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Research Report

Factors contributing to the adaptation aftereffects of facial expression

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ABSTRACT

Previous studies have demonstrated the existence of adaptation aftereffects for facial expressions. Here we investigated which aspects of facial stimuli contribute to these aftereffects. In Experiment 1, we examined the role of local adaptation to image elements such as curvature, shape and orientation, independent of expression, by using hybrid faces constructed from either the same or opposing expressions. While hybrid faces made with consistent expressions generated aftereffects as large as those with normal faces, there were no aftereffects from hybrid faces made from different expressions, despite the fact that these contained the same local image elements. In Experiment 2, we examined the role of facial features independent of the normal face configuration by contrasting adaptation with whole faces to adaptation with scrambled faces. We found that scrambled faces also generated significant aftereffects, indicating that expressive features without a normal facial configuration could generate expression aftereffects. In Experiment 3, we examined the role of facial configuration by using schematic faces made from line elements that in isolation do not carry expression-related information (e.g. curved segments and straight lines) but that convey an expression when arranged in a normal facial configuration. We obtained a significant aftereffect for facial configurations but not scrambled configurations of these line elements. We conclude that facial expression aftereffects are not due to local adaptation to image elements but due to high-level adaptation of neural representations that involve both facial features and facial configuration.

1. Introduction

Adaptation paradigms are commonly used to characterize the mechanisms and neural representations involved in the perception of various visual dimensions, such as color, orientation and frequency, among others. One classic example is the color aftereffect, where an observer perceives a green afterimage square after adapting to a red square for many seconds (e.g. Clifford and Rhodes, 2005). While simple color aftereffects can be explained by adaptation of color-opponency cells in the retina, recent experiments have also shown adaptation aftereffects for high-level visual stimuli such as faces, across such dimensions as identity, gender, race and expression (Fox and Barton, 2007; Leopold et al., 2001; Webster et al., 2004).

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All of these face adaptation studies have used similar paradigms that involve morphed faces. Essentially, subjects view a particular face during an adaptation period that lasts several seconds and then are shown ambiguous test images that are created by morphing between that face and another. Adaptation causes these subjects to respond that the morphed images are less similar to the face they had viewed during the adaptation period. This aftereffect is attributed to a reduction in neural responses evoked by the adapting face (Huber and O'Reilly, 2003). When an ambiguous image is viewed following adaptation, the responses in competing, unadapted representations of other faces are stronger than the response in the adapted representation, leading to a bias of perception towards unadapted stimuli (Leopold et al., 2001). This conceptualization of the origins of face aftereffects suggests that adaptation studies may be a useful and important means of probing the nature of the neural representations of faces and the organization of 'face space', the theoretical multidimensional relationship of facial representations in the human visual system (Rhodes et al., 1987; Valentine, 1991) and the impact of phenomena such as learning on these representations (Wilson and Diaconescu, 2006).

However, before such inferences about the neural representations of faces can be made from adaptation studies, one must first consider whether local adaptation to image elements in face stimuli might account for the observed aftereffects. Complex stimuli like faces, after all, are composed of many different local elements, which include line orientation, curvature and shape, all properties for which aftereffects have been described (Adams and Mamassian, 2002; Gibson and Rander, 1937; Regan and Hamstra, 1992; Suzuki, 2003; Suzuki and Cavanagh, 1998). If local adaptation to these image elements accounts for a significant portion of face aftereffects, this would significantly constrain the inferences about face space that can be derived from face adaptation studies.

Some studies have argued that if the aftereffect persisted despite changes in stimulus size or location, such invariance would argue against a significant contribution of local adaptation to image elements towards face aftereffects. Thus, Zhao and Chubb (2001) found that while aftereffects to distorted faces were largest when the adapting and test stimuli were of the same size, significant aftereffects could still be obtained even when the two stimuli differed in size by a factor of four. Leopold et al. (2001) found that the magnitude of the aftereffect was not altered even if the location of adapting and test stimuli differed by as much as 6°.

In a recent study of facial expression aftereffects, Fox and Barton (2007) showed that the aftereffects persisted even when adapting and test stimuli were images of different individuals, suggesting that neural representations of expression are identity-invariant. However, because expression aftereffects generated by incongruent identities were smaller than ones generated by congruent identities, a second identity-dependent representation of expression was also postulated (Fox and Barton, 2007). While identity-invariant expression aftereffects are unlikely to be the result of local adaptation to image elements, as the adapting and test stimuli are pictures of different people, identity-dependent expression aftereffects may reflect such local adaptation. To counter this, Fox and Barton (2007) noted that the magnitude of the identity-dependent expression aftereffect was not affected when the adapting stimulus was changed to a picture of the same expression in the same individual different from the image used to create the morphed test stimuli.

However, different depictions of the same expression by the same person are still highly similar. Thus, this finding (Fox and Barton, 2007) does not definitively exclude a role for local adaptation to image elements in expression aftereffects. For example, one could suppose that adaptation to tilt mediates aftereffects of the expression of anger because this emotion is usually associated with a downward tilt of the eyebrows. This tilt would still be present in two different images of the same person displaying anger. Likewise, adaptation to the curvature of the mouth could contribute to aftereffects of the expression of happiness across different images of the same person. The goal of the first experiment of this report, then, was to perform a more definitive examination of the role of local adaptation to image elements in the face expression aftereffect.

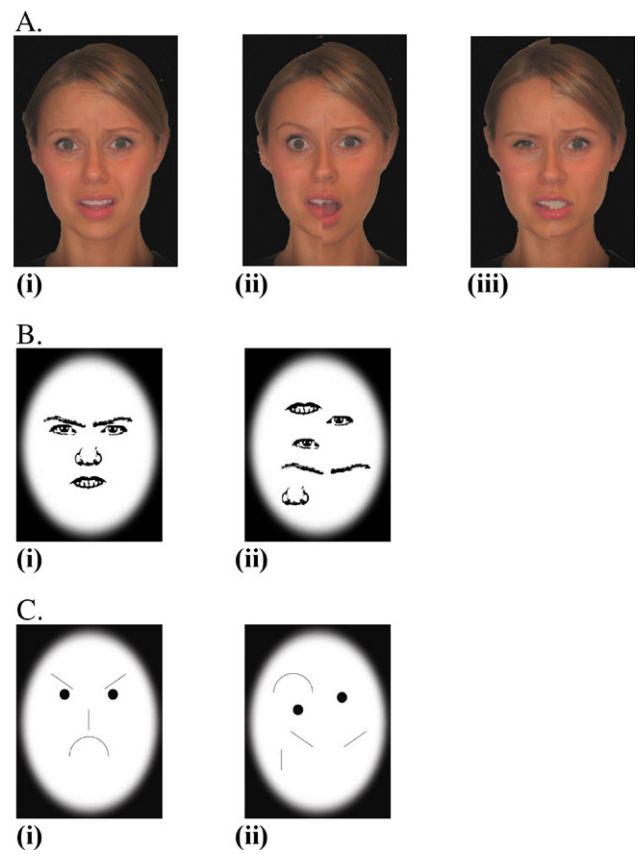

Fig. 1 – Examples of stimuli in the three experiments. (A) Experiment 1: (i) *normal-face* condition, using afraid face A; (ii) *quartered-face/consistent-expression* condition, with the upper right and lower left quarters from afraid face A and the lower right and upper left quarters from afraid face B; and (iii) *quartered-face/mixed-expression* condition, with the upper right and lower left quarters from afraid face A and the lower right and upper left quarters from angry face A. (B) Experiment 2: (i) *intact-face* condition; and (ii) *scrambled-face* condition. (C) Experiment 3: (i) *intact-schematic-face* condition; and (ii) *scrambled-schematic-face* condition.

Beyond the role of local adaptation to image elements, there is also the question of whether adaptation effects originate in representations of facial features or whole-face configurations. While facial features can clearly be recognized and exist independent of the whole-face context, many face-related phenomena are said to depend upon or reflect 'holistic' processing, in which the configuration and interrelation of features in their natural facial context is critical (de Heering et al., 2007; Goffaux and Rossion, 2006; Singer and Sheinberg, 2006; Tanaka et al., 1998; Yovel and Duchaine, 2006). To examine the role of both facial features and configuration in face adaptation, we performed two additional experiments, one in which features were presented without the normal facial configuration, and another in which the normal facial configuration was preserved but presented with minimal (or impoverished) feature information.

2. Results

2.1. *Experiment 1*

To determine whether expression aftereffects result from adaptation of high-level representations of facial expression or from local adaptation to image elements, we created hybrid face stimuli (Fig. 1A.iii) that lacked a consistent expression but which still possessed the same local elements of the normal faces used to generate an expression aftereffect (Fig. 1A.i). These faces were created by quartering the original pictures so that two diagonally opposite quarters (e.g. upper left and lower right) were taken from one facial expression (e.g. angry), and the remaining two from a different expression (e.g. afraid) (Fig. 2B). Our goal was to test whether these quartered stimuli

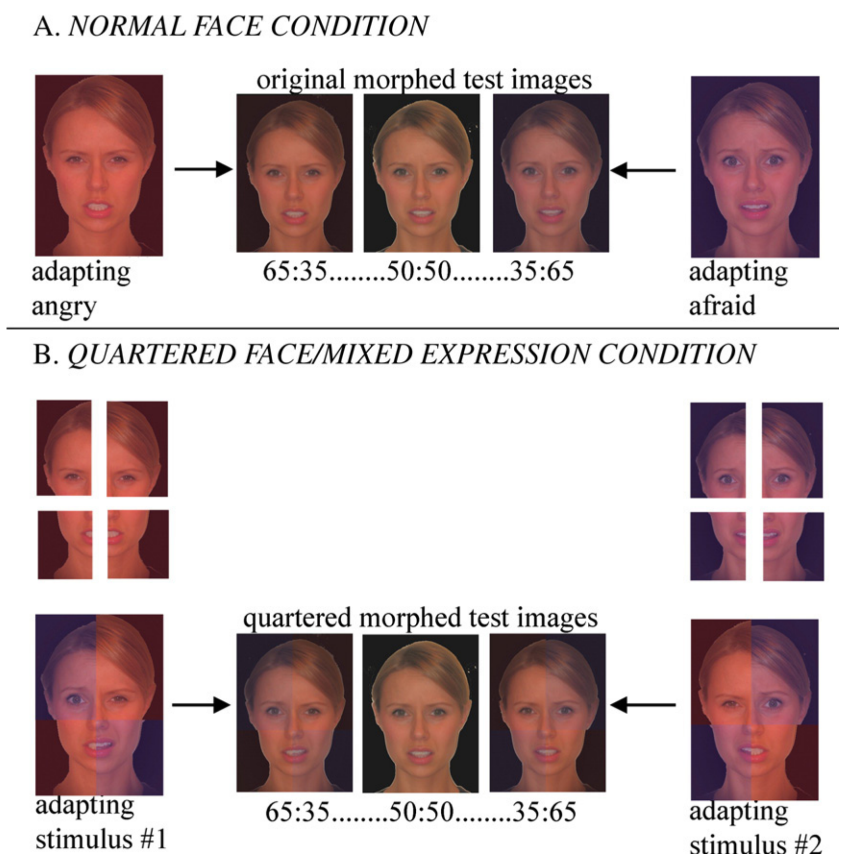

Fig. 2 – Creation of adapting and test stimuli in the *normal-face* and *quartered-face/mixed-expression* conditions. (A) *Normal-face* condition. The A versions of the Angry and Afraid images are shown. These will be used as adapting stimuli in the *normal-face* condition. A morph series is then generated between these two images, and 13 stimuli with morph mixtures ranging from 65% angry/35% afraid to 35% angry/65% afraid will be used as test stimuli for the adaptation effect. The smaller images shown are three representative images from this morph series: 65% angry/35% afraid, 50% angry/50% afraid and 35% angry/65% afraid morphed images. (B) *Quartered-face/mixed-expression* condition. The images used in the *normal-face* condition are divided into quarters and recombined into two images (1 and 2) that are a mixture of angry and afraid quarters, one (image 1) in which the upper right and lower left quarters are angry and the lower right and upper left quarters are afraid and another (image 2) that is the reverse. These will be used as adapting stimuli in the *quartered-face/mixed-expression* condition. A morph series is then generated between these two images, and 13 stimuli with morph mixtures ranging from 65% stimulus 1/35% stimulus 2 to 35% stimulus 1/65% stimulus 2 will be used as test stimuli for the adaptation effect. Smaller images show 35%/65%, 50%/50% and 65%/35% images taken from this series. (Note: the superimposed colors are for illustrative purposes only, to clarify the principle of stimulus design. These range from a red tinge for 100% angry to a blue tinge for 100% afraid, with morphs having intermediate values. Stimuli were not tinged in the experiment.)

generated aftereffects, and if so, how they compared to the aftereffects obtained by adaptation to faces with consistent facial expressions. As faces no longer contained consistent expressions, subjects did not perform an explicit expression-naming task but were asked to match the test face to one of the two adapting stimuli displayed on a choice screen (see Fig. 6). Thus, if expression aftereffects are simply due to local adaptation to image elements, significant aftereffects should be found with both types of stimuli; that is, regardless of the presence or absence of a strong consistent expression. On the other hand, if aftereffects arise solely from adaptation of a high-level representation of facial expression, there should be no measurable aftereffect when adapting to the quartered faces with ambiguous expressions.

Our experiment had three face conditions. In the *normal-face* condition, whole faces with strong expressions of anger or fear were used as adapting stimuli. In the *quartered-face/mixed-expression* condition, the normal faces were quartered and re-arranged to give stimuli with inconsistent expressions, ensuring that subjects were exposed to the same set of image quarters during the adapting phase of this condition as in the *normal-face* condition. Quartered stimuli were used as adapting stimuli and were also used to create quartered test stimuli. Last, we included a *quartered-face/consistent-expression* condition to control for the edges introduced during the process of quartering. In this condition, hybrid images were constructed from two different pictures of the same expression in the same individual. Again, these quartered stimuli were used for both the adapting and test stimuli.

In all three conditions, subjects adapted to one of two adapting stimuli at the extreme ends of a morph continuum and then were tested for aftereffects on test stimuli selected from the mid-region of the continuum. The analysis examined for effects of face condition and adapting stimulus, with aftereffects indicated by the presence of a significant effect of adapting stimuli. The results did show a significant main effect of adapting stimulus ($F(1,127)=101$, $p<0.0001$). More importantly, there was a significant interaction between face condition and adapting stimulus ($F(2,127)=21.17$, $p<0.0001$). Linear contrasts showed that there was a significant difference in response following adaptation to the two different adapting stimuli in the *normal-face* condition ($t=9.32$, $p<0.0001$) and also in the *quartered-face/consistent-expression* condition ($t=7.55$, $p<0.0001$), but not for the *quartered-face/mixed-expression* condition ($t=0.61$, n.s.) (Fig. 3). Thus, there were large aftereffects for the two conditions with adapting stimuli that displayed consistent expressions, but none when the facial expression in the adapting stimuli was inconsistent. Even though the images in the *quartered-face/mixed-expression* condition were produced from the same photographs and therefore contained the same local elements as in the *normal-face* condition, the aftereffect was abolished by disrupting the consistency of the displayed facial expression.

These results show that presenting the same local image elements in a way that reduces the coherence of the depicted expression eliminates the aftereffect. The loss of this aftereffect cannot be attributed to a distortion in the image introduced by the quartering process because a similar mixing of two different images in the *quartered-face/consistent-expression* condition did not reduce the magnitude of the aftereffect.

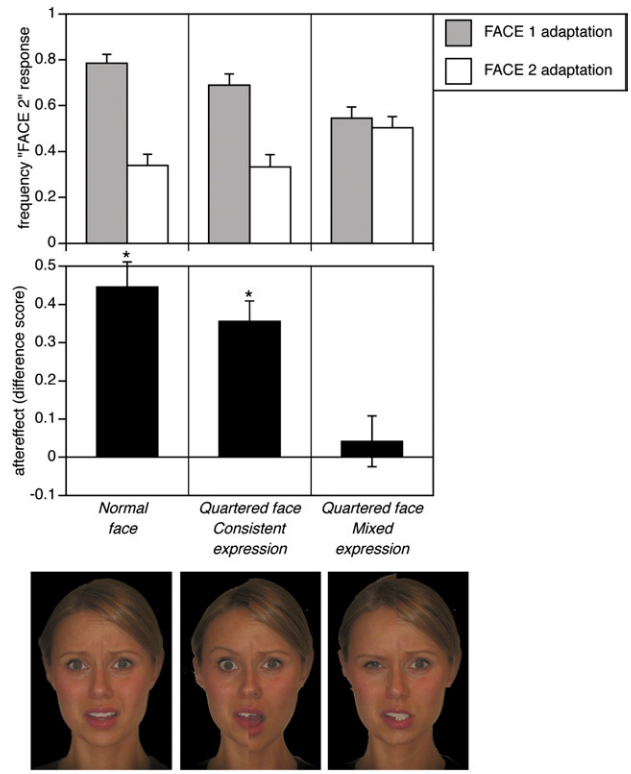

Fig. 3 – Results of Experiment 1. Top graph shows the mean frequency of responses that the test stimuli looked like Face 2 after adapting to either Face 1 or Face 2. Bottom graph shows the magnitude of the aftereffect, expressed as the mean difference score, which is calculated from the data in the top graph by subtracting for each subject the frequency of answering Face 2 after adapting with Face 2 from the frequency of answering Face 2 after adapting with Face 1 (if there is no aftereffect from previewing Face 1 or Face 2, the frequencies would be the same and the difference score would be zero). Data are shown for each of the three conditions (left = *normal-face*, middle = *quartered-face/consistent-expression*, right = *quartered-face/mixed-expression*) with error bars showing one standard deviation and asterisks denoting significant aftereffects. (For *normal-face* and *quartered-face/consistent-expression* conditions, Face 1 is Afraid and Face 2 is Angry.)

These findings indicate that the aftereffects in our experiment are not due to local adaptation to image elements such as orientation, curvature or shape. If such local adaptation occurred, we would have expected to see at least some aftereffects in the *quartered-face/mixed-expression* condition, whereas we found none.

The results of Experiment 1 also raise an interesting question. Within each quartered-image there were facial features in which expression could be identified; however, aftereffects were absent in the *quartered-face/mixed-expression* condition. Does this mean that simultaneous adaptation to two different facial expressions disrupts the resultant aftereffect or that adaptation of neural representations of facial expression does not occur at the level of facial features? Our second experiment was designed to address this issue.

2.2. Experiment 2

There is a large body of work suggesting that many aspects of face processing may occur holistically rather than at the level of components or individual features (de Heering et al., 2007; Goffaux and Rossion, 2006; Singer and Sheinberg, 2006; Tanaka et al., 1998; Yovel and Duchaine, 2006). The lack of an aftereffect in the *quartered-face/mixed-expression* condition of Experiment 1 is consistent with this view. However, the ambiguity of the overall expression in the *quartered-face/mixed-expression* condition may have obscured aftereffects generated by facial features. To determine if expression aftereffects can occur at the level of facial features, our second experiment compared aftereffects following adaptation to normal faces with those following adaptation to scrambled faces, in which facial configuration is disrupted but the expression remains consistent. If expression is represented at the level of individual features (e.g. eyes, mouth), then at least some aftereffects would be found in the scrambled condition.

This experiment had two conditions, both using thresholded facial images that allowed us to scramble images without producing edge artifacts (see Methods). The *intact-face* condition showed thresholded versions of faces with features in a normal arrangement in both the adapting and test stimuli, whereas the *scrambled-face* condition showed a scrambled arrangement of facial features in both the adapting and test stimuli.

We found a significant main effect of adapting stimulus, with a mean 19% difference in scores between adaptation to the angry versus the afraid images ($F(1,81)=17.1$, $p<0.0001$). However, there was no significant interaction between face condition and adapting stimulus ($F(1,81)=0.99$, p = n.s.). *A priori* linear contrasts showed significant aftereffects for both the *intact-face* condition ($t=3.634$, $p<0.0005$) and the *scrambled-face* condition ($t=2.220$, $p<0.03$) (Fig. 4).

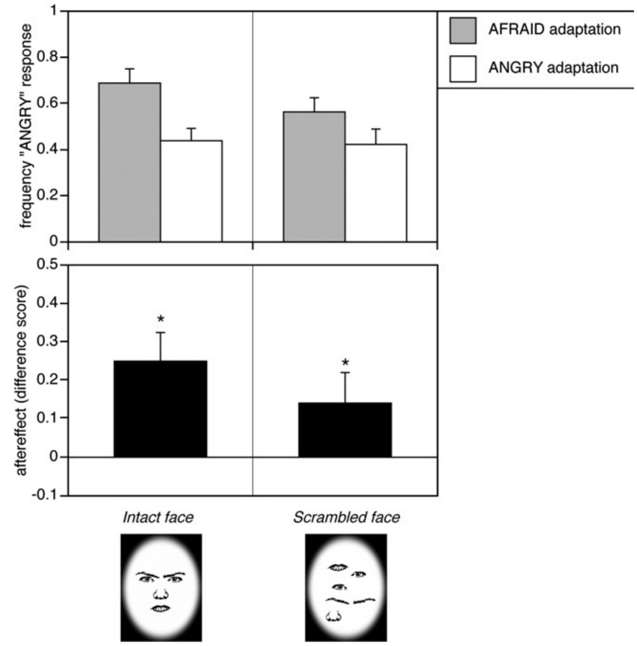

Fig. 4 – Results of Experiment 2. Top graph shows the mean frequency of responses that test stimuli looked 'Angry' after adapting to either Afraid or Angry thresholded faces. Bottom graphs show the magnitude of the aftereffect, expressed as difference scores, calculated from response scores as in Fig. 3, with error bars showing one standard deviation and asterisks denoting significant aftereffects. Data on the left are for the *intact-face* condition, data on the right are for the *scrambled-face* condition.

The results of Experiment 2 suggest that at least some of the expression aftereffect may be mediated at the level of facial features because an aftereffect was found in the *scrambled-face* condition. Thus, individual features are able to activate adaptable neural representations of expression even when the normal facial configuration was absent.

While the aftereffect in the *scrambled-face* condition appeared smaller than the aftereffect for the *intact-face* condition, the interaction between face condition and adapting stimulus was not significant. The lack of interaction might be interpreted as suggesting that the normal facial configuration does not contribute to the expression aftereffect. This would be surprising given the prominent role of configuration in many aspects of face processing. To determine if configuration contributed to the expression aftereffect, we performed a third experiment, in which the perception of expression depended upon the configuration of elements that on their own do not convey a significant expression signal.

2.3. Experiment 3

In Experiment 3, we used highly schematic faces made up of line and curve segments and circles. These geometric shapes, which form the individual features of the face, are devoid of expression on their own, but when placed within a facial configuration they combine to depict facial expressions (Fig. 1C). Thus, in a manner similar to Experiment 2, we compared expression aftereffects in an *intact-schematic-face* condition to those in a *scrambled-schematic-face* condition. If facial configuration does not contribute to the expression aftereffect (i.e. the aftereffects are based solely on the representation of individual facial features), then we would not find an expression aftereffect in either condition. If the aftereffects reflect local adaptation to image elements such as tilt and curvature, we would find significant and similar aftereffects in both conditions (contrary to the results of Experiment 1). Finally, if adaptation to facial configuration but not local elements contributes to expression aftereffects generated with these schematic images, then we would see significant aftereffects with the intact schematic faces but not with the scrambled ones.

This experiment also had two conditions. In the *intact-schematic-face* condition, line elements were combined in a face-like arrangement in both the adapting and test stimuli. In the *scrambled-schematic-face* condition, they were arranged in a non-face-like arrangement for both adapting and test stimuli.

There was no significant main effect of adapting stimulus ($F(1,33)=1.58$, n.s.). However, there was a significant interaction between face condition and adapting stimulus ($F(1,33)=4.39$, $p<0.044$). The linear contrasts showed a significant aftereffect in the *intact-schematic-face* condition ($t=2.372$, $p=0.024$), but not for the *scrambled-schematic-face* condition ($t=0.59$, n.s.) (Fig. 5).

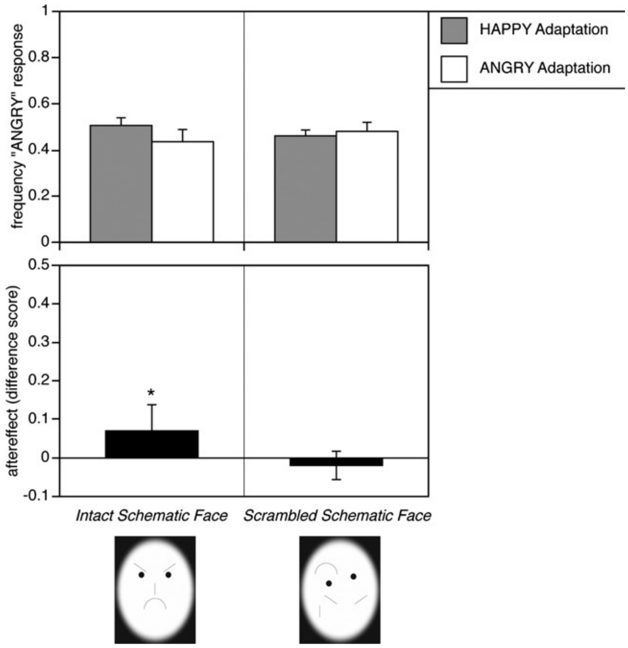

Fig. 5 – Results of Experiment 3. Top graph shows the mean frequency of responses that test stimuli looked 'Angry' after adapting to either Happy or Angry schematic faces. Bottom graphs show the magnitude of the aftereffect, expressed as difference scores, calculated from response scores as in Fig. 3, with error bars showing one standard deviation and asterisks denoting significant aftereffects. Data on the left are for the *intact-schematic-face* condition, data on the right are for the *scrambled-schematic-face* condition.

The findings in the *scrambled-schematic-face* condition of Experiment 3 reinforce the conclusion from Experiment 1: facial expression aftereffects do not originate from local adaptation to image elements like orientation and curvature. The difference between the *scrambled-face* condition in Experiment 2 and the *scrambled-schematic-face* condition in Experiment 3 is that the features of the highly schematic faces of Experiment 3 do not convey expression when viewed in isolation, being merely tilted lines and curves, whereas expression is still visible in the individual features of the faces in Experiment 2. Thus, when expression information is removed from the face parts, adaptation to these face parts does not generate an aftereffect, further reinforcing the conclusion from Experiment 1, that local adaptation to image elements like line orientation and curvature do not mediate the face expression aftereffect. However, when these curved and oriented segments are assembled into a face-like configuration, an expression aftereffect can be found even with these very basic schematic faces. Therefore, whereas Experiment 2 shows that features alone can generate some of the expression aftereffect, Experiment 3 demonstrates that facial configuration can generate an expression aftereffect. Both experiments show that a perceivable expression is the necessary component to generate an aftereffect. Again this supports the finding reported in Experiment 1 where aftereffects were only seen when a consistent expression was perceived in the adapting face.

3. Discussion

Previous studies have found aftereffects following adaptation to various aspects of faces, such as identity, race, gender and expression (Fox and Barton, 2007; Webster et al., 2004). This report focused on determining the basis of the facial expression aftereffect. We first considered the possibility that it was derived from local adaptation to image elements within the facial image, such as orientation, curvature and shape. By creating quartered faces with inconsistent expressions, we examined whether this local adaptation could generate an aftereffect in the absence of a coherent expressive signal. The result of Experiment 1 was clear: There were no aftereffects when there was no coherent expression. This suggests that neurons coding for local image elements are not the source of the expression aftereffects seen in this adaptation paradigm. This conclusion was also supported by the lack of aftereffects in the *scrambled-schematic-face* condition of Experiment 3, once again implying that tilt and curvature aftereffects were not the source of the facial expression aftereffects.

One possible reason for a greater aftereffect for images with consistent rather than mixed expressions may be that, not only do consistent images generate a coherent representation of expression, but these coherent representations also have a verbal label or name for the expression that images with mixed expressions lack, and that this may reinforce perception or recall during the task. However, our experiments were designed to minimize the use of a verbal label in all conditions, in that the task required subjects to choose one of two faces on a choice display, a task that does not require any verbal label. Also, in our previous report (Fox and Barton, 2007), the use of verbal labels alone as adapting stimuli did not generate any aftereffect in images of facial expression, indicating that representations at a verbal level do not contribute significantly to face expression aftereffects.

Experiment 2 examined whether local features alone could generate an aftereffect when facial expression was consistent, or if a whole-face configuration was necessary. This was motivated by a large body of literature showing that many aspects of face perception depend on 'holistic' processing (de Heering et al., 2007; Goffaux and Rossion, 2006; Singer and Sheinberg, 2006; Tanaka et al., 1998; Yovel and Duchaine, 2006). The results showed that it was possible to generate expression aftereffects without a whole-face configuration. However, this result does not imply that facial configuration does not contribute to expression aftereffects: Experiment 3 used schematic faces comprised of simple line elements that do not resemble a facial feature or convey a facial expression when viewed in isolation. This experiment showed that these expression-neutral elements generate an expression aftereffect only when arranged into a normal facial configuration. Thus, the results of Experiments 2 and 3 suggest the existence of both featural and configural aspects to the neural representations of expression.

Our prior report suggested that identity-dependent representations of expression might exist because adaptation effects were largest when images of the same person were used as both adapting and test stimuli (Fox and Barton, 2007). We have demonstrated in the current study that identity-dependent expression aftereffects are not the result of local adaptation to image elements of the faces. The existence of identity-dependent neural representations of expression is also consistent with a number of previous studies (Baudouin et al., 2002; Ganel et al., 2004; Schweinberger et al., 1999; Schweinberger and Soukup, 1998). For example, a recent study of neural responses in monkeys demonstrated that the responses of cells in the amygdala to facial expression depended upon the identity of the monkey demonstrating that expression (Kuraoka and Nakamura, 2006). In addition, responses to emotion and responses to facial identity were coded in the same phase of the response, consistent with an integrated processing of the two types of information (Kuraoka and Nakamura, 2006). In humans, another potential site for integration of identity and expression information may be the posterior superior temporal sulcus, which showed hemodynamic adaptation to both identity and expression in an event-related fMRI paradigm (Winston et al., 2004). The superior temporal sulcus and the amygdala are relatively high-level regions in the cortical hierarchy of visual processing (Felleman and Van Essen, 1991) and would be appropriate candidates for the hypothesized locus of neural populations generating the behavioral aftereffects in our experiment.

In contrast, local 'shape dimensions' such as curvature and particularly orientation (Werner and Chalupa, 2004) are represented in the lowest levels of the visual hierarchy, such as the striate cortex (area V1) (Hubel and Wiesel, 1962). While aftereffects for orientation do occur and are known to be based on changes in neural dynamics in V1 (Dragoi et al., 2000), our experiment suggests that these do not account for the identity-dependent component of the expression aftereffect. This may partly reflect the free-viewing nature of our adaptation period. Aftereffects in strictly retinotopically organized structures like the retina and V1 are highly localized and depend upon controlled fixation during the adaptation period. The absence of a requirement for maintained fixation may account for the lack of adaptation in the *quartered-face*s with mixed expressions in Experiment 1 and the scrambled line elements of Experiment 3. Allowing our subjects to freely move their eyes during the adaptation period may have allowed us to limit adaptation to representations in higher level cortical regions for object recognition, many of which are invariant to object location.

Experiments 2 and 3 showed that, on the one hand, the whole-face configuration is able to generate expression aftereffects, and yet, on the other, the configuration is not necessary if the features themselves are sufficiently expressive. This suggests that both holistic facial representations and facial features can generate expression aftereffects. One possible interpretation of these findings is that there are separate feature-based and holistic neural representations of facial expression, both of which can be adapted by their preferred stimuli. However, an alternative interpretation is that facial features alone are able to partially activate holistic representations of facial expressions, and that exposure to a feature collage will result in partial adaptation of these holistic representations. Indeed, neurophysiologic data show that face-responsive cells in monkey temporal cortex do respond partially to isolated features (Perrett et al., 1982). If so, one would expect a reduced aftereffect with scrambled faces than with whole faces. The results of Experiment 2 do suggest that the magnitude of the aftereffect for scrambled faces is less than that for whole faces, even though the interaction did not reach significance. Therefore, we consider that this possibility cannot be excluded. Regardless, the results argue against a single representation of expression in a holistic code that can only be accessed by holistic depictions. Rather, either holistic representations can be flexibly activated, strongly by whole faces or partially by fragmentary representations, or the system itself is flexible, in that it may contain multiple representations of expression, both feature-based and configurational, consistent with some recent computational models of face processing (Wallraven et al., 2005).

To conclude, our findings provide further data on the nature of the identity-dependent representation of expression in the human cortex. Our first experiment shows that these expression aftereffects cannot be attributed to well-known aftereffects for low-level shape dimensions such as orientation and curvature. Our data also show that aftereffects can be elicited through adaptation to an expressive face in a normal configuration, or to expressive local features alone, suggesting a degree of flexibility in these representations.

4. Experimental procedures

4.1. *Subjects*

Twelve subjects participated in all three experiments (8 female; age = 27.0 ± 10.8 years). All participants had normal or corrected-to-normal vision. The institutional review boards of Vancouver General Hospital and the University of British Columbia approved the protocol and all subjects gave informed consent in accordance with the declaration of Helsinki.

4.2. *Experiment 1*

4.2.1. *Stimuli*

We created three types of adapting stimuli to be used in the three conditions (Fig. 1A), which were the *normal-face* condition, the *quartered-face/consistent-expression* condition and the *quartered-face/mixed-expression* condition. All stimuli were created from the facial images of two individuals (one female, F22, and one male, M17) from the Karolinska Database of Emotional Faces (Lundqvist and Litton, 1998) showing one of two expressions (afraid or angry).

4.2.1.1. Normal-face condition. (i) Adapting stimuli: In the *normal-face* condition, these were unaltered images of F22 and M17, displaying anger or fear (Fig. 2A). The database has two images of each expression per person, which we labeled as A and B versions. We paired these arbitrarily to create an A pair and a B pair of afraid and angry images.

(ii) Test stimuli: Using these A and B pairs, our second step was to create test stimuli for the experiment by generating a morph series between the two opposite adapting stimuli of the same person, using FantaMorph 3.0 software (www.fantamorph.com). This created 4 morph series, an A and a B series for F22 and an A and a B series for M17 (i.e. angryA/afraidA indicates a morph between angry face A and afraid face A, whereas angryB/afraidB indicates a morph between angry face B and afraid face B). From these morph series, we selected for our test stimuli thirteen morphs that ranged from 35% angry/ 65% afraid to 65% angry/35% afraid in 2.5% steps. This range was chosen to ensure that the displayed facial expression was ambiguous for all test stimuli.

In the experiment, half of the subjects saw series A, in which the two adapting stimuli were angry face A and afraid face A and the test stimuli were selected from the morph series between angry face A and afraid face A. The other half saw series B, in which the adapting stimuli and all morphed test stimuli were derived from angry face B and afraid face B.

4.2.1.2. *Quartered-face/mixed-expression condition.*

(i) Adapting stimuli: We took the same unmorphed faces used as adapting stimuli in the *normal-face* condition and divided them into quarters, using Adobe Photoshop CS 8.0 (Adobe Systems, San Jose CA), with the tip of the nose serving as the center point of each face (Fig. 2B). We then recombined these quarters so that the upper left and lower right quarters were from the face showing one expression (e.g. afraid face A), whereas the lower left and upper right quarters were from the face showing the other expression (e.g. angry face A) (Fig. 1A.iii). Thus, the two adapting stimuli in the *quartered-face/mixed-expression* condition (Adapting stimulus 1 and Adapting stimulus 2 in Fig. 2B) were simply a mix of the two adapting stimuli used in the *normal-face* condition (Afraid and Angry stimuli in Fig. 2A). As subjects were exposed to both adapting stimuli (Afraid and Angry in the *normal-face* condition, and Adapting stimulus 1 and Adapting stimulus 2 in the *quartered-face/mixed-expression* condition), subjects saw precisely the same set of image quarters during adaptation in each of these experimental conditions, only in a different combination with the other quarters. Hence, the local image elements of the faces used as adapting stimuli were preserved across these two conditions, with the only differences being the consistency of the displayed expression in a single adapting image, and any edges introduced at the margins of the facial quarters (for which the *quartered-face/consistent-expression* condition served as a control). Quartering rather than halving ensured that both right and left hemifaces as well as upper and lower face halves in themselves contained a hybrid mixture, which was important because there is evidence that attention to faces differs between both the right and left and also the upper and lower halves (Barton et al., 2006; Butler et al., 2005; Shepherd et al., 1981).

(ii) Test stimuli: In the *quartered-face/mixed-expression* condition, these were created from the quartered images used as adapting stimuli (Fig. 2B). We generated morph series between Adapting Stimulus 1 and Adapting Stimulus 2 and selected as test stimuli the thirteen morphs that ranged from 35% Adapting stimulus 1/65% Adapting stimulus 2 to 65% Adapting stimulus 1/35% Adapting stimulus 2 in 2.5% steps. Note that this essentially resulted, for example, in a 35:65 morph image having two quarters with a 35% angry/65% afraid mixture and two quarters with a 65% angry/35% afraid mixture. Hence, as with the adapting stimuli, across the entire block the subjects saw exactly the same quarter images during the test phase in both the *normal-face* and *quartered-face/mixed-expression* conditions, merely combined in different ways in the single images.

Again, there were two versions of the test, one using the A images and one using the B images. Those subjects who saw series A images in the *normal-face* condition also saw quartered stimuli generated from the series A images in the *quartered-face/mixed-expression* condition, whereas those subjects who saw series B images in the *normal-face* condition saw quartered stimuli generated from the series B images in the *quartered-face/mixed-expression* condition. Thus, the experimental design was balanced within subjects with regard to stimulus components.

4.2.1.3. *Quartered-face/consistent-expression condition.*

(i) Adapting stimuli: To control for the potential effects of the quartering procedure in the *quartered-face/mixed-expression* condition, we created a third condition, the *quartered-face/consistent-expression* condition. Stimuli in this condition also had edges at the margins of the facial quarters but differed from the *quartered-face/mixed-expression* condition in that all quarters had a similar rather than different facial expression. These were created by combining quadrants from the A image and the B image of the same expression by the same person (Fig. 1A.ii), the same images used in the *normal-face* condition. As the second set of images used to create the adapting stimuli in the *quartered-face/consistent-expression* were not seen in the *normal-face* condition by that subject, low-level properties of the faces were not balanced for this condition within a particular subject, although they were balanced across subjects (see Procedure).

(ii) Test stimuli: We next created morphed images from these quartered adapting stimuli. There were again four morph series, two for F22 and two for M17. For each person, there was one morph series in which the left-upper and right-lower quadrants were derived from the A series of facial images and the right-upper and left-lower quadrants from the B series of facial images, and one morph series with the reverse arrangement. Again, we chose as test stimuli the thirteen morph images ranging from 35/65% to 65/35%.

4.2.2. *Apparatus*

Experimental procedure was implemented in SuperLab 1.71 software (www.cedrus.com). A Mac G4 PowerBook with a 17-in. wide-screen display was used in the setting of ambient background lighting and viewed from a distance of 57 cm. All stimuli were presented in the centre of the screen and subtended 12 deg × 15 deg of visual angle.

4.2.3. *Procedure*

All subjects learned the task through written instructions and a short practice session of ten trials before starting the experiment. Each trial (Fig. 6) began with a 5-s presentation of an adapting stimulus, which was one of the two endpoint images of a given morph series. This was followed by a 50-ms mask of random black and white pixels. The mask was followed by a 300-ms test stimulus, picked randomly from the series of 13 morphed images, corresponding to the method of constant stimuli. A choice screen was then presented, which displayed both adapting images side-by-side, labeled '1' and '2'. The displayed position of the two adapting stimuli (left versus right) on the choice screen varied throughout the experiment. This pattern of choice screens was balanced by randomly assigning half of the subjects to the opposite

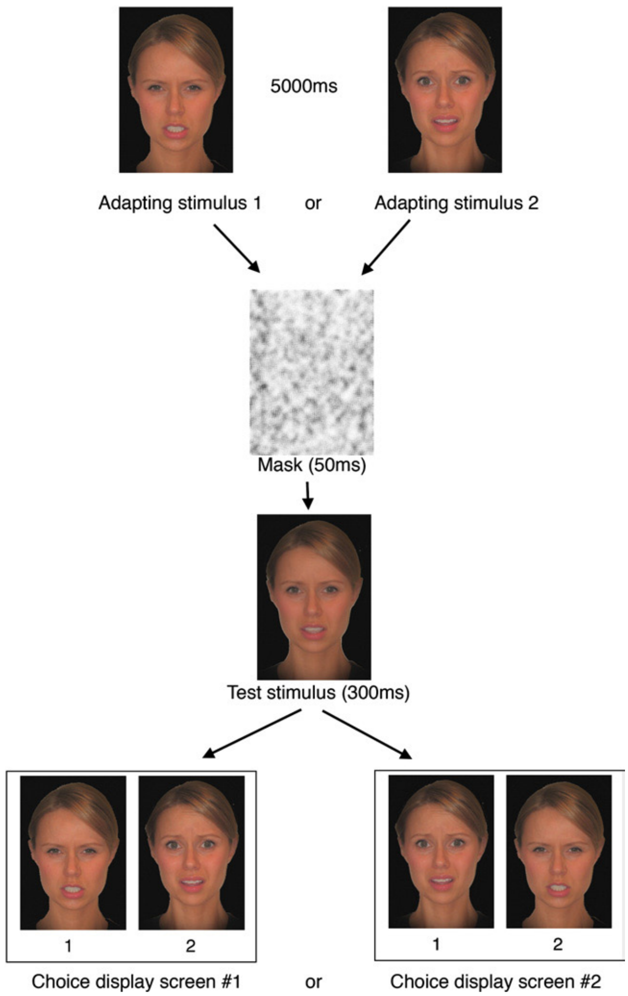

Fig. 6 – Example of a trial. Stimuli from the *normal-face* condition of Experiment 1 are used to demonstrate a typical trial. Each trial began with the presentation of one of two possible adapting face stimuli (i.e. either the afraid or angry face). The adapting stimulus was followed by the presentation of a mask. This was followed by the test stimulus, an image formed by morphing between the two possible adapting stimuli. One of two choice screens then followed, which presented the two possible adapting faces. At this point, the subject had to indicate which of the two faces the test image most closely resembled (i.e. either the angry or afraid face).

sequence of choice screens. The subject was asked to indicate with a keypress which of the two choice faces the test stimulus most strongly resembled. A 500-ms blank screen then appeared, followed by the start of the next trial.

The three different conditions (*normal-face*, *quartered-face/consistent-expression* and *quartered-face/mixed-expression*) were tested in separate blocks, with the order randomly determined for each subject. Subjects were also randomly assigned to one of four versions of the experiment. All four versions included both the male (M17) and the female (F22) face as stimuli. Two versions used the A series of images for the *normal-face* and *quartered-face/mixed-expression* conditions and the other two used the B series of images. These two experimental versions differed in turn by whether they used the first or the second of the versions of the *quartered-face/consistent-expression* condition.

Each pairing of a given test with a given adapting stimulus occurred only once. With thirteen test stimuli in each morph series for both the male and the female face, and each stimulus seen twice, once after each of the two non-morphed adapting stimuli (e.g. angry adapting stimulus and afraid adapting stimulus for the *normal-face* or *quartered-face/consistent-expression* conditions, and adapting stimulus 1 and adapting stimulus 2 for the *quartered-face/mixed-expression* condition), there were a total of 52 trials for each condition, all presented in random order within a block. With three blocks, there were a total of 156 trials.

4.2.4. *Analysis*

In the *normal-face* condition, the "afraid" response was assigned a value of 0, and the "angry" response was assigned a value of 1. For each adapting stimulus (angry or afraid), we calculated a score that was the proportion of responses where the subject selected the angry face across the full series of 13 test stimuli. As all 13 test stimuli were taken from the mid-range of the morph series and each stimulus was presented only once in each condition, morph level was not considered as a factor for further analysis. This response score, collapsed across all levels of morph, was our behavioral measure for the *normal-face* condition. The response score was calculated in a similar manner for the *quartered-face/consistent-expression* and the *quartered-face/mixed-expression* conditions.

A repeated measures ANOVA was performed with the response score as the dependent measure and significance levels set at $p<0.05$, using JMP IN 5.1 software (SAS Institute, www.jmpin.com). Face condition (*normal-face*, *quartered-face/consistent-expression*, *quartered-face/mixed-expression*) and adapting stimulus (image 1, image 2) served as within-subject factors. A *difference score* was calculated between the response score for the first adapting stimulus and that for the second (opposite) adapting stimulus. This difference score was used for graphical purposes only.

4.3. *Experiment 2*

4.3.1. *Stimuli*

We used the same faces as Experiment 1. In this experiment, however, each original image was manipulated in Adobe Photoshop CS 8.0 by applying a number of filters, including grayscale and high-pass, to create black-and-white thresholded images, so that scrambling of the features could be performed without leaving visible segmentation boundaries in the image. The thresholded images were used as adapting stimuli (Fig. 1B.i) and to generate the morphed test stimuli for the *intact-face* condition, in the same manner as in Experiment 1.

In the *scrambled-face* condition, the features (eyes, mouth, eyebrows and nose) of the non-morphed thresholded images were rearranged in an identical manner for all images, angry and afraid (Fig. 1B.ii). These served as the adapting and choice stimuli in the trials. The morphing process was then applied to these new scrambled configurations to generate the morphed test stimuli (hence, both adapting stimuli and test stimuli were identically scrambled arrangements in the *scrambled-face* condition), which at the featural level consisted of physical changes equal in magnitude to the test stimuli in the *intact-face* condition.

4.3.2. Procedure

Trials were similar to those in Experiment 1. Each began with a 5-s view of an adapting stimulus, followed by a 50-ms mask, a 300-ms view of a test stimulus and then the choice screen. There were two blocks of trials, one of 52 trials for the *intact-face* condition and one of 52 trials for the *scrambled-face* condition. With both blocks, there were a total of 104 trials. Half of the subjects began with the *intact-face* block and the other half with the *scrambled-face* block.

4.3.3. Analysis

As in Experiment 1, a repeated measures ANOVA was performed with the response score as the dependent measure, and face condition (*intact-face*, *scrambled-face*) and adapting stimulus (image 1 with angry elements, image 2 with afraid elements) as within-subject factors.

4.4. *Experiment 3*

4.4.1. Stimuli

We created a new set of stimuli with Adobe Illustrator CS 8.0. Angry and happy expressions consisted of simple black lines, curves and circles. Happy faces were used instead of afraid faces as it was difficult to convey fear in these schematic faces. For the *intact-schematic-face* condition, we arranged lines in a facial configuration within an oval outline, with tilted eyebrow lines and mouth curves in opposite directions to create the baseline adapting stimuli of angry and happy faces (Fig. 1C.i). Thirteen test stimuli were created by systematically changing the mouth curvature and eyebrow orientation between the 35%/65% and the 65%/35% points in the happy–afraid transition images in 2.5% steps, analogous to the morphed images in Experiment 1 and 2. Here the 50%/50% mid-position between happy and afraid was characterized with flat horizontal lines for the eyebrows and mouth. The adapting and the test stimuli for the *scrambled-schematic-face* condition were created in a similar fashion, but with the line elements in a non-facial configuration within the same oval outline (Fig. 1C.ii). Again, the adapting stimuli and the test stimuli had identical scrambled arrangements in the *scrambled-schematic-face* condition.

4.4.2. Procedure

Trials were similar to those in Experiments 1 and 2, with a 5-s viewing of one of the two adapting stimuli, followed by the 50-ms mask, the 300-ms test stimulus, and the choice screen showing the two possible extreme stimuli. There were two blocks, one for the *intact-schematic-face* condition and one for the *scrambled-schematic-face* condition. In each block, all 13 test stimuli were presented twice, once after each of the two adapting stimuli, for a total of 26 trials per block and 52 trials in the experiment.

4.4.3. Analysis

We ran a repeated measures ANOVA with the response score as the dependent measure, and face condition (*intact-schematic-face*, *scrambled-schematic-face*) and adapting stimulus (image 1 with angry elements, image 2 with happy elements) as within-subject factors.

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REFERENCES

Adams, W.J., Mamassian, P., 2002. Common mechanisms for 2D tilt and 3D slant after-effects. Vis. Res. 42 (23), 2563–2568.
Barton, J.J., Radcliffe, N., Cherkasova, M.V., Edelman, J., Intriligator, J.M., 2006. Information processing during face recognition: the effects of familiarity, inversion, and morphing on scanning fixations. Perception 35 (8), 1089–1105.
Baudouin, J.Y., Martin, F., Tiberghien, G., Verlut, I., Franck, N., 2002. Selective attention to facial emotion and identity in schizophrenia. Neuropsychologia 40 (5), 503–511.
Butler, S., Gilchrist, I.D., Burt, D.M., Perrett, D.I., Jones, E., Harvey, M., 2005. Are the perceptual biases found in chimeric face processing reflected in eye-movement patterns? Neuropsychologia 43 (1), 52–59.
Clifford, C.W.G., Rhodes, G., 2005. Fitting the Mind to the World: Adaptation and After-Effects in High-level Vision. Oxford University Press, Oxford.
de Heering, A., Houthuys, S., Rossion, B., 2007. Holistic face processing is mature at 4 years of age: evidence from the composite face effect. J. Exp. Child Psychol. 96 (1), 57–70.
Dragoi, V., Sharma, J., Sur, M., 2000. Adaptation-induced plasticity of orientation tuning in adult visual cortex. Neuron 28 (1), 287–298.
Felleman, D.J., Van Essen, D.C., 1991. Distributed hierarchical processing in the primate cerebral cortex. Cereb. Cortex 1 (1), 1–47.
Fox, C.J., Barton, J.J., 2007. What is adapted in face adaptation? The neural representations of expression in the human visual system. Brain Res. 1127 (1), 80–89.
Ganel, T., Goshen-Gottstein, Y., Ganel, T., 2004. Effects of familiarity on the perceptual integrality of the identity and expression of faces: the parallel-route hypothesis revisited. J. Exp. Psychol. Hum. Percept. Perform. 30 (3), 583–597.
Gibson, J.J., Rander, M., 1937. Adaptation, aftereffect and contrast in the perception of tilted lines. J. Exp. Psychol. 20, 453–467.
Goffaux, V., Rossion, B., 2006. Faces are "spatial"–holistic face perception is supported by low spatial frequencies. J. Exp. Psychol. Hum. Percept. Perform 32 (4), 1023–1039.
Hubel, D.H., Wiesel, T.N., 1962. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J. Physiol. 160, 106–154.
Huber, D.E., O'Reilly, R.C., 2003. Persistence and accommodation in short-term priming and other perceptual paradigms: temporal segregation through synaptic depression. Cogn. Sci. 27 (3), 403–430.
Kuraoka, K., Nakamura, K., 2006. Impacts of facial identity and type of emotion on responses of amygdala neurons. NeuroReport 17 (1), 9–12.
Leopold, D.A., O'Toole, A.J., Vetter, T., Blanz, V., 2001. Prototype-referenced shape encoding revealed by high-level aftereffects. [see comment]. Nat. Neurosci. 4 (1), 89–94.
Lundqvist, D., Litton, J.E., 1998. The Averaged Karolinksa Directed Emotional Faces—AKDEF.

Perrett, D.I., Rolls, E.T., Caan, W., 1982. Visual neurones responsive to faces in the monkey temporal cortex. Exp. Brain Res. 47 (3), 329–342.
Regan, D., Hamstra, S.J., 1992. Shape-discrimination and the judgment of perfect symmetry—dissociation of shape from size. Vis. Res. 32 (10), 1845–1864.
Rhodes, G., Brennan, S., Carey, S., 1987. Identification and ratings of caricatures—implications for mental representations of faces. Cogn. Psychol. 19 (4), 473–497.
Schweinberger, S.R., Soukup, G.R., 1998. Asymmetric relationships among perceptions of facial identity, emotion, and facial speech. J. Exp. Psychol. Hum. Percept Perform. 24 (6), 1748–1765.
Schweinberger, S.R., Burton, A.M., Kelly, S.W., 1999. Asymmetric dependencies in perceiving identity and emotion: experiments with morphed faces. Percept. Psychophys. 61 (6), 1102–1115.
Shepherd, J., Davies, G., Ellis, H., 1981. Studies of Cue Saliency. Academic Press, London.
Singer, J.M., Sheinberg, D.L., 2006. Holistic processing unites face parts across time. Vis. Res. 46 (11), 1838–1847.
Suzuki, S., 2003. Attentional selection of overlapped shapes: a study using brief shape aftereffects. Vis. Res. 43 (5), 549–561.
Suzuki, S., Cavanagh, P., 1998. A shape-contrast effect for briefly presented stimuli. J. Exp. Psychol. Hum. Percept. Perform. 24 (5), 1315–1341.
Tanaka, J.W., Kay, J.B., Grinnell, E., Stansfield, B., Szechter, L., 1998. Face recognition in young children: when the whole is greater than the sum of its parts. Vis. Cogn. 5 (4), 479–496.
Valentine, T., 1991. A unified account of the effects of distinctiveness, inversion, and race in face recognition. Q. J. Exp. Psychol., A 43 (2), 161–204.
Wallraven, C., Schwaninger, A., Bulthoff, H.H., 2005. Learning from humans: computational modeling of face recognition. Network 16 (4), 401–418.
Webster, M.A., Kaping, D., Mizokami, Y., Duhamel, P., 2004. Adaptation to natural facial categories. Nature 428 (6982), 557–561.
Werner, J.S., Chalupa, L.M., 2004. The Visual Neurosciences. MIT Press, Cambridge, Mass.
Wilson, H.R., Diaconescu, A., 2006. Learning alters local face space geometry. Vis. Res. 46 (24), 4143–4151.
Winston, J.S., Henson, R.N., Fine-Goulden, M.R., Dolan, R.J., 2004. fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. J. Neurophysiol. 92 (3), 1830–1839.
Yovel, G., Duchaine, B., 2006. Specialized face perception mechanisms extract both part and spacing information: evidence from developmental prosopagnosia. J. Cogn. Neurosci. 18 (4), 580–593.
Zhao, L., Chubb, C., 2001. The size-tuning of the face-distortion after-effect. Vis. Res.. 41 (23), 2979–2994.