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Brief facial emotion aftereffect occurs earlier for angry than happy adaptation

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ABSTRACT

Prolonged exposure to an emotional face biases our judgement of subsequent face stimulus toward the opposite emotion. This emotion aftereffect has been suggested to occur as early as 35 ms exposure duration in cartoon faces. In the current study, we are interested in investigating the time-course of brief emotional face adaptation, and the relationship between brief emotional face adaptation and prolonged emotional face adaptation. We adapted the subjects from 17 ms to 1000 ms with a happy or angry adapting face. We found that a facial emotion adaptation aftereffect started from 17 ms adapting duration for angry face adaptation, and from 50 ms for happy face adaptation. Factor analysis on the adaptation effects highlighted three different components: brief angry adaptation (17 ms, 34 ms, and 50 ms), prolonged angry adaptation (100 ms and 1000 ms), and happy face adaptation (from 17 ms to 1000 ms). We found that the brief angry face adaptation was negatively associated with the awareness of the adapting face, and the prolonged angry face adaptation was stronger in subjects who perceived the angry adapting face as more negative in valence. Together, these findings suggest that (1) facial emotion adaptation can be induced by brief (17 ms) adapting face presentation; (2) brief angry face adaptation may be related to early visual processing, whereas prolonged angry face adaptation may be related to adaptation at later and higher-level visual emotional processing; and (3) brief and prolonged adaptations may adapt different neural populations. Our findings thus shed light on the current understanding of the neural mechanisms of emotional face adaptation.

1. Introduction

Our vision system is constantly shaped by its past experience. When we are exposed to a face with a specific emotion (e.g., sadness) for an extensive duration, a subsequently presented neutral face will often be perceived as reflecting an emotion in the opposite direction (e.g., happiness). It has been suggested that this face aftereffect is induced via habituation of neural responses after exposure to a stimulus of a certain attribute (in this case a specific emotional expression), resulting in inhibition of behavioral response towards this attribute (Webster & MacLeod, 2011). It has been found that the longer the exposure duration is, the larger this adaptation aftereffect is in face identity (Rhodes, Jeffery, Clifford, & Leopold, 2007) and facial expression adaptation (Burton, Jeffery, Bonner, & Rhodes, 2016). As these time-course studies tested face adaptation strength for adapting durations of 1000 ms and above, we are interested to ask the following questions: can brief (e.g., 17 ms) stimulus exposure result in face adaptation with a similar aftereffect? What is the effect of adapting duration shorter than 1000 ms on face adaptation?

Adaptation is commonly observed in both low-level perception, such as curvature (Gibson, 1933; Mei, Dong, & Bao, 2017) and contrast (Solomon, Peirce, Dhruv, & Lennie, 2004), and higher-level perception, such as face (Fox & Barton, 2007; Leopold, O'Toole, Vetter, & Blanz, 2001; Strobach & Carbon, 2013). In face perception, adaptation was consistently illustrated in the processing of identity (Leopold et al., 2001; Moradi, Koch, & Shimojo, 2005), facial expression (Fox & Barton, 2007; Hsu & Young, 2004; Webster, Kaping, Mizokami, & Duhamel, 2004; Wolfe & Whitney, 2015), viewpoint (Fang, Murray, & He, 2007), gender and ethnicity (Webster et al., 2004), and facial attractiveness (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Ying, Burns, Lin, & Xu, 2019). The typical adaptation paradigm involves an adapting stimulus (e.g., an emotional face) shown for 100 ms – 16 s, and then a test face shown for 100 ms–1600 ms, after 100 ms to a few seconds inter-stimulus-interval (ISI) (Barrett & O'Toole, 2009; Burton et al., 2016; Fang & Murray, 2005; Fang et al., 2007; Hills, Holland, & Lewis, 2010; Kovács, Zimmer, Harza, & Vidnyánszky, 2007; Leopold, Rhodes, Muller, & Jeffery, 2005; Rhodes et al., 2007; Walther, Schweinberger, Kaiser, & Kovács, 2013; Wolfe & Whitney, 2015; Xu, Dayan, Lipkin, &

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Qian, 2008; Zimmer, Zban, Nemeth, & Kovács, 2015; for a review, see Strobach & Carbon, 2013). The strength of the aftereffects is usually measured by the change in response caused by the adapting stimulus. Previous time-course studies in adaptation found that the magnitude of the adaptation increases logarithmically as the adapting duration increases, and decreased exponentially as the ISI/test duration increases (Burton et al., 2016; Leopold et al., 2005; Mei et al., 2017; Rhodes et al., 2007).

In the literature, the briefest adapting duration for facial emotion adaptation (FEA) that has been reported was 35 ms to cartoon faces (Xu, Liu, Dayan, & Qian, 2012). In their study, the researchers observed that briefly presented sad cartoon faces (35 ms) was able to induce an adaptation effect to the subsequently presented cartoon faces (i.e., judging a neutral face as less sad), but the effect was weaker than prolonged adaptation (4000 ms). However, this same adaptation duration has not been reported in real faces. Additionally, other questions remain unanswered. One of the unanswered questions is whether a briefer adapting duration (e.g., 17 ms) can induce emotional face adaptation? The answer to this question could potentially reflect the extent to which low-level orientation/curvature perception and higher-level object/face perception (such as facial emotion) share common coding principles (Strobach & Carbon, 2013). For example, orientation adaptation was found to be possible with an adapting duration of 17–25 ms (Felsen et al., 2002). Adapting durations of 27 ms and 35 ms were sufficient to generate shape and curve adaptation aftereffects respectively (Suzuki, 2001; Xu et al., 2012). If FEA can be induced by a mere 17 ms adapting duration, it suggests that orientation adaptation might be contributing to the FEA.

Another important consideration is how brief FEA and prolonged FEA are related to each other. One of the most cited frameworks for understanding emotional face perception is proposed by Haxby, Hoffman, and Gobbini (2000). In their framework, all facial expressions undergo the same processing hierarchical procedure, from facial feature processing at the inferior occipital gyrus, to processing of facial movement at the superior temporal sulcus, and finally to the extended system for emotion perception at the amygdala or the insula. Thus, the facial emotion adaptation at higher levels processing may be inherited from its local feature processing (e.g., mouth curvature) at early processing (Xu et al., 2008). Relatedly, previous studies provided evidence that face-related adaptation (with adapting durations above 1000 ms) consisted of high-level visual adaptation by testing the size invariance (Hsu & Young, 2004; Zhao & Chubb, 2001) and location specificity (Afraz & Cavanagh, 2008; Xu et al., 2008) in face adaptation. In these studies, the aftereffect was weaker or diminished when the size and the location of the adapting face did not match with the test face. The reduction of the aftereffect was attributed to a reduced low-level adaptation that was subsequently inherited by the next stage in the processing hierarchy. In the current study, we investigate associations between different stages of emotional face perception via brief adaptation and prolonged adaptation, and any correlations therein. Specifically, if the prolonged FEA inherits adaptation from earlier stages it should correlate with the brief FEA.

This study aims to investigate the effect of brief adapting duration on FEAs. We ask two questions: (1) Can FEA be induced by brief presentation (e.g., 17 ms) of adapting face stimuli? We manipulated the adapting duration varying from 17 ms to 1000 ms and tested the subjects on their judgment of the subsequently presented face's emotion. (2) Are brief and prolonged FEAs associated with each other? If the information flow in emotional face perception is hierarchical, we expect that the two types of adaptations are related. Should this be the case, the adaptation at later stages of processing should inherit adaptation from earlier stages of processing. Two adaptation experiments were conducted. The experimental paradigms of the two experiments were the same except that the facial identities of the adapting face and the test face were swapped in the two experiments. Such manipulation is to test the reliability or replicability of results found. Since reducing presentation duration of an adapting face will inevitably reduce the visibility of the face, we also asked the subjects to complete an awareness check and examined the effect of the adapting face's awareness on the FEAs.

2. Methods

2.1. Participants

Twenty-three subjects (15 females, mean age = 24.73) and twenty-two subjects (17 females, mean age = 24.52), with normal or corrected-to-normal vision, were recruited from Nanyang Technological University, Singapore for Experiment 1 and Experiment 2 respectively. Informed consent to participate in the experiments was obtained from each subject prior to experiment. The data of one subject from Experiment 1 was removed from the analysis due to response abnormality (angry responses and happy responses failed to exceed 50% at any of the test faces in more than two blocks resulting in a flat psychometric curve fitted with the responses). As a result, twenty-two subjects' data was included in the analysis in Experiment 1. This study was approved by the Institutional Review Board (IRB) at Nanyang Technological University, Singapore, by the Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving human subjects.

2.2. Apparatus

The experiment was designed and run in Eprime2 (Psychology Software Tools, Inc.) on a Dell XPS 8700 (Intel Core i7) with Dell Ultrasharp U2412M 24-inch screen in the laboratory room at Nanyang Technological University, Singapore. The monitor's spatial resolution was 1920×1200 pixels, and the vertical refresh rate was 60 Hz. The chin rest was placed 57 cm away from the monitor to stabilize subjects' head position.

2.3. Visual stimuli

Faces of two male identities (PE and WF) were selected from the Picture of Facial Affect (PoFA; Ekman & Friesen, 1976) collection. The faces of WF (Angry: WF3-4; Happy: WF2-11) were used as the adapting faces and those of PE (Angry: PE2-21; Happy: PE2-26) were used as the test faces in Experiment 1. The facial identities of the adapting face and the test faces were swapped in Experiment 2. To generate the test faces, the neutral faces of WF (WF2-5) and PE (PE2-4) were also used. We used Morph Man 2016 (STOIK Imaging, Moscow, Russia) to morph the happy test face with his own neutral face to produce a face series ranged from 0% (happiest) to 50% (neutral), and morphed his angry test face with his neutral face to produce another face series ranged from 50% (neutral) to 100% (angriest). Out of the entire face series, we chose seven faces (20%, 30%, 40%, 50%, 60%, 70%, and 80% in proportion of angry level) as the test face set. The selected faces were resized and cropped using Photoshop CS5 (Adobe System Inc., CA, USA) such that they were all of the same size ($3.8^\circ \times 5^\circ$) and only the face region was shadowed with a grey background of the same average luminance as the faces. Therefore, the identities of the adapting face and the test face were different, but their sizes were the same and presented at the same location on the computer screen.

2.4. Procedure

We used the method of constant stimuli and the two-alternative forced choice paradigm (2-AFC) in the experiment. Subjects did not receive any feedback for their responses during the experiment.

This experiment investigated the FEA by brief adapting durations. We manipulated the adaptation duration (17 ms, 34 ms, 50 ms, 100 ms, and 1000 ms) and the emotion (angry and happy) of the adapting face.

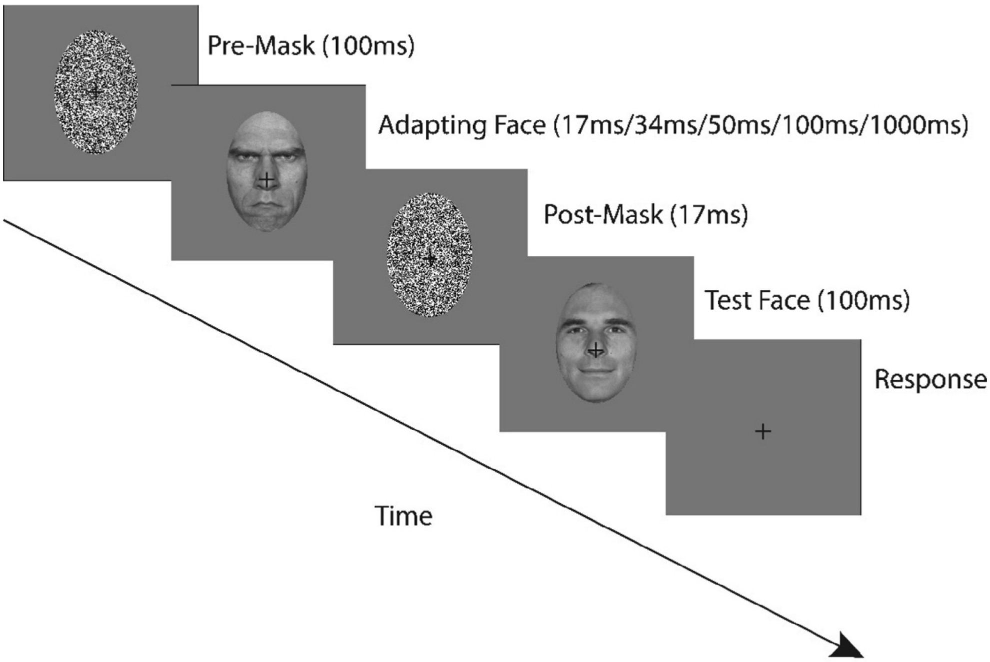

Fig. 1. The sequence of an adaptation trial. The trial started with a 100 ms pre-mask, then an angry or happy adapting face was presented on the screen. The presentation duration of the adapting face varied across blocks: 17 ms, 34 ms, 50 ms, 100 ms, and 1000 ms. After 17 ms post-mask, the test face (morphed from angry to happy) presented for 100 ms. Subjects were required to respond to the emotion of the test face as fast as possible or within 1000 ms. In the baseline, the adapting face was not presented. The mask, adapting face and test face were presented at the same location. The average luminance of the adapting face, mask, test face and background were matched in the experiment.

The condition without adapting face served as the baseline. Therefore, there were 11 conditions in total: baseline, adapting to angry or happy face for 17 ms, 34 ms, 50 ms, 100 ms, or 1000 ms. The conditions were presented in a randomized block design. Each condition had 15 repetitions of each test face. The order of the test faces within each condition was pseudo-randomized. To avoid a possible carry-over effect between the successive conditions, the subjects were asked to rest for the same duration as the adapting condition lasted (e.g., rested for 5 min for a 5-minute condition). Before data collection, practice trials were provided until the subjects felt comfortable with the task.

2.4.1. Adaptation task

The trial sequence is illustrated in Fig. 1. Each trial of the blocks began with a 100-ms Gaussian noise mask. After that, an adapting face appeared followed by a 17 ms post-mask at the center of the screen. The post-mask is provided to separate the adapting face from the test face. Following the post-mask, a test face was presented for 100 ms at the same location. The subjects had to judge whether the test face was angry or happy by pressing the keys “Z” and “M” respectively as fast as possible or within 1000 ms. The next trial began after a 1000 ms inter-trial interval.

2.4.2. Awareness check task

To assess their awareness of the adapting face under different durations, the subjects were instructed to complete an awareness check task after the completion of all experimental conditions in the adaptation and baseline tasks. The trial sequence of the awareness check task was the same as the experimental conditions, except that (1) the subjects were asked to report the emotion of the adapting face instead of the test face; (2) the duration and the emotion of the adapting face varies across trials; and (3) only the neutral face was used as the “test” face throughout the entire task. There were 15 repetitions for each adapting face in the awareness check task.

2.4.3. Stimulus validation task

Subjects in Experiment 2 also went through a stimulus validation task at the end of the experiment. In each trial, the subjects were asked to rate the intensity and valence of the presented face in a 7-point Likert scale (intensity: 1 = not emotional at all, 7 = very emotional; valence: 1 = very negative, 7 = very positive). Angry, neutral and happy faces of PE and WF were included. Each face appeared twice and thus there were 12 trials in total.

2.5. Data analysis

The decisions were extracted and analyzed from the subjects’ responses. The data from the trials with no responses were discarded. The decision for each condition was sorted into proportion of “angry” responses to each step of test face. The proportion of angry responses was plotted against the proportion of angry level of the test faces, and the resulting psychometric curve was fitted into a sigmoidal function with the following form:

$$f(x) = 1/[1 + e^{-a(x-b)}]$$

where b represents the value of the point of subjective equality (PSE), at which angry level of the test face generates 50% of angry responses, and $a/4$ indicates the slope at the PSE. The magnitude of facial emotion aftereffect (FEA) was measured by the difference in PSEs between an adaptation condition and the baseline condition. In the angry conditions, the more positive the value is, the stronger the adaptation effect is since the adaptation aftereffect is repulsive; whereas in the happy conditions, the more negative the value is, the stronger the adaptation effect is.

Next, we correlated the PSE shifts across duration conditions within emotion and across emotions to examine the relationship among the adaptation effects. Since visual inspection of the correlations suggested that the adaptation effects could be grouped into 3 categories, we performed a PCA factor analysis on the covariance matrix of the PSE shifts to verify our inspection. The number of components extracted was based on eigenvalue (e.g., Eigenvalue > 1 times the mean eigenvalue). We used Varimax as the rotation method. A PSE shift was said to be related to a component if its loading was greater than 0.4 or lower than −0.4 on that component. The resulted components were then correlated with the intensity ratings and the valence ratings of the adapting faces obtained from Experiment 2. This analysis was to test if any of the components was related to the high-level visual processing of the facial emotion.

Lastly, to investigate if the FEAs were affected by the awareness of the adapting faces, we correlated the PSE shifts with the recognition rates of the adapting faces within the same adaptation durations using

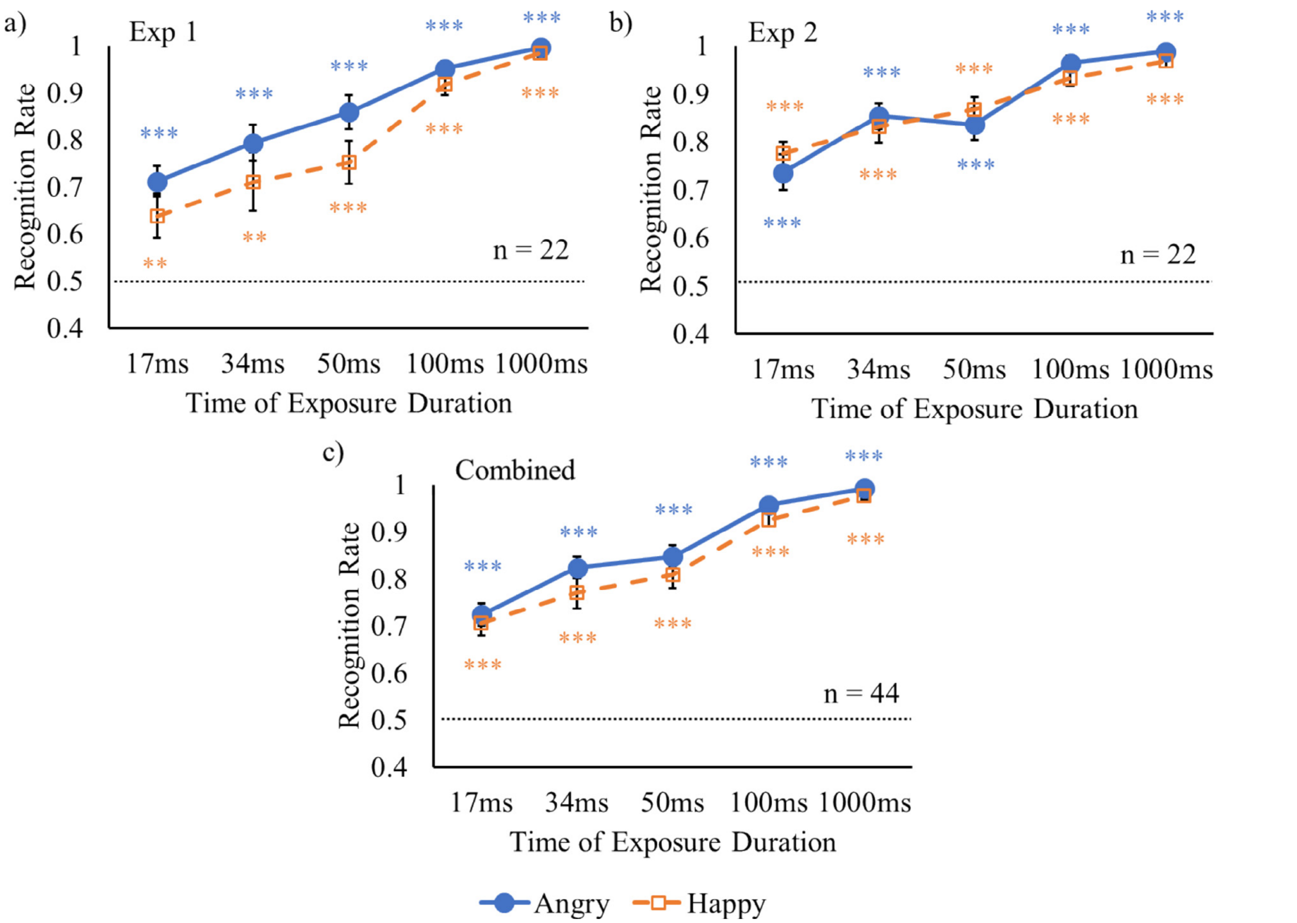

Fig. 2. Recognition rates of the adapting faces (a) in Experiment 1, (b) in Experiment 2, and (c) when combining data from Experiment 1 and Experiment 2. The dotted line indicates the chance performance (50%). The ** and *** indicates that the recognition rate of the angry (blue filled circle with solid line) or happy (orange open square with dashed line) adapting face significantly above chance performance at $p < .01$ and $p < .001$ respectively. Error bars indicate ± 1 standard error of mean. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

two-tailed Pearson's correlations. All statistical analyses were conducted in Matlab R2018a (Mathworks, MA, USA) and SPSS Statistics 25 (IBM, NY, USA).

3. Results

3.1. Adapting face awareness

We first examined how the awareness of the adapting faces was affected by its exposure duration. The results from the awareness check tasks of Experiment 1 (Fig. 2a) and Experiment 2 (Fig. 2b) reflected consistent reporting. The awareness of the adapting face increased as the adapting duration increased. On average, the recognition rates of all duration conditions were significantly higher than chance level, i.e., 50% ($ps < 0.01$).

3.2. Facial-emotion adaptation aftereffect

We then examined the FEA after adapting to the angry or happy face for 17–1000 ms. The FEA is quantified by the PSE shift of adaptation conditions from that of the baseline in psychometric curves. Individual psychometric curves for each condition are shown in Fig. 3(a and c). After adapting to the angry face (Fig. 3a), for example, the psychometric curves shift to the right of the baseline, indicating less angry responses (more happy responses), therefore, a repulsive aftereffect. The summary of aftereffects is shown in Fig. 3(b) for angry adaptor and (d) for happy adaptor. We found an earlier onset of FEA in the angry adaptation (17 ms) than the happy adaptation (50 ms). In angry adaptation conditions, it emerged as early as 17 ms (17 ms: $t(43) = 3.40$, $p = .001$; 34 ms: $t(43) = 2.71$, $p = .010$; 50 ms: $t(43) = 4.93$, $p < .001$; 100 ms: $t(43) = 5.35$, $p < .001$; 1000 ms: $t(43) = 5.67$, $p < .001$). In contrast, in happy adaptation conditions, the aftereffect was significant from 50 ms adaptation and onwards (50 ms: $t(43) = -2.22$, $p = .032$; 100 ms: $t(43) = -3.00$, $p = .004$; 1000 ms: $t(43) = -3.98$, $p < .001$).

3.3. Correlation across FEAs and factor analysis

To test if the adaptation aftereffects in different conditions were associated with each other, we performed pairwise correlation on the FEAs (measured by PSE shifts from the baseline) across conditions within the same adapting emotion (Tables 1 and 2) and across emotions from both experiments (Table 3). For angry face adaptation (Table 1), the FEAs at 17 ms, 34 ms and 50 ms were significantly correlated with each other ($ps < 0.05$). However, the FEAs at 100 ms were not correlated with any other adaptation duration except 1000 ms ($r = 0.74$, $p < .001$). The angry FEA at 1000 ms was significantly correlated with that at 50 ms ($r = 0.42$, $p = .005$) and was approaching significant correlation with that at 17 ms ($r = 0.30$, $p = .050$). Therefore, it appears that 100 ms may be the threshold duration differentiating the brief (17, 34, and 50 ms) and prolonged adaptation durations (100 and 1000 ms) for angry emotion. In contrast, the adaptation aftereffects of happy face were all correlated with each other ($ps < 0.01$, Table 2). Across the two emotions, the angry FEA at 34 ms was significantly

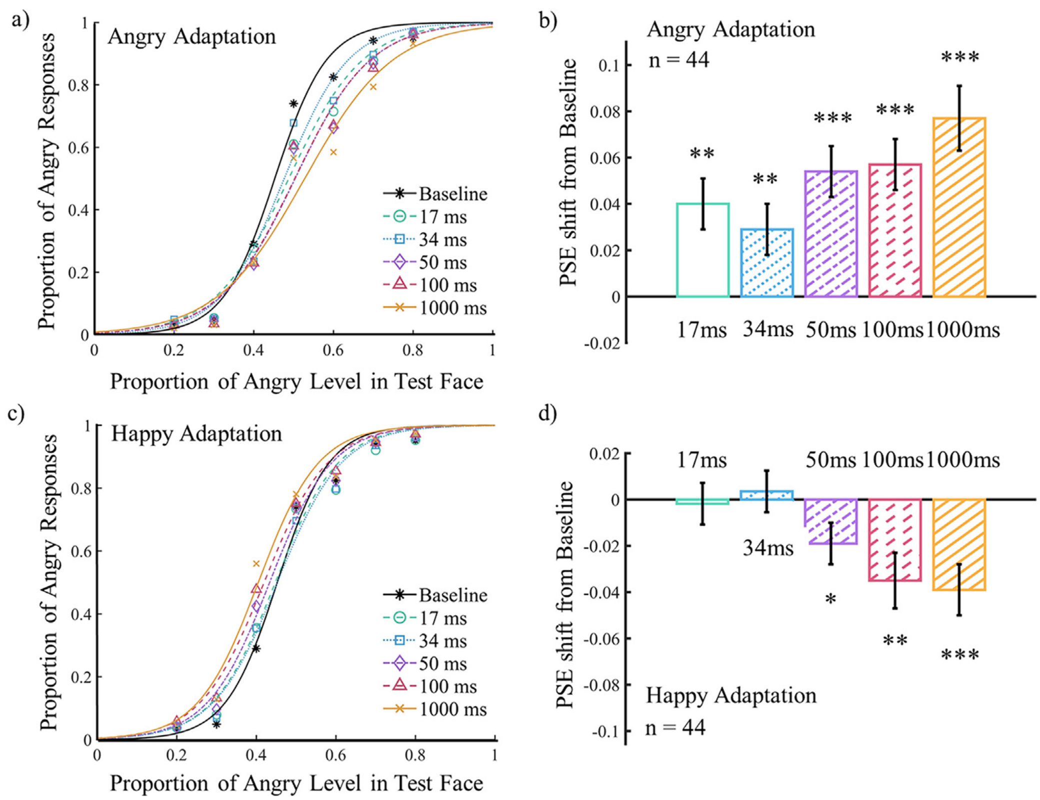

Fig. 3. Adaptation aftereffect on facial expression judgment. (**a, c**) Psychometric curves plotted as a function of the proportion of angry responses (averaged across all 44 participants) against the percentage of angry level in the test face when the adapting face was (a) angry or (c) happy under the following adapting duration conditions: 0 ms (baseline), 17 ms, 34 ms, 50 ms, 100 ms, and 1000 ms. (b, d) Summary of PSE shifts (adaptation aftereffect). A positive value indicates a rightward shift of psychometric curve, i.e., less angry responses towards the test faces after adapting to the angry face; whereas a negative value indicates the opposite, after adapting to the happy face. When the adapting face was (b) angry, the more positive the value is, the stronger the adaptation effect is, whereas when the adapting face was (d) happy, the more negative the value is, the stronger the adaptation effect is. $^{*}p < .05$, $^{**}p < .01$, $^{***}p < .001$. Error bars indicate ± 1 standard error of mean.

Table 1
Correlations of FEAs across angry face adaptation duration conditions.

Angry	17 ms	34 ms	50 ms	100 ms	1000 ms
17 ms		0.58^{***}	0.68^{***}	0.23	$0.30^{\sim}$
34 ms			0.36^{*}	0.04	0.09
50 ms				0.18	0.42^{**}
100 ms					0.74^{***}
1000 ms					

~ p < .06.
* p < .05.
** p < .01.
*** p < .001.

Table 2
Correlations of FEAs across happy face adaptation duration conditions.

Happy	17 ms	34 ms	50 ms	100 ms	1000 ms
17 ms		0.62^{***}	0.60^{***}	0.71^{**}	0.66^{***}
34 ms			0.57^{***}	0.58^{***}	0.62^{**}
50 ms				0.61^{***}	0.64^{**}
100 ms					0.72^{***}
1000 ms					

** *p* < .01.
*** *p* < .001.

correlated with all happy FEAs (*ps* < 0.001, Table 3); the angry FEA at 17 ms was significantly correlated with happy FEAs at 17 ms ($r = 0.42$, $p = .005$) and 100 ms ($r = 0.31$, $p = .044$).

Visual inspection of the correlation results suggested that the FEAs might be grouped into different categories. To verify our inspection, we conducted a factor analysis on the FEAs from both experiments. Minimally three components were identified (Table 4). The angry FEAs were split into two components: FEA at 17 ms, 34 ms and 50 ms were factorized into one component (Component 2) while those at 100 ms and 1000 ms were loaded into another component (Component 3).

Table 3
Correlations of FEAs between angry face adaptation and happy face adaptation duration conditions.

Angry\Happy	17 ms	34 ms	50 ms	100 ms	1000 ms
17 ms	0.42^{**}	0.26	0.26	0.31^{*}	0.23
34 ms	0.66^{***}	0.60^{***}	0.52^{***}	0.78^{***}	0.68^{***}
50 ms	0.20	0.07	0.07	0.14	0.09
100 ms	0.10	0.11	0.14	−0.14	0.16
1000 ms	0.08	0.09	0.15	−0.10	0.04

* *p* < .05.
** *p* < .01.
*** *p* < .001.

Table 4
Rotated component matrix on FEAs after PCA on covariance. Loadings higher than 0.40 are highlighted in bold font.

	Component 1	Component 2	Component 3
Angry 17 ms	0.26	**0.87**	0.12
Angry 34 ms	**0.78**	**0.46**	−0.06
Angry 50 ms	0.01	**0.90**	0.19
Angry 100 ms	0.07	0.04	**0.90**
Angry 1000 ms	< 0.01	0.27	**0.92**
Happy 17 ms	**0.81**	0.22	0.03
Happy 34 ms	**0.77**	0.03	0.09
Happy 50 ms	**0.78**	< 0.01	0.16
Happy 100 ms	**0.89**	0.17	−0.21
Happy 1000 ms	**0.89**	< 0.01	0.07

Furthermore, angry FEA at 34 ms was also loaded in the same component (Component 1) as all the happy FEAs.

3.4. Correlation between FEA components and stimulus validation ratings of the adapting face

To test if any of the components were related to any high-level

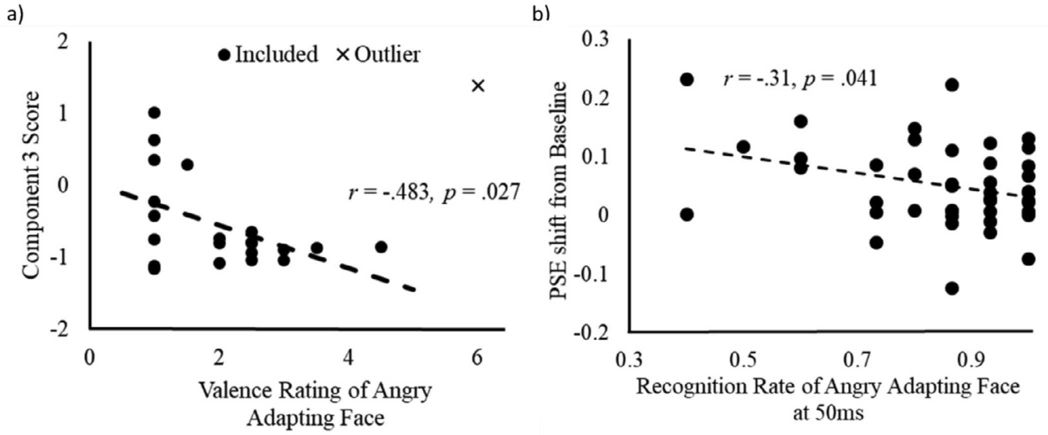

Fig. 4. Correlation between (a) the valence ratings of angry adapting face and Component 3 scores extracted by the factor analysis. The scores were normalized and centered to zero. Component 3 was negatively correlated with valance rating (1 = very negative; 7 = very positive) of angry adapting face; thus, the more negative the angry adapting face was rated, the stronger the prolonged angry face adaptation. Data from one subject was excluded from this analysis because his valence rating was identified as an outlier (marked by "×"); (b) the adapting face awareness and the angry FEA at 50 ms.

visual properties of emotional face perception, we correlated the component scores obtained from the factor analysis with the intensity ratings and the valence ratings of the adapting faces in Experiment 2. Since only the subjects from Experiment 2 did the stimulus validation task, we only included the data from these 22 subjects in this analysis. One subject's valence rating on the angry adapting face was found to be an outlier (rated 6 when the mean was 2.18 and the standard deviation was 1.30), so his/her valence rating was removed from the correlation analysis.

Of all three components, only Component 3, which is related to the angry prolonged FEAs (Table 4), was significantly and negatively correlated with the valence rating of the adapting face ($r = -0.48$, $p = .027$; Fig. 4a). The negative correlation indicates that the more negative in valence the adapting face was to the subjects, the stronger the prolonged angry face adaptation was. None of the other components were correlated with any of the ratings ($ps > 0.05$).

3.5. Correlation between FEAs and adapting face awareness

To test whether the awareness of the adapting face influenced the FEA, we correlated the awareness of the adapting face with its FEA within each adaptation duration. Pearson's correlation analysis showed that only the angry FEA at 50 ms reached significance ($r = -0.31$, $p = .041$, Fig. 4b). Therefore, surprisingly, the better the recognizability of the adapting angry face, the weaker the adaptation aftereffect; possible reasons are discussed in the *Discussion* section. On the other hand, the strength of happy FEAs was not correlated with any of the corresponding face awareness ($ps > 0.05$). Therefore, the awareness of the adapting face plays distinctive roles in happy or angry FEAs, dependent upon adaptation durations.

4. Discussion

We found that briefly adapting for 17 ms to angry faces generated significant FEA; whereas happy FEA requires a longer adapting duration, 50 ms. The FEAs can be grouped into three clusters: (1) angry FEAs at 17 ms, 34 ms, and 50 ms; (2) angry FEAs at 100 ms and 1000 ms; and (3) all happy FEAs and angry 34 ms. This hints that distinct neuron populations being adapted for angry and happy FEAs, and for brief and prolonged angry FEAs. In general, angry FEAs were stronger than happy FEAs. One might think this is because of the difference in the emotion intensity ratings of happy and angry adapting faces. However, the intensity ratings of the two emotions showed marginally significant difference ($t(21) = 2.05$, $p = .053$). Interestingly, we found that the prolonged angry FEA (100 ms and 1000 ms) was significantly correlated with the perceived valence of the adapting face suggesting that prolonged adaptation may be related to emotion processing.

Theoretical models suggest that emotional face processing follows a sequence of stages from early to late cortical areas (Duchaine & Yovel, 2015; Haxby et al., 2000). One may expect that the adaptation at the early processing stage should be carried over to that at the later stage (Hsu & Young, 2004; Kovács et al., 2007; Xu et al., 2008, 2012). The correlation between brief adaptation and prolonged adaptation was, however, not continuous in angry adaptation. It appears that distinct neuron populations were adapted for angry face adaptation for the two FEAs. One plausible explanation is that the brief angry face presentation (17–50 ms) adapted the early stage and the prolonged presentation (100–1000 ms) adapted the later stage of face processing. Our findings that the prolonged, but not the brief, angry FEA was stronger in subjects who perceived the angry adapting face as more emotionally negative suggests that the prolonged adaptation is related to a later stage of, and presumably higher-level, face processing. Previous studies have shown that FEA with comparable prolonged adapting durations survives size variation between adapting face and test face (Hsu & Young, 2004), and is transferrable from faces of different identities (Fox & Barton, 2007) and auditory emotional adaptors (Wang et al., 2017). The findings in the current study suggest that prolonged FEA may consist of the adaptation of high-level emotional information. However, this does not exclude the existence of low-level visual perception in prolonged adaptation in emotion perception.

Visual perception that are at the lower level than emotion perception can be adapted with brief adapting durations. This adaptation duration increases when the perception is more complex and at a higher-level. For example, 17 ms is sufficient for orientation adaptation (Felsen et al., 2002), while 27 ms were the briefest adapting duration for shape adaptation (Suzuki, 2001) and 35 ms for curve and cartoon face adaptations (Xu et al., 2012). Furthermore, 35 ms adaptation at the lower-level visual processing (e.g., curvature) was found to suffice to affect subsequent emotional face judgement (Xu et al., 2012). Therefore, brief low-level visual adaptation can propagate to the higher-level visual perception. One explanation to the brief angry FEA we observed at 17–50 ms is that it may be related to the adaptation of visual features that are at the lower level than facial emotion, such as orientation perception or shape perception. However, this does not exclude the possibility of the involvement of fast and coarse emotion perception.

The negative correlation observed between the awareness and the FEA at 50 ms in this study supports this possibility. Subjects who were more aware of the emotion of the briefly presented angry adapting face demonstrated a weaker FEA than those who were less aware of the emotion. The data from the subjects (Fig. 4b) suggest that there are relatively more subjects who were able to judge the faces' emotion correctly as angry, and this negative correlation was largely contributed by the few subjects who showed strong adaptation aftereffect even when they were not able to correctly discriminate the emotion of the adapting faces. This is not surprising, however, because past literature in psychophysics also showed that emotional face adaptation is possible even without awareness of the adapting emotion (Adams, Gray, Garner, & Graf, 2010; Burns, Martin, Chan, & Xu, 2017; Luo, Wang, Schyns, Kingdom, & Xu, 2015; but see Yang, Hong, & Blake, 2010). Furthermore, such adaptation without awareness might not be related to higher-level visual neural regions (e.g., fusiform face area, FFA) because it has been reported that the activation of these neural regions tends to attenuate when the visual stimuli were presented under awareness threshold (Jiang & He, 2006; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). In contrast, lower-level visual areas, e.g., primary visual cortex and extrastriate cortex (e.g., V4), and subcortical structures for early emotion categorical perception (e.g., amygdala, superior colliculus and pulvinar) were reported to be activated without visual awareness (Leopold & Logothetis, 1996; Luo et al., 2010; Motter, 1993; Pasley, Mayes, & Schultz, 2004; Tamietto & De Gelder, 2010; Tong, 2003; Williams et al., 2004). Therefore, the negative correlation observed between the awareness and the FEA at 50 ms in this study suggests that this brief FEA is related to the visual perception that is processed at or earlier than V4 (see Kohn, 2007 for a review), to the subcortical structures (Tamietto & De Gelder, 2010; but see Pessoa & Adolphs, 2010).

Notably, we have not demonstrated that prolonged angry FEA is completely isolated from adaptation at early processing stages. In fact, our finding that the angry FEA at 1000 ms but not at 100 ms was associated with that at 50 ms suggests the longer the adapting duration, the more the adaptation from early visual processing contributes to later and high-level visual adaptation. Arguably, this may be related to recurrent connections in the neural network (Felsen et al., 2002; Teich & Qian, 2002). Early studies found that brief exposure to an orientation for 17–25 ms can induce a repulsive orientation adaptation effect at V1 (Felsen et al., 2002). The strength of the aftereffect is weakened as the adaptation duration increases, and diminishes at 100 ms. The repulsive orientation adaptation reemerged as the adaptation duration increases to 400–500 ms (Dragoi, Sharma, Miller, & Sur, 2002; Müller, Metha, Krauskopf, & Lennie, 1999). This time-course of orientation adaptation may explain the brief angry FEAs' disconnection with 100 ms angry FEA and their reconnection with 1000 ms angry FEA.

Happy face adaptations were found to be associated across all adapting durations. Furthermore, these adaptations were also related to brief angry face adaptation only at 34 ms. If brief angry face adaptation is the result of low-level visual adaptation, happy face adaptation may be rooted in the same mechanism. In the literature, the perception of happy emotion was shown to be dependent upon the feature of the mouth region (Calder, Keane, Young, & Dean, 2000; Calvo, Fernández-Martín, & Nummenmaa, 2014; Eisenbarth & Alpers, 2011; Gosselin & Schyns, 2001; Wegrzyn, Vogt, Kireclioglu, Schneider, & Kissler, 2017) and mouth curvature (Dickinson & Badcock, 2013; Xu et al., 2008). For example, compared to perceiving negative emotions, people tend to pay more attention to the mouth region than eye regions when perceiving happy faces (Eisenbarth & Alpers, 2011). Hiding the mouth region impedes the accuracy and increases the reaction time in categorizing happy faces from other emotional faces (Calder et al., 2000; Calvo et al., 2014). Moreover, both brief or prolonged exposure to a concave curve can generate FEA such that the subsequently presented face was perceived as more happy (Xu et al., 2008, 2012). These findings highlight the possibility that curvature adaptation is vital for happy FEA. Interestingly, but unexpectedly, stronger happy FEA was associated with weaker brief angry FEA in the current study. Given the attention differences in facial features for happy (mouth region) and angry faces (eye regions) (Calvo & Nummenmaa, 2008), the inverse relationship between happy and angry FEAs may be explained by the differences in the foci of attention of our subjects - those showed stronger aftereffect by happy face adaptation may have paid more attention to the mouth region, and paid less attention to the eye regions which may contain essential information for brief angry face adaptation to occur.

One may argue that the absence of the brief happy FEAs is because the subjects could not see the adapting face (e.g., Yang et al., 2010; but see Adams et al., 2010; Burns et al., 2017). Our results from the awareness check task does not support such an argument. Across all conditions, subjects' performance was above chance; they thus could perceive all adapting faces accurately even when the exposure duration was as short as 17 ms (similar for angry and happy faces). Awareness of the adapting face itself, therefore, is not a sufficient criterion for brief FEA induction. Moreover, brief FEA appears to be emotion specific. This emotion specificity is consistent with the assertion that there are distinct, but maybe overlapping, neural pathways for processing faces with different emotions (Fusar-Poli et al., 2009; Vytal & Hamann, 2010).

Our results demonstrated that the FEAs were different for brief exposure and prolonged exposure to adaptors, and we argue that the brief FEA is related to early or coarse visual processing, while the prolonged FEA is related to the later and higher-level emotional processing. While we provided the evidence for the dissociation between brief and prolonged FEAs, future studies are invited to identify the particular brain regions, cortical or subcortical, activated for brief FEAs.

5. Conclusions

We report for the first time that brief adaptation (17 ms) to emotional faces generated significant aftereffect. Brief angry face adaptation, prolonged angry face adaptation, and happy face adaptation were not associated, suggesting that they may activate different neural populations. Prolonged angry FEA was stronger in subjects who perceived the angry adapting face as more negative, indicating that prolonged angry FEA is related to emotional processing. In contrast, brief angry FEA was stronger in subjects who were less aware of the adapting face, indicating that the brief FEA is associated with the early visual processing.

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