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Multi-level visual adaptation: Dissociating curvature and facial-expression aftereffects produced by the same adapting stimuli

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ABSTRACT

Adaptation aftereffects offer a critical window onto sensory processing in the brain. However, such sensory processing is hierarchical, progressing from the extraction of simple features to the representation of complex patterns. The way that adaptation depends on coordinated changes across different levels of the hierarchy has been studied. However, when a given adapting stimulus produces both a low- and a high-level aftereffect, it remains unclear whether the high-level aftereffect is a passive reflection of low-level adaptation, or whether it is generated, at least partially, *de novo* in high-level areas. We assembled the two key ingredients needed for investigating this question psychophysically. One ingredient involves perceptual tasks that depend rather exclusively on low or high levels of processing, and yet involve partially identical stimuli that inspire cross-level adaptation. For this, we considered the discrimination of curvature or facial expression using curves or cartoon faces. The other ingredient is spatial or temporal stimulus manipulations that limit adaptation to either low or high levels. For this, we used crowding and brief presentations. We found that crowding an adapting curve with flanking curves reduces the curvature aftereffect much more than the facial-expression aftereffect, and vice versa for crowding the adapting face with flanking faces. Additionally, reducing adaptation time to a cartoon face diminishes the curvature aftereffect more drastically than the facial-expression aftereffect. These results suggest that high-level aftereffects, even when generated by a low-level adaptor, are not completely inherited from lower levels, and offer a window into the determining factors.

1. Introduction

The hierarchical nature of visual processing is well established (Felleman & Van Essen, 1991; Ungerleider & Mishkin, 1982): Retinal images are first analyzed by low-level areas such as V1 to extract simple features like orientation and curvature; these features are then integrated in successive higher-level areas to form progressively more complex representations of shapes, objects, faces, etc. Similar hierarchies exist for other sensory modalities. However, the consequence of this hierarchical organization for what is perhaps the most prominent psychophysical tool for investigating sensation, namely adaptation, is not clear. Adaptation putatively leads to changes in responsivity, and thus perceptual aftereffects, at higher levels of the hierarchy. However, this could merely be inherited from changes that happen in lower levels, or be created *de novo*, or indeed both. It is essential to know how this might work in order to interpret and exploit adaptation correctly.

This issue has been discussed since very early studies of face aftereffects (Afraz & Cavanagh, 2009; Fox & Barton, 2007; Hsu & Young, 2004; Leopold & Rhodes, 2010; Leopold et al., 2001; Rhodes, Evangelista, & Jeffery, 2009; Webster & MacLeod, 2011; Webster & MacLin, 1999; Webster et al., 2004), and many subtleties are apparent. For instance, one key finding is that face aftereffects transfer from one (adapting) location to other, non-overlapping (test) locations, and from one image orientation or size to another orientation or size. Transfer is stronger the more closely adapting and test location, size and orientation match. One might hope to conclude from this that face adaptation is a high level phenomenon, assuming that face cells at higher levels of the visual system are invariant to these same manipulations, whereas cells at lower levels are not. However, although high-level cells are more invariant than low-level cells, their invariance is also only partial, and indeed highly heterogeneously so (Desimone et al., 1984; DiCarlo & Maunsell, 2003; Perrett et al., 1984; Rolls & Baylis, 1986; Schwartz et al., 1983; Tanaka et al., 1991; Tsao et al., 2006), and it is not possible to convict definitively the partial high-level neural transfer of the partial psychophysical transfer, or thus to rule out contributions from partial low-level neural transfer. The question

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of inheritance is meaningful only after establishing the low-level contribution. Equally, Leopold et al. (2005) found that face and orientation aftereffects have similar time courses of build-up and decay. However, although this finding suggests possible shared mechanisms for the two aftereffects, it also fails to address the issue of inheritance.

To investigate hierarchical nature of visual adaptation, we previously measured multiple aftereffects corresponding to different levels of processing, but generated by the *same* adapting stimulus (Xu et al., 2008). In one experiment, we adapted subjects to a curve and measured both the curvature aftereffect (with test curves) and the facial-expression aftereffect (with test faces) in separate blocks. We found that the curve adaptation produced both a curvature aftereffect and a facial-expression aftereffect when the stimuli were properly aligned. Since curvature is a low-level feature whose tuning first appears in V1 (Dobbins, Zucker, & Cynader, 1987; Hubel & Wiesel, 1965), our results indicate that local, low-level features do indeed contribute to face adaptation. Additionally, the facial-expression aftereffect appeared to be more specific to the adapted location than other face aftereffects (Xu et al., 2008). Finally, we also found a holistic component in face representation: an adapting curve produced a stronger facial-expression aftereffect when it was the mouth curve of a cartoon face than when it was presented alone. More recently, Dickinson et al. (2010) used a different paradigm to also demonstrate local contributions to global shapes, including faces, and Susilo et al. found that there are mid-level (face parts) contributions to face representation (Dennett et al., in press; Susilo, McKone, & Edwards, 2010).

Though revealing about the existence of some inheritance, our previous experiments do not distinguish the following two possibilities. First is that facial-expression areas do nothing more than inherit curve adaptation started in lower areas. Indeed, one may argue that our finding of a facial-expression aftereffect caused by curve adaptation (Xu et al., 2008) was trivial because curve adaptation changes perceived mouth curvature and thus facial expression. This argument implicitly assumes that facial-expression areas passively reflect curve adaptation in lower areas. This possibility predicts that the curvature and facial-expression aftereffects generated by the same adaptor cannot be dissociated: if the curvature aftereffect disappears so does the facial-expression aftereffect. The second possibility is that the facial-expression aftereffect is not completely inherited from curve adaptation started in lower areas, but partially results from direct adaptation in facial-expression areas. Specifically, although a curve is not the best stimulus for facial-expression cells, it may nonetheless activate and adapt cells tuned to one expression more strongly than those tuned to other expressions. This possibility predicts that the curvature and facial-expression aftereffects produced by the same adaptor can be partially dissociated under proper conditions, because one aftereffect is not a complete, passive reflection of the other.

Investigating the inheritance of aftereffects takes two ingredients that have not previously been assembled. First, for inheritance to be possible, we need to use two classes of stimuli, one targeted at lower levels, the other at higher levels, but with the lower level stimuli comprising a key part of the higher level ones. The curves and cartoon faces used in our previous study (Xu et al., 2008), with the mouth curve playing the cross-level role, satisfy this requirement. Second, we need manipulations that dissociate aftereffects that could happen across the levels. For this we took advantage of spatial or temporal manipulations of the stimuli that limit adaptation in such a way that provides just such dissociations. The first technique involves crowding, i.e. presenting flanking stimuli in close proximity to the adapting stimulus. Crowding impedes stimulus discriminability, yet likely leaves at least some activity associated with the stimulus intact, as suggested by observations that crowding can be specific to a processing level (Levi, 2008; Louie, Bressler, & Whitney, 2007) and be relieved by flanker grouping (Levi & Carney, 2009; Livne & Sagi, 2007, 2010; Martelli, Majaj, & Pelli, 2005; Pelli & Tillman, 2008; Saarela et al., 2009). Thus, by crowding the adapting curves with other curves, or the adapting faces with other faces, we might expect to dissociate effects at the different levels. Similarly, there are reports that very brief presentation of adapting and test stimuli impact low- and high-level aftereffects differently (Suzuki, 2001), presumably because of the different temporal properties of activity at low and high levels of processing. Again, we exploited this difference to provide a revealing dissociation.

We used these techniques to show that there is both inheritance and *de novo* creation of adaptation across the hierarchy. This makes for a rich space of possible interactions. Preliminary results were reported in an abstract (Xu, Dayan, & Qian, 2008).

2. Methods

2.1. Subjects

A total of 11 subjects, with normal or corrected-to-normal vision, participated in the four experiments of this study. Two subjects (one experimenter, PL, and one naïve subject) participated in all four experiments. The remaining subjects were naïve to the purpose of the study. Experiments 1 and 2 had five subjects and Experiments 3 and 4 had eight subjects. All the data were collected at Nanyang Technological University (NTU), Singapore. This study was approved by the Institutional Review Board and the Ethics Committee of Division of Psychology at NTU.

2.2. Apparatus

We used a 17 in. Samsung (Seoul, South Korea) SyncMaster 793 MB monitor controlled by an iMac Intel Core i3 computer. The monitor's spatial resolution was 1024×768 pixels, and the vertical refresh rate was 85 Hz. A chin rest was placed at distances of 57 cm (Experiments 1 and 2) and 75 cm (Experiments 3 and 4) from the monitor to stabilize subjects' head position. Each pixel subtended 0.032° and 0.024°, respectively, at these distances. We used a Minolta LS-110 photometer to measure luminance and linearize the monitors. All experiments were run in Matlab with Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

2.3. Visual stimuli

Visual stimuli were black (0.62 cd/m^2) on a white (69.89 cd/m^2) background. The Weber contrast was 0.99. A black fixation cross was always shown at the center of the screen. It consisted of a horizontal and a vertical line segment, each extending 0.45° (Experiments 1 and 2) or 0.34° (Experiments 3 and 4) in length, and 0.064° (Experiments 1 and 2) or 0.048° (Experiments 3 and 4) in width.

Examples of the stimuli we used are shown in Fig. 1. We generated cartoon faces composed of a circle for the face contour, two dots for the eyes, and a curve for the mouth (Xu et al., 2008). The eye and mouth levels were at one-third and two-thirds of the face diameter, respectively. The center-to-center distance between the eyes was one-third of the face diameter. The face contour had a diameter of 1.85° for Experiments 1 and 2, and 2.42° for Experiments 3 and 4. The smaller stimuli for Experiments 1 and 2 better accommodated an array of 5 faces in a crowding condition (see below). The widths of the face contour and the mouth curve, and the radius of the eye dots, were 0.096° for Experiments 1 and 2, and 0.073° for Experiments 3 and 4. The mouth curves had the same pixel lengths in all experiments, but because of the different

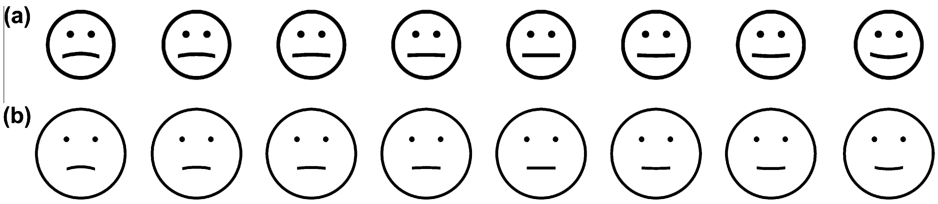

Fig. 1. Example visual stimuli. (a) Cartoon faces used in the crowding experiments (Experiments 1 and 2). (b) Cartoon faces used in the brief adaptation experiments (Experiments 3 and 4). For each set of faces, we also generated a set of curves identical to the mouth curves of the face set.

viewing distances, they were 0.99° for Experiments 1 and 2 and 0.75° for Experiments 3 and 4.

To create cartoon faces with sad to happy expressions, we varied the curvature of the mouth curve from concave to convex (Experiments 1 and 2: −0.63, −0.42, −0.21, −0.10, 0, 0.10, 0.21, 0.63; Experiments 3 and 4: −0.83, −0.55, −0.28, −0.14, 0, 0.14, 0.28, 0.55, in units of 1/°). We also generated the inverted version of the saddest and the happiest faces, and a set of isolated curves that were identical to the mouths of the corresponding cartoon-face set.

To avoid jagged edges of stimuli which may provide potential confounding cues to curvature or facial expression, we generated all stimuli with an anti-aliasing method (Matthews et al., 2003).

2.4. Procedure

We used the method of constant stimuli and the two-alternative forced choice paradigm (2AFC) in all experiments. Subjects received no feedback to their responses.

2.4.1. Experiment 1. Curve crowding

This experiment measured how crowding of the adapting curve affected the curvature and facial-expression aftereffects it produced. The adapting curve was the most concave curve of the curve set. It was either presented alone (no crowding) or with four horizontally aligned flanking curves (crowding), three on the fixation side and one the far side (Fig. 2). The flankers had the same absolute curvature as the adapting curve, but their signs (convex or concave) were chosen equally often at random in each trial. The center-to-center distance between two adjacent curves was 1.88° and the horizontal center-to-center distance between the fixation and the adapting curve (the fourth in the array) was 7.24°. The ratio of these numbers is 0.26, well within the limiting ratio of 0.5 at which crowding is induced (Bouma, 1970; Levi, 2008; Martelli, Majaj, & Pelli, 2005; Strasburger, Harvey, & Rentschler, 1991). The test stimuli were drawn either from the curve set, to measure the curvature aftereffect, or from the face set, to measure the facial-expression aftereffect; each test stimulus was presented alone without flankers (Fig. 2). Note that the test faces were horizontally aligned with the fixation point, and the adapting and test curves were at the same location as the mouth curve of the faces.

We label the resulting four adaptation conditions as c-c, c_{crowd}-c, c-f, and c_{crowd}-f, where the first letter (c) indicates the adapting stimulus was the most concave curve, the presence and absence of the subscript ("crowd") indicates crowding and no crowding, respectively, for the adapting curve, and the final letter indicates whether the test stimuli were the face set (f) or the curve set (c). For example, c_{crowd}-f means the adapting curve was presented with flankers and the test stimuli were the face set to measure the facial-expression aftereffect (Fig. 2). There were also two baseline conditions without adaptation (0-c for the test curves and 0-f for the test faces).

The total six conditions (0-c, c-c, c_{crowd}-c, 0-f, c-f, and c_{crowd}-f) were run in separate blocks with two blocks per condition. The order of the whole set of 12 blocks was randomly chosen for each subject. Each block had 10 repetitions of each test stimulus.

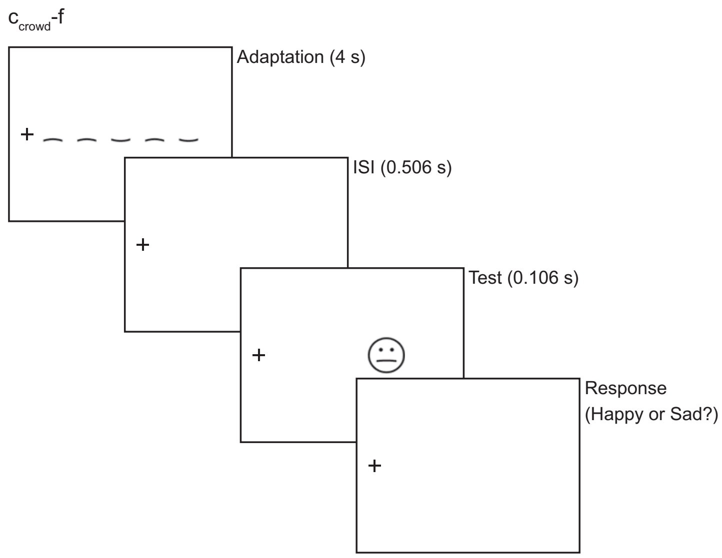

Fig. 2. Trial sequence for the c_{crowd}-f condition in Experiment 1. Subjects fixated on the cross and pressed the space bar to initiate a trial block. After 506 ms, the adapting curve (the 4th curve from the fixation) appeared with four flanking curves for 4 s. After a 506 ms ISI, a test face appeared for 106 ms. The mouth of the test face was at the same screen location as the adapting curve. A beep was then played to remind the subjects to press the "a" or "s" key to report happy or sad expression of the test face. In the actual experiments, the fixation cross was always at the screen center.

Therefore, over the two blocks for each condition, each test stimulus was repeated 20 times. Within each block, the order of the test stimuli was also randomized. To avoid possible carryover of adaptation from block to block, the subjects waited at least 10 min between successive blocks. Before data collection, each subject was also given sufficient practice trials until they felt comfortable with the task.

Subjects started each block by fixating at the fixation cross and then pressing the space bar. After 506 ms, for each adaptation block the adapting stimulus appeared for 4 s (Fig. 2). Following a 506 ms inter-stimulus interval (ISI), a test stimulus was shown for 106 ms. For the baseline blocks without adaptation (0-c and 0-f), only a test stimulus was shown for 106 ms in each trial. Finally, a 59 ms beep was played right after the test stimulus to remind the subjects to respond. When the test stimulus was a curve (0-c, c-c, and c_{crowd}-c blocks), subjects judged whether the center of the curve appeared to point up (concave) or down (convex) by pressing the "e" or "d" key. When the test stimulus was a face (0-f, c-f, and c_{crowd}-f blocks), subjects judged whether it appeared happy or sad by pressing the "a" or "s" key; for these three block types, we also randomly interleaved catch trials using the inversion of the saddest and happiest faces in the face set as the test stimuli to ensure that subject indeed judged the facial expression of the test faces, instead of the mouth curvature (see Section 3). The next trial began after a 1 s inter-trial interval.

Because of position specificity of the curvature and facial-expression aftereffects (Gibson, 1933; Xu et al., 2008), we aligned the adapting and test stimuli in all experiments so that the screen positions of the isolated curves and the mouth curves of the upright and inverted faces were always the same. For the crowding conditions, the adapting stimuli, not the flankers, were used for the alignment.

We later ran several conditions as additional controls (see Section 3). First, we repeated the 0-c, c-c and c_{crowd}-c conditions above but with the curve adaptation time in each trial reduced from 4 s to 1 s and the test stimulus duration increased from 106 ms to 200 ms to reduce the curvature aftereffect. These new conditions are termed 0-c′, c′-c′ and c'_{crowd}-c′. Second, we confirmed that crowding was effective. This was done by repeating the 0-c′ condition but presenting each test curve with flanking curves. This condition is termed 0-c'_{crowd}.

2.4.2. Experiment 2. Face crowding

This experiment measured how crowding of an adapting face affected the curvature and facial-expression aftereffects it produced. The procedure was identical to that for Experiment 1, including the extra control conditions, except that the adapting stimulus was the saddest cartoon face in the face set, and its crowding was achieved by four flanking cartoon faces. The mouth curves of the flanking faces had the same absolute curvature as the adapting face but their signs (convex, i.e., happy, or concave, i.e. sad) were chosen equally often at random in each trial. The whole collection of 10 conditions (corresponding to the 10 conditions performed in Experiment 1) are termed 0-f, f-f, f_{crowd}-f, 0-c, f-c, f_{crowd}-c, 0-f′, f′-f′, f'_{crowd}-f′, and 0-f'_{crowd}.

2.4.3. Experiment 3. Brief curve adaptation

This experiment measured how the time for which the adapting curve is exposed affected the curvature and facial-expression aftereffects it produced. We used 4-s (long) and 35 ms (brief) adaptation durations, with corresponding test durations of 118 ms (long) and 35 ms (brief). The short test duration was necessary for the short adaptation time in order to produce a sizable aftereffect (Suzuki, 2001; Suzuki & Cavanagh, 1998). The other aspects of the experiment were identical to those for Experiment 1 except that no flanker was used, the test faces had a larger diameter (2.42° vs. 1.85°) and shorter mouth curves (0.75° vs. 0.99°) (see Fig. 1), and the horizontal center-to-center distance between the fixation and the stimuli was 3.15°. There were four adaptation conditions termed c-c (long), c-c (brief), c-f (long), and c-f (brief), and four baseline, no-adaptation conditions termed 0-c (long), 0-c (brief), 0-f (long), and 0-f (brief), where the word in parenthesis indicates the long and brief conditions. Since each test type (curves or faces) had two presentation durations, each had two baseline conditions, long and brief.

2.4.4. Experiment 4. Brief face adaptation

This experiment measured how exposure time of the adapting face affected the curvature and facial-expression aftereffects it produced. The procedure was identical to that for Experiment 3 except that the adapting stimulus is the saddest cartoon face in the face set. The total of eight conditions (corresponding to the eight conditions in Experiment 3) were termed f-f (long), f-f (brief), f-c (long), f-c (brief), 0-f (long), 0-f (brief), 0-c (long), and 0-c (brief).

2.5. Data analysis

The data for each condition were sorted into fraction of "happy" or "convex" responses to each test stimulus. The test stimuli were parameterized according to the curvature of the test curves or the mouth curvature of the test cartoon faces. The fraction of happy or convex responses was then plotted against the test stimulus, and the resulting psychometric curve was fitted with a sigmoidal function of the form $f(x) = 1/[1 + e^{-a(x-b)}]$, where b gives the test-stimulus parameter corresponding to the 50% point of the psychometric function [the point of subjective equality (PSE)] and $a/4$ is the slope at the PSE. To test the hypotheses, we used two-tailed paired t test to compare subjects' PSEs or slopes for different conditions in an experiment. The aftereffect is measured as the difference between the PSE of an adaptation condition and the PSE of the corresponding baseline condition. We use the convention that repulsive aftereffects are negative.

3. Results

We previously showed that adaptation to a curve or a cartoon face generates both a curvature aftereffect and a facial-expression aftereffect (Xu et al., 2008). To understand how these aftereffects, which correspond to different levels of processing but are produced by the same adapting stimulus, depend on each other, we examined whether they can be dissociated via crowding and brief adaptation.

3.1. Crowding of the adapting curve reduced the curvature aftereffect much more than the facial-expression aftereffect

In the first experiment, we investigated whether crowding the adapting curve differentially affected the curvature and the facial-expression aftereffects it produced. We generated a set of cartoon faces whose mouth curvature varied from concave to convex so that their facial expressions varied from sad to happy (see Section 2). We also generated a set of curves that were identical to the mouths of the cartoon faces. The adapting stimulus was always the most concave curve in the curve set; it was presented either alone (no crowding) or with four flanking curves (crowding), in separate blocks. The test stimuli were taken either from the curve set, to measure the curvature aftereffect, or from the face set, to measure the facial-expression aftereffect, again in separate blocks. All the test stimuli were presented alone, without crowding.

The psychometric data from a naïve subject and fitted curves are shown in Fig. 3a. The fraction of the "convex" or "happy"

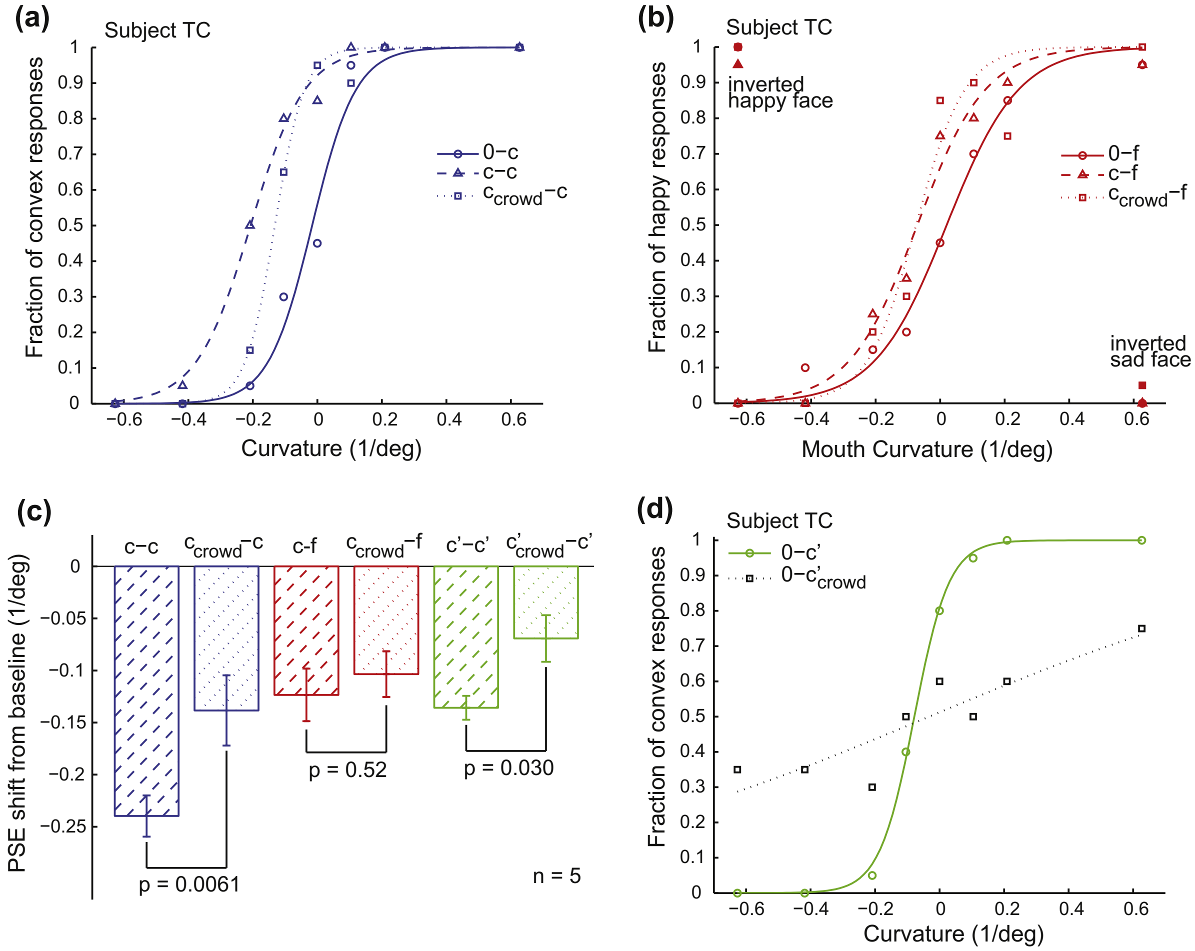

Fig. 3. The effect of crowding the adapting curve on the curvature and facial-expression aftereffects (Experiment 1). (a) Psychometric functions from a naïve subject on curvature judgment. The three blue curves represent no adaptation baseline (solid, 0-c), adaptation to a concave curve alone (dashed, c-c), and adaptation to the concave curve with flanking curves (dotted, c_{crowd}-c), all with the curve set as the test stimuli to measure the curvature aftereffect. (b) Psychometric functions from the same naïve subject on facial expression judgment. The three red curves represent the same three conditions but with the face set as the test stimuli to measure the facial-expression aftereffect (solid, 0-f; dashed, c-f; dotted, c_{crowd}-f). The results for the catch trials, in which the inverted happy and sad test faces were used, were shown as filled red dots, squares, and triangles for the 0-f, c-f, and c_{crowd}-f conditions, respectively. (c) Summary of all five subjects' data from the above conditions (blue and red bars) and the control experiment (green bars), in which the curvature aftereffect was reduced to match the facial-expression aftereffect in the absence of crowding (compare c′-c′ and c-f). We measure aftereffect as the average PSE shift of an adaptation condition from its baseline condition. The error bars represent ± SEM (the lengths equal 2 SEMs). The *p* value shown for each comparison was calculated using the two-tailed paired *t* test. (d) Psychometric functions from the same naïve subject as in panel (a) showing the crowding effect. The no-adaptation baseline condition was run without (solid curve, 0-c′) or with (dotted curve, 0-c'_{crowd}) crowding of the test curves. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

responses is plotted as a function of the curvature of the test curves, or the mouth curvature of the test faces. We first describe the three conditions involving curvature judgments on the test curves (blue curves and symbols in the figure). The blue solid curve represents the no-adaptation, baseline condition (0-c), the blue dashed curve represents the curve-adaptation condition without crowding (c-c), and the blue dotted curve represents the curve-adaptation condition with crowding (c_{crowd}-c). In all three conditions, the test stimuli were the same curve set and the subject judged the curvature of the test curve (always presented alone) in each trial. The leftward shift of the dashed vs. the solid blue curves indicates that after adapting to the concave curve alone, the subject perceived convex curvature in the test curves more frequently. This is the standard curvature aftereffect (Gibson, 1933). The new finding is that after adapting to the same curve but with crowding (the dotted blue curve), the curvature aftereffect is reduced.

We next describe the facial-expression aftereffects produced by the same adapting curve with and without crowding for the same subject (the red curves and symbols in Fig. 3b). The red solid curve represents the no-adaptation, baseline condition (0-f), the red dashed curve represents the curve-adaptation condition without crowding (c-f), and the red dotted curve represents the curve-adaptation condition with crowding (c_{crowd}-f). In all three conditions, the test stimuli were the same face set and the subject judged the facial expression of the test face (always presented alone) in each trial. The red dashed and dotted curves nearly superimpose, indicating that the adapting curve with and without crowding produced similar facial-expression aftereffects.

The results from five subjects (four of them naïve) are summarized in Fig. 3c. The mean aftereffects ± SEM for each adaptation condition are shown. Repulsive aftereffects are represented as being negative. The aftereffects for all the four adaptation conditions were significant compared with the corresponding baseline conditions (all *p*'s < 0.015, paired *t* test). More importantly, crowding of the adapting curve reduced the curvature aftereffect significantly ($p = 0.0061$) but not the facial expression aftereffect ($p = 0.52$), compared with the corresponding no-crowding conditions. This dissociation of the two aftereffects produced by the same adapting curve suggests that the facial-expression aftereffect is not all a passive reflection of the curve adaptation started in V1, but is at least partially generated *de novo* in high-level facial-expression areas. As mentioned in the Introduction, this suggests that the facial-expression aftereffect that our previous experiment (Xu et al., 2008) found to arise following curve adaptation, was not purely passively inherited from a curvature aftereffect.

Note that the slopes of the psychometric curves in panels *a* and *b* of Fig. 3 are unrelated to the crowding effect. This is because the curve crowding was only present, if at all, in the adapting phase, but not in the test phase during which the psychometric curves were measured. Thus, for all six conditions in panels *a* and *b* of Fig. 3, the test stimuli were always presented alone without crowding. The small slope differences among the curves in panels *a* and *b* are specific to this subject and do not represent a consistent pattern among the five subjects. The crowding effect was verified separately by the large slope difference of the curves in Fig. 3d, which is consistent among all subjects (see below).

A potential problem with the result in Fig. 3c is that without crowding, the adapting curve produced a much larger curvature aftereffect than facial-expression aftereffect (compare the c-c and c-f conditions in Fig. 3c). One may argue that this larger curvature aftereffect provided more room for reduction by crowding. We therefore did a control experiment in which we repeated the 0-c, c-c and c_{crowd}-c conditions but reduced the curve adaptation time from 4 s to 1 s and increased test time from 106 ms to 200 ms in each trial. These three new conditions are labeled 0-c′, c′-c′ and c'_{crowd}-c′ (green bars in Fig. 3c). Fig. 3c shows that without crowding of the adapting curve, the curvature aftereffect (c′-c′) was now comparable to the facial expression aftereffect (c-f) but curve crowding (c'_{crowd}-c′) still reduced the curvature aftereffect significantly ($p = 0.030$). Therefore, the dissociation of the two aftereffects cannot be attributed to different magnitudes of aftereffect under the no-crowding condition.

In the three conditions (0-f, c-f, and c_{crowd}-f) where the test stimuli were the face set and the subjects were asked to judge the facial expression, we sought to ensure that the subjects indeed judged the facial expression, instead of the mouth curvature. We thus randomly interleaved catch trials using inverted happy and sad faces as test stimuli (Xu et al., 2008). These inverted faces were the upside-down version of the saddest and happiest faces in the face set. Consequently, the mouth curvatures of the inverted sad and happy faces were identical to those of the happiest and saddest upright faces, respectively. If the subjects judged the mouth curvature, then the fraction of "happy" responses to the inverted sad and happy faces would be close to 1 and 0, respectively. On the other hand, if they judged facial expressions, then because the inverted sad and happy faces still appeared sad and happy, respectively, the fraction of "happy" responses should be close to 0 and 1, respectively. The actual data for the same naïve subject are at the lower-right and upper-left corners of Fig. 3b (filled red symbols), indicating that he indeed judged the facial expression as instructed. The average fraction of "happy" responses of all five subjects was 0.017 for the inverted sad face, and 0.91 for the inverted happy face. We conclude that the subjects judged facial expression, instead of the mouth curvature, of the test cartoon faces.

Finally, we confirmed that the crowding configuration indeed generated a crowding effect. We measured the subjects' curvature judgments when each test curve was presented with flankers (0-c'_{crowd}), and compared the result to that of no crowding (0-c′ above). Fig. 3d shows the comparison for the same naïve subject; as expected, the crowding configuration greatly reduced the slope of the psychometric function, and thus the curvature discriminability. For the five subjects, the mean slopes with and without crowding were 0.43 and 5.9, respectively, and the difference was significant ($p = 0.0026$). Thus, the crowding configuration was highly effective.

3.2. Crowding of the adapting face reduced the facial-expression aftereffect much more than the curvature aftereffect

We showed previously that adaptation to a cartoon face also generates both a curvature aftereffect and a facial-expression aftereffect (Xu et al., 2008). We therefore studied, in the second experiment, how crowding of the adapting cartoon face affects the two aftereffects. This experiment was the same as Experiment 1 above except that the adapting stimulus was the saddest face of the face set, and that in the crowding conditions, the adapting face was surrounded by four flanking faces.

The results from a naïve subject are shown in Fig. 4a. The red curves and symbols represent the three conditions in which subjects judged facial expression of the test faces. The red solid curve is the baseline condition without adaptation (0-f). After adapting to the sad face without crowding, the subject perceived happy expression more frequently in the test faces and the psychometric curve (red dashed curve, f-f) shifted to the left. This is the standard facial-expression aftereffect (Fox & Barton, 2007; Hsu & Young, 2004; Webster et al., 2004; Xu et al., 2008). When the adapting face was crowded by flanking faces, the shift of the psychometric curve (red dotted curve, f_{crowd}-f) from the baseline, and thus the facial-expression aftereffect, was reduced. Note that, as in Experiment 1, face crowding only occurred during the adaptation period of the f_{crowd}-f condition and the test faces for the three conditions were exactly the same without crowding.

The blue curves and symbols in Fig. 4b represent the conditions in which the same subject judged the curvature of the test curves with and without crowding of the adapting face. The blue solid curve is the no-adaptation, baseline condition (0-c). After adapting to the sad face (which had a concave mouth), the subject perceived convex curves more frequently, and the psychometric curve (blue dashed curve, f-c) shifted to the left, consistent with our previous report (Xu et al., 2008). When the adapting face was crowded by flanking faces, the psychometric curve (blue dotted curve, f_{crowd}-c) does not differ substantially from the no-crowding condition (f-c). Therefore, crowding of the adapting face did not affect the curvature aftereffect.

A summary of all five subjects' data is shown in Fig. 4c. The aftereffects for all four adaptation conditions were significant compared with the corresponding baseline conditions (all p's < 0.01, paired *t*-test). The crowding of the adapting face reduced the facial-expression aftereffect significantly ($p = 0.0044$) but not the curvature aftereffect ($p = 0.43$). Since without crowding, the adapting face produced a much larger facial-expression aftereffect (f-f) than the curvature aftereffect (f-c), we ran a control experiment in which we repeated the 0-f, f-f, and f_{crowd}-f conditions but reduced the adaptation duration from 4 s to 1 s and increased the test duration from 106 ms to 200 ms, in order to reduce the facial-expression aftereffect. The results from these new conditions, termed 0-f′, f′-f′, and f'_{crowd}-f′, are summarized as magenta bars in Fig. 4c. The figure shows that without crowding of the adapting face, the facial-expression aftereffect (f′-f′) was now comparable to the curvature aftereffect (f-c), and yet face crowding (f'_{crowd}-f′) still reduced the facial-expression aftereffect significantly ($p = 0.0085$).

As in Experiment 1, when the test stimuli were faces, we interleaved catch trials with inverted happy and sad faces to ensure that subjects judged facial expression instead of the curvature of the mouth. The average fraction of "happy" responses of all five subjects was 0.017 for the inverted sad face, and 0.85 for the inverted happy face, indicating that the subjects indeed judged facial expression as instructed. We also confirmed that our face-crowding configuration produced a crowding effect. We measured the subjects' facial-expression judgment on the face set when each test face was presented with flanking faces (0-f'_{crowd}), and compared the result with that of no crowding (0-f′ above). Fig. 4d

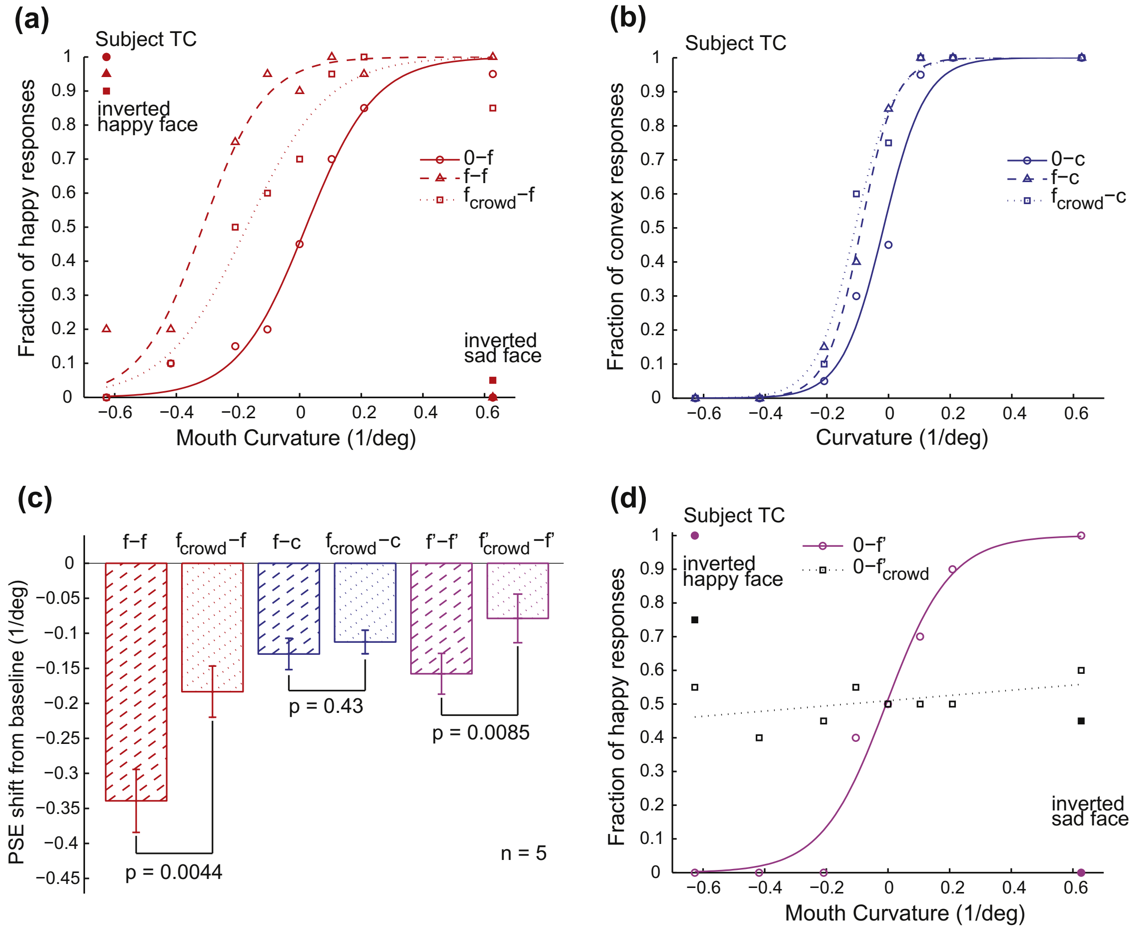

Fig. 4. The effect of crowding the adapting face on the curvature and facial-expression aftereffects (Experiment 2). The format is similar to that of Fig 3. (a) Psychometric functions from a naïve subject on facial expression judgment. The three red curves represent the same three conditions but with the face set as the test stimuli to measure the facial-expression aftereffect (solid, 0-f; dashed, f-f; dotted, f_{crowd}-f). The results for catch trials, in which inverted happy and sad test faces were used, were shown as filled dots, squares, and triangles for the 0-f, f-f, and f_{crowd}-f conditions, respectively. (b) Psychometric functions from the same naïve subject on curvature judgment. The three blue curves represent no adaptation baseline (solid, 0-c), adaptation to a sad face alone (dashed, f-c), and adaptation to the sad face with four flanking faces (dotted, f_{crowd}-c), all with the curve set as the test stimuli to measure the curvature aftereffect. (c) Summary of all five subjects' data on the above conditions (blue and red bars) and the control experiment (magenta bars), in which the facial-expression aftereffect was reduced to match the curvature aftereffect in the absence of crowding (compare f'-f' and f-c). (d) Psychometric functions from the same naïve subject as in panel (a) showing the crowding effect. The no-adaptation baseline condition was run without (solid curve, 0-f') or with (dotted curve, 0-f'_{crowd}) crowding of the test faces. The results from catch trials using inverted happy and sad faces are also shown as filled symbols. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

shows the comparison for the same naïve subject; the crowding configuration greatly reduced the slope of the psychometric function, and thus the facial-expression discriminability. For the five subjects, the mean slopes with and without crowding were 0.28 and 3.49, respectively, and the difference was significant ($p = 0.013$). Moreover, crowding with upright flanking faces also reduced the visibility of the inverted faces in the catch trials (compare filled black squares and filled magenta dots in Fig. 4d). For all five subjects, the average fractions of “happy” response to the inverted happy face were 0.75 and 0.99 for the crowding and no-crowding conditions, respectively; and the fractions of “happy” response to the inverted sad face were 0.39 and 0.03 for the crowding and non-crowded conditions, respectively.

To summarize the first two experiments, we found that crowding the adapting curve with flanking curves significantly reduced the low-level curvature aftereffect but not the high-level facial-expression aftereffect; conversely, crowding the adapting face with flanking faces significantly reduced the high-level facial-expression aftereffect but not the low-level curvature aftereffect. These results demonstrate a double dissociation of low- and high-level aftereffects produced by the same adapting stimuli.

3.3. Brief curve adaption reduces both the curvature and facial-expression aftereffects

In the first two experiments, we studied how crowding, which is a spatial manipulation, differentially affected the curvature and facial-expression aftereffects produced by the same adapting stimuli. In the following two experiments, we examined whether the dissociation of the two aftereffects may be realized with brief adaptation, a temporal manipulation. The motivation was the very different time courses of the activities of cells at low- and high-levels of the visual hierarchy in response to transient stimuli. In particular, activities at high levels persist for substantially longer than those at lower levels, perhaps as a form of reverberating memory (Miyashita & Chang, 1988). This raises the possibility that brief stimuli might activate high-level cells for longer, and thus adapt them more, than low-level cells. We investigated this possibility by comparing results from brief and elongated periods of adaptation. In the long paradigm, adaptation and test durations in each trial were 4 s and 106 ms, respectively; in the brief paradigm, these durations were both 35 ms. Thus, both the adapting and test durations were reduced in the brief condition.

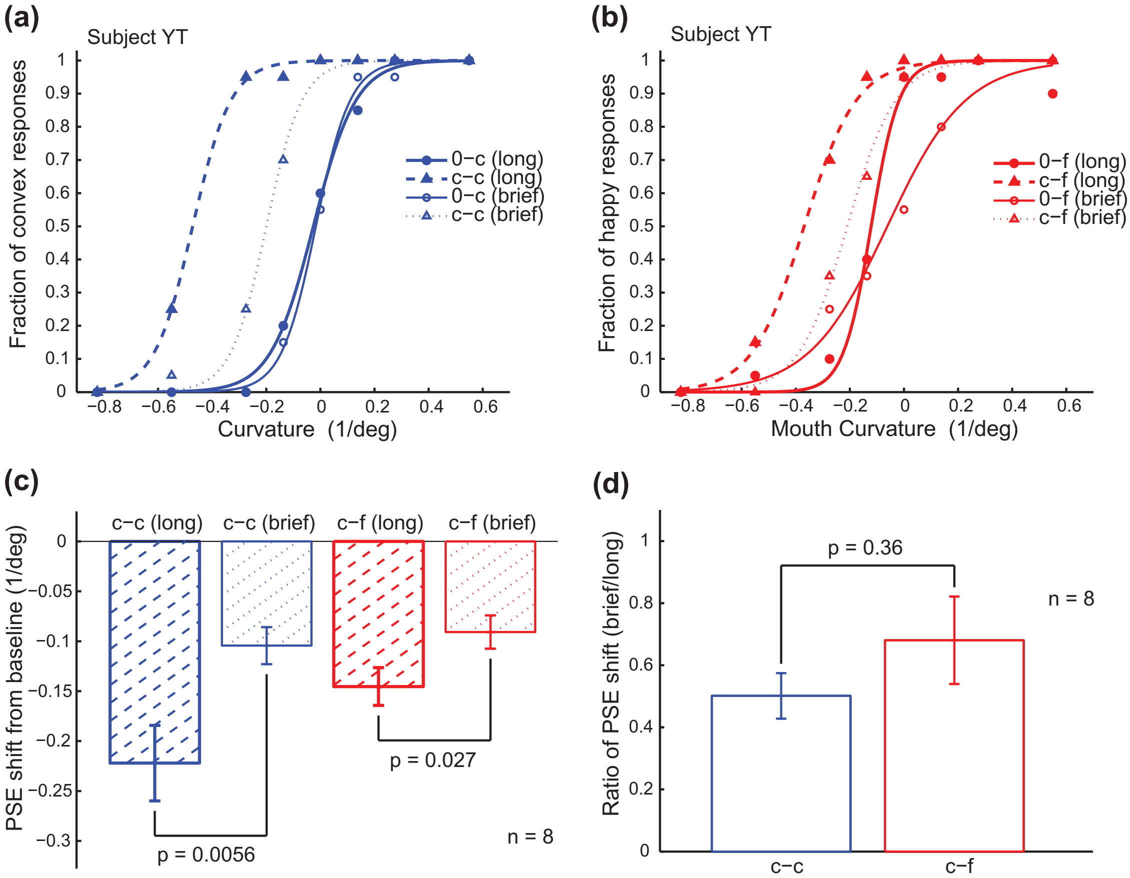

Fig. 5. The effect of brief curve adaptation on the curvature and facial-expression aftereffects (Experiment 3). The thick lines (filled symbols) and thin lines (open symbols) represent long and brief conditions, respectively. The blue and red colors represent curvature and facial expression aftereffects, respectively. (a) Psychometric functions from a naïve subject judging the curvature of the test curves under the following conditions: 0-c (long), no adaptation baseline with 106-ms test curves (blue filled dots and thick solid curve); c-c (long), adaptation to a concave curve for 4 s and test with 106-ms curves (blue filled triangles and thick dashed curve); 0-c (brief), no adaptation baseline with 35-ms test curves (blue open circles and thin solid curve); c-c (brief), adaptation to the concave curve for 35 ms and test with 35-ms faces (blue open triangles and thin dotted curve). (b) Psychometric functions from the same subject judging facial expression of the test faces under the following conditions: 0-f (long), no adaptation baseline with 106-ms test faces (red filled dots and thick solid curve); c-f (long), adaptation to the concave curve for 4 s and then test with 106-ms faces (red filled triangles and thick dashed curve); 0-f (brief), no adaptation baseline with 35-ms test faces (red open dots and thin solid curve); c-f (brief), adaptation to the concave curve for 35 ms and test with 35-ms faces (red open triangles and thin dotted curve). (c) Summary of all eight subjects' data. (d) Average ratios of the aftereffects produced by the brief and long paradigms. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

This is necessary to keep the aftereffects measureable (Suzuki & Cavanagh, 1998).

We first describe how brief curve adaptation affects curvature and facial-expression aftereffects (Experiment 3). In Fig. 5, thick and thin lines indicate long and brief paradigms, respectively; and blue and red colors indicate curve and face aftereffects, respectively. These are all based on curve adaptation. The psychometric functions from a naïve subject judging the curvature of the test curves are shown in Fig. 5a. The thick solid and dashed curves are the baseline [0-c (long)] and curve-adaptation [c-c (long)] conditions, respectively, using the long paradigm. The corresponding results for the brief paradigm [0-c (brief) and c-c (brief)] are shown as thin solid and dashed curves. Fig. 5a shows that compared with the long adaptation, the brief adaptation to a curve produced a much smaller curvature aftereffect. Fig. 5b shows that the similar result holds for the facial-expression aftereffect.

Fig. 5c summarizes all eight subjects' data (seven of them naïve). The aftereffects of all adaptation conditions are significant against their corresponding baseline conditions (all p's < 0.001, paired t-test). Moreover, the brief curve adaptation reduced both the curvature aftereffect ($p = 0.0056$) and the facial-expression aftereffect ($p = 0.027$), compared with the corresponding long conditions. To examine whether the degrees of the reduction are different between the two aftereffects, we calculated the aftereffect ratio between the brief and long paradigms for each aftereffect type (Fig. 5d). Although the brief curve adaptation reduced the curvature aftereffect more than the facial-expression aftereffect, as expected, the difference is not significant ($p = 0.36$).

We note that Fig. 3c shows a large difference between the c-c and c-f conditions whereas Fig. 5c shows a relatively small difference between the c-c (long) and c-f (long) conditions. This may be caused by the different face stimuli used in these experiments (cf. panels a and b of Fig. 1). Additionally, different subjects were used in these experiments.

3.4. Brief face adaption reduces the curvature aftereffect more than the facial-expression aftereffect

Finally, we describe how brief face adaptation affected the curvature and facial-expression aftereffect (Experiment 4). This experiment was identical to Experiment 3 above except that the adapting stimulus was a sad face instead of a concave curve. The results, in Fig. 6, are presented in a similar format as Fig. 5. The data from a naïve subject are shown in panels a and b of Fig. 6. Compared with the long paradigm, the brief paradigm greatly reduced the subject's curvature aftereffect (Fig. 6b) but not her facial-expression aftereffect (Fig. 6a).

Fig. 6c summarizes all eight subjects' data. The aftereffects of all adaptation conditions are significant against their corresponding baseline conditions (all p's < 0.044), and the brief face adaptation reduced both the curvature aftereffect ($p < 0.0001$) and the facial-expression aftereffect ($p = 0.0016$), compared with the corresponding long conditions. Fig. 6c also indicates that brief face adaptation reduced the curvature aftereffect much more than the facial-expression aftereffect. As in Experiment 3, we compared the degrees of reduction between the two types of aftereffects by calculating the aftereffect ratio produced by the brief and long paradigms (Fig. 6d). Unlike Experiment 3, Fig. 6d shows that the brief face adaptation reduced the curvature aftereffect significantly more than the facial-expression aftereffect ($p = 0.0020$). Therefore, brief face adaptation partially dissociates the low-level curvature aftereffect and the high-level facial-expression aftereffect.

4. Discussion

Adaptation is one of the most important ways by which we understand sensory processing. However, that such processing is hierarchical poses a central problem for interpreting adaptation, since aftereffects can arise from changes that happen at multiple levels, with one layer inheriting influences from layers below. As we discussed in the Introduction, although many studies have investigated and discussed multi-level contributions, notably in the context of face processing (Afraz & Cavanagh, 2009; Fox & Barton, 2007; Hsu & Young, 2004; Leopold & Rhodes, 2010; Leopold et al., 2001; Rhodes, Evangelista, & Jeffery, 2009; Webster & MacLeod, 2011; Webster & MacLin, 1999; Webster et al., 2004), difficulties with pinning down effects to particular levels mean that they have not directly addressed the question of aftereffect inheritance. A simple way to examine inheritance is to use a single adapting stimulus that can potentially exert effects at more than one level of the hierarchy, and to show that it is possible to dissociate the effects at these levels. We had previously suggested two classes of stimuli that showed suitable cross-level aftereffects (Xu et al., 2008); here we demonstrated clear signs of dissociation by manipulating spatial context, through layer-specific crowding, and temporal context, through the brevity of stimulus presentation.

The two classes of stimuli concerned were simple curves and cartoon faces, and the tasks involved discriminating curvature and facial expression. Our previous work showed that adaptation to a curve, or a cartoon face containing the curve as the mouth, produced both a curvature aftereffect and a facial-expression aftereffect (Xu et al., 2008). We consider these aftereffects as low- and

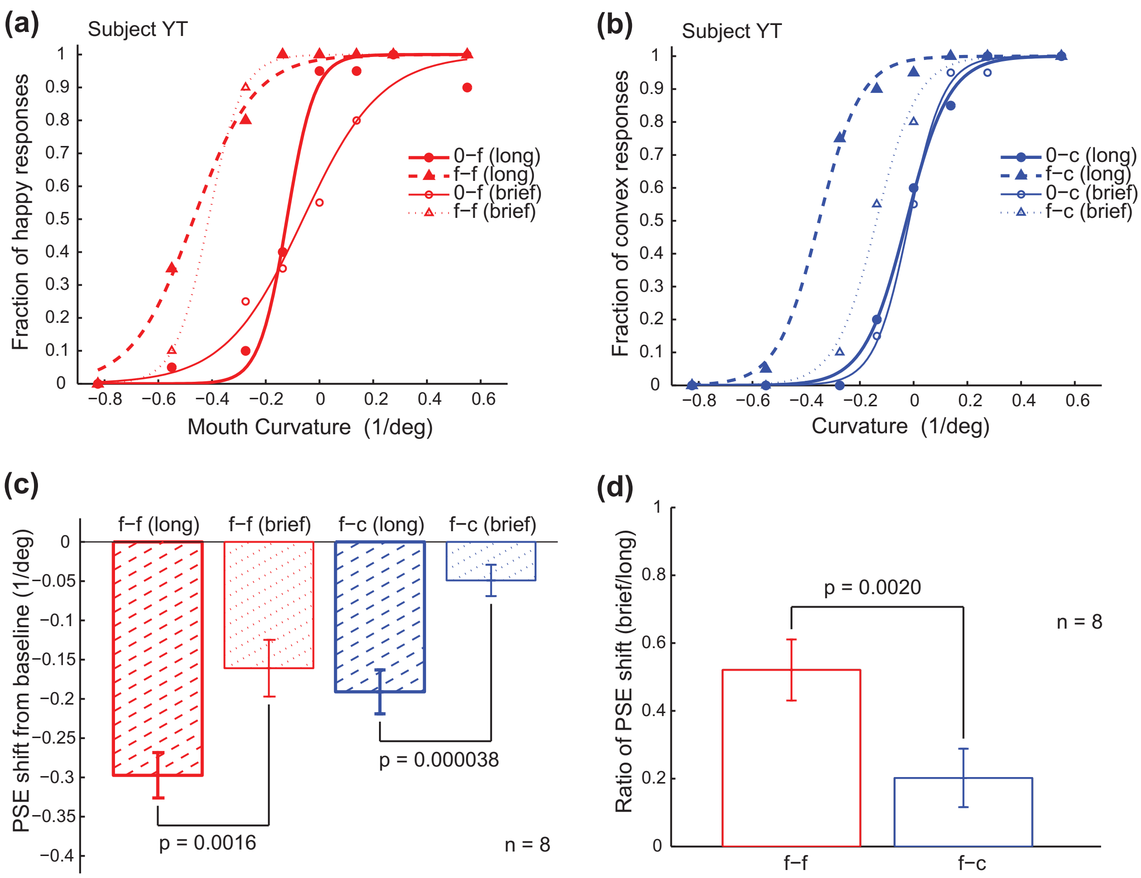

Fig. 6. The effect of brief face adaptation on the curvature and facial-expression aftereffects (Experiment 4). The format is similar to that of Fig. 5. The thick lines (filled symbols) and thin lines (open symbols) represent long and brief conditions, respectively. The blue and red colors represent curvature and facial-expression aftereffects, respectively. (a) Psychometric functions from a naïve subject judging the facial expression of the test faces under the following conditions: 0-f (long), no adaptation baseline with 106-ms test faces (red filled dots and thick solid curve); f-f (long), adaptation to a sad face for 4 s and test with 106-ms faces (red filled triangles and thick dashed curve); 0-f (brief), no adaptation baseline with 35-ms test faces (red open circles and thin solid curve); f-f (brief), adaptation to the sad face for 35 ms and test with 35-ms faces (red open triangles and thin dotted curve). (b) Psychometric functions from the same subject judging the curvature of the test curves under the following conditions: 0-c (long), no adaptation baseline with 106-ms test curves (blue filled dots and thick solid curve); f-c (long), adaptation to the sad face for 4 s and then test with 106-ms curves (blue filled triangles and thick dashed curve); 0-c (brief), no adaptation baseline with 35-ms test curves (blue open dots and thin solid curve); f-c (brief), adaptation to the sad face for 35 ms and test with 35-ms curves (blue open triangles and thin dotted curve). (c) Summary of all eight subjects' data. (d) Average ratios of the aftereffects produced by the brief and long paradigms. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

high-level, respectively, because curvature tuning starts as early as V1 (Dobbins, Zucker, & Cynader, 1987) whereas facial-expression selectivity occurs much later (e.g., STS) along the visual hierarchy (Hasselmo, Rolls, & Baylis, 1989; Haxby, Hoffman, & Gobbini, 2000; Winston et al., 2004; Xu et al., 2008) [although face or face-part tuning in early visual cortical areas has not been examined in detail].

We found that crowding the adapting curve with flanking curves reduced the curvature aftereffect by half, but failed to affect the facial-expression aftereffect significantly. The converse was true when the adapting face was crowded with flanking faces. Additionally, brief adaptation to a cartoon face reduced the curvature aftereffect much more than the facial-expression aftereffect. Brief curve adaptation also reduced the curvature aftereffect more than the facial-expression aftereffect, although this difference failed to reach significance. These results suggest that the facial-expression aftereffect is not all passively inherited from simple-feature adaptation started in lower-level areas; part of it must be generated by adaptation in facial-expression areas. In particular, when an adapting curve produces a facial-expression aftereffect, part of that aftereffect must result from the curve-driven response adaptation of facial-expression cells. In other words, the curve must activate and change responses of cells tuned to different facial expressions to different degrees. Obviously, our psychophysical experiments cannot pinpoint exact brain areas involved in adaptation. Nevertheless, we hope our experimental paradigm will prove useful for future physiological investigations.

Given our evidence of adaptation at both lower and higher levels, one of the most important questions is how they interact, be it additively (as suggested in Susilo, McKone, and Edwards (2010)) or in a non-linear manner. Although investigating this requires going substantially beyond our current experiments – for instance it would be helpful to physiologically measure adaptation effects in multiple visual areas produced by the same adaptor, we speculate that the interaction might be non-linear. First, our previous study showed that with typical (long) presentation durations, the facial-expression aftereffect produced by an adapting curve is highly specific to the location of the curve, suggesting a low-level origin of the aftereffect (Xu et al., 2008). Second, the first experiment of the current study (Fig. 3) showed that when the curvature aftereffect was greatly reduced by crowding the adapting curve, the facial-expression aftereffect was not much affected. It thus appears that adaptation in high-level face areas could be boosted when inheritance from lower levels is reduced. It would be interesting to examine this issue in future work.

We chose cartoon faces for our experiments because they contained the mouth curves as a well-defined low-level feature, which could also be used in isolation as adapting or test stimuli. This is an important aspect of our experimental design because it maximized cross-level adaptation between the curve and face stimuli (Xu et al., 2008), which in turn facilitated our investigation of the aftereffect inheritance question. Had we used other face types, the cross-level aftereffects would have been weaker (Xu et al., 2008), making it harder to conduct and interpret the dissociation experiments. Further, physiological experiments have shown that face cells respond to real and cartoon faces similarly (Freiwald, Tsao, & Livingstone, 2009). By randomly interleaving catch trials involving inverted test faces, we ensured that the subjects were indeed judging the facial expressions of the cartoon faces. Of course, real and cartoon faces do differ considerably, and in the future, it would be interesting to repeat our study with real faces.

With the same goal of maximizing cross-level aftereffects, we kept constant the size, orientation, and position of the curve stimuli and the mouths of the cartoon-face stimuli. Manipulations of these quantities have been widely used to exclude low-level contributions to face aftereffects (Afraz & Cavanagh, 2009; Fox & Barton, 2007; Hsu & Young, 2004; Leopold et al., 2001; Rhodes, Evangelista, & Jeffery, 2009). The purpose of our study, however, is different: we wanted to maximize, for example, the facial-expression aftereffect produced by an adapting curve in order to study whether the aftereffect is passively inherited from low-level adaptation or generated *de novo* in high-level face areas. Instead, in our design, we used spatial and temporal manipulations to achieve the required dissociation.

4.1. Brief adaptation

We borrowed the idea of using brief adaptation to separate effects at different levels from Suzuki (2001), who measured the orientation tilt aftereffect and a contour-distortion aftereffect at long (2.7 s) and brief (27 ms) adapting durations. He found that the orientation tilt aftereffect (putatively lower level) is much weaker at the brief than at the long adapting duration, whereas the contour-distortion aftereffect (putatively higher level) is about the same for the two adapting durations. We speculate that since activity at higher levels of the hierarchy tends to persist for longer periods after stimulus offset (Miyashita & Chang, 1988), brief adaptation should have more chance to work at those levels than lower down. However, in Suzuki's experiments, the orientation and contour-distortion aftereffects were unrelated, and indeed were induced by different adapting stimuli (an orientation and a contour, respectively). Consequently, his results cannot be used to draw inferences about the interdependence of aftereffects at different levels of processing. Our stimuli were designed to permit such inferences.

Our findings are partly consistent with Suzuki (2001)'s, in that making the face adaptation more brief reduced the lower level, curvature, aftereffect by more than the higher level, expression aftereffect. That making curvature adaptation briefer did not reduce the curvature aftereffect by significantly more than the expression aftereffect is a problem for this account. One possibility is that brief presentation of the adapting curve was insufficient to ignite persistent activity in the higher levels devoted to representing facial expressions.

4.2. Crowding

Restricting the length of adaptation was a mostly effective way of eliminating effects at the lower level, revealing the unique role for upper level aftereffects. However, it was not expected to eliminate effects at the higher level, to reveal what is possible at the lower level by itself. In order to do this, we turned to the spatial contextual phenomenon of crowding, in which stimuli that are sufficiently near to the adapting stimulus reduce its discriminability. Crowding is in general reduced when the nearby stimuli can form part of a perceptual whole (Martelli, Majaj, & Pelli, 2005; Pelli & Tillman, 2008), a fact that plays a crucial part in our design. It implies that although facial crowding would seem inevitably to contain curve crowding, since the faces contain the curves, this might actually not occur, since, from the perspective of the curves, the faces are perceptually whole. However, the faces would still crowd other faces (and curves crowd other curves). Stimuli that are crowded should lead to less adaptation. Indeed, this is exactly what we found – with aftereffects being selectively suppressed at the level where crowding remains effective.

Our results bear an interesting relation to those of previous studies that have examined the effect of reducing the visibility of adapting stimuli on aftereffects. First, and consistent with our results, Moradi, Koch, and Shimojo (2005) showed that the (higher level) face identity aftereffect did depend on the adapting face being visible. The case for stimuli associated with lower levels is more complex. Blake et al. (2006) showed that the motion aftereffect, another low-level aftereffect, is reduced when the adapting motion is made less visible by crowding or binocular rivalry. However, reducing the visibility of an adapting orientation stimulus only reduced the strength of a resulting aftereffect (the elevation of the contrast-detection threshold) if the adapting stimulus was low, but not high contrast. It would be interesting to use techniques such as ours to see if effects at higher levels could be partly responsible for this.

4.3. Statistical tests

We used paired *t*-tests to determine whether the crowding or duration manipulations differently affected the curvature and facial-expression aftereffects produced by the same adapting stimuli. One might argue that it would be better to use ANOVA to assess the interactions between manipulations (crowding vs. no-crowding or brief vs. long duration) and tasks (curvature vs. facial-expression judgments). We performed a within-subject, two-way ANOVA for each of the four experiments. We found that for the first three experiments, the ANOVA interaction and the paired *t*-test agree: when the paired *t*-test showed that a manipulation affected the curvature and facial-expression aftereffects differently (or similarly), the ANOVA showed a significant (or non-significant) interaction between the manipulation and task. The fourth experiment (Fig. 6), however, is an exception; here the *t*-test indicated that compared with the long face adaptation, the brief face adaptation reduced the curvature aftereffect more than the facial-expression aftereffect, but the ANOVA showed no significant interaction. The reason can be seen from Fig. 6c: decreasing presentation durations reduced the curvature and facial-expression aftereffects by roughly the same absolute amount [the difference between f-f (long) and f-f (brief) is similar to the difference between f-c (long) and f-c (brief)]. Since ANOVA uses a linear model, it considers the interaction between the duration and task non-significant. However, the question we investigated here concerns the relative reduction, measured by the aftereffect ratio between the brief and long conditions, and these ratios were quite different for the curvature and facial-expression aftereffects. Therefore, our hypothesis is better tested by the *t*-test of the ratios than by the ANOVA interaction. ANOVA is often used to avoid accumulation of type-I error caused by multiple comparisons. This is not relevant here because we are not looking for any significant result among multiple comparisons. Instead, our hypothesis specifically predicts that brief adaptation affects curvature aftereffect more than the facial-expression aftereffect. We thus believe that the paired *t*-test is more appropriate for our purposes.

4.4. Perspective

In summary, we found that controlled spatial and temporal manipulations can dissociate low-level curvature and high-level facial-expression aftereffects that are produced by the same adapting curve or face. These results suggest that high-level aftereffects are not completely inherited from adaptation started in lower levels. We argue that a given brain area partially inherits adaptation from lower areas and partially undergoes its own adaptation, and the relative contributions of these two factors depend on stimulus parameters/configurations and physiological properties of the areas. Of course, we have been rather imprecise about exactly what counts as lower and higher levels. Indeed, once one acknowledges the multiple, partially independent sites of adaptation, it becomes pressing to examine the nature of the interaction between levels, be it additive, interactive, or some combination of the two, and to seek richer classes of stimuli offering an even finer grain for dissociating the many intermediate levels of sensory processing.

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