Holistic crowding of Mooney faces

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An object or feature is generally more difficult to identify when other objects are presented nearby, an effect referred to as crowding. Here, we used Mooney faces to examine whether crowding can also occur within and between holistic face representations (C. M. Mooney, 1957). Mooney faces are ideal stimuli for this test because no cues exist to distinguish facial features in a Mooney face; to find any facial feature, such as an eye or a nose, one must first holistically perceive the image as a face. Through a series of six experiments we tested the effect of crowding on Mooney face recognition. Our results demonstrate crowding between and within Mooney faces and fulfill the diagnostic criteria for crowding, including eccentricity dependence and lack of crowding in the fovea, critical flanker spacing consistent with less than half the eccentricity of the target, and inner-outer flanker asymmetry. Further, our results show that recognition of an upright Mooney face is more strongly impaired by upright Mooney face flankers than inverted ones. Taken together, these results suggest crowding can occur selectively between high-level representations of faces and that crowding must occur at multiple levels in the visual system.

Introduction

Crowding refers to the phenomenon that an object or feature is generally more difficult to identify when other objects are presented nearby (Bouma, 1970; Levi, 2008; Pelli, Palomares, & Majaj, 2004; Stuart & Burian, 1962). The effects of crowding have been demonstrated using letters, digits, gratings, and faces (Andriessen & Bouma, 1976; Louie, Bressler, & Whitney, 2007; Martelli, Majaj, & Pelli, 2005; Pelli et al., 2004; Strasburger, Harvey, & Rentschler, 1991), and various characteristic features of crowding have been identified and studied with these stimuli. Crowding in normal vision occurs more robustly with increasing eccentricity, extending as far as half the retinal eccentricity of the target in the periphery, but occurring 1 degree (deg) or less when the target is in the fovea (Bouma & Andriessen, 1970; Pelli et al., 2004; Toet & Levi, 1992). Crowding also depends on the spacing between the target object and the flankers, in proportion to the target's eccentricity. Impairment of target identification as a result of crowding has been shown to be independent of the target size or the size of the flanking items (Levi, Hariharan, & Klein, 2002; Pelli et al., 2004; Strasburger et al., 1991). Crowding increases as the number of flankers and similarity between target and flankers increases (Kooi, Toet, Tripathy, & Levi, 1994), and is not alleviated with extra viewing time (Townsend, Taylor, & Brown, 1971).

It is well established that crowding can occur as a result of interference between low-level elementary features, which likely happens at a single, relatively early stage in visual processing (He, Cavanagh, & Intriligator, 1997; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Pelli et al., 2004). More recently, it has been shown that crowding may also occur between higher level representations in the visual system, such as between faces (Louie et al., 2007), thought to be processed holistically (Farah, 1995; Maurer, Le Grand, & Mondloch, 2002; Tanaka & Farah, 1993). Louie et al. (2007) tested this by presenting subjects with an upright face surrounded by upright or inverted faces and found selective crowding of upright faces by other upright faces. This did not happen for inverted faces or non-face objects. These results demonstrate that crowding occurs between higher-level representations, and not just between low-level elementary features such as edges or gratings. What counts as a "high-level" representation, though, is somewhat unclear. The results of Louie et al. (2007) could involve crowding between upright facial features (e.g. the face parts themselves or

the configuration of face parts). Crowding could also occur for holistic representations of faces. The purpose of the present experiment was to provide a direct test of holistic face crowding using Mooney faces (Mooney, 1957) (Figure 1).

Mooney faces were first used to examine the development of visual closure ability in young children (Mooney, 1957), and have since been used to investigate various aspects of intact and impaired face processing. Studies have found that, in general, Mooney faces are more difficult to recognize than photographs of faces, they are most easily and more rapidly identified as a face when they are in the upright orientation, and they activate known face-selective regions such as the fusiform face area (FFA) (Andrews & Schluppeck, 2004; George, Jemel, Fiori, Chaby, & Renault, 2005; Kanwisher, Tong, & Nakayama, 1998; Latinus & Taylor, 2005, 2006; McKeeff & Tong, 2007; Moscovitch, Winocur, & Behrmann, 1997). Mooney faces are advantageous stimuli for testing whether crowding operates at the level of holistic processing because the faces lack individual facial features and cannot be parsed or segmented by bottom-up processes in order to perceive the face. Since no cues exist to distinguish the cast shadows in a Mooney face, to find any facial feature, such as an eye or a nose, one must first holistically perceive the image as a face (Cavanagh, 1991; Kemelmacher-Shlizerman, Basri, & Nadler, 2008; Moore & Cavanagh, 1998). Therefore, holistic processing is a prerequisite for Mooney face perception.
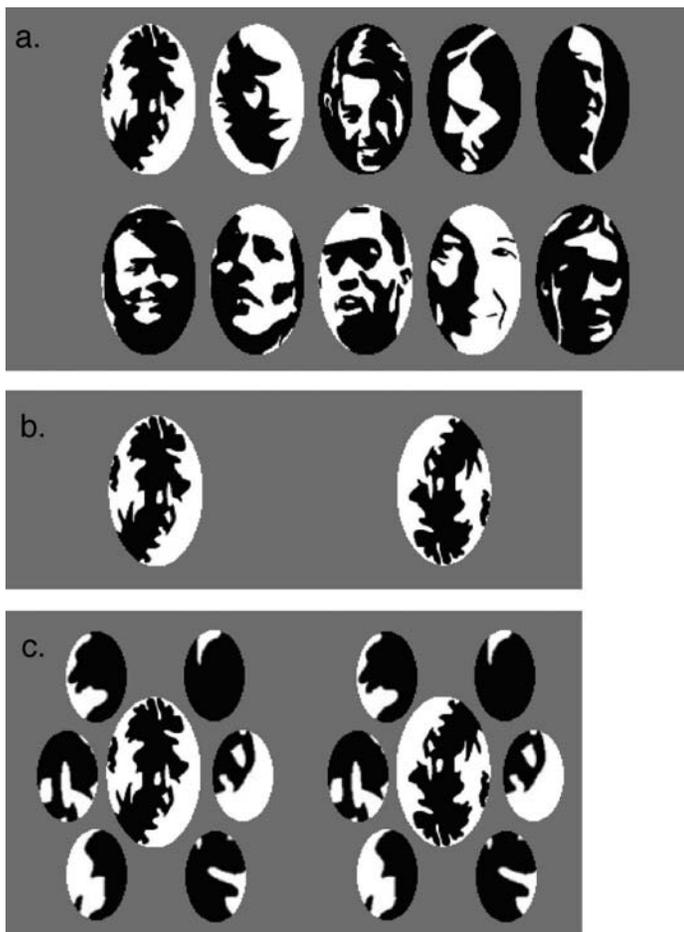

Figure 1. (a) Mooney face stimuli used in Experiments 1, 4, and 5 (top row are original faces used in Mooney, 1957), (b) upright (left) and inverted (right) without flankers, (c) upright (left) and inverted (right) with flankers. Each face was cropped to fit a 1.63 deg by 2.62 deg region when viewed from a distance of 60 cm. Each crowded face was surrounded by six 1.53 deg by 0.95 deg elliptically-shaped parts (flankers) created from the upright target face, randomly positioned. Flankers were presented with a fixed horizontal center-to-center spacing of 1.44 deg between the face and the flanker, unless otherwise noted. Stimuli were presented against a gray background.

Experiment 1: Crowding of a Mooney face

Experiment 1 sought to extend the results of Louie et al. (2007) by using Mooney faces to test whether crowding can occur at the level of a single holistic representation. The advantage of using these faces is that it is well-established that recognition of an upright Mooney face is not possible (at least initially) based on segmentable facial features—the whole must come before the parts. If Mooney faces are subject to crowding, it would suggest that there is a level of crowding that occurs independent of low-level crowding between facial features.

Method

Subjects

Subjects were eight undergraduate students (6 females, mean age = 23.5 ± 3.69 years) at the University of California, Davis, participating for course credit. All subjects had normal or corrected-to-normal visual acuity and were naïve to the faces and the purpose of the experiment. The study was approved by the Institutional Review Board at the University of California, Davis, and informed consent was obtained from all subjects.

Apparatus and stimuli

All experiments were conducted in a small testing room with the lights off. Stimuli were presented on a Tobii 17-inch LCD binocular eye tracker monitor (1024 × 768 pixels

resolution, 50 Hz data capture rate, 60 Hz refresh rate) to insure that subjects' gaze position did not deviate from fixation. A radius of 2 deg around the fixation point was used as the criteria for central fixation. Trials in which the participant's gaze shifted outside of this area (an average of 4 trials per participant) were removed from the analysis. Experiments were programmed and presented using Presentation version 11.3 (Neurobehavioral Systems).

Stimuli consisted of ten Mooney faces, 6 of which were male (Figure 1). Five of these faces were from the original collection of faces used in the Mooney study (Mooney, 1957). Faces were 99.8% Michelson contrast, and cropped to fit into a 1.63 deg by 2.62 deg region when viewed from a distance of 60 cm. Using a larger sized version of each face image (3 deg by 5 deg), six flankers were created by "cutting" elliptically-shaped sections from the upright target face. Each flanker was a 1.05 deg by 1.58 deg ellipse (Figure 1). In the crowded condition, the flankers were centered on an imaginary ellipse surrounding the target face (radii of the horizontal and vertical vertices were 1.44 deg and 2.2 deg, respectively). In this experiment, and unless noted otherwise, the flanker separation will be expressed as the horizontal center-to-center distance between target and flanker, and was fixed at 1.44 deg. Stimuli were presented against a gray background (77.23 cd/m^2).

Procedure

All experiments began with a five-point calibration routine on the eye tracker to accurately estimate the subject's gaze position during the task. Trials began with a 1 deg fixation point (red circle) presented at the center of the screen for 750 ms. A single face with (crowded) or without (uncrowded) its corresponding six flanker parts was shown at the fovea (0 deg) or at 3, 6, or 10 deg to the left or right of fixation for a duration of 250 ms (Figure 2). The eccentricity and visual field in which the face was presented were blocked and the order of blocks was randomized for each subject. The orientation of the face and the presence of flankers were randomized on each trial. Using a two-alternative forced-choice (2AFC) task, subjects were asked to respond with the press of a two-button mouse whether the target face was upright or inverted. Following the face presentation, the gray background screen remained until a response was received, advancing the experiment to the next trial. Subjects completed 40 trials at each eccentricity and on each side of fixation (total of 320 trials).

Results and discussion

Percentage of correct trials averaged across subjects is shown as a function of eccentricity in Figure 2. A
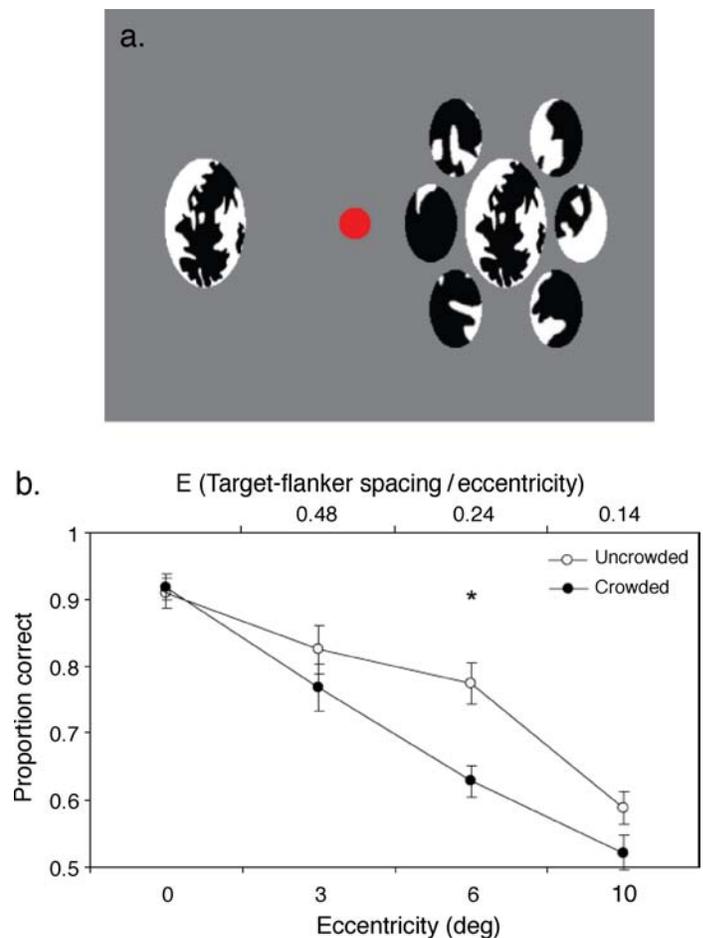

Figure 2. Example stimuli (a) and results (b) from Experiment 1. (a) Example of an uncrowded inverted face (left) and crowded inverted face (right) presented at 3 deg from fixation (Note that a single face was presented to one visual field per trial). (b) Orientation discrimination of a Mooney face was significantly impaired in the presence of flankers, as a function of increasing eccentricity ($F_{(3,5)}$ = 11.158, p = 0.012, η^2 = 0.870). Main effects of eccentricity ($F_{(3,5)}$ = 136.7, p = 0.001, η^2 = 0.988) and crowding ($F_{(1,7)}$ = 35.52, p = 0.001, η^2 = 0.835) were also observed. A significant difference between performance in the uncrowded and crowded conditions was found at 6 deg eccentricity ($t_{(7)}$ = 3.653, p = 0.008). Asterisks indicate significant differences between pairwise comparisons (p < 0.05). Error bars represent ±SEM across 8 subjects.

4 (eccentricity) × 2 (uncrowded or crowded) ANOVA revealed significant main effects of eccentricity ($F_{(3,5)}$ = 136.7, p = 0.001, η^2 = 0.988) and crowding ($F_{(1,7)}$ = 35.52, p = 0.001, η^2 = 0.835), and a significant interaction between eccentricity and crowding ($F_{(3,5)}$ = 11.158, p = 0.012, η^2 = 0.870) (Figure 2). Paired-samples t-tests (2-tailed) at each eccentricity showed a significant difference between performance in the uncrowded and crowded conditions only when faces were presented at 6 deg eccentricity ($t_{(7)}$ = 3.653, p = 0.008). These results

demonstrate that the orientation of a Mooney face can be discriminated in the periphery, supporting previous findings that face recognition in the periphery is possible, though more difficult than close to the fovea (Goren & Wilson, 2006; Louie et al., 2007; McKone, 2004). More importantly, the significant interaction establishes that flankers interfered with orientation discrimination of a face at larger eccentricities, consistent with other types of crowding (Levi, 2008; Pelli et al., 2004). Because Mooney faces lack individually segmentable facial features, and must first be processed holistically, these results suggest that the flankers were most likely interfering at the stage of holistic processing.

Experiment 2: Gender identification of a crowded Mooney face

The experiments above relied on discrimination of upright versus inverted Mooney faces, which first depends on the formation of a holistic representation of a face. However, to rule out the possibility that local cues (e.g. inferred lighting direction) may have facilitated orientation discrimination without requiring the actual recognition of the face, the current experiment required that subjects identify the gender of the Mooney face. In doing so, this task made it necessary that subjects recognize the stimulus as a face prior to identifying its gender.

Method

Subjects

Subjects were ten undergraduate students (6 females, mean age = 21.03 ± 3.04 years) at the University of California, Davis, with normal or corrected-to-normal visual acuity.

Stimuli and task

Stimuli were 10 male and 10 female Mooney faces. A single upright face was presented at the fovea (0 deg) or at 3, 6, or 10 deg to the left or right of fixation, either uncrowded or crowded by six flankers at a fixed horizontal center-to-center spacing of 1.44 deg (Figure 3). Visual field of the stimulus and eccentricity were blocked in a random order (block order was randomized between subjects), and gender of the target face and presence of flankers was randomized on each trial. Subjects completed 40 trials at each eccentricity and side of fixation (total of 320 trials). Subjects were asked to indicate with a button-press whether the face was male or female (2AFC).
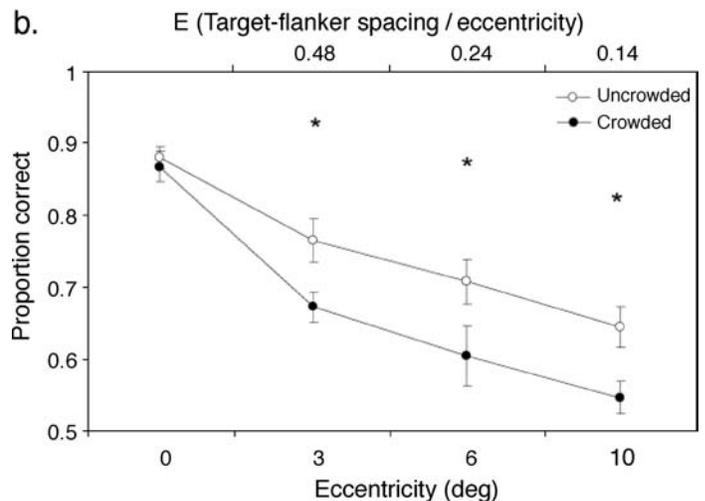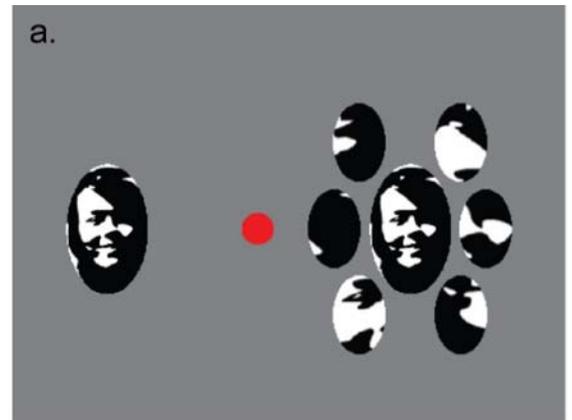

Figure 3. Example stimuli (a) and results (b) from Experiment 2. (a) Example of an uncrowded (left) and crowded (right) female face at 3 deg from fixation (Note that a single face was presented to one visual field per trial). (b) Gender identification of a Mooney face was significantly impaired in the presence of flankers ($F_{(1,9)}$ = 21.690, p = 0.001, η^2 = 0.707), and this crowding effect increased significantly with increasing eccentricity ($F_{(3,7)}$ = 6.896, p = 0.017, η^2 = 0.747). Flankers impaired performance at 3 ($t(9)$ = 2.751, p = 0.022), 6 ($t(9)$ = 4.080, p = 0.030), and 10 ($t(9)$ = 3.759, p = 0.040) deg eccentricity conditions, but not at the fovea. The results of this experiment confirm that under conditions requiring gender identification of the target face, subjects were impaired when the face was crowded and presented in the periphery. Therefore, we are able to rule out that the crowding effect observed in Experiment 1 was specific to orientation discrimination of the faces, possibly driven by some local cues that bypassed holistic processing of the faces. Asterisks indicate significant differences between pairwise comparisons (p < 0.05). Error bars represent ±*SEM* across 10 subjects.

Results and discussion

Figure 3 shows that there were main effects of eccentricity ($F_{(3,7)}$ = 43.809, p = 0.001, η^2 = 0.949) and

crowding ($F_{(1,9)}$ = 21.690, p = 0.001, η^2 = 0.707) on subjects' identification of the gender of the target face. A significant interaction between crowding and eccentricity was also found, showing that the crowding effect increased significantly with increasing eccentricity ($F_{(3,7)}$ = 6.896, p = 0.017, η^2 = 0.747). Identification of the gender of the face was significantly impaired by the presence of flankers at 3 deg ($t_{(9)}$ = 2.751, p = 0.022), 6 deg ($t_{(9)}$ = 4.080, p = 0.030), and 10 deg ($t_{(9)}$ = 3.759, p = 0.040) eccentricity, but not at the fovea ($t_{(9)}$ = 1.000, p = 0.343). These results confirm that under conditions requiring identification of the gender of the target face, subjects were impaired when the face was crowded and presented in the periphery. Therefore, we are able to rule out that the crowding effect observed in the previous experiment was specific to orientation discrimination of the faces, perhaps driven by some local cues that bypassed holistic processing.

Experiment 3: Spatial scaling of a Mooney face

The ability to recognize a face decreases with increasing eccentricity, partly as a result of crowding between features within the face (Martelli et al., 2005). Within-face crowding is relieved when the face size is increased such that the features have sufficient spacing from one another, referred to as critical spacing (Martelli et al., 2005). This spatial scaling can be described quantitatively in terms of E_2, which represents the eccentricity at which the foveal stimulus size must double in order to maintain foveal-level performance (Levi, Klein, & Aitsebaomo, 1985; Rovamo, Virsu, & Näsänen, 1978; Whitaker, Mäkelä, Rovamo, & Latham, 1992). The previous experiments showed that subjects' orientation and gender discrimination of an uncrowded Mooney face dropped with increasing eccentricity, which could have been the result of reduced acuity in the periphery or within-face crowding. Because perception of a Mooney face is guided primarily (at least initially) by top-down, holistic processing, we expect that it is unlikely that the observed decrement in performance is based purely on within-face crowding, which occurs at the level of facial features. Experiment 3 sought to determine the scaling rate (E_2) necessary to equate discrimination of a Mooney face in the periphery with performance obtained at the fovea. To determine whether crowding at the level of facial features may be operating on Mooney faces in a manner similar to that of grayscale faces, we measured the scaling factor required for Mooney faces as compared to the scaling factor for grayscale versions of the same faces.

Method

Subjects

Subjects were eight undergraduate students (6 females, mean age = 20.1 ± 1.78 years) at the University of California, Davis, with normal or corrected-to-normal visual acuity.

Stimuli and task

Images of 20 faces (10 male and 10 female) were obtained using the Google search engine and were edited using Adobe Photoshop CS2 to create two versions; one by converting to grayscale, applying a Gaussian blur filter and thresholding (Mooney faces) and one by converting to grayscale (grayscale faces) (Figure 4). To insure that performance at the fovea was equal for Mooney and grayscale faces, subjects were familiarized and tested with both sets of faces until performance reached at least 90% for each set. During the main experiment, subjects were asked to fixate on the center of the screen while a single face was shown (uncrowded) for 250 ms. Faces were presented first at the fovea and then at 3 eccentricities (3, 6, and 10 deg) randomized between subjects. Faces at the fovea were 1.12 deg by 1.73 deg in horizontal and vertical dimensions, respectively. At each eccentricity, six face image sizes were presented in random order. For the purpose of calculating scaling factors, horizontal dimensions of the face were used. At 3 deg, face sizes were
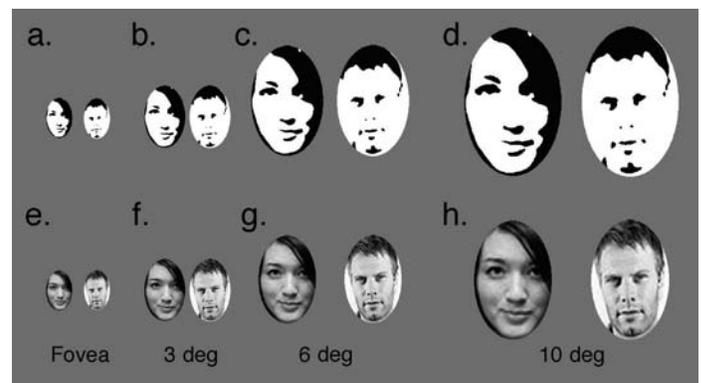

Figure 4. Example of a female and male Mooney (a–d) and grayscale (e–h) face at mean threshold sizes obtained from Experiment 3. Subjects were familiarized with both sets of faces prior to the experiment. Each face was presented for 250 ms, first at the fovea and then blocked randomly at 3, 6, and 10 deg from fixation. Faces at the fovea were 1.12 deg by 1.73 deg in horizontal and vertical dimensions, respectively. At each eccentricity, six face sizes were presented (3 deg: 0.75, 1.12, 1.49, 1.87, 2.24, and 2.61 deg, 6 deg: 1.12, 2.87, 2.24, 2.61, 1.98, and 3.35 deg, and 10 deg: 1.12, 1.87, 2.61, 2.98, 3.35, and 3.73 deg). Subjects were asked to indicate whether the gender of the face was male or female. Each face set was presented separately, counterbalanced between subjects.

0.75, 1.12, 1.49, 1.87, 2.24, and 2.61 deg. At 6 deg, face sizes were 1.12, 2.87, 2.24, 2.61, 1.98, and 3.35 deg. At 10 deg, face sizes were 1.12, 1.87, 2.61, 2.98, 3.35, and 3.73 deg. The task was a 2AFC procedure in which subjects were asked to indicate whether the gender of the face was male or female. Subjects completed a total of 400 trials. Each face type was presented separately, counterbalanced between subjects.

Results and discussion

Our findings revealed that the spatial scaling required for identifying the gender of Mooney faces in the periphery was similar to the scaling found for grayscale versions of the same faces (Figures 4 and 5). Overall, performance increased significantly with increasing face size, irrespective of eccentricity or face type ($F_{(5,3)}$ = 13.616, p = 0.028, η^2 = 0.958). No other significant effects or interactions were found. Importantly, there was no performance difference between gender discrimination of Mooney and grayscale faces at the fovea ($t_{(7)}$ = 1.038, p = 0.334). Individual subjects' performance at each eccentricity as a function of face size was fitted to a logistic function to find the "threshold" size at which performance matched 95% of foveal performance. Scaling factors were calculated by dividing the obtained threshold size by the foveal size of 1.12 deg, and then plotted against eccentricity and fitted with a line of least squares. The eccentricity at which the scaling factor doubled (E_2) was calculated as the inverse of the slope of the line of least squares (foveal scaling factor constrained to 1), for each subject. There was no difference in E_2 values obtained for discriminating Mooney (mean = 3.72 deg) and grayscale (mean = 4.89 deg) faces ($t_{(7)}$ = 0.365, p = 0.726), suggesting that the face types may involve similar amounts of within-face feature-based crowding (Figure 5). These E_2 values are similar to values reported previously for Vernier acuity (Whitaker et al., 1992), orientation discrimination (Mäkelä, Whitaker, & Rovamo, 1993), and faces (Mäkelä, Näsänen, Rovamo, & Melmoth, 2001; Melmoth, Kukkonen, Mäkelä, & Rovamo, 2000).

For comparison purposes, we also carried out a similar calculation as Martelli et al. (2005) to determine the effect of within-face crowding by measuring performance as a function of critical spacing (estimated from face size) at each eccentricity, for each face type. To approximate the spacing of the facial features, the average distance between the nose and the eyes and the nose and the mouth was calculated in proportion to the width of the target face for the grayscale version of the faces and found to be 26% of the face size. Individual subjects' critical spacing threshold was calculated from their threshold face size at each eccentricity and fitted with a line of least squares, assuming zero critical spacing at the fovea. As shown in Figure 5, critical spacing was significantly
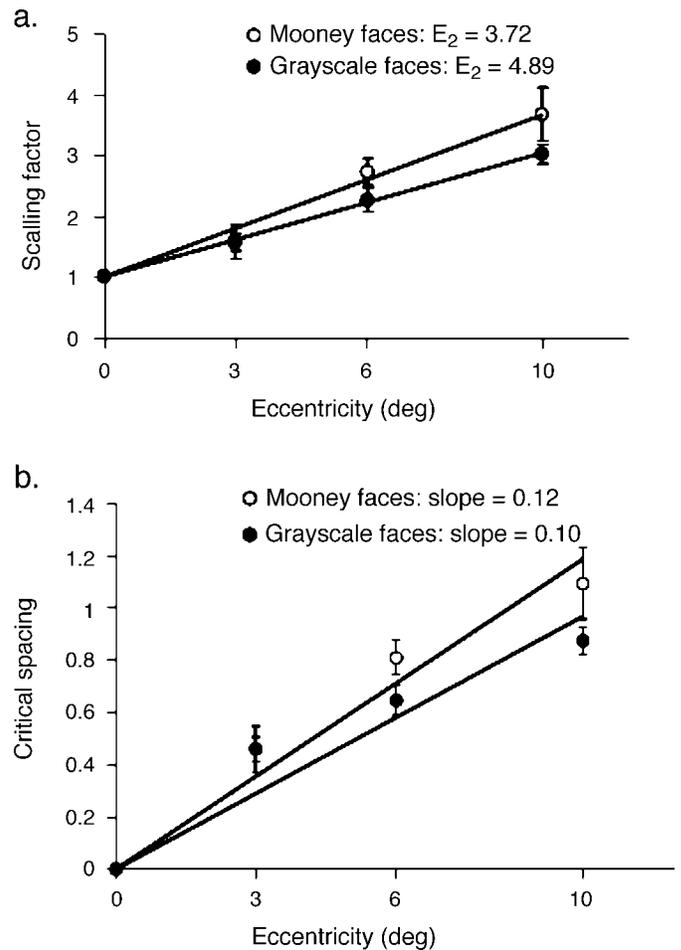

Figure 5. Scaling factor (a) and critical spacing (b) results from Experiment 3. (a) Mean spatial scaling factor plotted against eccentricity (foveal scaling factor constrained to 1) for identical Mooney and grayscale faces. Scaling factor at each eccentricity was calculated by dividing individual subjects' threshold face size by foveal face size of 1.12 deg and then fitted with a line of least squares. There was no difference in E_2 values for Mooney (mean = 3.72) and grayscale (mean = 4.89) faces ($t_{(7)}$ = 0.365, p = 0.726). (b) Critical spacing as a function of eccentricity for identical Mooney and grayscale faces. Critical spacing, estimated from the spacing between the nose and eyes and mouth in proportion to the width of the face, was found to be 26% of face size. Individual subjects' critical spacing was calculated from their threshold face size at each eccentricity and fitted with a line of least squares, assuming zero critical spacing at the fovea. Critical spacing was significantly proportional to eccentricity for both face types (Mooney: ($F_{(2,6)}$ = 19.132, p = 0.002, η^2 = 0.864), grayscale: ($F_{(2,6)}$ = 7.179, p = 0.026, η^2 = 0.705)), and slope values did not differ for Mooney (mean = 0.12) and grayscale faces (mean = 0.10) ($t_{(7)}$ = 0.800, p = 0.450). R^2 values of the fits were 0.96 for Mooney faces and 0.90 for grayscale faces. Error bars represent ±*SEM* across 8 subjects.

proportional to eccentricity for both face types (Mooney: ($F_{(2,6)}$ = 19.132, p = 0.002, η^2 = 0.864), grayscale: ($F_{(2,6)}$ = 7.179, p = 0.026, η^2 = 0.705)), and the slope values did not differ between face types ($t_{(7)}$ = 0.800, p = 0.450). For Mooney faces, critical spacing was proportional to eccentricity with a slope of 0.12, while for grayscale faces the slope was equal to 0.10. R^2 values of the fits were 0.96 and 0.90, respectively. These critical spacing values are consistent with the results presented in Martelli et al. (2005).

Do Mooney faces have facial features?

These results indicate that Mooney faces may contain facial features. This finding suggests the possible existence of within-face in addition to between-face crowding of Mooney faces. Based on the understanding that Mooney faces are initially perceived using shape-from-shading information and then segmented into facial features for discrimination purposes (Cavanagh, 1991; Kemelmacher-Shlizerman et al., 2008; Moore & Cavanagh, 1998), it is plausible that crowding of a Mooney face can occur by multiple mechanisms at multiple levels in the visual system. By this account, crowding may occur at the level of facial features, within the face (once the "face-ness" has been perceived), but there may also be crowding between the holistic representations of the faces that cannot be accounted for by within-face crowding alone. The following experiments will test the holistic level of crowing further.

Experiment 4: Effect of flanker spacing

One of the diagnostic criteria of crowding is based on the finding that the critical spacing between target and flanker scales with eccentricity (Bouma, 1970; Pelli et al., 2004; Pelli & Tillman, 2008; Strasburger et al., 1991; Toet & Levi, 1992). Critical spacing is the minimum spacing at which there is no observable effect of the flankers on identification of the target. In this experiment we measured performance when discriminating orientation of a Mooney face at 6 deg eccentricity as a function of horizontal center-to-center spacing between target face and flankers. The effect of crowding should be less when the separation is large, but stronger as the separation decreases.

Method
Subjects

Subjects were ten undergraduate students (7 females, mean age = 21.04 ± 2.73 years) at the University of California, Davis, with normal or corrected-to-normal visual acuity.

Stimuli and task

Face stimuli were the same as those used in Experiment 1, with the exception that five flankers (rather than six) were presented (Figure 6). Following fixation, a single Mooney
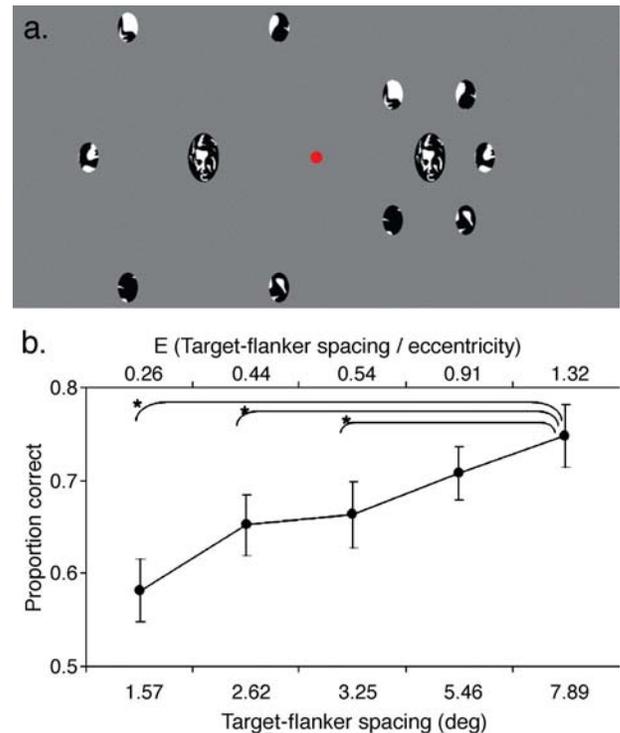

Figure 6. Example stimuli (a) and results (b) from Experiment 4. (Note that a single face was presented to one visual field per trial). Eccentricity of the target face was fixed at 6 deg and target-flanker spacing varied at one of five levels: 1.57, 2.62, 3.25, 5.46, or 7.89 deg. To remove the overlap between the fixation point and the inner flanker at the greatest spacing level, this flanker was removed. A significant decrease in performance was observed as a function of decreased center-to-center spacing between the target face and five flankers ($F_{(4)}$ = 3.625, p = 0.012, η^2 = 0.244). Performance at the largest spacing (shown on left of fixation) was confirmed to be equivalent to performance at the 6 deg uncrowded condition of Experiment 1. Paired-samples t-tests (2-tailed) between performance at each of the four closest spacing levels and performance at the largest spacing level revealed a significant difference only at the first three levels (1.57 deg: ($t_{(9)}$ = −9.156, p = 0.001), 2.62 deg ($t_{(9)}$ = −11.756, p = 0.001), 3.25 deg ($t_{(9)}$ = −3.730, p = 0.005)). The largest spacing at which flankers impacted orientation discrimination of the target face was 3.25 deg (shown on right of fixation), corresponding to an E (target-flanker spacing/eccentricity) value of 0.54 and closely following the half-eccentricity rule of crowding. Asterisks indicate a significant difference from the 7.89 deg spacing condition (p < 0.05). Error bars represent ±SEM across 10 subjects.

face, either upright or inverted, was presented at 6 deg eccentricity to the left or right of fixation for a duration of 250 ms. Flanker spacing was varied randomly from trial to trial between five levels: 1.57, 2.62, 3.25, 5.46, or 7.89 deg. To remove overlap between the fixation point and the most foveal middle flanker at the largest spacing level, this flanker was removed on all trials. The visual field in which the stimulus was presented was blocked (block order was randomized for each subject). Subjects completed 40 trials at each level of spacing (200 trials total). Subjects were asked to indicate whether the target face was upright or inverted (2AFC).

Results and discussion

Figure 6 shows the significant main effect of target-flanker spacing on performance. As expected, recognition of the orientation of the face decreased significantly as spacing (flanker density) decreased ($F_{(4)} = 3.625$, $p = 0.012$, $\eta^2 = 0.244$). Paired-samples *t*-tests (2-tailed) between performance at each of the four closest spacing levels and performance at the greatest spacing level (confirmed to be statistically equivalent to the 6 deg uncrowded condition of Experiment 1) revealed a significant difference at the first three levels (1.57 deg: ($t_{(9)} = -9.156$, $p = 0.001$), 2.62 deg ($t_{(9)} = -11.756$, $p = 0.001$), 3.25 deg ($t_{(9)} = -3.730$, $p = 0.005$)). The largest center-to-center spacing at which flankers impacted orientation discrimination was 3.25 deg, which corresponds to an E value (target-flanker spacing/eccentricity) of 0.54. These results are in agreement with Bouma's (1970) rule stating that crowding between target and flankers occurs when critical spacing is roughly half the target's eccentricity, and are similar to critical spacing values found by other groups (Levi, 2008; Pelli & Tillman, 2008). This dependency, along with the results of Experiments 1 and 2, meets the diagnostic criteria for crowding, distinguishing it from a masking process.

Experiment 5: Inner-outer flanker asymmetry

Asymmetry is a general property of peripheral crowding, and has been suggested as a diagnostic test (Bex, Dakin, & Simmers, 2003; Bouma, 1970; Petrov, Popple, & McKee, 2007; Toet & Levi, 1992). Specifically, flankers on the more eccentric (outer) side of the target impair recognition more than flankers on the more foveal (inner) side of the target. In this experiment we examined the effect of a single flanker placed on the left or right of the target face, along the horizontal meridian. Inner-outer asymmetry predicts a stronger crowding effect when the flanker is on the outer side of the target.

Method

Subjects

Subjects were ten undergraduate students (9 females, mean age = 20.1 ± 1.78 years) at the University of California, Davis, with normal or corrected-to-normal visual acuity.

Stimuli and task

Face stimuli were the same as those used in Experiments 1 and 4, with the exception that only one flanker (rather than six) was presented (Figure 7). A single Mooney face was shown at the fovea (0 deg) or at 3, 6, or 10 deg to the left or right of fixation, with visual field and eccentricity blocked in a random order. Each face was shown either uncrowded or with a single flanker positioned at a fixed horizontal center-to-center spacing of 1.44 deg on the left or right of the face along the horizontal meridian, randomly determined on each trial. This allowed us to test the hypothesis that a stronger crowding effect exists when the single flanker is located on the more eccentric (outer) side of the target face. Subjects completed a total of 640 trials. The task was a 2AFC procedure in which subjects were asked to indicate whether the target face was in an upright or inverted orientation.

Results and discussion

Our findings revealed a stronger crowding effect when the single flanker was located on the outer side of the target face (Figure 7). A 4 (eccentricity) by 3 (crowding condition: uncrowded, inner flanker, or outer flanker) ANOVA resulted in a main effect of eccentricity ($F_{(3,7)} = 27.533$, $p = 0.001$, $\eta^2 = 0.922$) and a significant interaction between eccentricity and crowding condition ($F_{(6,4)} = 20.121$, $p = 0.006$, $\eta^2 = 0.968$). Given this interaction, we conducted paired-samples *t*-tests (2-tailed) at each eccentricity level. As would be expected from Petrov et al. (2007), we found little difference between performance in the uncrowded condition and the single inner flanker condition at any eccentricity, indicating that a single flanker on the inner side of the target face only mildly interfered with face recognition. Significant crowding of the target face with a single flanker on the outer side was observed at 6 deg ($t_{(9)} = 2.878$, $p = 0.018$), illustrating that a single outer flanker is sufficient to disrupt face recognition in the periphery. A significant difference between the crowding effect of the inner and outer flanker was present at 10 deg ($t_{(9)} = 3.678$, $p = 0.005$) such that the outer flanker produced a greater crowding effect than the inner one. These results replicate and extend previous findings of flanker asymmetry in crowding (Banks, Larson, & Prinzmetal, 1979; Bex et al., 2003; Bouma,
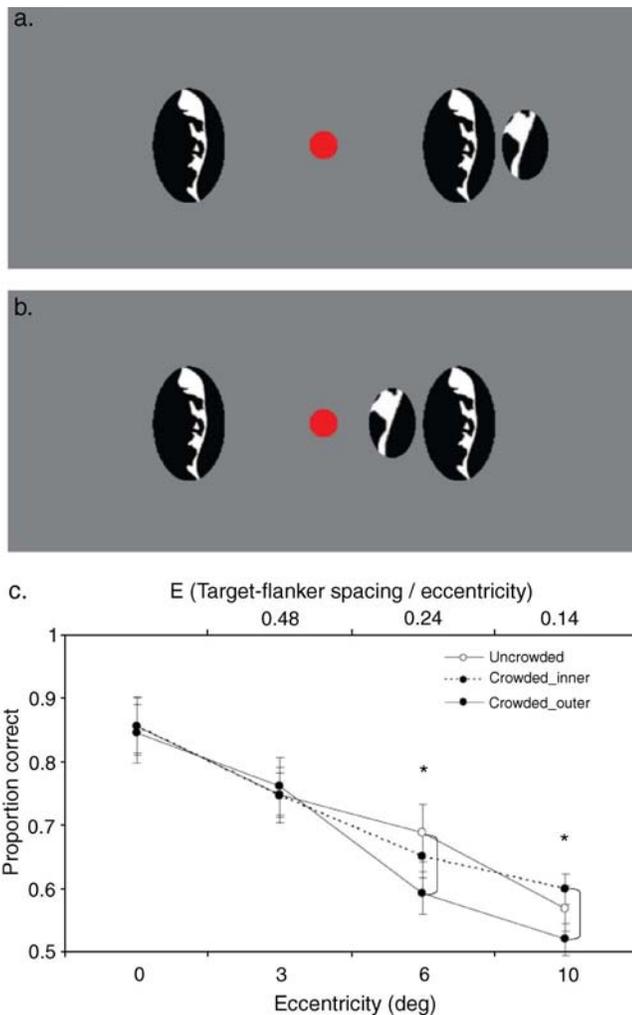
Figure 7. Example stimuli ((a) and (b)) and results (c) from Experiment 5. An example of an upright face uncrowded (a and b; left), an upright face crowded by an outer flanker (a; right), and an upright face crowded by an inner flanker (b; right) at 3 deg from fixation. (Note that a single face was presented to one visual field per trial). A significantly stronger crowding effect was present when a single outer (a) rather than inner (b) flanker was presented ($F_{(1,9)}$ = 4.920, p = 0.05, η^2 = 0.353), and this effect was stronger at higher eccentricities ($F_{(3,7)}$ = 4.695, p = 0.042, η^2 = 0.668). As would be expected, we found no significant difference between performance in the uncrowded and the single inner flanker conditions at any eccentricity, indicating that a single flanker on the inner side of the target face did not strongly interfere with face recognition. Significant crowding of the target face by a single flanker on the outer side was observed at 6 deg ($t_{(9)}$ = 2.878, p = 0.018), illustrating that a single outer flanker is sufficient to disrupt orientation discrimination in the periphery. A significant difference between performance in the inner and outer flanker crowding conditions was present at 10 deg ($t(9)$ = 3.678, p = 0.005) such that the outer flanker produced a greater crowding effect than the inner one. Together, these results are consistent with the inward-outward anisotropy that has been shown to be characteristic of crowding. Asterisks indicate significant differences between pairwise comparisons ($p < 0.05$). Error bars represent ±SEM across 10 subjects.

1970; Petrov et al., 2007), demonstrating that a single flanker on the outer side of the face target is more effective in peripheral crowding than a flanker on the inner side. Together, these results are consistent with the inward-outward anisotropy that is characteristic of crowding.

Experiment 6: Upright-inverted Mooney face flanker asymmetry

The results described above provide strong evidence for crowding of a holistically processed face representation, but leave unanswered the question of whether crowding can also occur selectively *between* holistic face representations. Experiment 6 tested gender identification of a Mooney face when flanked by six, either upright or inverted, Mooney faces. Based on studies showing that upright faces are processed holistically, while inverted faces rely on the extraction of individual facial features (Boutet & Chaudhuri, 2001; Farah, 1995; Maurer et al., 2002; Tanaka & Farah, 1993), the expectation is that if crowding occurs selectively between holistic representations, then gender identification of an upright target face should be more impaired when flanked by upright faces than by inverted faces.

Method
Subjects

Subjects were ten undergraduate students (7 females, mean age = 22.7 ± 2.75 years) at the University of California, Davis, with normal or corrected-to-normal visual acuity.

Stimuli and task

Target face stimuli were the same as those used in Experiment 2, and flankers were 20 different Mooney faces (10 male and 10 female) (Figure 8). A single upright Mooney face (1.53 deg by 2.48 deg) was presented at the fovea (0 deg) or at 3, 6, or 10 deg to the left or right of fixation for 250 ms. On each trial, the target face was shown either without flankers (uncrowded) or flanked (crowded) by six upright or inverted Mooney faces (3 male and 3 female). Flankers were the same size as the target face, and were presented at a fixed horizontal center-to-center spacing of 2.38 deg from the target face. Gender of the target face and identity, position, and orientation of the flanker faces were randomly determined on each trial. Visual field and eccentricity were blocked in random order (order was randomized between subjects). Subjects completed a total of 480 trials. The task was a 2AFC procedure in which subjects were asked to indicate whether the target face was male or female.

Results and discussion

The results of Experiment 6 revealed a selective and stronger crowding effect when the target Mooney face was surrounded by upright compared to inverted Mooney faces (Figure 8). A 4 (eccentricity) by 2 (flanker orientation: upright or inverted) ANOVA confirmed a significant main effect of eccentricity ($F_{(3,7)} = 64.231$, $p = 0.001$, $\eta^2 = 0.965$) and flanker orientation ($F_{(1,9)} = 17.257$, $p = 0.002$, $\eta^2 = 0.657$) (Figure 8). Paired-samples *t*-tests (2-tailed) revealed that upright face flankers impaired performance more than inverted flankers at 3 deg ($t_{(9)} = -3.236$, $p = 0.010$) and 6 deg ($t_{(9)} = -4.129$, $p = 0.003$), but no significant difference was found at the fovea or at 10 deg. A significant difference between performance in the
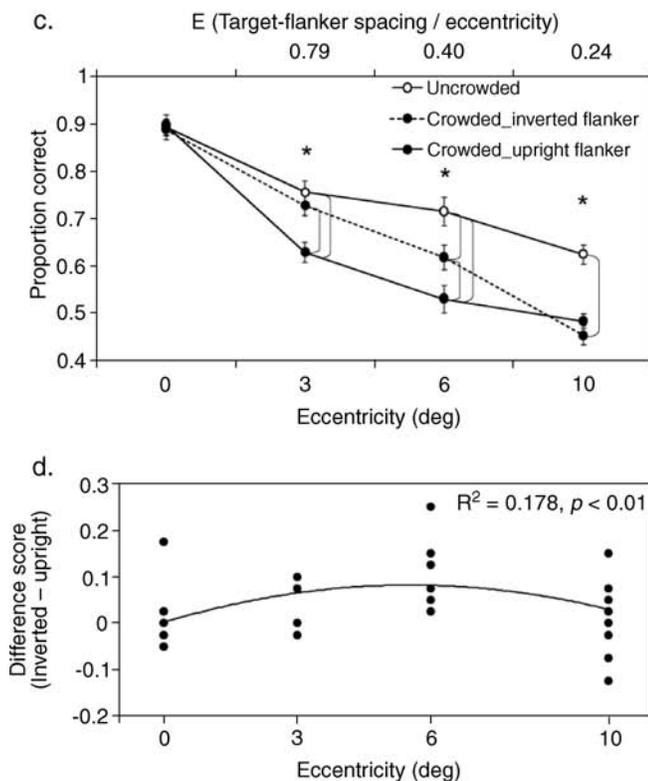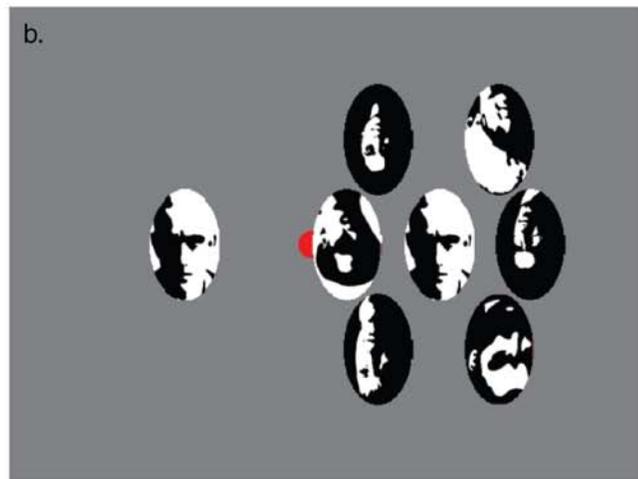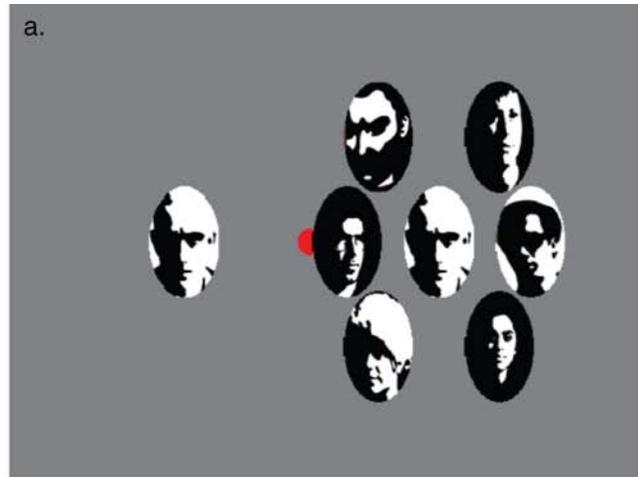

Figure 8. Example stimuli ((a) and (b)) and results ((c) and (d)) from Experiment 6. An example of an uncrowded male Mooney face (a and b; left), crowded by upright Mooney face flankers (a; right), and crowded by inverted Mooney face flankers (b; right) at 3 deg from fixation. Note that only one condition was presented per trial. Six flankers (half male) were presented with a fixed horizontal center-to-center spacing of 2.38 deg between the target face and the flanker. (c) A significant main effect of eccentricity ($F_{(3,7)} = 64.231$, $p = 0.001$, $\eta^2 = 0.965$) and flanker orientation ($F_{(1,9)} = 17.257$, $p = 0.002$, $\eta^2 = 0.657$) was confirmed. Paired-samples *t*-tests (2-tailed) revealed that upright face flankers impaired performance more than inverted flankers at 3 deg ($t_{(9)} = -3.236$, $p = 0.010$) and 6 deg ($t_{(9)} = -4.129$, $p = 0.003$), but no significant difference was found at the fovea or at 10 deg. A significant difference between performance in the uncrowded and upright face flanker conditions was found at 3 deg ($t_{(9)} = -3.581$, $p = 0.006$), 6 deg ($t_{(9)} = -4.271$, $p = 0.002$), and 10 deg ($t_{(9)} = -5.749$, $p = 0.0001$), and between performance in the uncrowded and inverted face flanker conditions at 6 deg ($t_{(9)} = -2.567$, $p = 0.030$) and 10 deg ($t_{(9)} = -3.399$, $p = 0.008$). Asterisks indicate significant differences between pairwise comparisons ($p < 0.05$). Error bars represent ±*SEM* across 10 subjects. (d) To test the hypothesis that crowding is occurring selectively between holistic face representations and in an eccentricity-dependent manner, we fit individual subjects' difference scores (performance in the inverted minus upright face flanker conditions) with a second-order polynomial ($f(x) = (ax^2 + bx + c)$). If the null hypothesis, that the net crowding effect of upright flankers is not eccentricity-dependent, were true, the data should be better fit with a linear function. We used Akaike's information criterion (AIC) method for comparing the likelihood of the two models: second-order polynomial versus linear. The second-order function was more likely the correct model for the data (difference in AIC = 4.72, IR = 10.61; the second-order fit was 10 times more likely to be correct). This finding shows that upright face flankers selectively crowd an upright Mooney face more strongly than inverted face flankers, and do so only in the range of eccentricities where crowding is expected to occur. This supports the conclusion that, in addition to within-face crowding, there is selective crowding between holistic representations of faces.

uncrowded and upright face flanker conditions was found at 3 deg ($t_{(9)} = -3.581$, $p = 0.006$), 6 deg ($t_{(9)} = -4.271$, $p = 0.002$), and 10 deg ($t_{(9)} = -5.749$, $p = 0.0001$), and between performance in the uncrowded and inverted face flanker conditions at 6 deg ($t_{(9)} = -2.567$, $p = 0.030$) and 10 deg ($t_{(9)} = -3.399$, $p = 0.008$). Compared to results obtained from Experiment 2, which used smaller parts of the face as flankers (at a center-to-center spacing of 1.44 deg), upright face flankers interfered with identification of the target face more than face parts at 10 deg ($t_{(9)} = 2.669$, $p = 0.026$), but there was no difference in the crowding effect of inverted face flankers and face parts at any eccentricity.

Figure 8 shows that upright Mooney face flankers were more effective at crowding recognition of an upright Mooney face than inverted flankers. Is this simply a generic interference resulting in an overall decrease in performance across all eccentricities? Or, is this specifically an effect of crowding? If the difference between upright and inverted face flankers is due to holistic crowding, then the impairment in performance should only be found within a range of eccentricities, beyond which accuracy in both flanker orientation conditions is expected to fall to chance levels. Such a pattern would appear as a hyperbolic-shaped function, with little to no difference in performance between upright and inverted flankers at 0 and 10 deg eccentricities, and a strong difference at intermediate eccentricities (Figure 8). To test this hypothesis we fit a second-order polynomial ($f(x) = (ax^2 + bx + c)$) to individual subjects' difference scores (performance in the inverted minus upright face flanker conditions) and compared the fit to the null hypothesis that the crowding effect of upright flankers is not eccentricity-dependent and therefore better fit with a linear function. We used Akaike's information criterion (AIC) method for comparing the likelihood of the two models: second-order polynomial versus linear. In this method of model comparison, a lower AIC indicates a better model fit (Motulsky & Christopoulos, 2003). The difference in AIC between the two models is computed, from which an information ratio (IR) is derived, reflecting the likelihood that one of the two models is correct. Our results establish that the second-order function was more likely the correct model for the data (difference in AIC = 4.72, IR = 10.61; the second-order fit was 10 times more likely to be correct) (Figure 8). This finding shows that upright face flankers selectively crowd an upright face more strongly than inverted face flankers, and that they do so only in the range of eccentricities where crowding is expected to occur. This supports the conclusion that, in addition to low-level crowding between face features, there is selective crowding between holistic representations of faces.

The selective crowding between upright Mooney faces is not explained simply by attributing it to the "similarity" of the target and flankers. Although crowding is modulated by similarity (Kooi et al., 1994), similarity in that context refers to the basic, low-level features of the target

and flankers. To confirm that a greater similarity between upright flanker faces and upright target faces is not driving the differential crowding effects observed, we conducted further analyses of the data.

Although it has been shown that one cannot recover information about lighting direction of a Mooney face without first identifying the face (Kemelmacher-Shlizerman et al., 2008; McKone, 2004; Moore & Cavanagh, 1998), we repeated the analysis after controlling for direction of the light source. Stimuli used in Experiment 6 consisted of 8 target faces with a light source from the right and 12 target faces with a light source from the left, so to equate the number of target faces with a light source from the left and right we randomly removed 4 target faces with a leftward light source. The results were identical to the original analysis, revealing significant main effects of eccentricity ($F(3, 7) = 70.973$, $p = 0.001$, $\eta^2 = 0.968$) and flanker orientation ($F(1, 9) = 16.043$, $p = 0.023$, $\eta^2 = 0.721$).

To further rule out the possibility that upright face flankers were more similar to the upright target face than inverted face flankers, and consequently that low-level similarities may have been the source of the crowding effect observed, we conducted a pixel-level cross-correlational analysis of target and flanker faces. We computed the pixel-wise Pearson r value for each possible pair of target/ flanker faces, and resulting r values were converted to Fisher z scores for purposes of direct comparison. No difference was found between the correlation of upright flanker faces with target faces (mean z = 0.103, $SD = 0.18$) and the correlation of inverted flanker faces with target faces (mean z = 0.099, $SD = 0.17$) ($t(399) = -0.263$, $p = 0.793$). The correlations for both flanker orientations were significantly above zero (upright: $t(399) = 11.39$, $p = 0.0001$, inverted: $t(399) = 11.92$, $p = 0.0001$), illustrating that upright and inverted faces share some featural information (e.g., the background in all images tends to be dark). However, since there was no differential correlation for upright versus inverted flankers, we conclude that low-level features between upright and inverted Mooney face flankers such as pixel color or position, lighting direction, and background color are indistinguishable. Rather, the upright Mooney faces are only "similar" in that they share "faceness," and are perceived holistically.

Overall, these results replicate and extend the findings of Louie et al. (2007) by showing selective interference between holistic representations of Mooney faces that is eccentricity dependent, thus demonstrating that crowding can occur at a level beyond that of within-face crowding.

General discussion

The experiments reported here used Mooney faces— known to rely on holistic processing—to examine the

existence of crowding of high-level representations. The results demonstrate that orientation and gender of a Mooney face can be discriminated in the visual periphery and that this discrimination is significantly worse when the face is surrounded by flankers. The effect of crowding increased with eccentricity, increased as flanker spacing decreased, and was not observed when the faces were presented at the fovea. Critically, there was selectively more crowding when an upright Mooney face was flanked by other upright Mooney faces, but less so when flanked by inverted Mooney faces. These results extend those of Louie et al. (2007) by providing evidence that crowding can occur between holistic representations of faces, independent of low-level crowding of facial features within a face.

The detrimental effect of flankers seen here is the result of crowding and not ordinary masking or some other phenomenon. The results of each of the experiments above reflect the diagnostic criteria of crowding, including eccentricity and flanker spacing dependence and inner-outer asymmetry. Experiment 1 confirmed that discriminating the orientation of a Mooney face in the periphery, but not the fovea, was impaired by the presence of surrounding flankers. Experiment 2 employed a gender identification task to rule out the possibility that local orientation cues contributed to the results of the first experiment and again established an eccentricity-dependent effect of flankers. Experiment 3 measured gender identification of Mooney and grayscale faces as a function of face size to test the scaling factor required for equating foveal and peripheral performance. The scaling factor for Mooney faces was statistically similar to that of grayscale faces. Experiment 4 confirmed that orientation discrimination in the periphery (at 6 deg) was significantly affected by target-flanker spacing, meeting one of the signature diagnostic criteria used to distinguish crowding from ordinary masking (Levi et al., 2002; Pelli et al., 2004; Toet & Levi, 1992). Experiment 5 measured crowding as a function of a single flanker's spatial position, either on the inner or outer side of the face, and showed that an outer flanker interferes with orientation discrimination significantly more than an inner flanker, verifying flanker asymmetry and confirming that crowding and not lateral masking or surround suppression are responsible for the observed decrement in performance in the presence of flankers. Finally, Experiment 6 showed that gender identification of upright target faces was more impaired by upright flanker faces than inverted flanker faces, demonstrating that holistic representations of upright faces can selectively crowd each other. Together, these results demonstrate that Mooney faces can be processed in the periphery and that crowding both within and between Mooney faces exists at eccentric locations. Thus, in addition to lower-level featural representations, holistic representations are also subject to crowding.

To directly compare the effect of crowding between the different experiments we conducted a meta-analysis on the

individual difference scores obtained from each experiment as well as the average difference score from Experiments 1, 2, and 5 (outer flanker condition) (Figure 9). Difference scores were calculated by subtracting performance on crowded trials from performance on uncrowded trials at each eccentricity. Overall, difference scores were significantly positive across eccentricity ($F_{(3,141)}$ = 5.642, p = 0.001). A one-way ANOVA examining difference scores (collapsed across all eccentricity levels) between the three different crowding experiments revealed no significant difference based on experiment ($F_{(3,141)}$ = 0.949, p = 0.419). Comparisons between the average difference score and the null hypothesis (difference score = 0) at each level of eccentricity confirms that crowding significantly impacted performance at 3 deg ($t_{(37)}$ = 3.351, p = 0.002), 6 deg ($t_{(37)}$ = 6.282, p = 0.0001), and 10 deg ($t_{(37)}$ = 5.984, p = 0.0001)
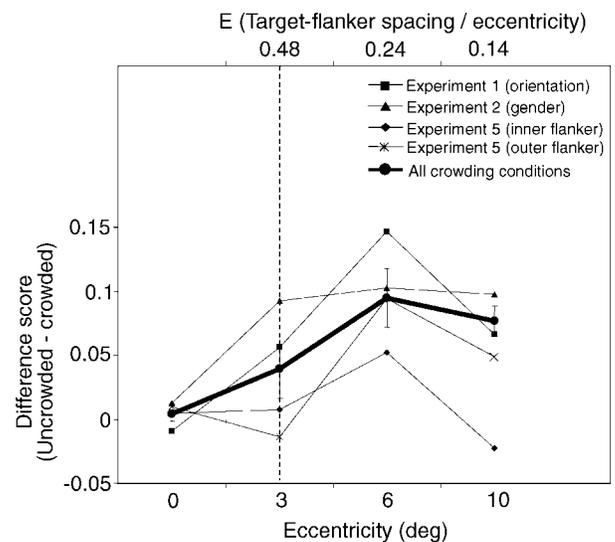

Figure 9. Meta-analysis to compare the crowding effect between Experiments 1, 2, and 5. Difference scores from each experiment were calculated by subtracting mean performance on crowded from uncrowded conditions. Scores were significantly positive across eccentricity for the four conditions combined ($t_{(111)}$ = 7.943, p = 0.001). A one-way ANOVA examining difference scores (collapsed across all eccentricity levels) between the three experiments (excluding the inner flanker condition of Experiment 5) revealed no significant difference between crowding conditions ($F_{(2,111)}$ = 2.298, p = 0.278). Comparisons between the mean difference score across experiments and the null hypothesis (difference score = 0) confirmed that crowding significantly impacted performance at 3 deg ($t_{(27)}$ = 3.062, p = 0.005), 6 deg ($t_{(27)}$ = 6.508, p = 0.0001), and 10 deg ($t_{(27)}$ = 4.815, p = 0.0001) eccentricity. Crowding was not observed at the fovea in any of the experiments. This analysis demonstrates that at the closest eccentricity where crowding was detected (3 deg), target-flanker spacing was close to 0.5E, verifying that performance across tasks was impacted by crowding-specific processes. Error bars represent ±*SEM* across 28 subjects.

eccentricity. This analysis verifies that performance was impacted by crowding-specific processes by establishing that the crowding effect was present when critical target-flanker spacing was less than half the target's eccentricity. Slight deviations from this critical spacing value between experiments may depend on stimulus characteristics and may also be important.

In a separate analysis, performance on the first ten novel target face trials was calculated across all subjects and Experiments 1, 2, and 5. The crowding effect remained intact and dependent on eccentricity, ruling out the possibility that perceptual learning or familiarity played a role in the crowding results.

The current models of spatial crowding range from low- to high-level explanations. One existing model proposes that the inability to identify a crowded target item in the periphery is the result of interference between low-level elementary features within the same receptive field (Flom, Heath, & Takahashi, 1963; Kooi et al., 1994) or excessive feature integration within an "integration field" (Pelli et al., 2004). Another explanation is that crowding is the result of a higher-level limited resolution of spatial attention (He, Cavanagh, & Intriligator, 1996; He et al., 1997; Intriligator & Cavanagh, 2001). It has also been suggested that crowding may facilitate the representation of groups of items when the ensemble is more informative than the individual object, perhaps by computing a "compulsory average" (Parkes et al., 2001). Ensemble coding has been found for low-level elementary features such as line and grating orientation, dot size, and has recently been extended to include higher-level face recognition (Ariely, 2001; Haberman & Whitney, 2007; Parkes et al., 2001). According to this model, higher-level crowding may facilitate the summary statistical representation of groups of faces. Whether or not each of these mechanisms exists in the visual system and contributes to crowding at a different level of processing remains to be fully understood, but our results suggest that multiple mechanisms and multiple stages of crowding should be examined.

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