Vision Research 105 (2014) 189–198

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Effects of face feature and contour crowding in facial expression adaptation

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ARTICLE INFO

Article history:
Received 1 February 2014
Received in revised form 8 October 2014
Available online 25 October 2014

Keywords:
Visual crowding
Visual adaptation
Object recognition
Feature integration
Holistic face perception
Facial expression judgment

ABSTRACT

Prolonged exposure to a visual stimulus, such as a happy face, biases the perception of subsequently presented neutral face toward sad perception, the known face adaptation. Face adaptation is affected by visibility or awareness of the adapting face. However, whether it is affected by discriminability of the adapting face is largely unknown. In the current study, we used crowding to manipulate discriminability of the adapting face and test its effect on face adaptation. Instead of presenting flanking faces near the target face, we shortened the distance between facial features (internal feature crowding), and reduced the size of face contour (external contour crowding), to introduce crowding. We are interested in whether internal feature crowding or external contour crowding is more effective in inducing crowding effect in our first experiment. We found that combining internal feature and external contour crowding, but not either of them alone, induced significant crowding effect. In Experiment 2, we went on further to investigate its effect on adaptation. We found that both internal feature crowding and external contour crowding reduced its facial expression aftereffect (FEA) significantly. However, we did not find a significant correlation between discriminability of the adapting face and its FEA. Interestingly, we found a significant correlation between discriminabilities of the adapting and test faces. Experiment 3 found that the reduced adaptation aftereffect in combined crowding by the external face contour and the internal facial features cannot be decomposed into the effects from the face contour and facial features linearly. It thus suggested a nonlinear integration between facial features and face contour in face adaptation.

1. Introduction

Prolonged exposure to one visual attribute (e.g., sadness of faces) biases the perception of subsequently presented visual stimuli toward the opposite attribute (e.g., happiness of faces). This phenomenon is known as visual adaptation. Visual adaptation is used to probe the short-term plasticity of the visual system. There are at least three consequences of visual adaptation: normalization (extreme stimuli become less extreme, and closer to the average/neutral point, e.g., after adapting to a sad face, sad test face becomes less sad), aftereffect (perception of the attributes of test stimuli shifts away from that of the adapter, e.g., neutral test face appears happy) and discriminability (sensitivity of test stimuli near the adapter increases, e.g., discriminability of sad test faces is increased). Sensitivity of test stimuli attributes similar to those of the adapter is increased by adaptation for both simple and complex stimuli, such as orientation (Clifford et al., 2001; Regan & Beverley, 1985), contrast (Abbonizio, Langley, & Clifford, 2002; Greenlee & Heitger, 1988), motion direction (Phinney, Bowd, & Patterson, 1997), speed (Bex, Metha, & Makous, 1999; Clifford & Wenderoth, 1999; Krekelberg, van Wezel, & Albright, 2006), gender (Yang et al., 2011), face viewpoint (Chen et al., 2010), and trustworthiness (Keefe et al., 2013). However, the cause of this increased sensitivity remains unclear. Specifically, this raises the question: what properties of object perception are changed because of adaptation?

Discriminability of adapting stimulus can be manipulated by multiple psychophysical techniques, such as crowding. Surrounding a stimulus by similar stimuli (flankers) reduces discriminability of the stimulus, the crowding effect. Adapting to a crowded stimulus does not reduce the adaptation aftereffect for simple features, such as oriented bars at high contrast (He, Cavanagh, & Intriligator, 1996; Rajimehr, Montaser-Kouhsari, & Afraz, 2003).

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http://dx.doi.org/10.1016/j.visres.2014.10.014
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More recent studies suggest, however, that reducing the discriminability of the adapting face by crowding with flanking faces (Louie, Bressler, & Whitney, 2007) reduces the aftereffect for complex stimuli (e.g., faces) at low contrast. Blake et al. (2006) resolved this controversy by showing that crowding does not reduce the aftereffect for simple features (e.g., orientation-dependent threshold-elevation aftereffect, TEAE) at high-contrast, but does so for simple features at low contrast, suggesting the existence of response saturation for adapting stimuli at high contrast levels.

Face crowding is used in discrimination tasks to see if subjects are able to identify the detailed information of a face, such as facial expression, given that they can detect the presence of the face. Visual crowding is an automatic but unwanted binding or grouping of flankers and target. It thus makes the target's details hard to identify. Face crowding can be induced by presenting similar faces nearby the target face (multiple faces) (Louie, Bressler, & Whitney, 2007), or by manipulating the distance among facial features (within the same face), which is internal feature crowding or self-crowding (Farzin, Rivera, & Whitney, 2009; Martelli, Majaj, & Pelli, 2005). Both can reduce the discriminability of facial expression of the crowded face. It has been shown that crowding the adapting face by face flankers can reduce the facial expression aftereffect (Xu et al., 2012). However, the effect of internal feature crowding or self-crowding, is relatively less studied. Furthermore, can external face contour crowding affect facial expression discriminability, as internal feature crowding does? Among all the facial features, the mouth is essential for facial expression judgment, especially for happy or sad emotion (Chen & Chen, 2010; Gosselin & Schyns, 2001). Presenting facial features (e.g., nose) or face contour near the mouth will likely induce crowding effect, and we would expect to see its effect on facial expression adaptation.

Therefore, three questions remain: (1) Which form of crowding, internal feature crowing or external contour crowding, is more effective in reducing discriminability of facial expression? (2) How are the adaptation properties (e.g., aftereffect and sensitivity) related to the discriminability of the adapting face? (3) Can the combined crowding effect by both external face contour and internal facial feature be decomposed into the effects from the face contour and facial features linearly?

In the present study, we used visual crowding to manipulate the facial expression discriminability (FED) to address the above questions. We varied the distance of facial features and/or face contour to the mouth to generate a series of faces, and examined its effect on facial expression judgment of these faces. We then investigated the facial expression aftereffect (FEA) by adapting to these faces.

2. Experiment 1

Our first experiment investigated the effect of crowding induced by different manipulations of surroundings to the mouth – facial features, face contour, or hair. Effect of crowding is related to the proximity and similarity between the target and the flankers such that the more similar the target and flankers are, the larger the crowding effect is (e.g., presenting flanking faces near the target face). This suggests strong grouping between the target face and flanking faces. However, few studies have explored grouping among distinct low-level features (such as different facial features) to form a coherent high-level perception (such as a face image), with the exception of within-face or facial feature crowding (Farzin, Rivera, & Whitney, 2009; Martelli, Majaj, & Pelli, 2005). Martelli, Majaj, and Pelli (2005) found that self-crowding of facial features (internal feature crowding) could induce crowding effects by reducing the distance among face parts (independent of size), just like crowding words by reducing the distance between letters. In comparison, crowding induced by face contour has been largely overlooked, because most facial information (e.g., identity and emotion) is sufficiently contained in facial features. We aim to investigate whether external crowding (induced by face contour) is effective in reducing the discriminability of facial emotion in Experiment 1.

In this experiment, to induce stronger grouping, we introduce a new form of crowding to generate a new set of face stimuli by reducing the size of the face contour, in addition to the internal feature crowding (Farzin, Rivera, & Whitney, 2009; Martelli, Majaj, & Pelli, 2005). These faces are labeled as *external contour and internal feature crowded faces*. In comparison, the *internal feature crowded faces* are generated by reducing the distances of other facial features (nose, eyes, and eye brows), but keeping the size of the facial features and face contour the same as the uncrowded expanded caricature face (similar to the feature crowding studies by Martelli, Majaj, & Pelli, 2005).

2.1. Methods

2.1.1. Observers

Ten subjects, with normal or corrected-to-normal vision, participated in Experiments 1. Two of the subjects were experimenters (PL and AC), and the others were naïve to the purpose of the study. All subjects were allowed sufficient practice on facial expression judgment of caricature faces before data collection for each condition. All subjects were given written consent before testing. This study was approved by the Ethics Committee of the Division of Psychology, and the Internal Review Board (IRB) at Nanyang Technological University, Singapore, in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving human subjects.

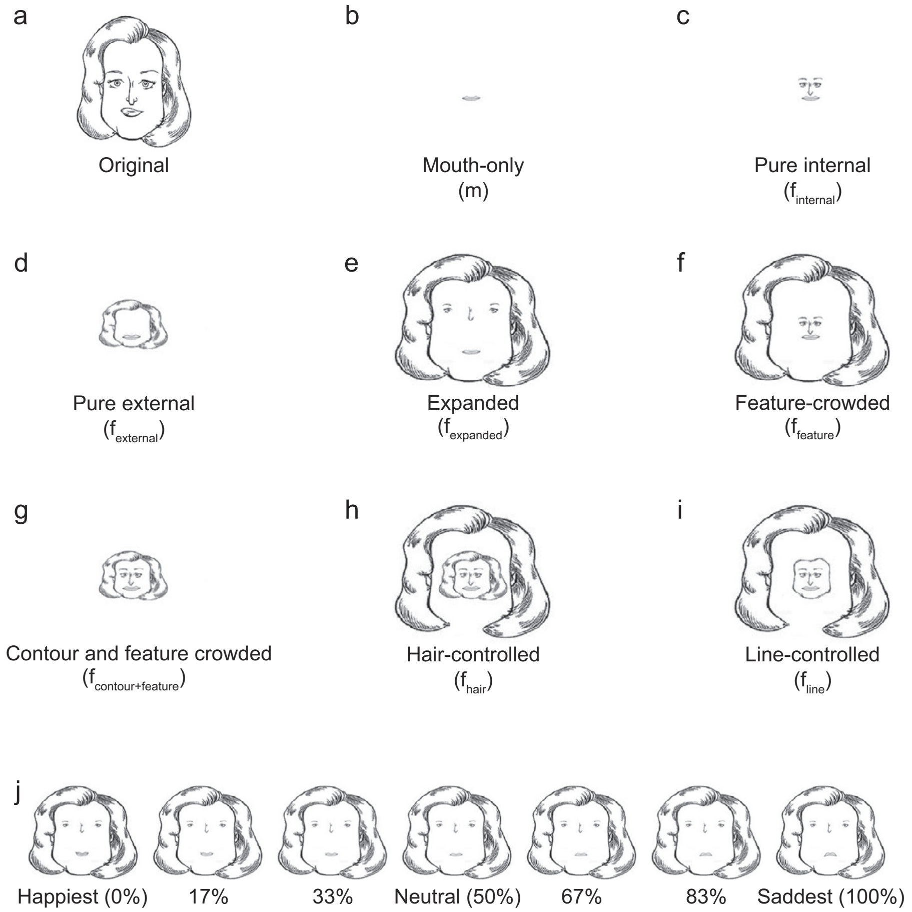
2.1.2. Apparatus

Stimuli were presented on a 17-in. Samsung monitor (SyncMaster 793MB) with a refresh rate of 85 Hz and a spatial resolution of 1024 × 768. The monitor was controlled by an iMac Intel Core i3 computer. Subjects were seated in a dimly lit room and viewed the stimuli from a distance of 57 cm. Each pixel on the screen subtended a visual angle of 0.032° at this distance. A chin rest was used to stabilize the subject's head position. A Minolta LS-110 photometer measured the luminance values. All experiments were run in Matlab (V2010a for Mac) with Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

2.1.3. Stimuli

Caricature faces were used in the experiments. We selected a caricature face ($f_{\mathrm{originial}}$, Fig. 1a) from the Lar DeSouza database (http://www.lartist.com/celebrity.htm) and then modified facial features, especially the mouth shape to make the curvature more salient and flexible for facial expression manipulation. We generated seven caricature face images for the experiments by modifying the facial features and face contour of the original caricature face using Adobe Photoshop CS5 (Adobe Systems Incorporated, California, U.S.A.). All faces had the same facial features (mouth, nose, eyes and eye brows), sized $0.77° \times 0.26°$, $0.26° \times 0.57°$, $0.42° \times 0.38°$, and $0.42° \times 0.42°$, respectively. We extracted the facial features to create the mouth-only image (m, Fig. 1b), pure internal facial-feature-crowded face (f_{internal}, Fig. 1c), and pure external face-contour-crowded face (f_{external}, Fig. 1d).

During the task, we required the subjects to maintain fixation on a cross, and the faces were presented in the periphery (center-to-center distance between the face and fixation point was 3.45° horizontally and 0.29° vertically). Therefore, to ensure a clear view of the facial expression of the faces in the periphery, we enlarged the distances between facial features of the original



Original

Mouth-only
(m)

Pure internal
$(f_{internal})$

Pure external
$(f_{external})$

Expanded
$(f_{expanded})$

Feature-crowded
$(f_{feature})$

Contour and feature crowded
$(f_{contour+feature})$

Hair-controlled
(f_{hair})

Line-controlled
(f_{line})

Happiest (0%) 17% 33% Neutral (50%) 67% 83% Saddest (100%)

Fig. 1. Face stimuli. (a) Original face from the website ($f_{original}$). (b) Mouth-only image (m). (c) Pure internal facial-feature-crowded face ($f_{internal}$). (d) Pure external face-contour-crowded face ($f_{external}$). (e) Expanded face ($f_{expanded}$), in which the distance among facial features increased as compared to the original face. (f) Internal feature-crowded face ($f_{feature}$) with distance between features reduced from the expanded face but with facial features of the same size as in the expanded face. (g) External contour and internal feature crowded face ($f_{contour+feature}$) with a shrunken face contour in addition to facial features of reduced distance. (h) Hair-controlled face (f_{hair}), a contour-crowded face with an additional hair part from the expanded face. (i) Line-controlled face (f_{line}), similar to the hair-controlled face with the exception that the inner hair was removed but the contour line remained. (j) Example of expanded faces as test stimuli, varying from happiest to saddest expression as indicated by the percentage of sadness. The mouth curvature and the corresponding percentage of sadness of these faces are 0.033 (0%), 0.025 (17%), 0.013 (33%), 0.010 (50%), −0.013 (67%), −0.025 (83%), and −0.033 (100%).

caricature face but maintained face contour size to generate an uncrowded expanded face ($f_{expanded}$, Fig. 1e). The size of the entire face was 6.19° × 5.26°. It was displayed slightly higher and to the right of the fixation point, with a center-to-center distance of 3.45° horizontally and 0.29° vertically, with a small gap (0.13°) between the edge of the fixation point and the nearest edge of the face contour. The center-to-center distances from the mouth to the face contour, nose, left eye, and right eye were 1.28°, 1.53°, 2.01°, and 1.96°, respectively. We then generated the internal feature-crowded face by reducing the distance among facial features ($f_{feature}$, Fig. 1f). The size of all face parts (contour, mouth, nose and eyes) remained the same. The new center-to-center distance from the mouth to the nose, left eye, and right eye was 0.26° (17%), 0.35° (18%), and 0.22° (11%), respectively (values in parentheses are the percentages of new distances compared to the corresponding distances in the uncrowded expanded face). External contour and internal feature crowding ($f_{contour+feature}$, Fig. 1g) was introduced in this study by reducing the face contour size (including the hair) in addition to shortening the distance of facial features, as with the internal feature crowded faces. The face contour size was 2.74° × 1.98°, about 17% of the expanded face.

To examine the contribution of the complete curly hair to aftereffect, we created a sixth face, i.e., the hair-controlled face (f_{hair}, Fig. 1h) in which a large hair part surrounded the external contour-crowded face. To further investigate the cause of the contour crowding, we created a seventh face, i.e., the line-controlled face (f_{line}, Fig. 1i) in which there is a thin line surrounding the mouth and other facial features, instead of the complete curly hair contour.

The mouth was always presented at the same location on the computer screen for all seven types of faces (Fig. 1c–i) and the mouth-only image (Fig. 1b).

Each of the eight face/mouth stimulus types (Fig. 1b–i) consisted of seven face/mouth images, with facial expressions varying from happy to sad. To construct the stimuli, we first created three basic images with happy (proportion of sadness = 0), neutral (proportion of sadness = 0.5) and sad (proportion of sadness = 1.0) expressions by modifying the mouth curvature in Adobe Photoshop. Using MorphMan 4.0 (STOIK Imaging, Moscow, Russia), we then morphed the sad face/mouth with the neutral face/mouth to generate two images with the proportion of sadness at 0.67 and 0.83, and morphed the happy face/mouth with the neutral face/mouth to generate two images with the proportion of sadness at 0.17 and 0.33. A sample of these faces is shown in Fig. 1j. We also measured mouth curvature for each of the seven faces by identifying the large circle that best matched the mouth shape. The reciprocal of the circle radius was defined as the curvature of the corresponding mouth. A positive value corresponded to a “happy” mouth and a negative value indicated a “sad” one. Mouth-curvature values for the seven faces were 0.033 (0%), 0.025 (17%), 0.013 (33%), 0.010 (50%), −0.013 (67%), −0.025 (83%), −0.033 (100%). Values in parentheses are the sadness proportion of the faces.

The mouth area in the faces had an average luminance of 53.80 cd/m^2. A black (1.04 cd/m^2) fixation cross was always presented at the center of the white (80.16 cd/m^2) screen. It consisted of two line segments, each 0.447° in length and 0.064° in width.

2.1.4. Procedure

In this experiment, subjects judged facial expression (happy or sad) of the caricature face/mouth images. The test stimulus was from the face sets of “f_{expanded}”, “f_{feature}”, “$f_{\text{contour+feature}}$”, “$f_{\text{hair}}$”, “$f_{\text{line}}$”, “$f_{\text{internal}}$”, and “$f_{\text{external}}$” faces and the mouth ($m$), resulting in eight baseline conditions: 0–m, 0–f_{internal}, 0–f_{external}, 0–f_{expanded}, 0–f_{feature}, 0–$f_{\text{contour+feature}}$, 0–$f_{\text{hair}}$, and 0–$f_{\text{line}}$. Zero (0) corresponded to the absence of the adapter (no adaptation) in Experiment 1. The mouths of the test stimuli were at the same location on the computer screen. The eight conditions were presented in separate blocks, with two blocks per condition, and sixteen blocks in total. Each block had ten repetitions of each test stimulus. In the two blocks for each condition, each test stimulus was repeated 20 times. There was a 10-min break between two consecutive blocks. Subjects first practiced on the 0–f_{expanded} condition to become familiar with the experiment. Before data collection for any condition, subjects were asked to practice the task for a few trials until they indicated that they were ready for the experiment (usually 3–5 trials).

Subjects started the experiment in each block by fixating on the fixation cross and pressing the space bar. After 506 ms, a test stimulus from the “f_{expanded}” face set (for the “0–f_{expanded}” condition) was presented for 59 ms. A 59 ms beep (900 Hz) was then played to remind subjects to report the facial expression of the test stimulus. Subjects had to make a two-alternative forced choice (2-AFC) judgment by pressing either the “A” or “S” key on the keyboard to indicate whether the test face was happy or sad, respectively. A 1 s blank inter-trial interval was then presented before moving on to the next trial. Subjects were asked to keep their eyes on the central fixation cross. No feedback was given on their responses at any time.

2.1.5. Data analysis

Data for each condition were sorted into the fraction of “sad” (concave) responses to each test stimulus. The test stimuli were parameterized according to the proportion of sadness, with the happiest face defined as 0 and the saddest face as 1.0. The fraction of sad responses was then plotted against the proportion of sadness of the test stimulus. The resulting psychometric curve was fitted with a sigmoidal function in the form of $f(x) = 1/[1 + e^{-a(x-b)}]$, where b is the test-stimulus parameter corresponding to 50% of the psychometric function [point of subjective equality (PSE)] and $a/4$ is the slope of the function at the PSE. We used a two-tailed paired t-test to compare subjects’ PSEs or the slopes for different conditions in the experiment. These analyses were performed in Matlab. Other data analyses (e.g., analysis of variance (ANOVA) and correlation) were performed in SPSS. Each subject went through all conditions in this experiment and the following experiments (within-subject design). Therefore all tests (t tests and ANOVA) are within-group tests.

2.2. Results: Experiment 1

Results from a naïve subject judging caricature facial expressions under various conditions are shown in Fig. 2a and b. The fraction of sad responses was plotted as a function of the percentage of sadness in the test faces. In Fig. 2a, surrounding the mouth with facial features (0–f_{internal}) or face contour (0–f_{external}) did not reduce the mouth’s discriminability (0–m) – reflected by the slope of the psychometric curves. In Fig. 2b, presenting facial feature near the mouth within its critical distance (f_{feature}) did not reduce the facial expression discriminability significantly, compared to the expanded face (f_{expanded}) ($p = 0.18$). However, presenting both facial features and face contour, hair, or a thin line within the critical distance of the mouth ($f_{\text{contour+feature}}$, f_{hair}, and f_{line}) reduced the discriminability of facial expression significantly (p’s = 0.016, 0.020, and 0.023 respectively).

We expected a systematic and significant slope reduction in crowded conditions compared with uncrowded conditions (Xu et al., 2012). Results from ten subjects are summarized in Fig. 2c. The mean slope ± SEM for each condition is shown. The slopes for all eight conditions (0–m, 0–f_{internal}, 0–f_{external}, 0–f_{expanded}, 0–f_{feature}, 0–$f_{\text{contour+feature}}$, 0–$f_{\text{hair}}$, and 0–$f_{\text{line}}$) were significantly different from zero (chance performance) (t tests, $p < 0.05$). The slopes were similar for 0–m, 0–f_{internal}, and 0–f_{external} (Fig. 1b–d) with the presence of facial features or contour near the mouth in Fig. 2c. But the slope decreased from 0–f_{expanded} to 0–f_{line} (Fig. 1e–i). Interestingly, the three faces (0–$f_{\text{contour+feature}}$, 0–$f_{\text{hair}}$, and 0–$f_{\text{line}}$, Fig. 1g–i) with similar distances from facial features and face contour or line closest to the mouth had the lowest and most similar slopes ($p = 1.0$, ANOVA), and significantly reduced from the uncrowded expanded face (0–f_{expanded}, p’s = 0.016, 0.02, and 0.023, respectively, paired t-tests). We think that may be because we presented the flanking facial feature and contour/line within the critical distance from the fixation point to the target mouth in these three faces. Crowding the mouth with facial features (f_{feature}) did not reduce its discriminability significantly, compared to uncrowded expanded face (f_{expanded}) ($p = 0.18$, paired t test). But adding face contour to feature crowding had a significant effect ($f_{\text{contour+feature}}$, $p = 0.016$). As the face stimuli were presented to the right of the fixation point, visual stimuli presented at the left of the mouth (mouth is considered as the main target for facial expression judgment) is on the radial line from fixation point, which is suggested to be more effective in crowding than on the tangent line, the radial–tangential anisotropy (Pelli et al., 2007; Petrov & Popple, 2007; Toet & Levi, 1992). This anisotropy may be a possible reason for the above finding.

3. Experiment 2

Our second experiment investigated whether crowding affects the facial expression aftereffect. Similar to crowding, adaptation also occurs at multiple levels (e.g., tilt aftereffect, MAE, and face aftereffect). To probe multiple-level processing along the cortical hierarchy, cross-level adaptation has been used to show that adapting to a simple curve or mouth alone could bias the judgment of facial expressions of cartoon and real faces (Xu et al., 2008), which suggests a local component, curvature of the mouth, in face adaptation. A recent study (Xu et al., 2012) found that crowding the adapting curve with flanking curves reduces the curvature aftereffect more than the facial expression aftereffect, and vice versa for crowding the adapting face with flanking faces. This finding suggests that although information can be transferred across multiple levels, the effect of crowding on adaptation is more or less specific to its own level of processing. However, this study crowded target face with flanking faces. It thus leaves the question whether and how self crowding, e.g., internal feature crowding or external contour crowding has the same effect on adaptation. Experiment 1 crowded the mouth with facial feature and contour and found a significant crowding effect in such faces ($f_{\text{contour+feature}}$, f_{hair}, and f_{line}). In Experiment 2, we hypothesize that the crowding the adapter will reduce its facial expression aftereffects.

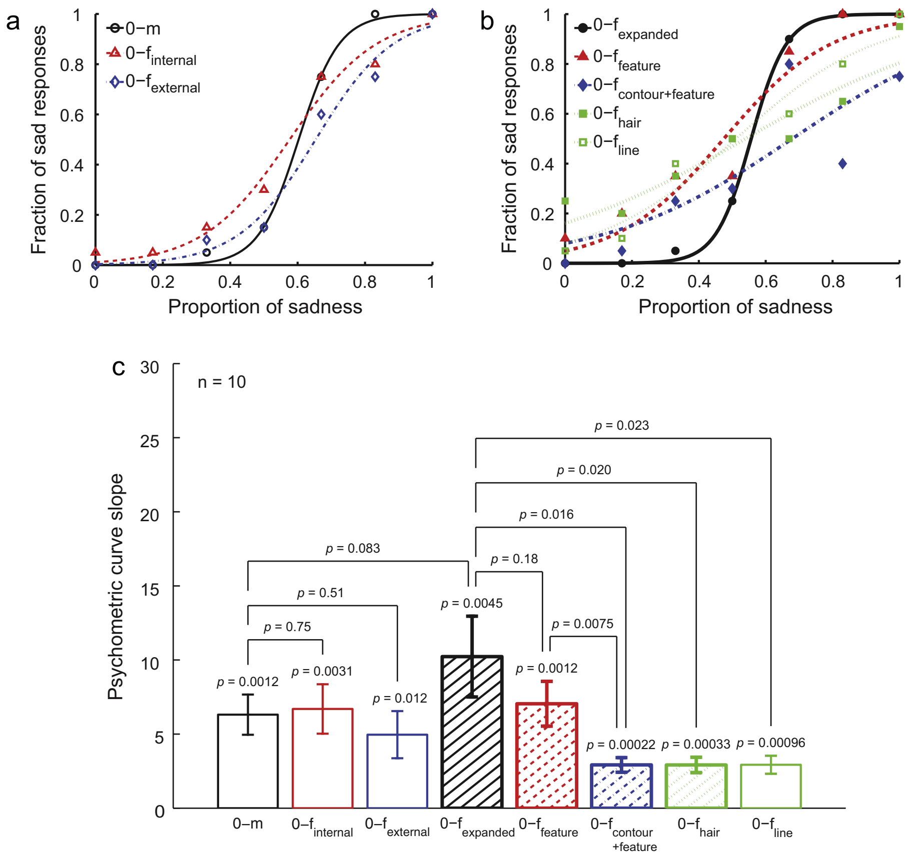


Fig. 2. Effect of crowding on facial expression judgment. (a) Psychometric functions from a naïve subject (LZ). 0–m, judgments of mouth-only images (black solid curve, open circle); 0–f_{internal}, facial expression judgments of pure internal feature-crowded faces (red dashed curve, open triangle); 0–f_{external}, facial expression judgments of pure external contour-crowded faces (blue dash-dotted curve, open diamond). (b) Psychometric functions from the same naïve subject (LZ). 0–f_{expanded}, facial expression judgments of expanded faces (black solid curve, filled circle); 0–f_{feature}, facial expression judgments of feature-crowded faces (red dashed curve, filled triangle); 0–$f_{\text{contour+feature}}$, facial expression judgments of contour and feature crowded faces (blue dash-dotted curve, filled diamond); 0–f_{hair}, facial expression judgments of hair-controlled faces (green dotted curve, filled square); 0–f_{line}, facial expression judgments of line-controlled faces (green dotted curve, open square). (c) Summary of data for all ten subjects under the eight conditions. For each condition, the average slope of the psychometric curve at the point of subjective equality (PSE) location (i.e., discriminability) was plotted. Error bars represent standard error of the mean (SEM, lengths equal 2 SEMs). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1. Methods

3.1.1. Observers

The same ten subjects from Experiment 1, with normal or corrected-to-normal vision, participated in Experiment 2. All subjects were allowed sufficient practice on facial expression judgment of caricature faces before data collection for each condition. All subjects were given written consent before the experiment.

3.1.2. Apparatus and stimuli

The apparatus was the same as in Experiment 1. The caricature faces with different forms of crowding in Experiment 1 were used as adapting stimuli for Experiment 2. The adapting faces were the happiest faces (with 0% proportion of the sad face) from the face morphs. To ensure the discriminability of the test faces, test stimulus was always from the set of uncrowded expanded face (f_{expanded}) that ranged between the full happy and sad expression (of the same person) at mouth-curvature values for the seven test faces: 0.033 (0%), 0.025 (17%), 0.013 (33%), 0.010 (50%), −0.013 (67%), −0.025 (83%), −0.033 (100%). Values in parentheses are the sadness proportion of the faces, with a total of seven possible morph values from the f_{expanded} face set. The facial expression of the test face was randomly selected from the face set and presented in each trial. The mouth was always presented at the same location on the computer screen for all adapting and test faces, and the mouth-only image.

3.1.3. Procedure

This experiment investigated the effect of discriminability of the adapting face/mouth on facial expression aftereffect (FEA). There were a total of nine conditions in this experiment, including the baseline condition (0–f_{expanded}). The nine conditions (0–f_{expanded}, m–f_{expanded}, f_{internal}–f_{expanded}, f_{external}–f_{expanded}, f_{expanded}–f_{expanded}, f_{feature}–f_{expanded}, $f_{\text{contour+feature}}$–$f_{\text{expanded}}$, f_{hair}–f_{expanded}, and f_{line}–f_{expanded}) were tested in separate blocks, with two blocks per condition as in Experiment 1. The block order was randomly selected for each subject.

Subjects started the experiment by focusing on the fixation cross and pressing the space bar in each block session. After 506 ms, the adapting stimulus (m, f_{internal}, f_{external}, f_{expanded}, f_{feature}, $f_{\text{contour+feature}}$, f_{hair}, or f_{line}) appeared for 4 s (Fig. 3 for trial sequence). Following a 506 ms inter-stimulus interval (ISI), a test stimulus randomly selected from the "f_{expanded}" face set was shown for 59 ms. This short test stimulus duration was selected to enhance aftereffects (Wolfe, 1984). The mouths of the adapting and test faces had the same position on the screen. After that, a 59 ms beep (900 Hz) was played to remind subjects to report the facial expression of the test stimulus. Subjects had to make a 2-AFC judgment by pressing the "A" or "S" key to indicate whether the test face

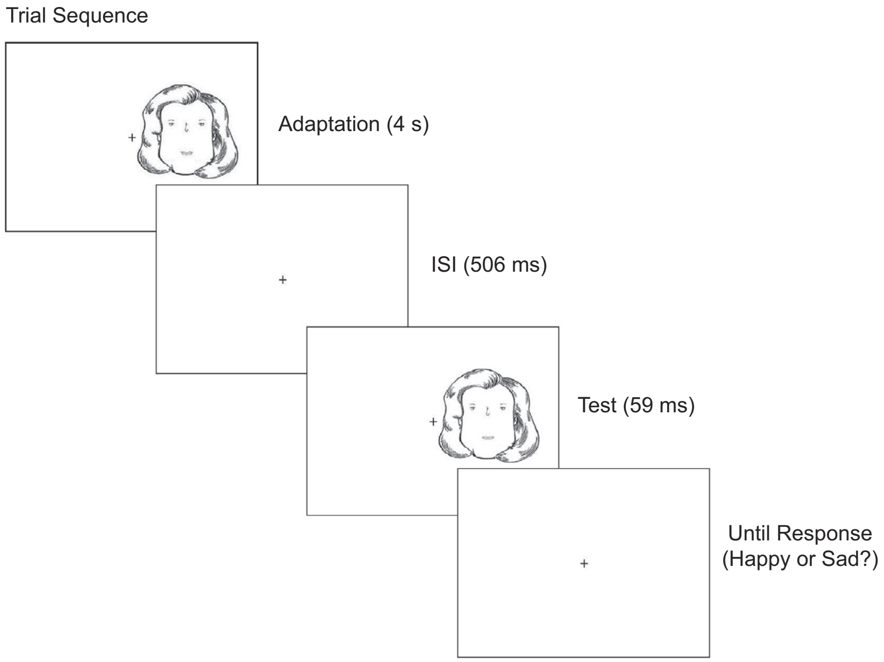


Fig. 3. Trial sequence for the f_{expanded}–f_{expanded} condition in Experiment 2. Subjects fixated on the central cross and pressed the space bar to initiate a trial block. After 506 ms, the adapting face appeared for 4 s. After a 506 ms ISI, a test face appeared for 59 ms. The mouth of the test face was at the same screen location as the mouth of the adapting face. A beep was then played to remind subjects to press the "A" or "S" key to report a happy or sad expression of the test face. In the actual experiments, the fixation cross was always at the screen center.

was happy or sad. A 1 s blank inter-trial interval was then presented before the next trial started. For baseline blocks without adaptation, no adapting stimulus was shown, and the test stimulus was from the "f_{expanded}" face set as in the baseline condition in Experiment 1 (0–f_{expanded}). Subjects were asked to maintain eye fixation on the central fixation cross. No feedback was given on their responses at any time.

3.1.4. Data analysis

Similar to Experiment 1, we fit the data with a sigmoidal function and obtained both PSE and slope for each psychometric curve for the baseline condition and the eight adaptation conditions. Aftereffect was measured as the difference between the PSE of an adaptation condition and the PSE of the corresponding baseline condition. We used the convention that repulsive aftereffects were negative. We used two-tailed paired *t* tests and analysis of variance (ANOVA) to compare subjects' PSEs or the slopes for different conditions in Experiment 2. We used Pearson correlation to examine the relationship between the curve slope in corresponding baseline conditions (discriminability of the adapting face) in Experiment 1 and the aftereffect magnitude (FEA) or the curve slope (discriminability of test faces, FED) in adaptation conditions in Experiment 2. These analyses were performed in Matlab or SPSS.

3.2. Results: Experiment 2

We investigated whether discriminability of the adapting stimuli influenced facial expression adaptation. We adapted subjects to one of the faces/mouth in Fig. 1b–i, and tested their performance on facial expression judgment of the expanded faces (f_{expanded}, Fig. 1e). First, if FEA depended on the discriminability of the adapting stimulus, we expected to find a reduction of FEA in crowded conditions.

FEA is measured by the shift of the point of subjective equality (PSE) in adaptation conditions from its baseline. Conventionally, a negative aftereffect indicates that the aftereffect is repulsive. A summary of the results from all ten subjects is shown in Fig. 4a. The mean aftereffect ± SEM for each adaptation condition is presented. The aftereffects for three of the adaptation conditions (m–f_{expanded}, f_{expanded}–f_{expanded}, and f_{feature}–f_{expanded}) were significantly different from baseline ($p < 0.05$, paired *t* tests) and one condition (f_{external}–f_{expanded}) was marginally significant ($p = 0.066$). Aftereffects for the remaining conditions (f_{internal}–f_{expanded}, $f_{\text{contour+feature}}$–$f_{\text{expanded}}$, f_{hair}–f_{expanded}, and f_{line}–f_{expanded}) were not significant.

As expected, for the three crowded face adaptation conditions ($f_{\text{contour+feature}}$–$f_{\text{expanded}}$, f_{hair}–f_{expanded}, and f_{line}–f_{expanded}), we found a significant reduction in FEA (p's = 0.0023, 0.00055, and 0.0039, respectively) from the uncrowded face adaptation condition (f_{expanded}–f_{expanded}). Interestingly, although pure internal feature crowded face (f_{internal}–f_{expanded}) and pure external contour crowded face (f_{external}–f_{expanded}) did not have significant crowding effects and thus subjects could clearly judge its facial expression, their FEAs were not significant either (p's = 0.26 and 0.066 respectively). Given that both are incomplete faces, it may suggest that presenting facial features or face contour near the mouth reduces the local component (mouth) adaptation in FEA significantly, compared to the uncrowded local adaptation condition (m–f_{expanded}). Likewise, internal feature crowded face (f_{feature}–f_{expanded}) generated a significantly smaller but significant FEA compared to uncrowded expanded face (f_{expanded}–f_{expanded}) adaptation ($p = 0.015$). The difference between internal feature crowded face (f_{feature}) and pure internal crowded face (f_{internal}) is that the former has the hair that is the same as the test faces (f_{expanded}), indicating the importance of background similarity in face adaptation (Wu et al., 2009).

We then examined whether FEA is correlated with the adapting face discriminability. Fig. 4b shows the correlation between the adapting face discriminability and FEA. Contrary to expectation, we did not find a significant correlation ($r = -0.026$, $p = 0.82$, $df = 78$) between the adapting face discriminability (measured by the slope of the psychometric curve at the PSE) and its FEA (measured by the PSE shift from the baseline condition).

Then what is correlated with the discriminability of the adapters in adaptation? We went on further to examine the relation between discriminabilities of the adapter and test faces. Fig. 4c shows the

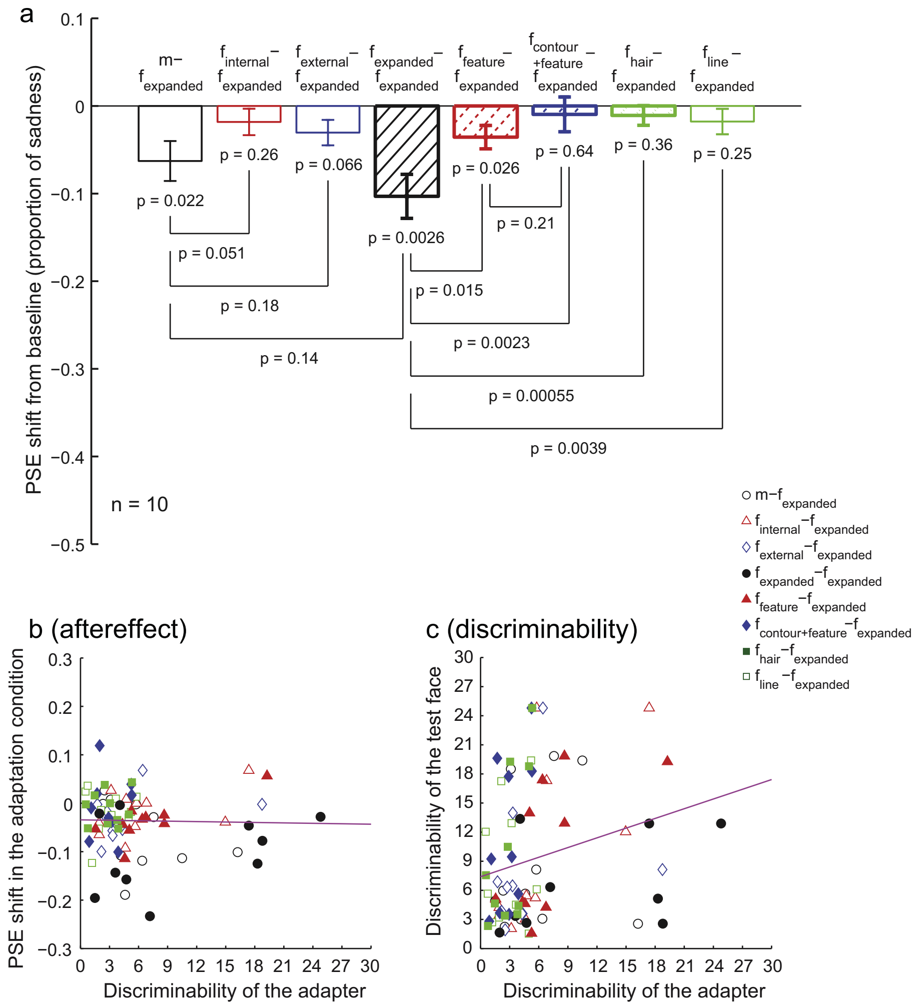


Fig. 4. Correlation between facial expression aftereffect and discriminability of the adapting stimulus (Experiment 2). (a) Summary of data from ten subjects for all conditions. FEA was measured as the average PSE shift of an adaptation condition from the baseline condition. Error bars represent ± SEM (lengths equal 2 SEMs). The *p*-value shown for each comparison was calculated using two-tailed paired *t* tests. (b) Correlation between FEA and adapting face/mouth discriminability was $r(78) = -0.026$, $p = 0.82$. Black open circles, red open triangles, and blue open diamonds represent $m\text{–}f_{\text{expanded}}$, $f_{\text{internal}}\text{–}f_{\text{expanded}}$, and $f_{\text{external}}\text{–}f_{\text{expanded}}$ conditions, respectively. Black filled circles, red filled triangles, blue filled diamonds, green filled squares, and green open squares represent $f_{\text{expanded}}\text{–}f_{\text{expanded}}$, $f_{\text{feature}}\text{–}f_{\text{expanded}}$, $f_{\text{contour+feature}}\text{–}f_{\text{expanded}}$, $f_{\text{hair}}\text{–}f_{\text{expanded}}$, and $f_{\text{line}}\text{–}f_{\text{expanded}}$ conditions, respectively. Discriminability was measured as the slope of the psychometric curve. (c) Correlation between adapting and test stimuli discriminability was $r(78) = 0.24$, $p = 0.032$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

correlation between discriminability of the adapter and discriminability of the test faces, measured by the slopes of their psychometric curves. The colors and conditions are the same as those in Fig. 4b, except the *y*-axis is the facial expression discriminability of the adapting face (slope). Interestingly, we found a significant positive correlation ($r = 0.24$, $p = 0.032$, $df = 78$) between the discriminabilities of the adapting and the test stimuli. Since discriminability is an indicator of sensitivity, the current result suggests that sensitivities to the adapting and test stimuli were correlated – that is, the more discriminable the adapting face is, the more discriminable the test face will be after adapting to this face. Previous studies suggested that adaptation improved sensitivity (or discriminability) of the test faces that are similar to the adapting face (Chen et al., 2010; Keefe et al., 2013; Yang et al., 2011). Our current findings suggest that the improved sensitivity of the test stimuli may be related to the improved sensitivity of the adapter during adaptation.

4. Experiment 3

The above second experiment found a reduction in FEA for adapting to the contour and feature crowded face ($f_{\text{contour+feature}}$, Fig. 1g) and testing on expanded faces (f_{expanded}, Fig. 1e). However, the contour and feature crowded face differed from expanded faces on both facial feature distance and face contour. Thus, to investigate the effects of face contour and the facial feature distance separately, we designed the third study by testing facial expression judgment on internal feature crowded faces (f_{feature}). There were three adapters: expanded (f_{expanded}), external contour and internal feature crowded ($f_{\text{contour+feature}}$), and internal feature crowded (f_{feature}) faces. The first adapting face (f_{expanded}) differed from the test face (f_{feature}) on facial feature distance; and the second adapting face ($f_{\text{contour+feature}}$) differed from the test face (f_{feature}) on face contour size. We therefore are able to separately evaluate the effects of facial feature distance and face contour size on FEA. If face contour plays an important role in adaptation, we would expect the contour and feature crowding will reduce FEA significantly.

4.1. Methods

4.1.1. Observers

A total of five subjects participated in Experiment 3 (including two, subject AC and LZ, from Experiment 1 and 2). All subjects were allowed sufficient practice on facial expression judgment of

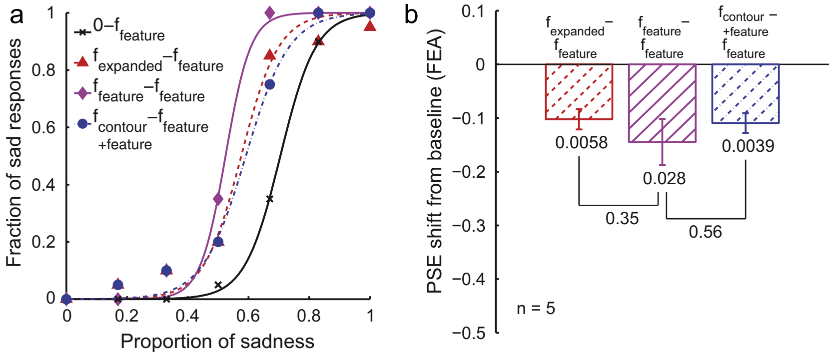


Fig. 5. Effect of crowding on FEA tested on feature-crowded faces (Experiment 3). (a) Psychometric functions from a naïve subject (RK). 0–$f_{feature}$, no adaptation baseline (blue solid curve, cross); $f_{expanded}$–$f_{feature}$, adaptation to the expanded face (red dashed curve, filled triangle); $f_{feature}$–$f_{feature}$, adaptation to the feature-crowded face (magenta solid curve, filled diamond); $f_{contour+feature}$–$f_{feature}$, adaptation to the contour and feature crowded face (blue dash-dotted curve, filled circle). Test stimuli in all four conditions were from the feature-crowded face set ($f_{feature}$). (b) Summary of data from five subjects under the above conditions. For each condition, the average PSE shift of an adaptation condition from the baseline condition (i.e., FEA) was plotted. Error bars represent ± SEM (lengths equal 2 SEMs). The *p* value shown for each comparison was calculated using two-tailed paired *t* test. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

caricature faces before data collection for each condition. All subjects were provided written consent before the experiment.

4.1.2. Apparatus, stimuli and procedure

The apparatus, stimuli, and procedure were the same as in Experiment 2, except the test stimuli were feature crowded faces ($f_{feature}$). The adapting stimuli were the feature crowded ($f_{feature}$), contour and feature crowded ($f_{contour+feature}$) or uncrowded expanded faces ($f_{expanded}$). Experiment 3 consisted of four conditions in total: $f_{expanded}$–$f_{feature}$, $f_{feature}$–$f_{feature}$, $f_{contour+feature}$–$f_{feature}$, and 0–$f_{feature}$ (baseline).

4.2. Results: Experiment 3

In this experiment, we swapped the adapter and test stimuli in Experiment 2, and tested facial expression judgments of feature crowded faces ($f_{feature}$), to separately evaluate the effects of facial feature distance and face contour size on FEA. We compared facial expression aftereffect generated by adapting to the expanded face ($f_{expanded}$–$f_{feature}$) or the contour and feature crowded face ($f_{contour+feature}$–$f_{feature}$) with the aftereffect generated by adapting to the feature-crowded face ($f_{feature}$–$f_{feature}$). The comparison between $f_{expanded}$–$f_{feature}$ and $f_{feature}$–$f_{feature}$ conditions indicates the effect of feature crowding on adaptation alone. Interestingly, this effect is not significant ($p = 0.35$). The comparison between $f_{contour+feature}$–$f_{feature}$ and $f_{feature}$–$f_{feature}$ conditions indicates the effect of contour crowding alone. Surprisingly, this effect is not significant either ($p = 0.56$). Overall, we found that all three conditions generated very similar aftereffects (Fig. 5b, $p = 0.569$, ANOVA). In $f_{expanded}$–$f_{feature}$ condition, although the adapting face ($f_{expanded}$) has clear discriminability, it is less similar to the test face ($f_{feature}$), compared to the $f_{feature}$–$f_{feature}$ condition. Therefore, clear discriminability and less similarity between the adapter and test faces actually did not change the FEA, indicating the tradeoff between crowding and stimulus similarity.

The above findings that neither feature nor contour crowding alone is significant in reducing FEA suggest that the reduced FEA in $f_{contour+feature}$–$f_{expanded}$ in Experiment 2 is not a simple linear addition of the crowding effects induced by face contour and facial feature separately. Thus, the findings from Experiment 2 and 3 may suggest a nonlinear interaction of crowding effects brought by facial features and face contour in FEA. However, note that the test faces ($f_{feature}$) had a relatively lower discriminability (though not significant) than uncrowded expanded faces ($f_{expanded}$).

5. Discussion

Three experiments were carried out to investigate the effect of crowding on facial expression adaptation. Experiment 1 revealed that crowding the mouth with both face contour and facial feature reduced discriminability of facial expression, but it did not when only crowding with facial feature (0–$f_{internal}$) or face contour alone (0–$f_{external}$). Experiment 2 found that the reduced discriminability in contour and feature crowding resulted in reduced facial expression aftereffect (FEA). However, interestingly, although feature crowding did not reduce discriminability, its FEA was significantly reduced as compared to the uncrowded expanded face adaptation. Therefore, we did not find a significant correlation between the discriminability of the adapting face and its FEA. Instead, we found a significant positive correlation between the discriminabilities of the adapting and test faces. This result may help explain the previous findings that adaptation improves sensitivity (or discriminability) of the test faces that are similar to the adapting face (Chen et al., 2010; Keefe et al., 2013; Yang et al., 2011). Experiment 3 showed that crowding the mouth by face contour did not reduce FEA ($f_{contour+feature}$–$f_{feature}$ compared to $f_{expanded}$–$f_{feature}$), neither did crowding by facial features alone ($f_{feature}$–$f_{feature}$). Therefore, the reduced FEA in contour and feature crowded face cannot be linearly decomposed or attributed to the crowding effects by face contour and facial features and thus suggests a nonlinear integration between the two.

5.1. Visual crowding and discriminability

The mouth plays an important role in facial expression perception. Specifically, the curvature of the mouth indicates happy or sad emotion (Chen & Chen, 2010; Gosselin & Schyns, 2001). In the current study, we used visual crowding to manipulate the discriminability of the adapting stimuli. We crowded the mouth part by other facial features, face contour or a combination of both to reduce discriminability. Comparing the face images of $f_{contour+feature}$, f_{hair}, and f_{line}, we found that all three had the same face contour line near the mouth, but different surrounding complexity; and f_{hair} was the most complex face image with more lines near the mouth. However, all three faces had very similar magnitude of discriminability (Fig. 2c). This suggests that when the complexity of the surroundings reached a certain level, discriminability could not be reduced any further. This may be related to the critical distance in crowding. Bouma's law suggests that presenting flankers within the distance of 0.5 × the eccentricity of the target (mouth) results in crowding effect (Levi, 2008; Pelli, 2008).

A study by Martelli, Majaj, and Pelli (2005) suggested that faces are processed like words by parts or non-holistically when crowding occurs among features within a face (self-crowding). We utilized this self-crowding (feature-level crowding) technique but differentiated the effects of the external face contour and the internal facial features on crowding. This is of particular interest because (1) the face contour is on the same radial line as the mouth, which is more effective in inducing crowding effect (Toet & Levi, 1992); (2) the mouth in a face contour can be easily or automatically combined toward the perception of a face holistically, which could be the reason for the higher discriminability of expanded face than the mouth alone ($0–f_{\text{expanded}}$ vs. $0–m$).

A recent single cell recording study of crowding (Crowder & Olson, 2013) in macaque monkeys found that the neural activities in area V1 reduced gradually when the distance between the flankers (e.g., "K", "P", "Y", "T") and the target (e.g., "X") decreased. This suggests that the strength of the signal was reduced by the flankers, providing neurophysiological evidence for the current findings.

5.2. Facial expression aftereffects, visibility, and discriminability of the adapting stimuli

Facial aftereffects, such as face identity or facial expression aftereffect, are modulated by adapting stimulus visibility or awareness of the adapting stimulus (Adams et al., 2010; Moradi, Koch, & Shimojo, 2005; Yang, Hong, & Blake, 2010). These studies used binocular rivalry or continuous flash suppression (CFS) to manipulate the visibility of the adapting stimulus. In the current study, we used visual crowding to manipulate discriminability. As pointed out by Whitney and Levi (2011), visual crowding impairs object identification but not detection or visibility. Therefore, in our experiments, the mouth was still visible to the subjects but they could not report its details (e.g., curvature). Interestingly, we did not find a significant correlation between the discriminability of the adapter and its aftereffect (FEA). However, the relative order of adapters in discriminability ($f_{\text{contour+feature}} < f_{\text{feature}} < f_{\text{expanded}}$) resulted in the same ranking order of facial expression aftereffects (FEAs, $f_{\text{contour+feature}} - f_{\text{expanded}} < f_{\text{feature}} - f_{\text{expanded}} < f_{\text{expanded}} - f_{\text{expanded}}$). This suggests that discriminability of the adapting stimulus is still important in face adaptation. The fact that we did not observe a significant correlation may be because of saturation effect, such that majority of the adapting face or visual stimuli did not yield significant aftereffects due to crowding effect or lack of background similarity.

Furthermore, because of the nonlinearity relationship between the face parts in FEA (Xu et al., 2011a), adapting to the whole face generated a larger aftereffect than adapting to the summation of its face parts (the mouth and mouthless face). This might offer a different perspective: the aftereffects generated by partial faces or the mouth alone may not only be affected by the discriminability of the adapting stimulus, but also the nonlinear mechanism in adaptation, specifically the missing information from the whole holistic face or the background of the mouth. When only full faces were considered (f_{expanded}, f_{feature}, $f_{\text{contour+feature}}$, f_{hair}, and f_{line}), all the other faces except f_{feature} had a significantly smaller discriminability than the expanded face (f_{expanded}) (Fig. 2c), and their FEAs were also significantly smaller than that of the expanded face (Fig. 4a). Moreover, there were only two conditions that generated significant FEAs ($m–f_{\text{expanded}}$ and $f_{\text{feature}}–f_{\text{expanded}}$), besides the uncrowded expanded face adaptation condition ($f_{\text{expanded}}–f_{\text{expanded}}$). For these two adaptation conditions, the former ($m–f_{\text{expanded}}$) replicated our previous findings in cross-level adaptation (Xu et al., 2008), indicating a strong local component in FEA. The later ($f_{\text{feature}}–f_{\text{expanded}}$) may suggest the importance of a similar discriminability and/or image background between the adapting and test face (discriminability of f_{feature} vs. f_{expanded} is $p = 0.18$, Fig. 2c) in producing a significant FEA. Therefore, the aftereffect generated by adapting to full faces was influenced by the discriminability of the adapting faces, though the magnitude between the two is not linearly correlated.

Note that our current findings are based on the adaptation to happy faces or adapting to sad faces previously (Xu et al., 2008, 2012). We have not tested other facial emotions, such as anger or surprise. Therefore, we should be cautious to generalize our findings to other types of facial expressions. However, face adaptation has been found to occur in different expressions (happy-angry, disgust-surprise, and fear-contempt) or even different facial attributes, such as gender and ethnicity (Webster et al., 2004).

5.3. Discriminability of the adapting stimuli and test faces

It has been shown that adaptation increases the sensitivity of the test stimuli near the adapter for both simple stimulus attributes like grating orientation (Regan & Beverley, 1985) and complex stimulus attributes like face viewpoint (Chen et al., 2010), gender (Yang et al., 2011) or trustworthiness (Keefe et al., 2013). The reason for this increased discriminability in test faces near the adapter remains uncertain. However, our current study indicated that the increased sensitivity on test stimuli after adaptation might be due to the increased sensitivity of the adapter during adaptation. Neural recordings from anaesthetized monkeys found that multiple tuning properties changed after adaptation (Kohn & Movshon, 2004) and usually this change was a shift toward the adapter. For the bell-shaped tuning function, this shift increased the slope or discriminability of the adapter.

5.4. Spatial layout of the flankers – radial–tangential anisotropy

The radial–tangential anisotropy in crowding suggests that if the flankers and the target are on the same radial line from the fixation point, the crowding effect is stronger (Pelli et al., 2007; Petrov & Popple, 2007; Toet & Levi, 1992), and it is weaker when they are on the tangent line. Some other studies suggested that crowding is stronger when the flankers and the target are horizontally aligned than vertically aligned in the four quadrants of visual field or are within the same visual field (Feng, Jiang, & He, 2007) than in separate visual fields (Liu et al., 2009). In our experiments, we horizontally aligned the adapting and test stimuli to the right of the fixation point. This spatial arrangement may increase the effect of crowding in pure external crowded faces (f_{external}, Fig. 1d), as the face contour (flanker) is horizontally aligned with the mouth target – along the radial line from the fixation point. In comparison, the arrangement in the pure internal crowded faces (f_{internal}, Fig. 1c) may be less effective in introducing crowding effect, since the other facial features (eyes and nose) are vertically aligned with the target mouth – along the tangent line from the fixation point. However, this is not the case, as both did not reduce the discriminability of the mouth significantly ($0–f_{\text{internal}}$ vs. $0–m$, $p = 0.75$, and $0–f_{\text{external}}$ vs. $0–m$, $p = 0.51$ in Fig. 2c).

The contour and feature crowded face ($f_{\text{contour+feature}}$), on the other hand, has both facial feature crowding and face contour crowding, radially and tangentially, and the effect of the two may be nonlinearly integrated. This may be a possible explanation for the significant crowding effect in contour and feature crowded faces but not in feature crowded faces ($0–f_{\text{contour+feature}}$ vs. $0–f_{\text{feature}}$ in Fig. 2c). When we presented the test stimuli below the fixation cross such that the other facial features are in the radial line of the mouth in a separate experiment, all the three test faces (expanded, feature crowded, and contour and feature crowded faces) were very hard to identify their facial expressions (unpublished data).

Such radial–tangential anisotropy was not observed in facial expression aftereffect, as both feature crowded faces (f_{feature}) and contour and feature crowded faces ($f_{\text{contour+feature}}$) reduced the facial expression aftereffect significantly, compared to adapting to uncrowded expanded faces (f_{expanded}). Interestingly, all three types of faces (whether with crowding or not) generated similar magnitude of aftereffects on feature crowded faces in Experiment 3. Therefore, the mechanism of radial–tangential anisotropy in crowding remains to be further explored.

5.5. Is this facial expression aftereffect local?

In the above experiments, the locations of the mouth of the adapting and test faces are aligned on the computer screen. The FEA generated by adapting to mouth alone stimulus (condition "m–f_{expanded}") was significant ($p = 0.022$). This FEA was slightly but not significantly lower than the full face adaptation (condition "f_{expanded}–f_{expanded}") in magnitude ($p = 0.14$, Fig. 4a). Therefore, the facial expression aftereffect can be explained by local low-level curve adaptation. In our previous experiments, we moved the adapting mouth or curve away from the test mouth, the aftereffect disappeared (Xu et al., 2008). Moreover, when we moved the entire adapting face away from the test face in location, the FEA diminished quickly (Xu et al., 2011b). Therefore, the observed FEA in the current study is probably caused by mouth adaptation, a low-level curve adaptation.

Acknowledgments

This work is supported by the Singapore MOE AcRF Tier 1, NTU HSS RCC45, NTU SUG, and CoHASS Incentive Scheme (HX). We thank April Ching for help with data collection and Drs. Olwen Bedford and Anthony Hayes for their helpful comments on the manuscript.

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