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Selectivity of facial aftereffects for changes in gender and expression

A thesis submitted in partial fulfillment of the requirements for the degree of
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by

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ABSTRACT

The ability to perceive and distinguish faces is a fundamental role of the visual system, though how the visual system accomplishes this goal remains poorly understood. A common method used to explore the neural mechanisms underlying face perception is to examine face adaptation aftereffects. For instance, when an observer views a distorted face (e.g. contracted) for a prolonged period of time, a normal face will appear to be distorted in the opposite direction (e.g. expanded). Several studies have utilized these adaptation aftereffects in order to investigate how adaptation transfers across different types of faces, to test whether common or separate neural pathways code different facial attributes. Two attributes that are thought to be processed by largely separate neural subsystems are the expression and identity of the face. In the present study, we examined the selectivity of face aftereffects for differences in gender or expression, in order to further elucidate how expression and identity are encoded in the brain. We tested the prediction that adaptation should show stronger transfer across changes in facial expression because expression changes do not alter the perceived identity of faces. The results of this study showed weak selectivity for changes in expression or gender, as well as modest differences between these two forms of natural facial variation. The results thus were inconsistent with the proposal that variant features of the face, like an expression change, will have less influence on adaptation than an invariant change, like gender or identity. Instead, the results suggest that changes in expression or gender have comparable effects, and may be represented in similar ways at least with regard to the mechanisms mediating face adaptation.

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INTRODUCTION

Faces are among the most important social stimuli for humans, for we devote more time looking at faces than any other object (Haxby et al. 2000). Face perception allows us to identify familiar faces, recognize emotions, and communicate non-verbally. These abilities are thought to depend upon specialized neural processes and pathways including the fusiform gyrus, which is located in the right temporal lobe of the brain (McCarthy et al., 1997). This is supported by the fact that individuals with damage to the fusiform gyrus often develop prosopagnosia and lose the ability to recognize faces (Whiteley and Warrington, 1977). However, it remains unclear exactly how the brain encodes and represents faces.

Invariant and Variant Characteristics

One of the most impressive capacities of face perception is the ability to distinguish and recognize different identities. Even infants have the ability to recognize a familiar face, for they can readily distinguish their mother from a stranger (Nelson, 2001). In addition, humans are capable of recognizing a face even though faces exhibit constant change. For example, whether an individual is smiling or frowning or seen from different angles or under different lighting, we still perceive the same individual despite natural facial alterations. A common question posed by visual scientists is how the brain represents identity independently of these stimulus changes. These studies address how the visual system can extract and represent “invariant” characteristics, or the facial features that define identity, which may include an individual’s gender, ethnicity, and face shape.

Faces also contain information by how they vary. These “variant” characteristics are the changeable aspects of the face and play an important role in general social communication. The most common example is facial expressions. Other examples of variant characteristics include age, mood, and health. The changeable facial features inform others of the present state of a person.

Because variant and invariant facial characteristics seem to provide different types of information, it has been proposed that the two categories are processed in separate pathways. Bruce and Young (1986) proposed that expression was processed in a pathway that recognized facial movements, such as moving the mouth to talk or express emotions, and identity was processed in a pathway that recognized the properties that defined a particular face. Furthermore, it is believed that invariant characteristics must be processed separately from variant characteristics, because, if not, face movements would cause a person to report a different identity (Haxby et al., 2000). The notion of separate pathways for invariant and variant characteristics has been supported by studies using neural recordings from face-sensitive cells in the visual system. In macaque monkeys, these recordings revealed that the superior temporal sulcus is activated by facial expressions, while the inferior temporal gyrus responds to identity (Hasselmo et al., 1989). Similar areas in the human brain, such as the superior temporal sulcus and lateral fusiform gyrus, have also been noted to respond to expression and identity separately by using fMRI, a neuroimaging technique (Haxby et al. 2000, Hasselmo et al., 1989).

Although identity and expression appear to be processed by separate pathways, there is some evidence to suggest an interaction between identity and expression as well. In a study by Gothard et al. (2007), it was observed that the amygdala receives input from

the inferotemporal cortex and superior temporal sulcus, areas noted to respond to identity and expression, correspondingly. This suggested that identity and expression might be integrated in other areas of the brain.

Adaptation

In addition to neural recordings and neuroimaging studies, the interaction between identity and expression has been investigated using adaptation studies. An adaptation study requires an observer to stare at, or adapt to, an image for a brief period of time (i.e. seconds or minutes), and then test how this prior exposure affects the appearance of stimuli shown subsequently. Adaptation studies are commonly used to examine the perception of many visual attributes, such as color, motion, and faces, for adaptation provides scientists with a noninvasive method of altering the neural code and understanding the underlying mechanisms of perception within the brain.

Adaptation induces changes in perception because it changes the sensitivity and thus relative responses to neurons. Neurons that experience prolonged stimulation become desensitized and decrease in activity. Once the stimulation is removed, neurons that were less adapted become more sensitive, and thus are more active. This sensitivity adjustment offers an effective tool to demonstrate selective neural sensitivities to several different stimulus dimensions. Once an observer has adapted to a particular stimulus for a prolonged amount of time, the observer will perceive a negative aftereffect in a neutral stimulus. A common example of the adaptation paradigm is the tilt aftereffect. When an observer adapts to a line with a particular orientation, the observer perceives subsequent lines to be tilted in the opposite orientation. During adaptation, the neurons that respond to the particular adapt line orientation become desensitized, and therefore the neurons

that respond to the other orientations are stimulated more readily and produce the negative aftereffect.

These negative aftereffects can also occur for face adaptation. Although face adaptation aftereffects are less understood than the tilt aftereffect, there are several face dimensions that can create strong face aftereffects. Human observers are exceptionally sensitive to configural properties of face images, and thus are very sensitive to change in configuration produced adaptation (Webster & MacLin, 1999). For example, Webster and MacLin (1999) discovered if a face image is manipulated by distorting the image, a test image will appear to be distorted in the opposite direction. Therefore, when an individual adapts to an expanded face, a test image will appear more contracted than normal, and vice versa (Figure 1). It has been suggested in an EEG study conducted by Burkhardt et al. (2010) that separate neural populations encoded expanded and contracted faces. Similarly, when an observer adapts to a male face, a neutral, androgynous image will appear more female, and vice versa (Webster et al., 2004).

Face adaptation aftereffects are suggested to reflect adjustments in processes that enable an individual to distinguish between faces with relatively few differences while also allowing for the ability to identify the same face from physically different images (Yamashita et al., 2005). Moreover, adaptation may consistently influence how faces are perceived in normal situations, which may allow face perception to be calibrated according to the specific group of faces that populate an individual's environment (Webster et al., 2004). Moreover, face adaptation may facilitate the ability to recognize those around us (Rhodes et al., 2010).



Figure 1. Face adaptation aftereffects produced by distorted face images. Adaptation to a contracted face makes a test face appear too expanded, therefore the null image to the observer is actually physically contracted. Adapting to an expanded face produces the opposite aftereffect.

Selectivity of Face Adaptation

Face adaptation produces obvious aftereffects. However, the strength of the aftereffect depends upon how similar the stimuli appear. In a study by Yamashita et al. (2005), the authors examined the selectivity for aftereffects on different image configurations including size, color, contrast, spatial frequency, and contrast polarity. Selectivity of aftereffects refers the notion that face adaptation aftereffects can be stronger for faces that are more similar. Yamashita et al. (2005) found that face aftereffects had weak selectivity for changes in size, color, and contrast. On the contrary, stronger selectivity was observed for changes in spatial frequency and contrast polarity. For instance, when the observer adapted to image with a certain size, a test image with the same size or a different size produced a similar aftereffect, thus resulting in weak selectivity. Conversely, when an observer adapted to an image with a certain spatial frequency range, a test image with the same spatial frequency produced a larger aftereffect than a test image with a different spatial frequency range, thus resulting in stronger selectivity (Figure 2). The authors suggested that the difference in selectivity strength was due to adaptation being contingent upon how similar the face stimuli appear. Perhaps the change in spatial frequency made the stimuli appear to have different identities, while the change in size allowed the stimuli to retain similar identities.

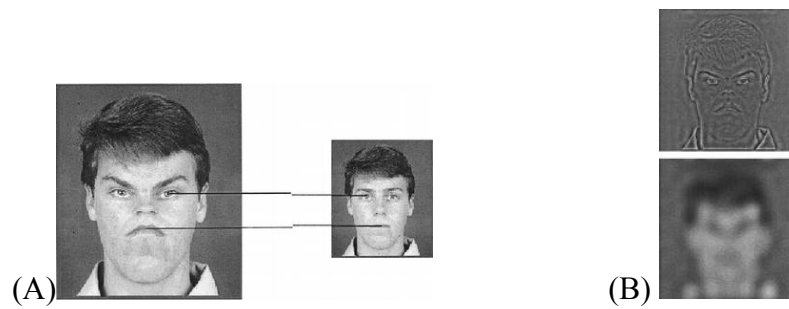


Figure 2. Comparison of the figural differences, size and spatial frequency, in the Yamashita et al. (2005) study. (A) Change in size does not seem to alter identity of face image, and therefore produces little selectivity for the adaptation. (B) Change in spatial frequency does seem to alter identity, and therefore produces a stronger selectivity.

Selectivity for Identity and Expression

In the Yamashita et al. (2005) study, the authors also tested whether the identity of a face influences the selectivity of different individual faces. The study found that adaptation was selective for actual differences between individual faces. Although it appears that face stimuli with similar identities produce larger aftereffects than images with different identities, it remains uncertain if face stimuli with similar identities produce the same aftereffects when variant face characteristics (e.g. expression) are altered.

Similar to face identity adaptation, adapting to a particular expression can cause an aftereffect of an opposite expression. For example, Rutherford et al. (2008) found that after an observer adapted to a face image with a negative emotion, a happy aftereffect was produced. Also, when the observer adapted to a happy face, a sad aftereffect was generated. Although expression changes can produce strong aftereffects, researchers are trying to determine if adapting to expressions is equivalent to adapting to identities.

In a study by Fox and Barton (2007), the authors examined face adaptation aftereffects produced by face images with expressions in order to determine the neural representation of expression. The results of their study suggested two different neural representations of face expression. Fox and Barton (2007) found that when an observer adapted to a face with a certain identity and expression, an aftereffect was produced on a test face with the same expression but a different identity. This suggests a neural representation of expression that is independent of identity. However, greater aftereffects were produced when the face stimuli were of the same identity but different expressions, suggesting a second neural representation of that expression is also dependent of identity.

Additional research also suggests overlapping neural pathways of identity and expression. In a study by Ellamil et al. (2008), the authors observed that adapting to expression is reduced when the identity is altered. If expression and identity were processed in distinct pathways, as suggested in the Bruce and Young (1986) study, then changing the identity of a face should not affect how an observer adapts to expression. However, in the Ellamil et al. (2008) study, some expression adaptation still occurred, similarly to the Fox and Barton (2007) study, implying a pathway involving an identity-independent representation of expression. The results of the Ellamil et al. (2008) study propose asymmetrical pathways for identity and expression: identity is relatively independent of expression, whereas expressions can either be independent of or dependent on identity. The asymmetric pathways may indicate that identity processing is less variable than expression processing.

In regards to selectivity, current research thus may indicate that changes in expression are less selective than changes in identity. Moreover, when an observer adapts to a face with a certain expression and tests on the same face with a different expression, the aftereffect is stronger than when the face stimuli have the same expression but different identities. According to Yamashita et al. (2005), this may be because the visual system allows stronger adaptation between face images that are more likely to represent the same identity.

In this study, we tested the proposal of Yamashita et al. (2005) by asking whether adaptation shows stronger transfer (i.e. less selectivity) when faces differ in their variant properties than when they differ in their invariant attributes. To test this we examined how adaptation aftereffects transferred between face images that differed in gender or

expression. For both, the adaptation was to a distortion in the face, and thus the same configural change was used for both types of face attributes. Observers were presented with distorted adapt faces that were either male or female and happy or fearful. Then, the observers were tested on faces that were the same as the adapt face, differed in expression, differed in gender, or differed in both attributes. We then asked how well aftereffects transferred across each difference. These comparisons allowed us to test whether adaptation behaves in similar ways for variant and invariant facial characteristics.

There were three possible outcomes in these experiments. First, there could be no selectivity, and all of the face images would produce similar aftereffects. Second, there could be no selectivity for expression, but some selectivity for gender. This outcome would suggest that expression is represented as belonging to the same face and that selectivity is established at a high, face-specific level of visual processing that extracts an invariant representation of identity. Finally, the results could simply show more selectivity the more the faces differ physically. That is, either an expression or a gender change could reduce the transfer because they reflect physical differences in the face images. This would suggest that selectivity depends on how similar the faces appear physically and might imply an adaptation effect at a lower level of visual processing. The results thus allow us to distinguish between different possible models of how faces are adapted and represented in the brain.

METHODS

Subjects

The subjects included the author and advisor and four additional observers. All subjects had normal or corrected-to-normal vision acuity.

Stimuli

The stimuli for this study consisted of full color frontal view images of Dutch female and male faces with happy and fearful posed expressions. The faces were collected from the Radboud Face Database (<http://www.socsci.ru.nl:8180/RaFD2/RaFD?p=main>). The images were presented on a SONY RGB monitor.

The images were distorted by a local expansion or contraction of the face relative to a midpoint on the nose. In order to distort the images, we used a program similar to the program used in the study by Webster and MacLin (1999). Each face image was distorted in finely graded steps in order to produce 100 images, which ranged from fully contracted (stimulus level 0) to fully expanded (level 100), with the original face corresponding to a level of 50 (Figure 3).

Procedure

Observers adapted to either a single distorted face image or two opposing face images for two minutes. In the single face condition, the adapt face image was either a happy male, happy female, fearful male, or fearful female, and was shown either contracted or expanded. The opposing face condition involved adapting to two face images that differed either in expression or in gender and had opposing distortions (i.e. adapting to a contracted happy male and an expanded happy female). After the two-minute adaptation period, observers were presented with test face images, which were

displayed 1.5 times smaller than the adapt images to reduce low-level aftereffects. Low-level aftereffects refer to actual physical similarities between the images, such as size.

For the single face adapt condition, the observers were presented with four different test face images. The test images consisted of a face that was the same as the adapt, differed in expression, differed in gender, or differed in expression and gender. In the opposing faces adapt condition, the observers were presented with test face images that were the same as the adapt images. The test faces for both faces were shown for one second and alternated with four-second readaptation intervals and the observers made a forced-choice response to indicate whether the face appeared “too contracted” or “too expanded.” Test faces were randomly selected from the generated image arrays, and the distortion level varied in staircases to estimate the level that appeared undistorted to the observer.

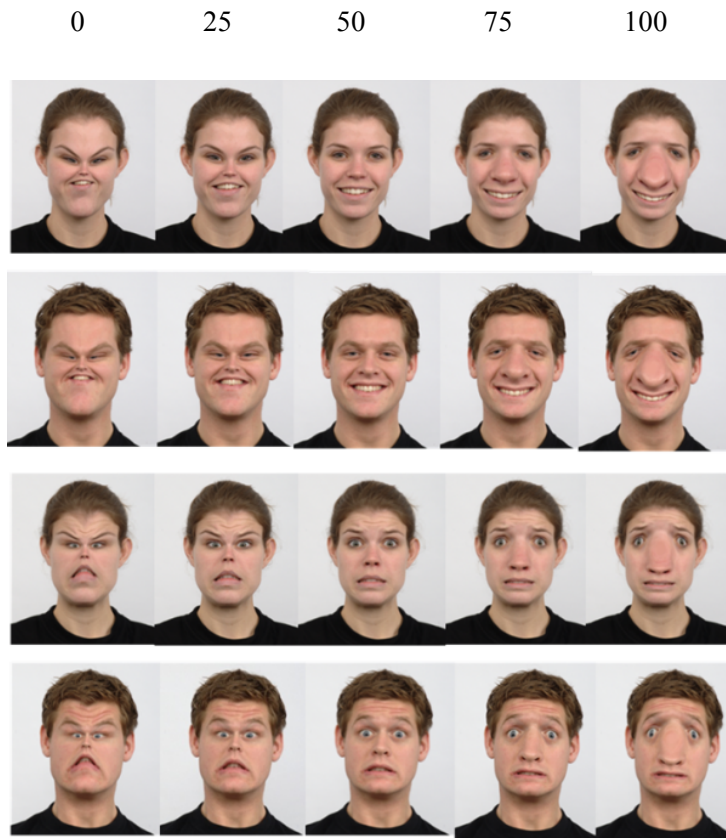


Figure 3. Face distortion array for each face type. From top to bottom, the faces include a happy female, happy male, fearful female, and fearful male. The 100 images in the array varied from fully contracted (0) to fully expanded (100) along the horizontal and vertical axis of the original images.

RESULTS

Preliminary Work

In a preliminary study, we examined the selectivity of facial aftereffects for changes in facial expression in order to determine whether a change in expression was equivalent to adaptation to the “same” or a “different” face. The images were distorted by a local horizontal expansion or contraction of the face relative to a midpoint on the nose. Observers adapted for two minutes to either a single distorted face or to an alternation between two faces with opposite distortions, in which the face(s) were from the same individual with a different expression or different genders with the same expression. Test faces were the same as the adapt face(s) or a face with a different expression or gender. In adaptation to either the single or opposing face pairs, the aftereffects showed weak selectivity for the change in expression and almost complete transfer. Also, the transfer was nearly equivalent to the changes in gender of the face images, showing little difference in selectivity between faces differing in expression and differing in gender. These pilot results thus suggested that expression and gender differences influenced the adaptation in similar ways. However, a problem with this experiment is that the neutral, undistorted faces were difficult to judge. In an attempt to make observers more sensitive to the distortions, we changed the stimuli from horizontal-only distortions to both horizontal and vertical distortions for the subsequent experiments.

Experiment 1

In this experiment we investigated the transfer of adaptation from a single adapting face to either the same or a different face. The observers adapted for two minutes to a single face image that was a happy male, a happy female, a fearful male, or a fearful female. The observer was then tested on four face images that were the same as the adapt, different in expression, different in gender, and different in expression and gender (Figure 4), with the displayed face chosen at random on each trial. The aftereffects were assessed as the difference in the null settings after adapting to an expanded face versus a contracted face (Figure 5). These differences showed strong transfer of the adaptation across all four different test faces. Using the Kruskal-Wallis one-way ANOVA, we found a significant difference between the transfer of the adaptation across all of the test faces ($H(3) = 16.26, p < 0.001$). Pairwise, we also found a significant difference between when the test face was the same as the adapt and when the test face differed in expression ($Q = 3.05, p < 0.05$), and also between when the test face was the same as the adapt and when the test face differed in expression and gender ($Q = 3.80, p < 0.05$). However, there was no significant difference between when the test face was the same as the adapt and when the test face differed in gender. The strength of the aftereffect was not significantly different for the images that differed in expression and differed in gender, thus showing similar selectivity for expression and gender.

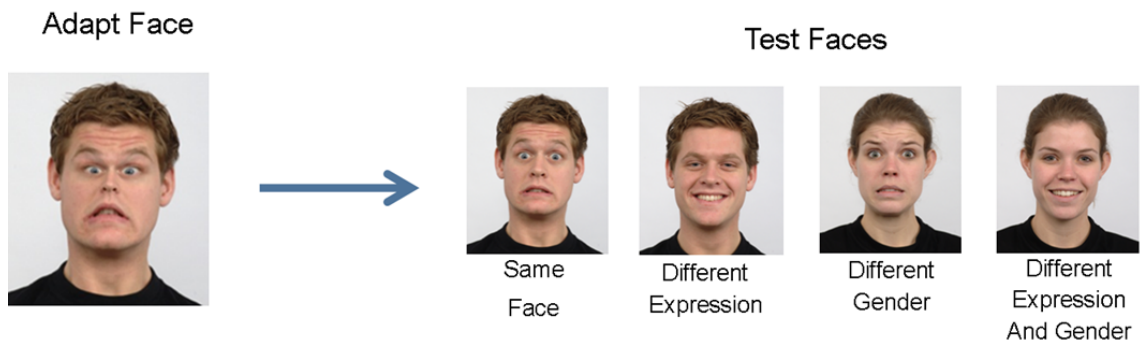


Figure 4. Single adapt image. After adapting to a single face image, the observers were presented with one of four test face images, which included the same adapt face, a face differing in expression, a face differing in gender, and a face differing in both expression and gender. The four test faces were randomly interleaved during the test and adapt top-up sequence until the null point was determined for each face.

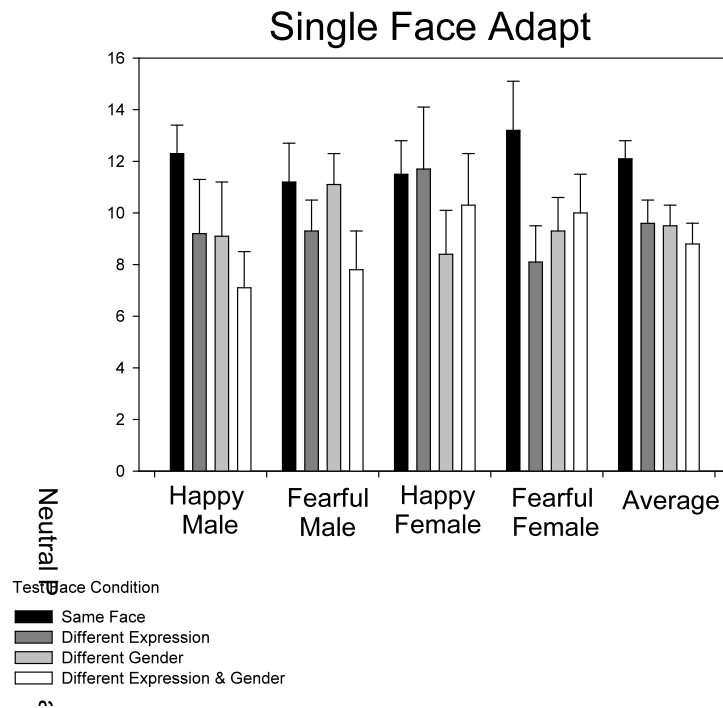


Figure 5. Transfer of adaptation across individual faces. The aftereffects were measured by taking the difference in the perceived neutral point for each test face after adapting to an expanded face versus a contracted face. The adapt images are listed from left to right: happy male, fearful male, happy female, and fearful female. The final set of graphs represents the combined results for all adapt face images. Each different shaded bar represents the aftereffect produced for each test face, which include a face that is the same as the adapt, a face that differs in expression, a face that differs in expression, and a face that differs in both expression and gender. The results were averaged across five observers.

Experiment 2

For the second experiment, we further explored the selectivity for expression and gender by looking at contingent adaptation aftereffects for expression and gender. The observers were adapted for two minutes to a one-second alternation between two opposing faces with opposite distortions that differed in either gender or expression (Figure 6). The test faces consisted of two interleaved faces that were the same as the adapt faces. There were significant contingent aftereffects for the adapting face pairs that differed in expression ($t(46) = 5.04, p < 0.001$), and for the adapting face pairs that differed in gender ($t(46) = 3.92, p < 0.001$). However, as in the first experiment, we again found that the magnitude of the contingent aftereffect was similar whether the face pairs differed in expression or in gender (Figure 7).

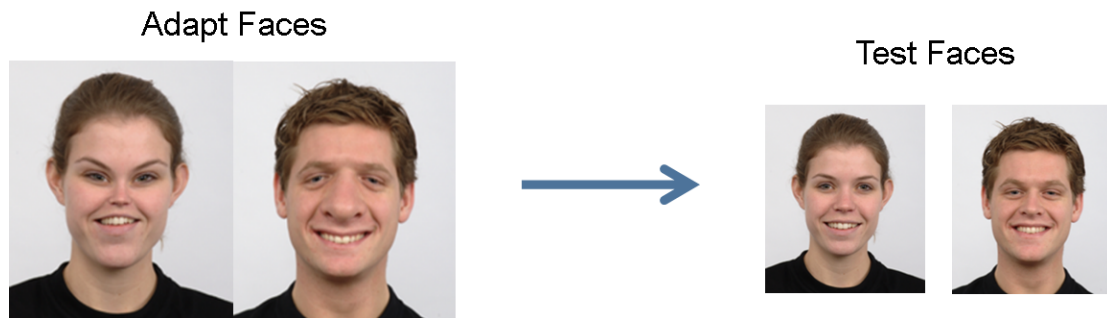


Figure 6. Opposing face adapt. Observers adapted to two opposing images with opposite distortions that differed in either gender or expression. This is an example of opposing face images that differ in gender.

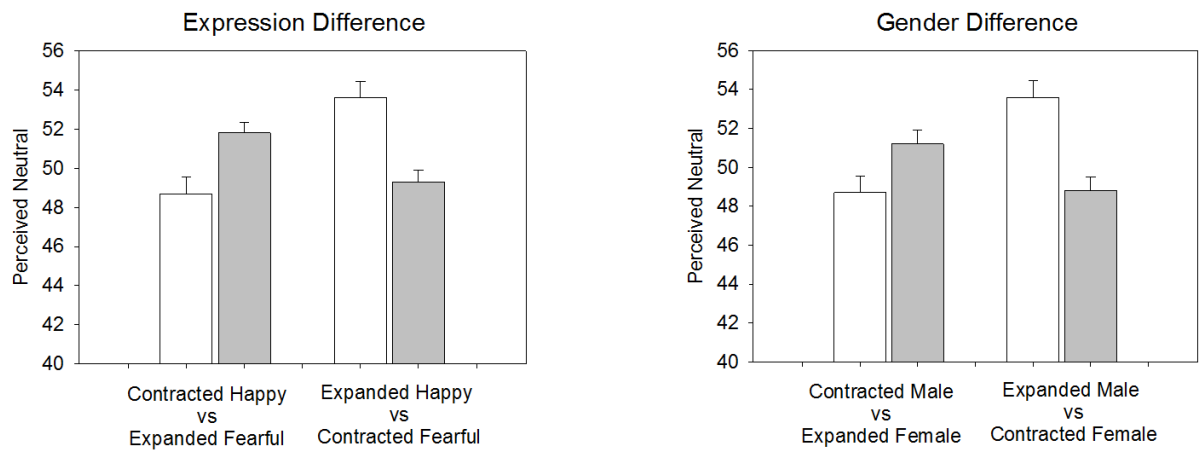


Figure 7. Contingent adaptation for expression and gender individual faces. In the first graph, we compared the contingent aftereffects when the opposing adapt faces were contracted happy versus expanded fearful and expanded happy versus contracted fearful. For the second graph, we compared the contingent aftereffects when the opposing adapt faces were contracted male versus expanded female and expanded male versus contracted female. The results were averaged across three observers.

Experiment 3

In the preceding experiments, we utilized only two faces, which could have been perceived as two identities rather than separate genders. Moreover, we had no way of controlling the magnitude of the identity difference relative to the expression difference. Thus a possible confound with the results was that “gender” and “expression” really do differ in the selectivity of the adaptation, but the gender differences may have been weak in the specific pair of faces we tested. In the final experiment, we tested the contingent adaptation aftereffects for actual attributes of expression and gender. For this, we used ten female and ten male faces with the same happy and fearful expressions (Figure 8). The observer adapted to these twenty faces, which were interleaved with each other and differed in their distortion and in either gender or expression (Figure 9). Thus, for example, in a condition looking at the difference between expression, all the adapt faces of one expression would be expanded, and the adapt faces with the other expression would be contracted. In this way the adapting distortions were tied to the particular expression or gender but not to a particular individual. The results of this experiment showed significant selective aftereffects for the expression difference ($t(7) = 5.52, p < 0.001$), and for a difference in both expression and gender ($t(15) = 5.37, p < 0.001$). However, for the gender difference the selectivity was non-significant ($t(7) = 1.12, p = 0.15$). Thus in this case the selectivity of the aftereffects appeared to largely depend on the differences in expression (Figure 10).

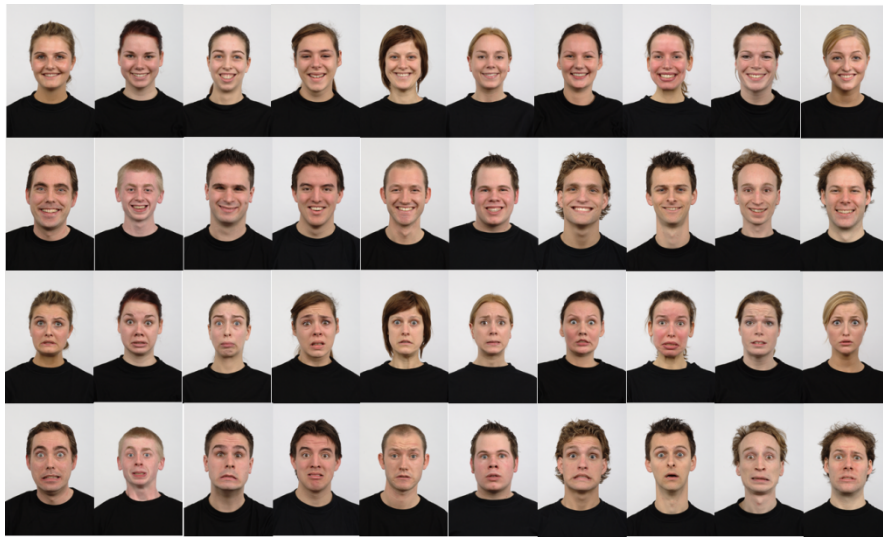


Figure 8. Multiple female and male faces. An array of ten different female faces and ten different male faces with posed happy and fearful expressions. These faces were also taken from the Radboud Face Database.

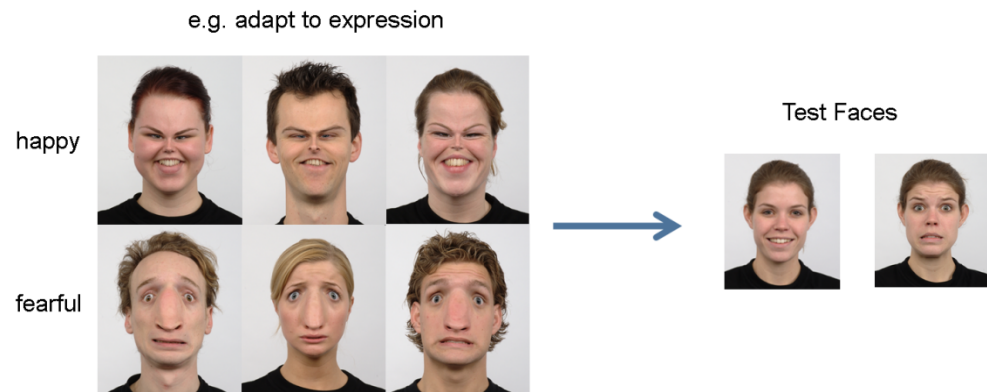


Figure 9. Multiple face adapt. Observers adapted to ten female and ten male faces that were distorted based on the difference being examined. For example, when we tested the expression difference, the adapt faces with a happy expression were contracted and the faces with a fearful expression were expanded. The test faces were of two different faces, which were not included in the twenty adapt faces, but had the same attributes as the two adapting face sets..

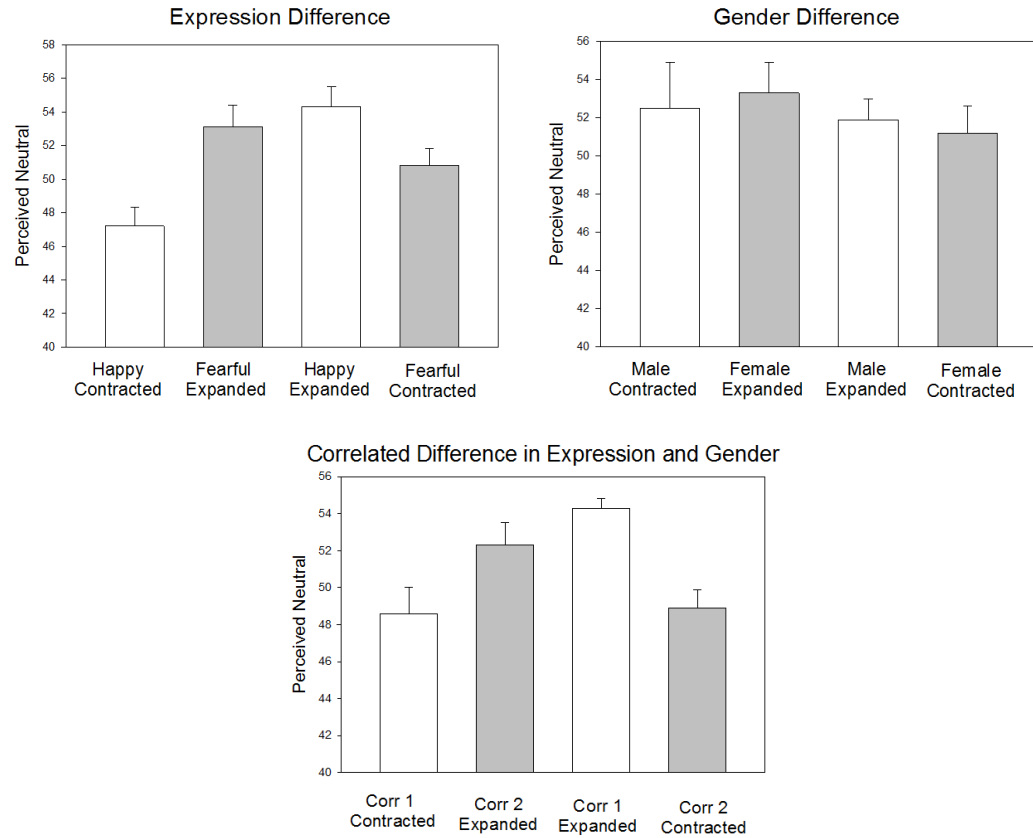


Figure 10. Contingent adaptation for identity-independent attributes of expression and gender. The graph for the expression difference shows the contingent aftereffects when the observer adapted to contracted happy versus expanded fearful faces, and to expanded happy versus contracted fearful faces. For the gender difference, the graph shows the contingent aftereffects when the observer adapted to contracted male versus expanded female faces, and to expanded male versus contracted female faces. The graph for the correlated difference in expression and gender shows when the observer adapted to contracted faces with a particular gender and expression versus expanded faces with the opposite gender and expression. The results were averaged across two observers.

DISCUSSION

The purpose of this study was to investigate the selectivity of adaptation aftereffects for faces that differed in gender and expression in order to further understand how invariant and variant characteristics of faces are processed in the brain. Previous studies have suggested that there is a greater transfer of adaptation across faces that appear to come from the same identity (Yamashita et al., 2005), and that there is more transfer across expression for identity aftereffects than vice versa (Fox and Barton, 2007; Fox et al. 2008). However, in our experiments, we found that distortion aftereffects for faces showed only weak selectivity for changes in expression or gender, and moreover, that the two types of natural facial variation yielded similar results.

One reason we believe our experiments showed weak selectivity for changes in gender and expression is that the male and female face images in Experiment 1 and 2 appeared too similar to each other. Also, in Experiment 3, perhaps the reason why the expression difference produced a stronger selectivity than the gender difference is that the difference between happy and fearful faces appears greater to the observer than the difference between the male and female faces. Of course, there is now way to physically equate a difference in gender and expression. Additionally, for all experiments, the weak selectivity for a difference in gender and expression could be due to the observers adapting to particular feature of the face, such as the nose, that did not seem to change when the expression or gender was altered.

Nevertheless, regardless of the basis for these effects, our results show that the selectivity for expression was as strong, or stronger (as seen in Experiment 3), than a change in the gender or specific identity of the face. The results of this study thus seem

to be inconsistent with the proposal that face aftereffects show more transfer when faces appear to come from the same individual. Instead, the results may suggest that figural aftereffects for faces may be modulated in similar ways for both variant (e.g. expression) and invariant (e.g. gender) attributes of the face. This could imply that adaptation affects face coding in similar ways within the visual pathways coding variant and invariant properties, or that the adaptation arises before these pathways diverge.

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