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Short Note

Retinotopy of Facial Expression Adaptation

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Abstract

The face aftereffect (FAE; the illusion of faces after adaptation to a face) has been reported to occur without retinal overlap between adaptor and test, but recent studies revealed that the FAE is not constant across all test locations, which suggests that the FAE is also retinotopic. However, it remains unclear whether the characteristic of the retinotopy of the FAE for one facial aspect is the same as that of the FAE for another facial aspect. In the research reported here, an examination of the retinotopy of the FAE for facial expression indicated that the facial expression aftereffect occurs without retinal overlap between adaptor and test, and depends on the retinal distance between them. Furthermore, the results indicate that, although dependence of the FAE on adaptation-test distance is similar between facial expression and facial identity, the FAE for facial identity is larger than that for facial expression when a test face is presented in the opposite hemifield. On the basis of these results, I discuss adaptation mechanisms underlying facial expression processing and facial identity processing for the retinotopy of the FAE.

Keywords

Face processing, facial expression, retinotopy, adaptation

1. Introduction

Faces provide a wealth of information essential to social communication. We can easily assess a person's identity and emotional state from facial information. What are the underlying neural mechanisms for face processing? To address this question, many studies have used a face adaptation paradigm (Adams *et al.*, 2010; Afraz and Cavanagh, 2008; Anderson and Wilson, 2005; Fox and Barton, 2007; Jiang *et al.*, 2006; Leopold *et al.*, 2001; Matsumiya, 2012, 2013; Moradi *et al.*, 2005; Rhodes *et al.*, 2004; Ryu *et al.*, 2008; Skin-

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ner and Benton, 2010; Webster *et al.*, 2004; Webster and MacLin, 1999). This paradigm is a powerful means to investigate the neural representations involved in face processing. One measure of such adaptation is the face aftereffect (FAE). In the FAE, adaptation to a face belonging to a facial category causes a subsequently neutral face to be perceived as belonging to an opposite facial category.

One of the most important questions related to the FAE is whether it reflects specific neural processes of face perception (Zimmer and Kovacs, 2011). When the adaptation and test faces are presented on the same retinal position, the FAE will be caused by adaptation of low-level feature processing and higher-level face processing. To distinguish aftereffects for faces from aftereffects for low-level features, it is important to determine the specificity of the FAE. Previous psychophysical studies have shown that FAEs can tolerate large degrees of retinal translation (i.e., position invariance — Leopold *et al.*, 2001; Melcher, 2005; Moradi *et al.*, 2005), which is different from the characteristics of low-level feature adaptation. Electrophysiological studies have reported that the inferior temporal neurons show selective responses to faces (Afraz *et al.*, 2006) and have very large receptive fields up to 30° (Desimone *et al.*, 1984; Gross *et al.*, 1972; Ito *et al.*, 1995; Logothetis *et al.*, 1995; Schwartz *et al.*, 1983; Tovee *et al.*, 1994). These findings suggest that face-selective neurons in higher-level areas of the cortex that have large receptive fields can adapt and might represent the neural basis of FAEs (Rhodes and Leopold, 2011; Zimmer and Kovacs, 2011).

However, several electrophysiological studies have reported much smaller receptive fields for neurons in the inferior-temporal cortex, as small as 2.5° (DiCarlo and Maunsell, 2003; Op De Beeck and Vogels, 2000; Rolls *et al.*, 2003). This implies that FAEs can change depending on the retinal position even though the FAE reflects the adaptation of higher-level face processing, not low-level feature processing. Recent studies have reported retinal position specificity of the FAE in the gender-specific FAE (Kovacs *et al.*, 2005, 2007), the facial identity aftereffect (Afraz and Cavanagh, 2008) and the facial expression aftereffect (Xu *et al.*, 2008). These results suggest that the FAE relies on both position-invariant and position-specific representations. However, other recent studies have suggested that not all aspects of FAEs can be attributed to a common mechanism (Storrs and Arnold, 2012; Zhao *et al.*, 2011), so it is unclear whether the characteristic of position specificity of the FAE in one facial aspect is the same as that of the FAE in another facial aspect. In this study, I addressed this issue by making use of facial expression aftereffects and facial identity aftereffects. To compare position specificity of the facial expression aftereffect with that of the facial identity aftereffect, I replicated the experiment of Afraz and Cavanagh (2008) for the facial expression aftereffect.

2. Methods

2.1. Participants

One woman and three men (aged 21–39 years) participated in experiments where the adaptation and test stimuli were images of the same person. Four men (aged 22–41 years) participated in an additional experiment where the adaptation and test stimuli were images of different persons. Participants had normal or corrected-to-normal vision.

2.2. Apparatus and Stimuli

Participants sat in a dark room with their head immobilized by forehead and chin rests at a distance of 37 cm from a display. Visual stimuli were presented on a 19-inch cathode ray tube monitor (Samsung SyncMaster 997MB, 1280 $\times$ 1024 pixels, 75 Hz refresh rate) controlled by a computer (Dell Precision T3400) running Reachin API (Reachin Technologies). Visual stimuli consisted of a realistic computer graphics (CG) face and a gaze point. An exemplar of the front view of a male face was taken from a human model included in a CG software application. Adaptation stimuli consisted of two facial expressions (happy and sad) generated by the CG software on the exemplar. Test stimuli consisted of morphed faces on a happy-to-sad continuum created with a morphing software application. The morph rate of the face was varied from -35% to 35% in 14% increments (Fig. 1a). Zero represented an averaged face between happy and sad and positive to negative values corresponded to sad to happy. Face stimuli were approximately 3° of the visual angle in diameter and were presented at 3° of visual angle eccentricity from the gaze point (Fig. 1b). Local adaptation was avoided by slightly moving adaptation stimuli around the presentation location during adaptation. Adaptation stimuli moved back and forth smoothly along a short path around a display circle spanning an 11.25° sector (0.6° of the visual angle) of an imaginary circle at 11.25°/s. The midpoint of the 11.25° sector was defined as the adaptation location for the corresponding stimulus.

2.3. Procedure

FAE magnitude was measured by the method of constant stimuli. Each trial began with a red gaze point presented at the center of the display. While looking at the gaze point, the participant adapted to the face stimulus for 5 s. Then, 0.1 s after the adaptation stimulus disappeared, the test stimulus was presented for 0.5 s. Figure 1b depicts the stimulus sequence. After test presentation, the participant made a two-alternative forced-choice response to classify the test stimulus as happy or sad. The adaptation location was at the right side of the display, which was 0° on the display circle (see Fig. 1b). The location of the test stimulus was randomly chosen from five positions (0°, 22.5°, 45°, 90° and

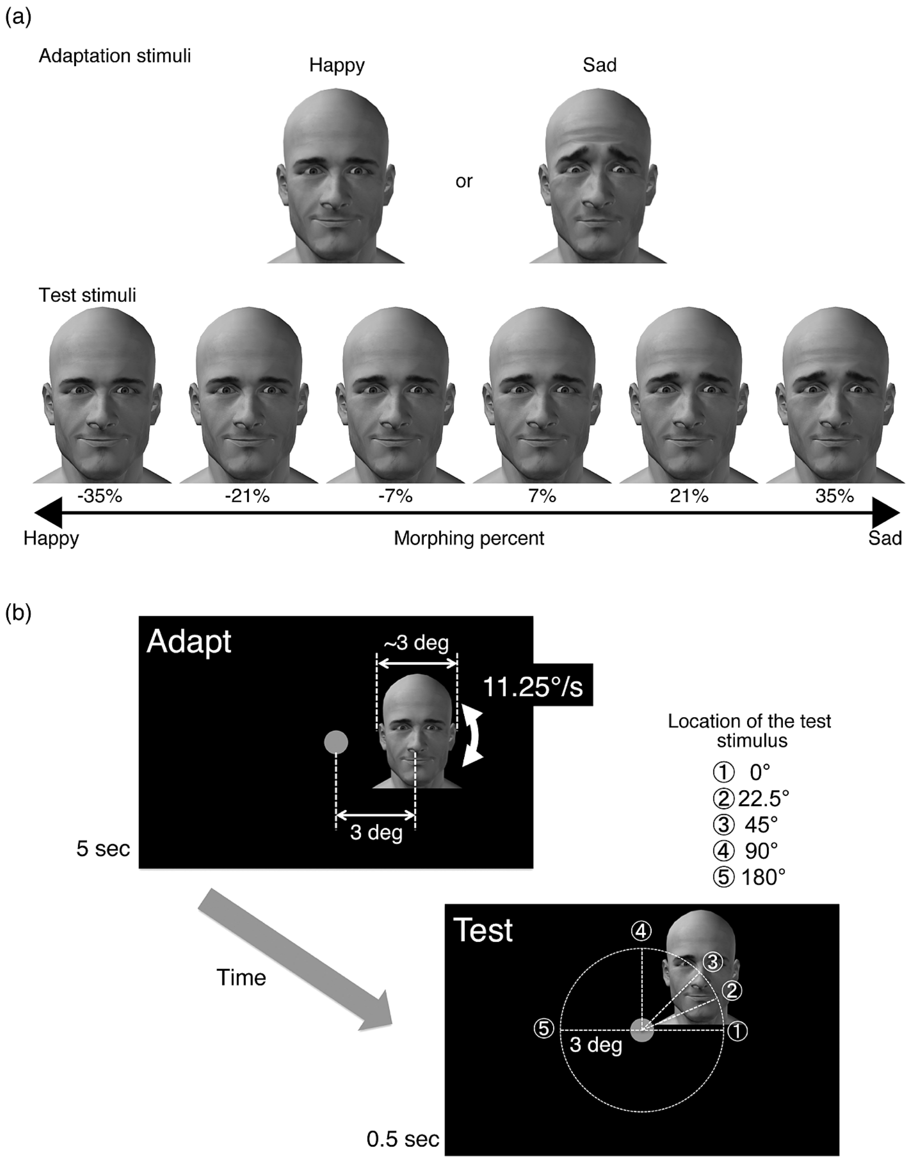

Figure 1. Visual stimuli and procedure. (a) Adaptation and test stimuli. Adaptation stimuli consisted of two types of facial expressions (happy and sad). Test stimuli were created by morphing a continuum from happy to sad faces. (b) Procedure. During adaptation, the participant saw an adaptation stimulus for 5 s while looking at the fixation point. The adaptation stimulus moved back and forth along a short path around a display circle that spanned an 11.25° sector of an imaginary circle at a speed of 11.25°/s. A test stimulus was then presented for 0.5 s. The location of the test stimulus was randomly chosen from five positions on the display circle (0°, 22.5°, 45°, 90° and 180°).

180°) on the display circle (Fig. 1b). The test stimulus was randomly selected from six different morphing levels.

Two adaptation conditions were defined as follows: (1) adaptation to a happy face and (2) adaptation to a sad face. Each participant performed the experiment in five sessions of 60 trials for each adaptation condition with the order counterbalanced.

3. Results and Discussion

Figure 2a shows the percentage of sad responses for the happy and sad face adaptation conditions for each location on the display circle for one participant. As shown in Fig. 2a, adaptation to the sad facial expression shifted the psychometric curve from the condition of adaptation to the happy facial expression such that test faces were perceived as having the opposite facial expression. To calculate FAE strength at each given location on the display circle, 50% criterion values (PSEs) were estimated by Probit analysis. FAE strength was defined as the shift in the PSE between happy and sad face adaptation conditions (Fig. 2b). Figure 2b indicates that the FAE occurs even when the adaptation and test faces are in different locations. FAE strength significantly increased from zero when the test face was presented within the 45° location on the display circle (0°: $t_3 = 13.18$, $p < 0.001$; 22.5°: $t_3 = 6.17$, $p < 0.01$; 45°: $t_3 = 4.78$, $p < 0.05$). These results indicate that the facial-expression aftereffect can tolerate large degrees of retinal translation between adaptation and test stimuli, which suggests position invariance for the FAE that supports the view that facial information is coded in a non-retinotopic visual representation (Leopold *et al.*, 2001).

However, Fig. 2b shows significant strength changes in FAE depending on the distance between adaptation and test stimuli ($F_{4,3} = 13.33$, $p < 0.001$). FAE strength gradually decreased with adaptation-test distance and did not significantly increase from zero when the test face was presented beyond the 90° location on the display circle (90°: $t_3 = 2.20$, $p = 0.12$ n.s.; 180°: $t_3 = 1.88$, $p = 0.16$ n.s.). Importantly, the adaptation and test faces were presented in this study at the same retinal eccentricity (3° of the visual angle) from the gaze point (see Fig. 1b). Therefore, the decline in FAE strength observed cannot be explained by a decline in recognition that occurs in the retinal periphery. These results indicate a retinotopy of the FAE for facial expression.

Could the observed aftereffects occur from adaptation to local changes in shape? A recent study suggested similar adaptation mechanisms underlying face gender and tilt aftereffects (Zhao *et al.*, 2011). Therefore, I conducted an additional experiment where the adaptation and test stimuli were images of different persons. If the aftereffects observed in the present study were due to adaptation to facial expression and not to local changes in shape, the af-

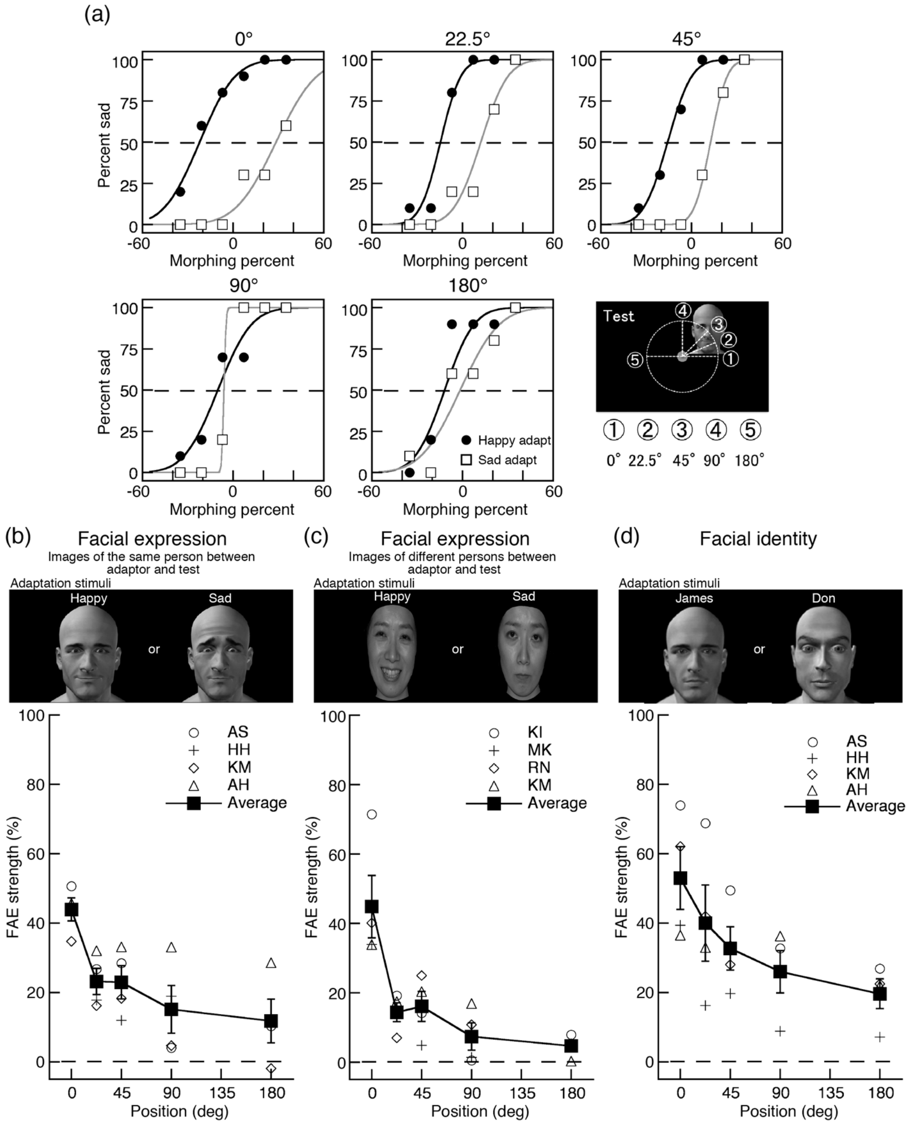

Figure 2. Results. (a) Psychometric facial expression discrimination curves for the five locations on the display circle for one participant. Adaptation to two adaptation conditions is shown: happy face (solid circle) and sad face (open square). (b) Strength of the facial expression aftereffect when the adaptation and test stimuli were images of the same person. (c) Strength of the facial expression aftereffect when the adaptation and test stimuli were images of different persons. (d) Strength of the facial identity aftereffect. Each symbol type, except the solid square, represents a different participant. Solid square represents the average strength of face aftereffects ($n = 4$). Error bars represent standard error of the mean.

tereffects should transfer across images of different persons (Fox and Barton, 2007). In this experiment, adaptation stimuli consisted of two photographs (happy and sad facial expressions) of a woman, not just those created with the morphing software (Fig. 2c). However, the test stimuli were identical to the CG faces used in the original experiment (Fig. 1a). In other words, the adaptation stimuli depicted a different gender from the test stimuli and were created in a different way from the test stimuli. The results shown in Fig. 2c indicate a similar pattern to that shown in Fig. 2b. Figure 2c shows significant changes in the strength of the FAE depending on the distance between the adaptation and test stimuli ($F_{4,3} = 10.16$, $p < 0.001$). FAE strength increased significantly from zero when the test face was presented within the 45° location on the display circle (0°: $t_3 = 4.98$, $p < 0.05$; 22.5°: $t_3 = 5.31$, $p < 0.05$; 45°: $t_3 = 3.70$, $p < 0.05$), but not when the test face was presented beyond the 90° location (90°: $t_3 = 1.88$, $p = 0.16$ n.s.; 180°: $t_3 = 2.93$, $p = 0.06$ n.s.). These results suggest that the observed aftereffects were not due to adaptation to local changes in shape and they confirm a retinotopy of the FAE for facial expression.

To compare position specificity of the facial expression aftereffect with that of the facial identity aftereffect, I again replicated the experiment of Afraz and Cavanagh (2008) using the same method as for facial-expression aftereffects (see 2.2. *Apparatus and Stimuli* and 2.3. *Procedure*). In this experiment, adaptation stimuli consisted of two individual faces (James and Don) generated by the CG software application (Fig. 2d). Test stimuli consisted of a James-to-Don face morph continuum created with the morphing software application. The morph rate of the face was varied from −44% to 44% in 8% increments. Figure 2d shows that FAE strength gradually decreases with increasing distance between adaptation and test stimuli ($F_{4,3} = 10.93$, $p < 0.001$), which confirms a retinotopy of the FAE for facial identity. FAE strength significantly increased from zero across all test face locations (0°: $t_3 = 5.86$, $p < 0.01$; 22.5°: $t_3 = 3.64$, $p < 0.05$; 45°: $t_3 = 5.22$, $p < 0.05$; 90°: $t_3 = 4.26$, $p < 0.05$; 180°: $t_3 = 4.58$, $p < 0.05$), which suggests position invariance for the facial identity aftereffect. These results are consistent with the findings of a previous study (Afraz and Cavanagh, 2008).

A comparison of the position specificity between the facial-expression and facial-identity aftereffects (Fig. 2b, c and d) provides several implications for adaptation mechanisms underlying face processing. First, FAE strength decreased with adaptation-test distance for both facial identity and facial expression. Indeed, the FAEs were larger when the adaptation and test faces were presented on the same retinal position compared with when they were presented in the opposite hemifield, which is consistent with the findings of previous studies (Kovacs *et al.*, 2005, 2007). This result suggests that there is an FAE that occurs with retinal overlap between the adaptation and test faces for both facial expression and facial identity processing. This could be explained by adaptation of face-selective neurons with relatively small receptive fields (DiCarlo and Maunsell, 2003; Op De Beeck and Vogels, 2000; Rolls *et al.*, 2003). Second, there was a smaller FAE even when the adaptation and test faces were presented without retinal overlap. This result suggests that there is also a spatially non-specific effect of the FAE (Burr and Morrone, 2005; Melcher, 2005) for both facial identity and facial expression. This could be explained by adaptation of face-selective neurons with large receptive fields (Desimone *et al.*, 1984; Gross *et al.*, 1972; Ito *et al.*, 1995; Logothetis *et al.*, 1995; Schwartz *et al.*, 1983; Tovee *et al.*, 1994). Thus, these findings suggest that, for both facial identity and facial expression, the FAE includes at least two effects: the retinal overlap effect and the spatially non-specific effect.

However, the present study also shows the difference in FAE magnitude between the facial-expression and facial-identity aftereffects. For test faces presented beyond the 45° location on the display circle, the FAEs for facial identity were strong (Fig. 2d) but the FAEs for facial expression were quite weak (Fig. 2b and c). This result suggests that the magnitude of the spatially non-specific effect of the FAE is different between facial identity and facial expression. A possible explanation for the result is that the spatially non-specific effect may be more local for the facial expression aftereffect than for the facial identity aftereffect. This is consistent with the recent view that the facial-expression aftereffect may be much more local than the gender- and identity-specific FAE (Zimmer and Kovacs, 2011).

The present findings reveal a negative correlation between facial expression aftereffect strength and adaptation-test distance and provide evidence for the retinotopy in facial expression aftereffects, which is consistent with the earlier results of Afraz and Cavanagh (2008). This suggests that facial expression information is coded not only in a non-retinotopic visual representation but also in a retinotopic visual representation in much the same way as reported for facial identity information (Afraz and Cavanagh, 2008).

Although the present results indicate that the facial expression aftereffect still occurs in a relatively large displacement (2.3°) of the adaptation stimulus relative to the test face, this finding does not agree with that of Xu *et al.* (2008) where a small displacement (0.9°) eliminated the facial expression aftereffect. This discrepancy could be explained by the difference in adaptation stimuli. Xu *et al.* (2008) used a simple concave or convex curve (corresponding to the mouth) as the adaptation stimulus and found that adaptation to such a simple feature caused the facial expression aftereffect for a subsequently presented face. This aftereffect disappeared with the small displacement of the adaptation feature stimulus relative to the test face. The present study used a happy or sad face as the adaptation stimulus and showed that adaptation to such a face caused the facial expression aftereffect for a subsequently presented face.

Therefore, it is likely that the adaptation stimulus used in the present study taps a higher level of processing more strongly than the adaptation stimulus used by Xu *et al.* (2008).

Traditional models of face perception have proposed separate neural processing routes for facial identity and facial expression and distinct visual representations within each of these domains (Bruce and Young, 1986; Haxby *et al.*, 2002). However, more recent studies have proposed an alternative view that visual representations of facial identity and facial expression are coded by a single representational system (Calder and Young, 2005; Dailey *et al.*, 2002; Skinner and Benton, 2010). The present study provides evidence of the retinotopy of the FAE not only for facial identity but also for facial expression and suggests that the FAE is stronger for facial identity than for facial expression when the test face is presented in the opposite hemifield. Taken together, these findings imply a difference in representation between facial identity and facial expression, in support of the traditional model.

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