Examinations of identity invariance in facial expression adaptation

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Abstract

Faces provide a wealth of information essential to social interaction, including both static features such as identity, as well as dynamic features such as emotional state. Classic models of face perception propose separate neural processing routes for identity and facial expression (Bruce and Young, 1986), but more recent models suggest these routes are not independent of each other (Calder and Young, 2005). Using a perceptual adaptation paradigm, the present study attempted to further examine the nature of the relation between the neural representations of identity and emotional expression. In Experiment 1, adaptation to the basic emotions of anger, surprise, disgust, and fear resulted in significantly biased perception away from the adapting expression. A significantly decreased aftereffect was observed when the adapting and test faces differed in identity. Using a statistical model that separates surface texture and reflectance from underlying expression geometry, Experiment 2 found a similar decrease in adaptation when the face stimuli had identical underlying prototypical geometry but differed in the static surface features supporting identity. These results provide evidence that expression adaptation depends on perceptual features important for identity processing and thus suggest at least partly overlapping neural representations for identity and facial expression.

Keywords: emotion, perception, face space, neural representation, expression morph, computational model

Humans are social beings and face perception is an essential aspect of social cognition. Faces provide a great amount of information critical to social interaction, including both static features such as information about a person's age, gender, race, and identity, as well as dynamic or changeable features such as those that communicate one's internal emotional state (Haxby et al., 2000; Calder and Young, 2005). Classic models of face perception (Bruce and Young, 1986) propose separate, specialized, and parallel processing routes for these distinct feature sets, in particular the recognition of identity and facial expression. A functional analysis suggests that it is advantageous to be able to identify a person regardless of their facial expression, with an abstract, invariant representation of an identity transferred across different facial expressions much like how it transfers across different view points. Conversely, since it is also useful to be able to infer the same emotional states from similar expressions of different individuals, abstract, invariant representations of different facial expressions would need to be transferred across different people.

Supporting this functional segregation, research shows that distinct neural processes may support identity and facial expression analyses. A double dissociation between the ability to identify faces and the ability to interpret expressions has been observed in both brain-damaged patients (e.g., Kurucz and Feldmar, 1979; Kurucz et al., 1979; Shuttleworth et al., 1982; Bruyer et al., 1983) and healthy subjects (Bruce, 1986). The separation between the processing of static invariant (e.g., identity) and dynamic variable (e.g., expression) aspects of faces has also been observed in neurophysiological studies, with the former involving the inferior temporal gyrus (the middle fusiform gyrus in humans), (Kanwisher et al., 1997; Grill-Spector et al., 2004) and the latter involving the superior temporal sulcus (Haxby et al., 2000; Narumoto et al., 2001;

Winston et al., 2004). In addition, neuropsychological and neuroimaging evidence suggests the recognition of categorically distinct prototypical emotions depends on further differentiated neural representations, such as the amygdala for fear (e.g., Adolphs et al., 1999; Calder et al., 2001b; Anderson et al., 2003) and the right anterior insula for disgust (e.g., Phillips et al., 1998; Anderson et al., 2003).

Recent behavioral studies, however, suggest that the neural representations and processes of identity and facial expression may not be entirely independent of each other. Variations in identity interfere with the speed of expression classification (Schweinberger and Soukup, 1998; Ganel and Goshen-Gottstein, 2004). Viewing different expressions improves identity recognition of familiar faces (Kaufman and Schweinberger, 2004) and learning the identity of unfamiliar faces (Baudouin et al., 2000). Computational analyses of identity and facial expression have further shown the potential overlap between identity and expression representations. Employing principal component analysis, Calder et al. (2001a) found substantial overlap between the components important for identity and expression discrimination in a statistical model such that identity discrimination was still possible when restricting analysis to components selective for expression discrimination and vice versa. Neuroimaging studies have also found a large overlap in activation patterns and associated processes drawn upon during identity and facial expression recognition tasks (e.g., LaBar et al., 2003).

Adaptation paradigms provide a way of further investigating the neural representation of faces (Fox and Barton, 2007a) and refining current theories on the independence or dependence of identity and facial expression from each other. Adaptation is the decrease over time in the responsiveness of a neural representation to a constant stimulus, which is believed to fatigue the neural mechanisms associated with the processing of a particular feature of that stimulus (Köhler and Wallach, 1944). The result is a biased perception of the stimulus towards its opposite (e.g., figural aftereffects) (Webster et al., 2004). Adaptation has been observed for a variety of visual features such as size, orientation, curvature, spatial frequency, motion, and complex and natural images (Webster and MacLin, 1999). In particular, aftereffects have now also been observed with distorted faces (e.g., contracted or expanded, changed spatial frequency) that are size-, retinal position-, and orientation-invariant (e.g., Leopold et al., 2001; Zhao and Chubb, 2001; Rhodes et al., 2003). Higher-order adaptation to natural facial categories such as gender, ethnicity, attractiveness, and identity has also been shown (e.g., Leopold et al., 2001; Rhodes et al., 2003; Webster et al., 2004).

In addition to static facial features, adaptation has been shown for dynamic features such as facial expression (Hsu and Young, 2004; Webster et al., 2004; Fox and Barton, 2007a), with repeated exposure to an expression significantly biasing perception away from the adapting expression. For example, repeated exposure to a face expressing happiness will reduce sensitivity to perceiving happiness in facial expression mixtures (e.g., a happiness-disgust morphed expression). Thus, studies have separately shown that adaptation can be used to interrogate the neural representations supporting both identity and expression recognition. However, little work has focused on the interaction of identity and expression in facial adaptation, which would have important consequences for examining the independence of identity and expression neural representations.

Recently, Fox and Barton (2007a) investigated whether facial expression adaptation generalizes across different identities. If facial expression adaptation results from modulation of identity-independent/expression-dependent representations, then they should be resilient to changes in identity between the adapting and test stimuli. Expression aftereffects, although present, were significantly diminished when the adapting and test stimuli had differing identities. These results are consistent with some common neural process supporting identity and expression processing. However, it is unclear to what extent reduced expression adaptation is due to changes in identity or expression features. Any decreases in identity-expression cross-adaptation not only reflect differences in static features supporting identity, but may also originate in differences in dynamic features supporting expression appearance. For instance, individuals may differ in the degree to which their expressions match underlying prototype geometry. Differences in expression geometry across individuals may preclude undiminished adaptation.

To examine whether expression aftereffects are identity invariant—that is, are preserved when the identity is altered between the presentation of the adapting and test stimuli—we attempted to more precisely determine the cause of the reduced expression aftereffect by carefully controlling facial features associated with identity and expression with a visual statistical model of facial appearance (Craw and Cameron, 1991). Experiment 1 examined identity-expression cross-adaptation using emotions thought to depend on specialized limbic and paralimbic neural substrates. Experiment 2 analyzed whether differences in expression geometry or features supporting identity accounted for reduced expression adaptation across identities. This was achieved by generating novel realistic facial stimuli via factoring face images into their geometrical (i.e., shape) and surface (i.e., texture and reflectance) properties (Craw and Cameron, 1991). This afforded a novel computational method for mapping different facial identities onto identical prototypical expression geometry and a direct test of whether expression adaptation is robust to changes in surface identity when expression form is held constant.

Experiment 1

Materials and Methods

Participants. Thirty-two participants contributed data for analysis (20 females; $M = 19.56$ years, $SD = 2.20$ years). All were undergraduate students at the University of Toronto who volunteered for experimental credit towards their Introduction to Psychology course or were recruited via posters and paid $10 for their participation. All had normal or corrected-to-normal vision. All were unaware of the purpose of the experiment and informed consent was obtained from each participant before the experiment started in accordance with the ethics guidelines at the university.

Stimuli and Apparatus. Grayscale images of two female individuals were obtained from Ekman and Friesen's Pictures of Facial Affect (POFA) dataset (Ekman and Friesen, 1976). Each individual posed four different expressions: anger, disgust, fear, and surprise. The two individuals were selected because they yielded the highest facial expression recognition rates in the POFA dataset. The four emotions were chosen on the basis of behavioral findings that anger and surprise and disgust and fear pairs are judged as most dissimilar (Susskind et al., 2007).

The images were processed for experimental display using MATLAB 7.0. All faces were cut out from the background image using a polygonal region defined by a consistent facial contour labeling scheme. Pixels inside the polygonal region defining the face were histogram-equalized to remove variability due to lighting differences across faces. All of the faces were then commonly aligned to remove global differences in size, rotation, and translation using a generalized Procrustes transformation (Goodall, 1991) on a set of 68 feature point locations including the contour, eyebrows, eyes, nose, and mouth. Each face was cropped to a common face box and resized to 337 x 328 pixels, maintaining the aspect ratio of the common face box.

Test faces for the two-alternative forced choice task before and after the adaptation phase were drawn from morph continua consisting of 100 images each, with the first image (left end, 0%) of a facial expression gradually turning into another expression by the 100th image (right end, 100%). The category boundary or neutral point is the percentage or morph level at which the image will be equally likely perceived as either the left or right end of the continuum. The anger and surprise images of the same identity face were morphed together using FantaMorph 3.0 and the morphing sequence was stored as 100 frames of a movie file. The disgust and fear images of the same identity face were morphed in the same way.

The experiment program was written using Visual Basic 6.0. A PC was used to present the stimuli on a uniform grey background with the monitor mounted approximately 50 cm in front of the participant. The participants pressed either a red or green button on the keyboard to make a two-alternative forced-choice response but were not given specific instructions for which hand to use. All instructions appeared on the monitor.

The independent variables were the continuum from which the test faces were drawn (anger-surprise or disgust-fear; between-subjects), the identity of the adapting face (same as or different from the continuum; between-subjects), and the adapting expression (left side of continuum = anger/disgust or right side = surprise/fear; within-subjects), resulting in four groups (continuum/adapting identity): anger-surprise/same identity, anger-surprise/different identity, disgust-fear/same identity, and disgust-fear/different identity. The dependent variable was the difference between the pre- and post-adaptation category boundaries (i.e., post minus pre). A negative value meant the boundary shifted towards the left end of the continuum (anger or disgust) while a positive value meant it shifted towards the right end (surprise or fear).

Procedure. Participants carried out the experiment individually. Participants were randomly assigned to the four groups. The experimental procedure is illustrated in Fig. 1. During the pre-adaptation phase, a test stimulus (i.e., an individual frame from a continuum) was presented for 500 ms on each trial followed by a prompt screen with two response options, which was shown until a response was made. The participant classified the image as one of two emotions, which corresponded to the two ends of the continuum, by pressing either the red (left choice) or green (right choice) button. A double, randomly interleaved staircase procedure (Cornsweet, 1962) was used to present the stimuli and to estimate the continuum category boundary (i.e., the morph level at which either of the two responses was equally likely) (Webster et al., 2004). Each of the two staircases started at one end of the continuum or the other. The morph level of the test stimulus on each trial was increased or decreased in steps of two depending on the response to the previous trial, for each of the two staircases. If, for example, the image was selected from the left end of the anger-surprise continuum and the participant judged “anger”, the next image would be selected from 2 steps up (i.e., towards the right or surprise end). The image would keep increasing in morph level (i.e., moving to the right) until the participant judged “surprise”, at which point the staircase would reverse (counted as 1 reversal) and the next image would be 2 steps down (i.e., back towards the left or anger end). The same dependency would occur for the staircase starting from the right/surprise end. The staircase procedure terminated after 12 reversals for each staircase. The morph levels at which each of the staircases’ 12 reversals occurred were averaged and the two resulting values were averaged in turn, which was taken as the category boundary (neutral point) between the two expressions.

During the adaptation phase, the participant was instructed to look at one of the original images from one end of the continuum continuously for 180 s but was not given specific fixation instructions. During the post-adaptation phase, the participant again classified test stimuli into one of two emotions to re-estimate the reversal points using the procedure from the pre-adaptation phase, but with the adapting image shown for 5 s in between each of the test images. There was an interstimulus interval of 250 ms between the adapting and test stimuli during which a uniform grey background was shown. After a short break, the three phases were repeated with the adapting face chosen from the other end of the continuum. The order in which the two adaptation blocks were presented was randomized across participants.

Results

An alpha level of .05 was used for all statistical tests. A three-way analysis of variance (ANOVA) for mixed-designs with continuum, adapting identity, and adapting expression tested for the effects of identity and facial expression on adaptation. The dependent measure was the difference between the pre- and post-adaptation category boundaries (post minus pre). Consistent with expression adaptation, there was a robust main effect of adapting expression, $F(1, 28) = 326.56$, $p < .001$, with adaptation to the left end of the continuum shifting the category boundary to the left ($M = -16.63$, $SD = 10.57$) and adaptation to the right end (100%) shifting it to the right ($M = 18.39$, $SD = 9.15$). Thus, adapting to anger or disgust resulted in seeing less anger or disgust in faces. There were no main effects of continuum, $F(1, 28) < 1$, or identity, $F(1, 28) = 2.35$, $p = .14$. The lack of a main effect of identity was qualified by a significant interaction of identity and expression, $F(1, 28) = 17.59$, $p < .001$, with adaptation to a different identity leading to significantly smaller boundary shifts (i.e., expression aftereffects) than adaptation to the same identity (Fig. 2). Restricting analysis to same identity revealed highly robust adaptation, $F(1, 14)$

= 302.09, $p < .001$. Although significantly diminished, there remained evidence of significant expression aftereffects for different identity trials as well, $F(1, 14) = 81.63$, $p < .001$.

Discussion

Consistent with previous facial expression adaptation studies (Hsu and Young, 2004; Webster et al. 2004; Fox and Barton 2007a), the perception of facial expressions were reliably and noticeably biased by prolonged exposure to images of facial expressions. Fatiguing the representation of a facial expression led to reduced sensitivity to that expression, decreasing the likelihood of perceiving that expression and increasing the likelihood of perceiving a competing expression. Although this expression aftereffect occurred both when the identities of the adapting and test faces were the same and when they were different, a significantly larger aftereffect was observed when the adapting and test faces were from the same individual. This is consistent with the reduced expression adaptation across identities reported by Fox and Barton (2007a) as well as partial sparing, suggesting a significant degree of overlapping and/or interacting identity and expression neural representations.

One potential complication with this interpretation is that the same identity condition used identical adaptation and test images, following prior work on expression adaptation (Hsu and Young, 2004; Webster et al., 2004). Thus, differences across identities may reflect differences in low-level visual features, rather than high-level featural similarity. However, adaptation reflecting redundancy in local luminance is unlikely as subjects were given ample time to move their eyes during adaptation. Nevertheless, we further explore this issue in Experiment 2.

Another plausible explanation for reduced expression adaptation across individuals is that individuals differ in extent to which they convey emotion when producing an expression. Different identity exemplars may present substantial variance in the intensity and precise form of expression features and thus may match expression category prototypes to differing degrees. As such, it may be differences in the changeable features that support expression geometry in different individuals that accounts for decreased expression adaptation across identities, and not identity change itself,

To explore the contributions of the above, we developed faces for Experiment 2 where expression shape (i.e., feature geometry) and surface texture and reflectance could be manipulated separately. If the decrease in expression adaptation across identities was due to individual differences in expression geometry and how they may differently match neural representations of an expression prototype, then holding the expression geometry constant should result in the same size expression aftereffects regardless of identity. We generated images of identical geometry/shape and warped surface textures from different identity information on to these shapes (see Fig. 3). This allowed an examination of whether the identity-related decrease in adaptation reflected changes primarily in identity while holding expression geometry constant. Expression geometry was computed by the average across exemplars in an expression category to more closely align with an underlying expression prototype, which may further limit variance in adaptation across identities. We examined the influence of a small horizontal distortion of the underlying facial geometry of one of the adapting faces. This allowed a determination of whether greater adaptation for the same identity merely reflected presenting the identical image during the adaptation and test trials. We also examined whether change in gender features in addition to identity altered expression adaptation. Finally, Experiment 2 manipulated identity as a within-subjects measure to allow greater sensitivity in detecting the effect of identity on expression adaptation.

Experiment 2

Materials and Methods

Participants. Thirty-two participants contributed data for analysis (22 females; *M* = 19.31 years, *SD* = 1.38 years). All were undergraduate students at the University of Toronto who volunteered for experimental credit towards their Introduction to Psychology course or were recruited via posters and paid $10 for their participation. All had normal or corrected-to-normal vision. All were unaware of the purpose of the experiment and informed consent was obtained from each participant before the experiment started in accordance with the ethics guidelines at the university.

Stimuli and Apparatus. Grayscale images of two female and two male individuals (240 x 240 pixels) were obtained from POFA (Ekman and Friesen, 1976). Although there was no significant difference between the two continua in the first experiment, the anger-surprise continuum displayed the numerically largest effects of identity on expression adaptation (see Fig. 2) and thus was used for Experiment 2. The same image processing steps used to prepare the stimuli for Experiment 1 were performed on the faces for this experiment with additional steps to remove differences in the facial geometry between faces posing a given expression. The first additional step was to create anger and surprise prototype geometries by averaging each of the 68 feature point locations across all of the faces in the anger and surprise categories, respectively. Then, each of the four anger faces and each of the four surprise faces were separately warped to the corresponding prototype anger or surprise shape using a piecewise affine warp defined on a

Delaunay triangulation (Goshtasby, 1986) of the feature points. This manipulation resulted in removing geometrical differences between identities posing a particular expression while retaining variance in surface reflectance characteristic of each identity (Craw and Cameron, 1991). Thus, realistic synthetic faces were created that differed in identity and gender but overall held expression geometry constant (Fig. 3), rendering a novel stimulus set of matching prototypic expressions of differing identities. In addition, to examine whether greater adaptation for the same identity reflects using the identical image, we performed a small horizontal compression of the underlying facial geometry of one of the two adapting faces (surprise).

The experiment program was written using Visual Basic 6.0. A PC was used to present the stimuli on a uniform grey background with the monitor mounted approximately 50 cm in front of the participant. The participants pressed either a red or green button on the keyboard to make a two-alternative forced-choice response but were not given specific instructions for which hand to use. All instructions appeared on the monitor.

The independent variables were adapting expression (anger or surprise; between-subjects), the gender of the adapting face (same as or different from the continuum; between-subjects), and the identity of the adapting face (same as or different from the continuum; within-subjects). The dependent measure was the difference between the pre- and post-adaptation category boundaries (post minus pre).

Procedure. To examine whether facial identity information was retained when warped onto a prototypical expression geometry, prior to the adaptation task, participants performed an identification task in which they identified each of the adapting faces showing anger or surprise by choosing one out of the four surrounding unprocessed POFA neutral expression images. The same adaptation procedure as in Experiment 1 was used for this experiment with a few minor modifications. The double, randomly interleaved staircase procedure still terminated after 12 reversals, but the first 3 reversals led to increments/decrements of 8 steps, the next 4 reversals to 4 steps, and the last 5 reversals to 2 steps. Before continuing with the second adaptation block, participants viewed a random sequence of images (each shown for 125 ms for 1 minute to speed up the decay of the adaptation effect) drawn from the set of test images, which were pixelated (cell size = 30 x 30 pixels) and randomly flipped horizontally, vertically, or both. The order in which the two adaptation blocks were presented was randomized across participants.

Results

To see whether warping the face points to the prototype position would retain the identity of the face, a one-sample chi-square test analyzed the participants' accuracy in the identification task. Average accuracy (56.25%) was significantly greater than chance (25%), $\chi 2(1, N = 64) = 33.33$, $p < .001$, suggesting that discriminative identity information was conveyed in the surface reflectance properties of the face after identity-specific shape information was removed. This is further illustrated in Fig. 3, where altering surface texture and reflectance while holding expression geometry constant yielded faces of distinct identities.

A four-way ANOVA for mixed-designs was employed with the adapting identity's gender (same or diff as continuum) and facial expression (anger vs. surprise) as between-subjects factors, and the adapting identity (same vs. different) as a within-subjects factor. The dependent measure was the difference between the pre- and post-adaptation category boundaries (post minus pre). There was a significant main effect of adapting expression, $F(1, 28) = 9.89$, $p = .004$, with adaptation to anger shifting the boundary towards the left or anger side ($M = -6.17$, $SD = 9.74$) and adaptation to surprise shifting the boundary towards the right or surprise side ($M =$

4.44, *SD* = 13.80) of the morph continuum. That is, the adapting expression shifted the categorical boundary closer to the expression prototype. Replicating Experiment 1, there was a significant identity by expression interaction, $F(1, 28) = 7.61$, $p = .01$, with adaptation to a different identity than the test faces leading to smaller boundary shifts (i.e., expression aftereffects) than adaptation to the same identity (Fig. 4). Follow-up analyses revealed robust same identity (i.e., same texture) adaptation even when the shape of adapting and test stimuli differed along the horizontal dimension (surprise, pre vs. post), $F(1, 15) = 14.37$, $p < .002$, being highly similar (8.64, SE = 3.52) to adaptation with the identical image (8.52, SE=2.65). There was no statistical evidence of expression aftereffects for different identity trials, when there was a change in both surface texture and shape, $F(1, 15) < 1$. The identity by expression interaction was not further modified by changes in gender between the adaptation and test faces, $F(1, 28) < 1$. This lack of effect of gender in addition to identity may however reflect a floor effect, as there was little evidence of adaptation after identity change.

Discussion

Consistent with the first experiment, in Experiment 2 facial expression perception was noticeably biased by adaptation to images of facial expressions. That is, adapting to an expression pushed the category boundary towards the prototype, requiring the expression to be more prototypical to be correctly categorized. Similar to the first experiment, facial expression aftereffects were larger when the identities of the adapting and test faces were the same. This identity modulation of expression adaptation was not an artifact of using the identical image in same identity condition, as a change in the horizontal aspect ratio between the adaptation and test faces in Experiment 2 resulted in robust adaptation of similar magnitude to adaptation found with the identical image. In addition, identity influences on expression aftereffects remained when a computational model of expression appearance was used to hold expression geometry constant across identities. As such, differences in expression geometry in different individuals cannot fully account for the reduction in identity and expression cross-adaptation. Since identity information was retained despite identical expression structures, the decreased cross-adaptation likely reflects differences in visual features supporting identity.

Of note was that the expression aftereffect, although still significant, was less statistically reliable in the second experiment compared to the first. The difference is most likely due to changes in experimental design. First, the facial expression comparison was within-subjects for Experiment 1 and between-subjects for Experiment 2, opting for adapting identity to be a within subject manipulation. Second, Experiment 1 contained twice the number of trials assessing the adaptation effect since two continua were used (anger-surprise and disgust-fear) and only one continuum in Experiment 2 (anger-surprise). Nevertheless, despite this reduced expression adaptation in Experiment 2, there remained a highly reliable influence of identity on expression adaptation.

General Discussion

Our findings show that expression adaptation is reduced when identity is manipulated. This robust reduction in adaptation was present even when the shape of expression features were held constant (i.e., same expression geometry) across individuals. Reduced adaptation across identities provides support for partially overlapping neural representations of identity and facial expression. If identity and expression processing depended on entirely segregated streams of processing, then altered identity should be represented as changes in a neural population vector in an identity system, having minimal influence on such representations on expression-dedicated neural systems. As such, changes in identity would not result in changes in expression adaptation. Contrasting with this neural model of independent expression and identity processing, identity changes had robust influences on expression adaptation. Nevertheless, there was evidence that adaptation was not entirely abolished following identity change. This is consistent with the presence of some level of identity-independent representation of emotional expression processing. Such findings are consistent with Calder and Young's (2005) proposal that identity and expression may be initially coded by a single representational system rather than through separate processing routes involved in the extraction and separation of different facial cues.

Experiment 2 attempted to preserve facial features informative for expression perception by equating geometrical shape features of the compared adapting faces. Our manipulation was designed to test whether the remaining surface reflectance information would preserve identity while minimizing expression differences. Our results show that expression adaptation is attenuated even when the shape features of the adapting face are equated to those of the continuum target face, thus indicating that the identity information in the texture interferes with expression adaptation. However, this argument may be complicated by evidence that surface reflectance properties in the shape-normalized image also convey important information for expression processing. That is expression information is not only carried by the shape features but also surface texture. Countering that notion, Calder et al (2001) show that shape information is more informative than surface reflectance for discriminating facial expressions in a PCA model, and that texture information such as bright teeth in smiles is largely redundant with shape features such as upturned and open lips. Much of the perceptually meaningful information conveyed by faces is in the phase structure rather than the frequency domain, indicating that shape features (edges and discontinuities in the face image) are more important than detailed surface texture (Bartlett, Movellan, & Sejnowski, 2002). In addition, computational systems employing local edge detection such as Gabor wavelets (Littlewort et al, 2006) perform well at expression recognition across a large degree of lighting conditions also indicating the high information value of edge features. Nevertheless, surface reflectance contributes to expression perception as supported by findings that a PCA representation combining shape and surface reflectance features performs better than either shape or reflectance alone (Calder et al, 2001).

Whereas identity adaptation has been shown to be robust to certain transformations of the face (Jiang et al., 2006), the current study indicates that expression adaptation is less so. This divergence may suggest that identity and expression features depend on distinct types of representations, counter to our suggestion of overlapping visual features in neural processing of identity and expression. However, the nature of transformations employed in these studies is quite distinct, with differences between identity and expression adaptation reflecting the use of rigid versus non-rigid transformations between adaptation and test stimuli. Previous studies examining identity adaptation have shown that identity adaptation is robust to rigid transformations, as in viewpoint (Jiang et al., 2006). Changes in facial expression adaptation related to identity, as done in the present studies, reflect a non-rigid transformation between adaptation and test stimuli. Thus, expression adaptation may be reduced by the non-rigid movement of facial features supporting identity. This is particularly striking in Experiment 2 where the shape features of adapting and test stimuli were generated based on an identical expression prototype. Despite the underlying commonality in expression geometry, expression adaptation was significantly disrupted. That is, large reductions in expression adaptation were found even when the underlying shape of features was held constant (i.e., shape of eyes, nose, mouth, outline of face), but surface features supporting identity was non-rigidly varied. This suggests the representation of non-rigid surface texture and reflectance patterns may be common to both identity and expression adaptation as shown by PCA (Calder et al., 2001a). However, it is important to consider whether rigid transformations of expression identity (e.g., viewpoint) would also alter expression adaptation. Future studies would need to demonstrate that expression adaptation is robust to rigid transformations, further suggesting that expression and identity representations call upon shared neural substrates.

One concern is that facial adaptation may influence neither identity nor facial expression processing themselves, but an earlier common visual representation. That is, identity and expression processing may occur in parallel at an abstract, high-level of processing at neural loci downstream of facial adaptation effects. By contrast, the neural locus of the intersection of identity and expression as revealed through facial adaptation is unlikely at very low levels of visual representation as visual fixation was not maintained through the adaptation and test phases. Consistent with an intermediate to high level locus, as mentioned above, identity adaptation has been shown to generalize across viewpoint (Jiang et al., 2006). This suggests that facial adaptation is at a level above view-dependent coding, where these lower-order representations are integrated into a view-independent representation of identity. We propose it is at this level that represents the common neural locus of adaptation between identity and expression. However, as mentioned above, it would be of interest in future studies to establish that expression adaptation indeed occurs at a similar view-independent level of representation.

What is the precise neural representation supporting expression adaptation? The separation between the processing of static invariant and dynamic variable aspects of faces has been proposed to involve the inferior temporal gyrus (the lateral fusiform gyrus in humans) (Kanwisher et al., 1997; Grill-Spector et al., 2004) and the superior temporal sulcus (Haxby et al., 2000; Narumoto et al., 2001; Winston et al., 2004). Neuroimaging evidence suggests that the high-level interaction between identity and facial expression likely occurs in the latter. The superior temporal sulcus (STS) contains cells sensitive to both expression and identity (Perrett et al., 1984) and also exhibits adaptation to both facial characteristics (Winston et al., 2004). Specifically, identity-dependent neural representations of facial expressions have been identified in humans in the posterior STS, which is responsive to both identity and expression (Winston et al., 2004). By contrast, identity-independent neural representations of expression have been found in the middle STS, which is responsive to expression but not identity (Winston et al., 2004). The present results suggest perceptual adaptation to facial expressions depends conjointly upon the posterior and middle STS, with the former representing identity-based expression adaptation and the latter representing more abstract expression-based adaptation. The reduction in adaptation we observed related to changing identity likely reflects that expression adaptation depends to a large degree on the posterior STS. However, as this reduction was not always absolute, the amount of spared adaptation across individuals may depend on the middle STS.

The evidence of identity-dependent and -independent representations in the STS suggests there is some form of functional asymmetry in how identity and facial expression coding overlap wherein identity processing is relatively view- (e.g., Jiang et al., 2006) and expression-independent (e.g., Fox and Barton, 2007b), but expression processing may be relatively view- and identity-dependent. Indeed, identity and familiarity have been shown to modulate judgments of facial expression while judgments of identity are unaffected by expression, suggesting an asymmetric relationship between identity and expression (Schweinberger & Soukop, 1998). It may be that expression processing relies more on integrative mechanisms than identity processing (Calder and Young, 2005). Compared to identity recognition, where there is a scarcity of evidence that facial identity interacts with other facial cues, expression recognition may make use of information from a variety sources. This is suggested by evidence of multiple systems for processing expressions and emotions (e.g., Phillips et al., 1998; Adolphs et al., 1999), of the multimodal analysis of expression (i.e., convergence of facial, vocal, and dynamic components) (e.g., de Gelder and Vroomen, 2000; Dolan et al., 2001), and of the co-processing of expression with other facial cues from dynamic sources such as gaze and lip speech (e.g., Adams and Kleck, 2003, 2005) much of which is supported by the STS (Haxby et al., 2002). Whereas dynamic cues need to be constantly monitored during social interaction this is not true for static facial identity. The dependence on such dynamic integrative mechanisms for expression relative to identity processing suggests a functional and thus neuroanatomic asymmetry. While expression processing is influenced by changes in identity—a situation rarely encountered by perceptual systems—identity processing maybe relatively robust to dynamic changes in the face, such as expression—a situation encountered in all social interactions.

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Captions to Figures

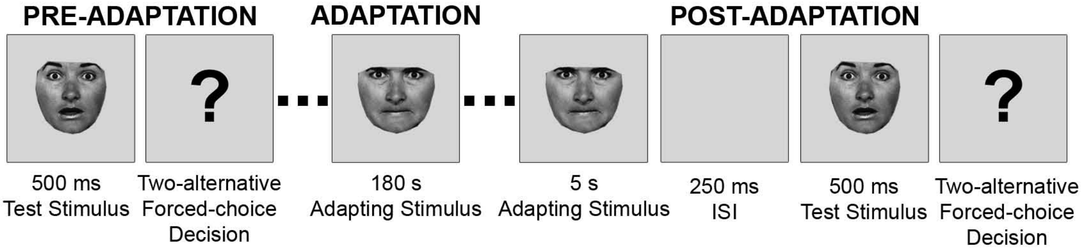
Figure 1. Schematic of Experiment 1 procedure.

Figure 2. Mean difference between the pre- and post-adaptation category boundaries from Experiment 1 for the anger-surprise (A, B) and disgust-fear (C, D) continua as a function of adapting expression (A = anger, B = surprise, C = disgust, D = fear) and identity (same as the test face = black bars or different from the test face = white bars). A negative value represents a boundary shift towards the left end of the continuum (anger or disgust) while a positive value represents a shift towards the right end (surprise or fear). Bar length represents magnitude of adaptation. Error bars represent the standard error of the mean.

Figure 3. Examples of the anger (left panel) and surprise (right panel) facial warp stimuli used in Experiment 2 with geometrical differences in expression between identities removed but variance in surface reflectance characteristic of each identity retained. The shape schematics in the left and right panels depict the underlying shapes for anger and surprise to which face features were warped.

Figure 4. Mean difference between the pre- and post-adaptation category boundaries from Experiment 2 for the anger-surprise continuum as a function of adapting expression (A = anger, B = Surprise) and identity (same as the test face = black bars or different from the test face = white bars). A negative value represents a boundary shift towards the anger (left) end of the

continuum while a positive value represents a shift towards the surprise (right) end. Bar length represents magnitude of adaptation. Error bars represent the standard error of the mean.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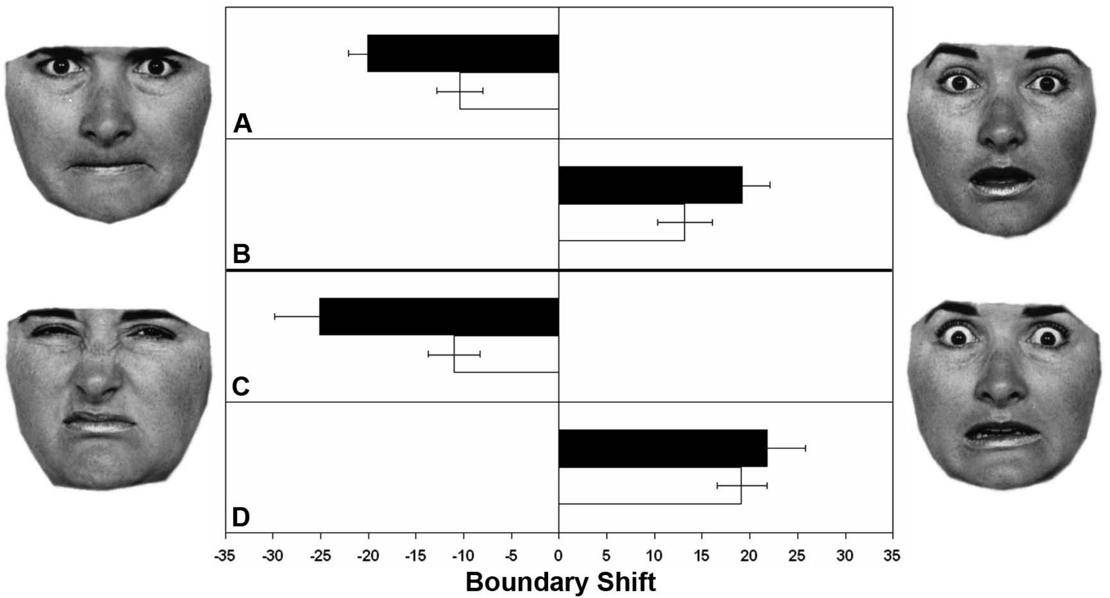
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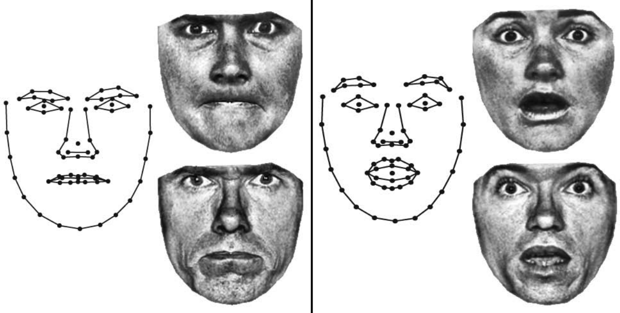

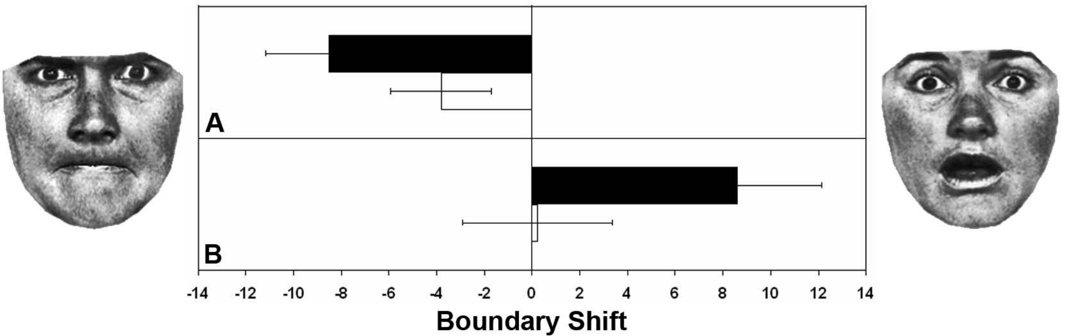
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