rule out the possibility of attention contributing to the observed effect that we found. Siman Tov et al. (2007) show that faces appearing in the LeVF activate the contralateral retinotopic cortex and the fronto-parietal attention network to a much greater extent than those appearing in the RVF [70]. This may indicate that attention is not uniformly distributed and therefore inputs from the LeVF are more prominent to face processing and to our perception.

Although inverted faces keep the local features and spatial relations of the faces intact, the stimuli and their holistic structure are unfamiliar to the visual system and this leads to the face inversion effect [41–43], where people are worse when performing a task on inverted faces relative to upright faces. Here we used inverted faces to try and account for any effects that may be due to the low-level physical features of the faces stimuli. As expected from the literature, we found worse performance for inverted faces compared to upright faces, and this was true for central faces as well as for parafoveal inverted faces (see Fig. 2a and Tables 1 and 2). In fact, it seems from our results that the face inversion effect may increase with eccentricity. Earlier studies show that processing of inverted face recruits both face specific and also non-face related mechanisms that include parietal attention-related foci [42,47,71–73], all of which may reflect inefficient coding of inverted faces.

In conclusion, our investigations of face discrimination at foveal and parafoveal regions revealed that as expected, faces, inverted faces, houses, and shape discrimination performance is reduced as a function of eccentricity. We found a LeVF bias for both faces and inverted faces, and the face inversion effect that was evident at parafoveal locations. It has been shown that different anatomical structures (which are likely to reflect different computational processes) spatially overlap with the modular category-related peaks [26] as well as with the foveal-peripheral preferences in high-order visual cortex. Based on these anatomical and neuroimaging activation findings in high-level visual cortex, we anticipated finding that face and house performance would reflect the cortical organization (i.e. finding differences between face and house performance), but instead we found that face and house performance were comparable, a finding that cannot be fully attributed to low level basic vision, to high-level visual cortex biases, or to top-down attentional aspects. Thus, we suggest that multiple factors, from bottom up low level mechanisms to top down high level mechanisms, are all likely to contribute to perceptual performance across the visual field.

Acknowledgments

This work was supported by ISF grant no. 1485/18 to SGD. We thank Yoram Bonneh, Inbal Ziv, Oren Kadosh and Uri Polat for their assistance, and the Computer Vision Laboratory, Faculty of Computer and Information Science, University of Ljubljana, Ljubljana, Slovenia, and the Secondary School Centre, Velenje, Slovenia, for allowing us to use the CVL Face Database (http://www.lrv.fri.uni-lj.si/facedb.html).

Author Contributions

OK and SGD designed the experiments. OK ran the experiments and analysed the data. OK and SGD wrote the paper.

Competing Interests Statement

All authors (OK and SGD) declare that they do not have any conflicts of interests.

Figures

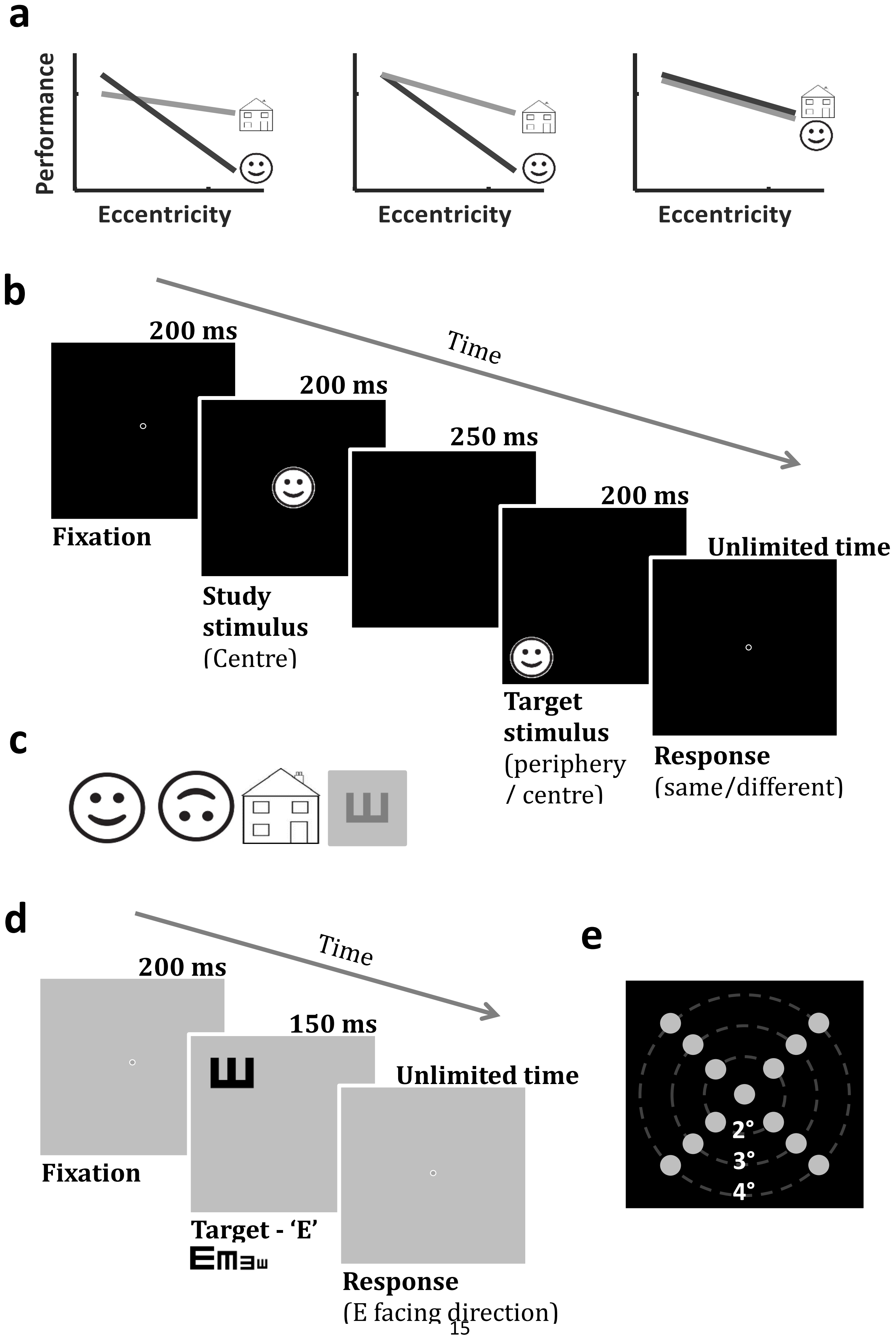
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Figure 1. Predicated outcomes and experimental design. (a) Proposed models for face and place-related processing as would be reflected in face and house discrimination performance across the parafoveal eccentricities. Left – face discrimination would outperform house discrimination at the centre and house discrimination would be less affected by eccentricity than face discrimination at parafoveal eccentricities. Middle – face and house discrimination would show similar performance at the centre but houses would be less affected by eccentricity (showing less reduction in performance than faces across the parafoveal eccentricities). Right - face discrimination would not show superiority to house discrimination at any parafoveal location. (b) Representative timeline of a face discrimination "same" trial at 4° eccentricity (left lower visual field). Each trial started with a fixation circle appearing for 200ms followed by a central study face appearing for 200ms, and after a 250ms ISI a target face appeared for 200ms in 1 of 13 randomly chosen locations at central or parafoveal eccentricities (see panel e). The participant's task was to report if the target face was the same as ("same" condition) or different than ("different" condition) the study face. (c) Conceptual representations of the 4 different category discrimination experiments (See Methods for specific details). (d) Timeline of a single trial in the 'VA' tumbling E experiment, representing part of a separate staircase procedure performed at 9 different locations (centre, 2° and 4° eccentricity). Trials from the different staircases (in the different locations) were interleaved randomly (see Methods). (e) The 13 possible locations for the target stimuli in the category discrimination experiments (see panel c). In each discrimination experiment there were 50 trials in each location (25 "same", and 25 "different" trials). In the E discrimination experiment we only tested performance at central, 2° and 4° eccentricity locations, overall 9 locations with 40 trials in each location (20 "same", and 20 "different" trials).

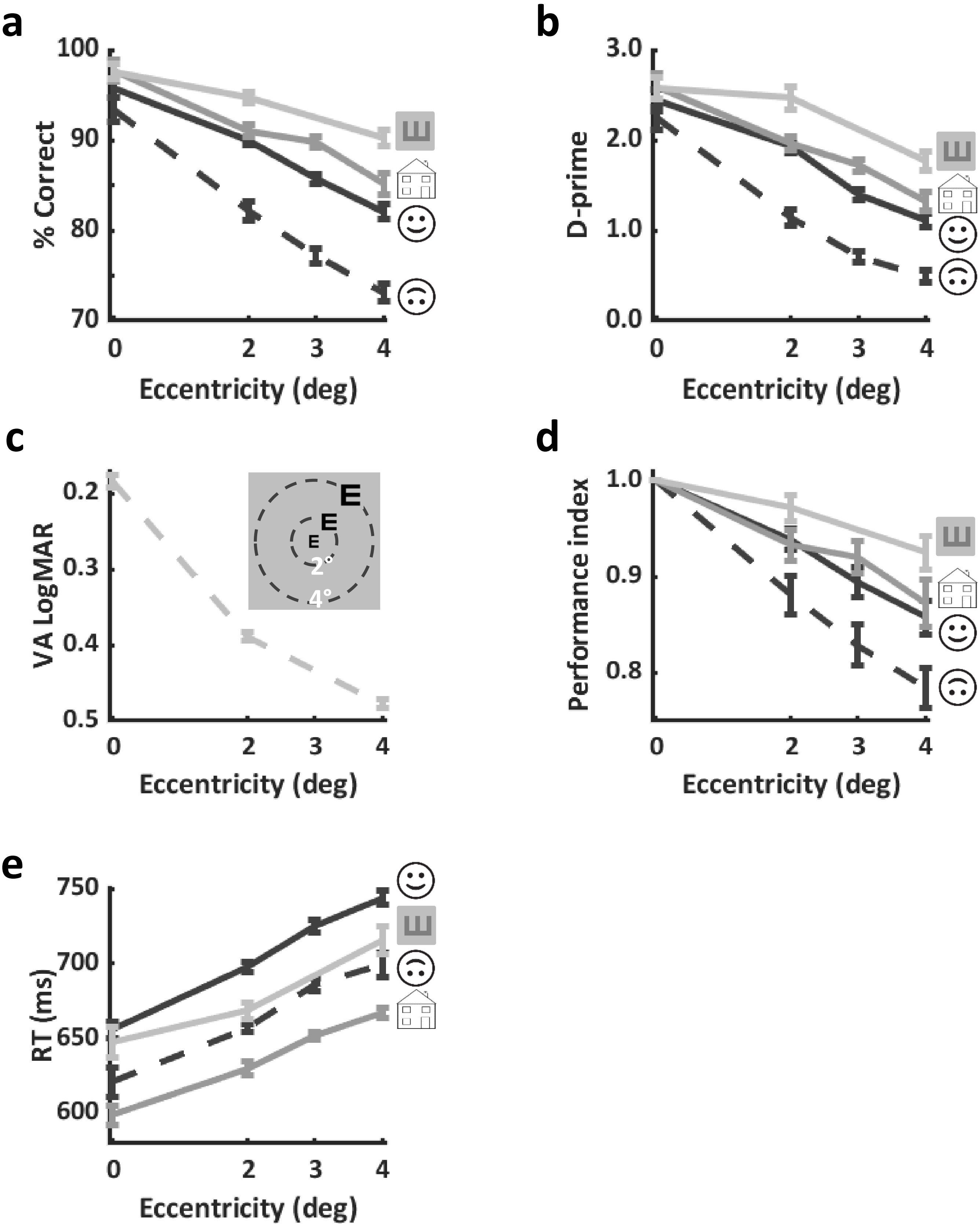
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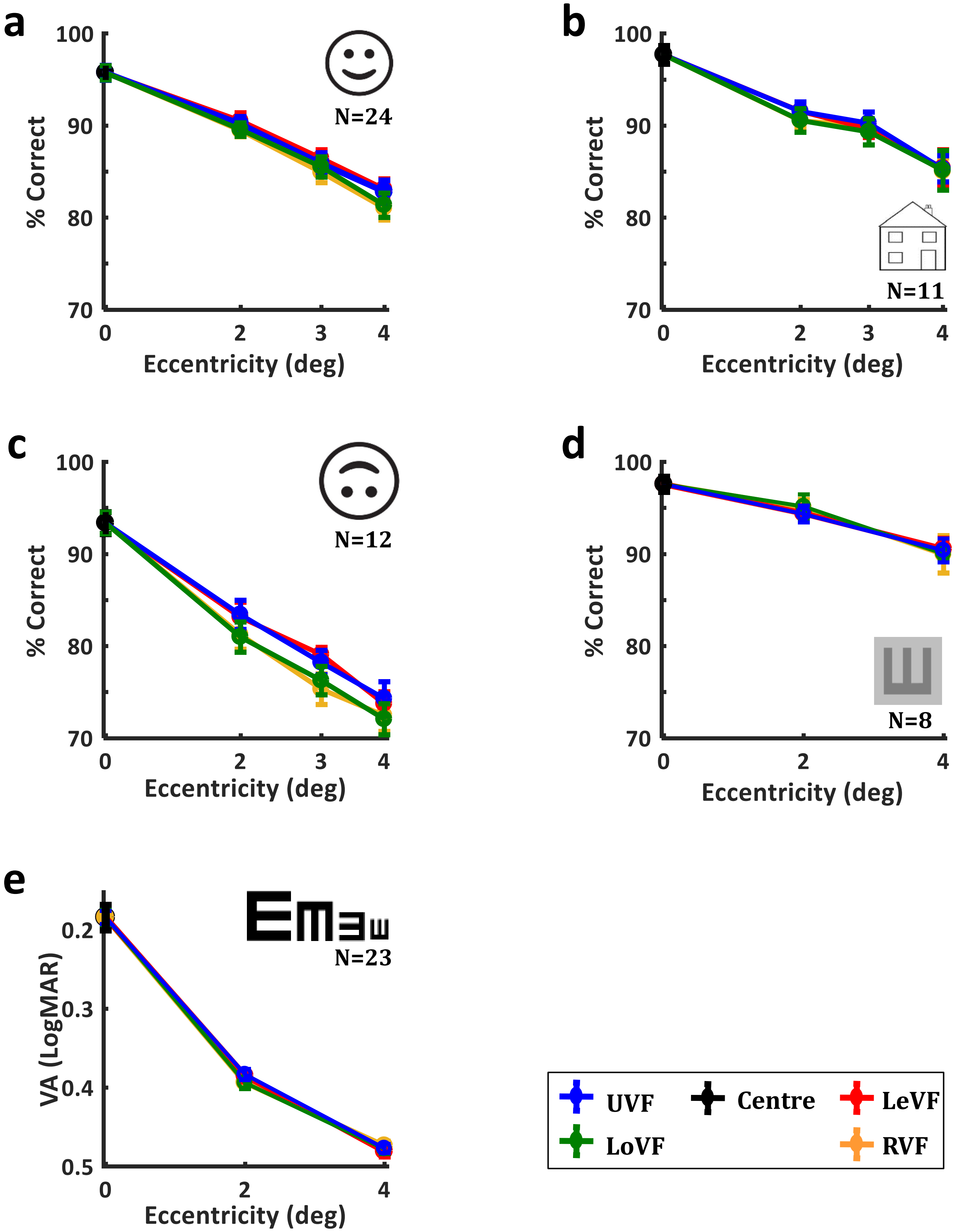
Figure 2. Experimental results. (a) Accuracy and (b) d-prime for each of the discrimination experiments by eccentricity. As can be seen performance declines with eccentricity for each of the categories, and there was no significant difference between upright face and house performance (see Results). There was a significant face inversion effect also evident at parafoveal eccentricities. (c) 'VA' tumbling E experimental results by eccentricity. As can be seen at 2° visual acuity seems to decline relative to the centre by an average of 0.2 LogMAR units which correspond to 2 lines on the ETDRS chart, and an additional decline of another line on the ETDRS chart for 4°. (d) Performance index (relative to performance at the centre of the visual field) calculated for each discrimination experiment) to estimate the rate of decline in performance relative to best vision at the centre. Here too, there was no significant difference between face and house performance (see Table 2 for further details). (e) RT (median) for the different discrimination experiments as a function of eccentricity. Note that house performance was faster than upright faces across eccentricities, including at the centre.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70
% Correct
0
2
3
4
Eccentricity (deg)
N=12
d
100
90
80
70
% Correct
0
2
4
Eccentricity (deg)
N=8
e
0.2
0.3
0.4
0.5
VA (LogMAR)
0
2
4
Eccentricity (deg)
N=23
UVF
Centre
LeVF
LoVF
RVF

Figure 3. Accuracy for the discrimination experiments by visual fields. Performance in each of the discrimination tasks ((a) upright faces, (b) houses, (c) inverted faces, (d) E shape, (e) tumbling E VA) declines with eccentricity for each of the categories. No significant differences between upper (in blue) and lower (in green) visual fields were found for any category. Upright and inverted faces performance was significantly higher in the left (in red) relative to the right (in yellow) visual field.

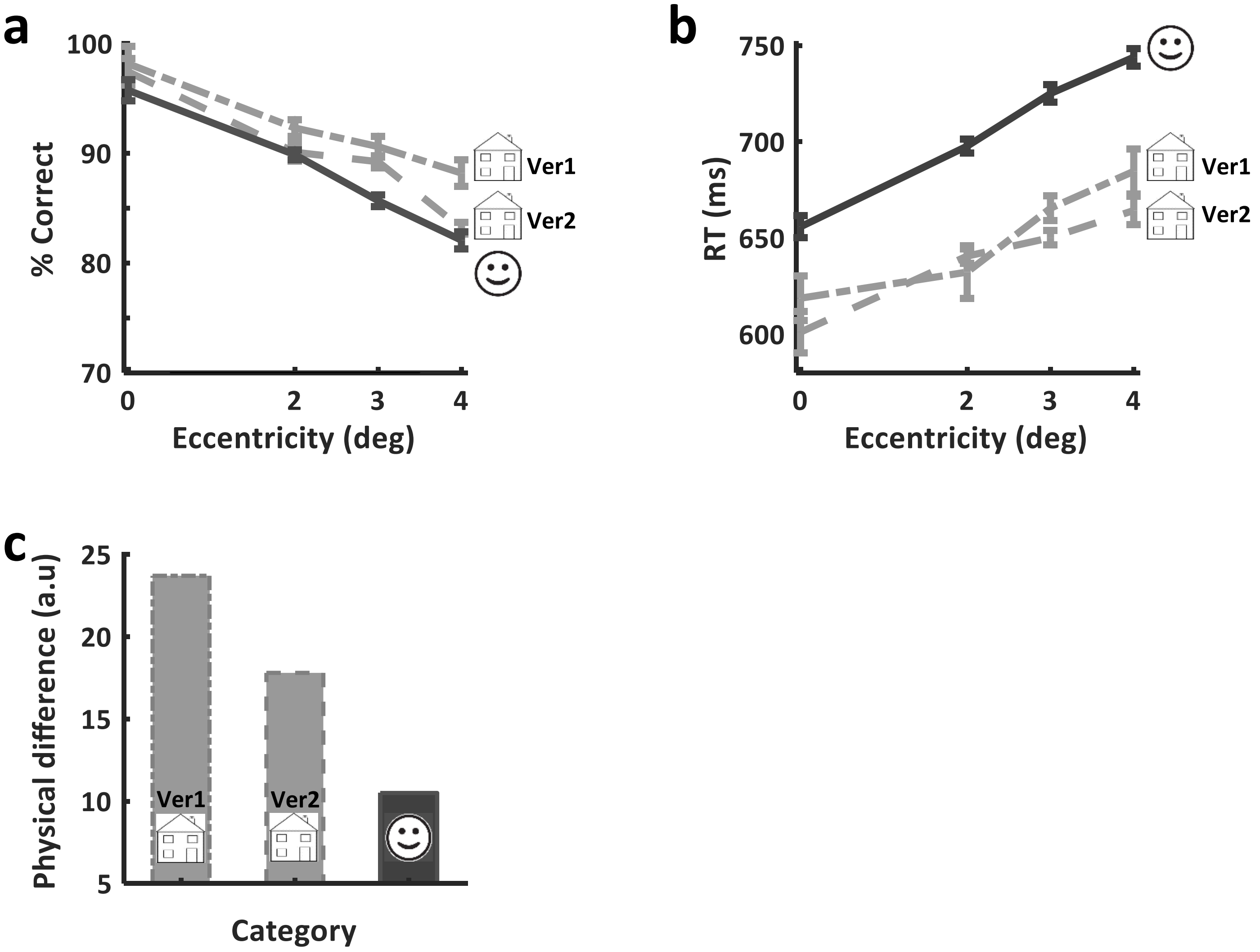

Figure 4. Low level physical differences relative to performance. The physical differences between image pairs (either from the face experiment, or from each of the house discrimination versions) are compared to performance differences. (a) The effect of the physical difference on accuracy. No significant difference in performance between both versions of house discrimination and face discrimination was found, but there was a small but significant difference between the two house versions (see Results). (b) The effect of the physical difference on RTs. No significant difference between both versions of house discrimination were found, but as reported in the Results, houses performance was significantly different (faster) than face discrimination. (c) Mean physical difference between pairs of stimuli in the face discrimination task (on the right) and two versions of the house discrimination task (Ver1 on left and Ver2 in the middle). Both house versions showed bigger physical difference than the face task, with a significant difference between the two house versions. For the face – house differences, while houses image pairs showed bigger physical difference than face image pairs, there was no accuracy difference and only an RT effect. However, the physical differences between the house versions was not reflected in performance. Furthermore, inverted faces, with physical differences as those of upright faces, showed significantly different accuracy and RTs. Therefore, physical differences are may only partially account for performance.

Tables

		Discrimination				Visual acuity
		Faces (n=24)	**Inverted faces (n=12)**	**Houses (n=11)**	**Shape (n=8)**	**Tumbling E (n=23)**
Accuracy	Centre	95.73 ± 0.96	93.36 ± 1.3	97.68 ± 1.2	97.57 ± 0.86	0.18 ± 0.008
	2°	89.86 ± 0.45	82.21 ± 1.03	91.03 ± 0.65	94.73 ± 0.61	0.38 ± 0.005
	3°	85.67 ± 0.52	77.21 ± 0.82	89.78 ± 0.57	NA	NA
	4°	82.07 ± 0.77	73.12 ± 0.98	85.2 ± 1.21	90.21 ± 0.85	0.47 ± 0.005
D-prime	Centre	2.44 ± 0.11	2.24 ± 0.12	2.59 ± 0.13	2.57 ± 0.12	NA
	2°	1.92 ± 0.06	1.14 ± 0.09	1.96 ± 0.07	2.46 ± 0.13	NA
	3°	1.39 ± 0.06	0.7 ± 0.06	1.71 ± 0.07	NA	NA
	4°	1.11 ± 0.07	0.49 ± 0.07	1.31 ± 0.1	1.77 ± 0.11	NA
RT (ms)	Centre	655.8 ± 5.6	621.16 ± 9.7	598.7 ± 6.6	647.8 ± 10.1	579.5 ± 10.7
	2°	697.7 ± 3.6	656.91 ± 2.8	629.8 ± 4.6	668.7 ± 5.6	590.4 ± 7.4
	3°	725 ± 4.5	686 ± 4.5	651.7 ± 2.5	NA	NA
	4°	743.9 ± 4.5	699.2 ± 8.3	666.9 ± 3.3	715.8 ± 9.1	620.6 ± 8.1
PI	Centre	1 ± 0	1 ± 0	1 ± 0	1 ± 0	1 ± 0
	2°	0.93 ± 0.01	0.88 ± 0.01	0.93 ± 0.01	0.97 ± 0.01	0.46 ± 0.02
	3°	0.89 ± 0.01	0.82 ± 0.02	0.91 ± 0.01	NA	NA
	4°	0.85 ± 0.01	0.78 ± 0.02	0.87 ± 0.02	0.92 ± 0.01	0.38 ± 0.02

Table 1. Summary of experimental results for each experiment by eccentricity. Mean ± SE are provided for accuracy, d-prime, and performance index; median ± SE are provided for reaction times for all experiments. Accuracy (discrimination experiments) is reported in % correct, visual acuity (tumbling E experiment) is reported in LogMAR units. Reaction time (RT) is reported in ms. Performance index represents proportion out of 1. NA - data not available

	Factor	**Main effect**	**Interaction**	**Post hoc (Bonferroni/Dunn)**
Accuracy	Ecc	F(2,153)=53.829 **p<0.0001**	F(6,153)=1.903 p=0.083	
	Centre, 2Deg			**p<0.0001**
	Centre, 4Deg			**p<0.0001**
	2Deg, 4Deg			**p<0.0001**
	Category	F(3,153)=18.311 **p<0.0001**		
	Upright faces, Inverted faces			**p<0.0001**
	Upright faces, Houses			p=0.1169
	Upright Faces, Shape			**p=0.001**
	Inverted faces, Houses			**p<0.0001**
	Inverted faces, Shape			**p<0.0001**
	Houses, Shape			p=0.905
RT	Ecc	F(2,219)=7.705 **p=0.0006**	F(8,219)=0.181 p=0.993	
	Centre, 2Deg			p=0.0812
	Centre, 4Deg			**p<0.0001**
	2Deg, 4Deg			**p=0.0143**
	Category	F(4,219)=9.941 **p<0.0001**		
	Upright faces, Inverted faces			p=0.0518
	Upright faces, Houses			**p=0.0016**
	Upright faces, Shape			p=0.3601
	Upright faces, VA			**p<0.0001**
	Inverted faces, Houses			p=0.261
	Inverted faces, Shape			p=0.4882
	Inverted faces, VA			**p=0.0029**
	Houses, Shape			p=0.0916
	Houses, VA			p=0.101
	Shape , VA			**p=0.0008**
Performance index	Ecc	F(1,146)=24.199 **p<0.0001**	F(4,146)=0.308 p=0.872	
	2Deg, 4Deg			**p<0.0001**
	Category	F(4,146)=243.549 **p<0.0001**		
	Upright faces, Inverted faces			**p=0.0027**
	Upright faces, Houses			p=0.8491
	Upright faces, Shape			p=0.046
	Upright faces, VA			**p<0.0001**
	Inverted faces, Houses			p=0.0068
	Inverted faces, Shape			**p<0.0001**
	Inverted faces, VA			**p<0.0001**
	Houses, Shape			p=0.1077
	Houses, VA			**p<0.0001**
	Shape , VA			**p<0.0001**

Table 2. Summary of statistical analyses across experiments. Statistical analysis was performed using non-repeated measures two-way ANOVA on accuracy, RT and performance index between factors (eccentricity and category). This was followed by Bonferroni/Dunn post-hoc tests. F statistics are provided with corresponding p values. Bold represents significant effects (including post-hoc Bonferroni/Dunn corrections).

		Discrimination				**Visual acuity**
		Faces (n=24)	**Inverted faces (n=12)**	**Houses (n=11)**	**Shape (n=8)**	**Tumbling E (n=23)**
UVF	2°	90.1 ± 0.6	83.4 ± 1.5	91.5 ± 0.9	94.3 ± 0.7	0.38 ± 0.007
	3°	85.8 ± 0.7	78.2 ± 1	90.2 ± 1.3	NA	NA
	4°	82.8 ± 0.8	74.2 ± 1.48	85.2 ± 1.1	90.3 ± 1	0.47 ± 0.004
Centre	0°	95.7 ± 1.1	93.3 ± 1.4	97.6 ± 1.4	97.5 ± 1	0.18 ± 0.009
LoVF	2°	89.5 ± 0.5	80.9 ± 1.3	90.5 ± 1.1	95.1 ± 1.3	0.39 ± 0.008
	3°	85.5 ± 0.8	76.2 ± 1.3	89.3 ± 1.1	NA	NA
	4°	81.3 ± 1.1	72 ± 1.6	85.1 ± 1.6	90 ± 0.4	0.47 ± 0.004
RVF	2°	89.45 ± 0.5	81.23 ± 1.5	90.51 ± 0.8	95.05 ± 0.7	0.39 ± 0.004
	3°	84.9 ± 0.6	75.31 ± 1.3	89.95 ± 0.7	NA	NA
	4°	81.03 ± 1	72.46 ± 1.4	85.02 ± 1	89.96 ± 1.8	0.47 ± 0.005
Centre	0°	95.73 ± 1.1	93.36 ± 1.4	97.68 ± 1.4	97.57 ± 1	0.18 ± 0.009
LeVF	2°	90.52 ± 0.7	83.11 ± 1.3	91.55 ± 0.7	94.4 ± 0.6	0.38 ± 0.006
	3°	86.43 ± 0.6	79.07 ± 0.6	89.65 ± 0.7	NA	NA
	4°	83.11 ± 0.7	73.71 ± 1	85.39 ± 1.5	90.54 ± 1.1	0.48 ± 0.005

Table 3. Summary of experimental results for each experiment according to visual field. Accuracy (mean ± SE) in discrimination experiments is reported in % correct, visual acuity (mean ± SE) in the tumbling E experiment is reported in LogMAR units. Same notations and units as in Table 1.

		Factor	Main effect	Interaction	Post hoc (Bonferroni/Dunn)
Faces	UVF-LoVF	VF	F(1,23)=0.688 p=0.415	F(2,46)=0.349 p=0.707	
		UVF-LoVF			p=0.415
		Ecc	F(2,46)=39.11 **p<0.0001**		
		4Deg, 3Deg			**p=0.0002**
		4Deg, 2Deg			**p<0.0001**
		3Deg, 2Deg			**p<0.0001**
	RVF-LeVF	VF	F(1,23)=4.605 **p=0.042**	F(2,46)=0.345 p=0.709	
		RVF-LeVF			**p=0.042**
		Ecc	F(2,46)=39.026 **p<0.0001**		
		4Deg, 3Deg			**p=0.0002**
		4Deg, 2Deg			**p<0.0001**
		3Deg, 2Deg			**p<0.0001**
Inverted faces	UVF-LoVF	VF	F(1,11)=2.154 p=0.17	F(2,22)=0.015 p=0.985	
		UVF-LoVF			p=0.17
		Ecc	F(2,22)=19.056 **p<0.0001**		
		4Deg, 3Deg			**p=0.011**
		4Deg, 2Deg			**p<0.0001**
		3Deg, 2Deg			**p=0.0027**
	RVF-LeVF	VF	F(1,11)=5.296 **p=0.041**	F(2,22)=0.345 p=0.709	
		RVF-LeVF			**p=0.0419**
		Ecc	F(2,22)=19.217 **p<0.0001**		
		4Deg, 3Deg			**p=0.0106**
		4Deg, 2Deg			**p<0.0001**
		3Deg, 2Deg			**p=0.0026**
Houses	UVF-LoVF	VF	F(1,10)=0.292 p=0.6	F(2,20)=0.063 p=0.938	
		UVF-LoVF			p=0.6
		Ecc	F(2,20)=11.325 **p=0.0005**		
		4Deg, 3Deg			**p=0.002**
		4Deg, 2Deg			**p=0.0002**
		3Deg, 2Deg			p=0.3413
	RVF-LeVF	VF	F(1,10)=0.239 p=0.635	F(2,20)=0.39 p=0.682	
		RVF-LeVF			p=0.635
		Ecc	F(2,20)=11.054 **p=0.0006**		
		4Deg, 3Deg			**p=0.0022**
		4Deg, 2Deg			**p=0.0002**
		3Deg, 2Deg			p=0.3581

Shape	UVF-LoVF	VF UVF-LoVF	F(1,7)=0.036 p=0.855	F(1,7)=0.686 p=0.434	p=0.855
		Ecc 4Deg, 2Deg	F(1,7)=17.077 **p=0.007**		**p=0.0071**
	RVF-LeVF	VF RVF-LeVF	F(1,7)=0.001 p=0.978	F(1,7)=0.167 p=0.694	p=0.978
		Ecc 4Deg, 2Deg	F(1,7)=13.91 **p=0.007**		**p=0.0074**
VA Tumbling E	UVF-LoVF	VF UVF-LoVF	F(1,22)=0.621 p=0.439	F(1,22)=0.862 p=0.363	p=0.439
		Ecc 4Deg, 2Deg	F(1,22)=206.459 **p<0.0001**		**p<0.0001**
	RVF-LeVF	VF RVF-LeVF	F(1,22)=0.026 p=0.873	F(1,22)=3.685 p=0.068	p=0.873
		Ecc 4Deg, 2Deg	F(1,22)=202.987 **p<0.0001**		**p<0.0001**

Table 4. Summary of statistical analyses according to visual field for all experiments. Statistical analysis was performed using repeated measures two-way ANOVA on accuracy between factors (eccentricity and visual field), followed by Bonferroni/Dunn post hoc test. Same notations as in Table 2.

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