Research Report

What is adapted in face adaptation? The neural representations of expression in the human visual system

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ABSTRACT

The neural representation of facial expression within the human visual system is not well defined. Using an adaptation paradigm, we examined aftereffects on expression perception produced by various stimuli. Adapting to a face, which was used to create morphs between two expressions, substantially biased expression perception within the morphed faces away from the adapting expression. This adaptation was not based on low-level image properties, as a different image of the same person displaying that expression produced equally robust aftereffects. Smaller but significant aftereffects were generated by images of different individuals, irrespective of gender. Non-face visual, auditory, or verbal representations of emotion did not generate significant aftereffects. These results suggest that adaptation affects at least two neural representations of expression: one specific to the individual (not the image), and one that represents expression across different facial identities. The identity-independent aftereffect suggests the existence of a ‘visual semantic’ for facial expression in the human visual system.

1. Introduction

Facial expression is an important vehicle for social communication. The perception and interpretation of facial expression provides us with clues about the emotional state of those with whom we interact. Disordered perception of facial expression is a feature of neurological disorders such as autism and Asperger syndrome, and may contribute to the social disruption experienced by patients with these diagnoses (Hefer et al., 2005). Understanding the neural representation of facial expression is important to advancing our knowledge of how the human visual system organizes and extracts socially relevant perceptual signals.

Current concepts of facial recognition suggest parallel processing of facial identity and facial expression in both cognitive and anatomic models, based largely on human functional imaging experiments that supplement earlier neurophysiological data from monkeys (Bruce and Young, 1986; Haxby et al., 2000; Andrews and Ewbank, 2004; Eifuku et al., 2004). Processing of facial identity may be a specific role of the fusiform face area, located in the inferior occipitotemporal cortex (Haxby et al., 2000; Barton, 2003; Grill-Spector et al., 2004), whereas facial expression may be preferentially processed in the superior temporal sulcus, located in the lateral occipitotemporal cortex (Haxby et al., 2000). The superior temporal sulcus appears to be involved in recognizing the changeable aspects of the face (Haxby et al., 2000), such as direction of gaze (Pelphrey et al., 2003), mouth movements (Puce et al., 1998; Callan et al., 2004), as well as expression (Winston et al., 2004). In addition, fMRI shows that activity in
the superior temporal sulcus is selectively increased when attention is directed towards emotion in facial images (Narumoto et al., 2001).

While these data suggest that expression may have a specific neuroanatomic substrate in the superior temporal sulcus, they are less clear on the nature of the representations contained within that substrate. Recent work using adaptation paradigms and aftereffects have suggested a means of exploring the neural representations of faces. Previous reports have shown that aftereffects (biased perceptions following sensory adaptation to a stimulus) exist not only for photo-receptor-based phenomena such as color (Allan et al., 1997; Nieman et al., 2005), but also for cortically based phenomena such as motion (Snowden and Milne, 1997; Seiffert et al., 2003), tilt in two dimensions (Adams and Mamassian, 2002), slant in three dimensions (Domini et al., 2001), and, more recently, for faces (Leopold et al., 2001; Webster et al., 2004; Yamashita et al., 2005).

One of these reports has documented aftereffects specific to facial identity (Leopold et al., 2001). When shown a series of morphed faces that varied between a target face and its ‘anti-face’ (one with the opposite structural characteristics to the target face), subjects were more likely to perceive the identity of the target face in an ambiguous morphed image after they had been exposed to the ‘anti-face’. Another study found similar aftereffects for a variety of facial properties beyond identity, including gender, race, and expression (Webster et al., 2004). This second study confirmed that an adaptation paradigm can be a useful tool to probe the neural populations involved in perceiving expression. However, the conclusions that can be made from its results, about the neural representations of expression, are limited because their adapting stimulus was the same image as the one used to generate the morph series. Therefore, one cannot determine whether this adaptation is of expression in general, expression in a specific face, or expression in a specific image.

Our objective was to systematically explore how differences in the adapting stimulus affected the production of aftereffects on expression perception, thereby better defining the neural representations of facial expression. Our initial hypothesis was that there should be a neural representation of expression that generalizes across different facial identities. For facial expression to be a truly useful social cue, it is important to be able to infer similar emotional states from similar expressions on the faces of different people. If so, we predicted that we would find adaptation aftereffects even if the faces of different people were used as the adapting stimuli and the probe stimuli.

2. Results

2.1. Experiment 1: an identity-independent representation of expression

In the first part of this study, we contrasted the effects of four different adapting conditions on the production of an expression-based aftereffect (Fig. 1). This was done for three different series of morphed images, one from angry to afraid, one from sad to happy, and one from disgusted to surprised. The first adapting condition consisted of images that were identical to those used to derive the morphed images which served as probes of the aftereffect. This ‘same-image’ condition also served to replicate the findings of the prior study cited (Webster et al., 2004). The second and third conditions used adapting stimuli which were faces of different individuals showing one of the expressions used in the probe series. The second condition had the same gender as the probe (‘different-person/same-gender’), while the third condition had a different gender (‘different-person/different-gender’). The last condition simply presented a word on the screen, naming one of the expressions. This ‘verbal’ condition was performed to determine if simply evoking the expression through a verbal semantic association was enough to generate facial expression aftereffects. If there is indeed a generalized representation of expression in the human visual system, then we would expect to see aftereffects in the different-person conditions. Strong aftereffects in the verbal condition would suggest an even more general non-visual representation of facial expression.

Our initial analysis tested for main effects of adapting condition, expression pair (i.e., angry/afraid, sad/happy, disgusted/surprised), gender of the probe face, and test version (see Experimental procedure). There was no significant main effect of expression pair, indicating that similar aftereffects were obtained for all three emotional axes (Fig. 2A). There were also no significant main effects of the gender of the probe face or the version of the test, and no significant two-way, three-way, or four-way interactions involving these variables. Therefore the data were collapsed across version, gender of probe face, and expression pair in the following analyses.

There was a significant main effect of adapting condition on aftereffects [F(3,47) = 1.656, p < 0.0001] (Fig. 2B). As reported in another study (Webster et al., 2004), the likelihood of reporting an emotion in an ambiguous probe face was reduced if subjects were adapted to the same image, expressing that emotion, which was used to create the morph series. Our same-image condition generated a similar aftereffect, where judgments of expression in the probe stimuli were biased towards the expression opposite to that displayed in the adapting stimuli [t(59) = 12.540, p < 0.0001]. The magnitude of this aftereffect was sizeable, being a 22.62% (SEM = 1.80%) difference in the probability of expression choice between the two adapting conditions (i.e., Angry and Afraid). However, we also found that aftereffects were generated using images from persons different from those seen in the probe series of morphed images, as adapting stimuli. Significant shifts in emotional judgments were produced in both the different-person/same-gender condition [6.40%, SEM = 1.92%; t(59) = 3.339, p = 0.001] and different-person/different-gender condition [7.06%, SEM = 1.44%; t(59) = 4.887, p < 0.0001]. In contrast to the clear aftereffects induced by different-person conditions, the verbal condition did not generate a significant aftereffect on the perception of facial expression [0.05%, SEM = 1.44%; t(59) = 0.38, p = 0.970].

Post hoc Bonferroni comparisons between the different adapting conditions showed that the difference between aftereffects of the different-person/same-gender and different-
person/different-gender conditions was not significant ($\Delta = 0.65\%$; $p = 1.00$), indicating that expression adaptation generalizes across gender. Further comparisons showed that the same-image aftereffect was significantly larger than the aftereffects of all other conditions, including the different-person/same-gender condition ($\Delta = 16.22\%$; $p < 0.0001$), the different-person/different-gender condition ($\Delta = 15.56\%$; $p < 0.0001$), and the verbal condition ($\Delta = 22.57\%$, $p < 0.0001$). The insignificant aftereffect of the verbal condition was significantly smaller than the same-image condition, and the different-person/different-gender condition ($\Delta = 6.35\%$, $p = 0.059$).

This first experiment confirmed the existence of a neural representation of facial expression that generalizes across facial identity, and that adaptation can occur across this generalizable representation of expression. As such, this represents what might be termed an abstract ‘visual semantic’ for expression, where expression is not coded as a particular appearance of a particular face, but as some shared configuration among all faces when a person is experiencing a certain emotional state. However, whether this is a visual semantic that is face-specific or that is generalizable to other visual depictions of emotion is an open question. Although a verbal semantic association was insufficient to generate an aftereffect, this may be attributable to intensity differences in the adapting stimuli. Emotional words (2.92, SEM=0.54) were rated as less intense than emotional faces (5.17, SEM=0.27) and this rating difference was significant [$t(82)=3.216$, $p=0.002$]. Thus the lack of aftereffect to verbal stimuli may be due to an adapting stimulus which was too weak to elicit such an effect. It is therefore still possible to ask whether this semantic representation is purely visual or if it is multi-modal in nature.

Fig. 1 – Example of an adapting trial, with samples of stimuli used in all the different adapting conditions in the first and second experiments. These stimuli were taken from the afraid condition. After the adapting stimulus is shown for 5 s, there is a short mask serving as an inter-stimulus interval, followed by the probe stimulus. This is an ambiguous image from the morphed series, in this case between angry and afraid. Subjects then make a two-alternative forced choice decision on the expression displayed in the probe stimulus (note: the faces pictured here are taken from the authors’ collection, while actual experimental stimuli were taken from the Karolinska Database of Emotional Faces).
Finally, another question is suggested by the observation that the same-image condition generated a much stronger aftereffect than the different-person conditions. The implication is that there must be some neural representation that is adapted in the same-image condition but not in the two different-person conditions. The results of this first experiment do not clarify whether this neural representation is specific to the image or specific to the individual.

2.2. Experiment 2: an identity-dependent representation of expression

Our second experiment was designed to test these three issues: (i) is the ‘visual semantic’ an abstract facial representation or a more general visual representation; (ii) is there a multi-modal expression aftereffect; (iii) is the larger same-image aftereffect a result of adaptation to identity or image. In experiment 1 we showed that there was no difference between the 3 expression pairs, therefore we restricted experiment 2 to one expression pair (angry/afraid). Again four adapting conditions were used. The first was a repeat of the same-image condition. The second was a same-person/different-image condition, in which the identity between adapting and probe stimulus was held constant, but a different image (different from the image used to create the morph series) of that individual displaying one of the morphed expressions was used. The contrast between this and the same-image condition would reveal whether the strong aftereffect generated in the same-image condition is an adaptation to a specific image showing expression or to a specific person showing expression. The third adapting condition, the visual/non-facial condition, used pictures of anger and fear that did not involve human faces, namely Darwin’s (1899) dogs. While it is true that facial information is not completely removed from these images of Darwin’s dogs, it was believed

Fig. 2 - (A) Aftereffects for each of the three expression pairs used in the first experiment. For each expression pair there were two adapting runs, one for each of the two opposing expressions. Aftereffects are reported as the difference score between the trials using one adapting stimulus (e.g., angry) and trials using the opposite adapting stimulus (e.g., afraid). (B) Pooled aftereffects from all three expression pairs, again reported as the difference score. Error bars indicate one standard error. Significant aftereffects are denoted with an asterisk (*) and non-significant aftereffects either not denoted or denoted (n.s.). SI = same-image, DP/SG = different-person/same-gender, DP/DG = different-person/different-gender, V = verbal. Inset graphs show, for the different adapting conditions, the probability of choosing Expression 2 as a function of the percentage of Expression 2 in the probe stimulus, fitted with sigmoid functions. The solid lines represent the data for Expression 1 as the adapting stimulus (i.e., angry, happy, disgusted) and the dashed lines represent the data for Expression 2 (i.e., afraid, sad, surprised) in the expression pairs.
that these images could still provide evidence for a more general visual semantic representation of emotion beyond that for human faces. Finally, the fourth, auditory condition examined whether expressions of emotion heard in neutral German sentences read with emotional prosody could generate cross-modal aftereffects on judgments of facial expression.

As in the first experiment, the initial analysis demonstrated that the aftereffect was significantly affected by adapting condition \(F(3,15)=1.208, p<0.0001\) but not by gender of the target face \(F(1,15)=0.006, p=0.595\) or test version \(F(1,15)=0.021, p=0.316\), and that there were no significant two-way or three-way interactions between these variables. Therefore the data were collapsed across test version and gender of probe face in the following analyses (Fig. 3).

The same-image condition produced a significant aftereffect [26.54%, \(\text{SEM}=3.80\); \(t(19)=6.976, p<0.0001\)], similar in magnitude to that of the same-image condition in experiment 1 \(t(38)=0.077, p=0.939\). Furthermore, adaptation to the same-person/different-image condition resulted in an aftereffect equally as large as the same-image condition \(30.38\%, \text{SEM}=2.98; t(19)=10.203, p<0.0001\). The visual/non-facial condition generated a trend to a weak aftereffect \(4.23\%, \text{SEM}=2.98; t(19)=1.191, p=0.248\). This lack of an auditory aftereffect could not be attributed to emotionally less intense stimuli in the auditory condition, as the auditory stimuli \(7.00, \text{SEM}=0.44\) were rated as significantly more intense than the face stimuli \(5.17, \text{SEM}=0.27\) \(t(82)=-2.662, p=0.009\).

Post hoc Bonferroni comparisons between the different adapting conditions showed that the strong aftereffects of the same-image and same-person/different-image conditions were not significantly different \(\lambda=3.85\%, p=1.00\), and the weak or non-existent aftereffects of the visual/non-facial and auditory conditions also did not differ \(\lambda=0.38\%, p=1.00\), due in large part to the large standard deviation of the auditory condition \(14.44\%). The visual/non-facial aftereffect was significantly smaller than the aftereffects observed in the same-image condition \(\lambda=22.31\%; p<0.0001\) and the same-person/different-image condition \(\lambda=26.15\%; p<0.0001\), and the aftereffect of the auditory condition was also significantly smaller than those in the same-image condition \(\lambda=26.54\%, p<0.0001\) and the same-person/different-image condition \(\lambda=26.54\%, p<0.0001\).

Finally, as a further examination of the trend in the visual/non-facial aftereffect, we compared this aftereffect with the different-person aftereffect (collapsed across gender) from the first experiment (angry/afraid expression pair only), using an independent samples t-test. The visual/non-facial aftereffect, while smaller \(\lambda=4.81\%) was not significantly smaller than the different-person aftereffect \(t(58)=1.362, p=0.178\). Of note, the emotional faces and the dogs received emotional ratings that were not significantly different \(5.17, \text{SEM}=0.27\) for faces, \(4.58, \text{SEM}=0.50\) for dogs, \(t(82)=0.840, p=0.403\).

3. Discussion

The results of these two experiments suggest that at least two neural representations of facial expression exist in the human visual system (Fig. 4). First, the fact that aftereffects can be generated from the faces of different people confirms our hypothesis that a neural representation of expression that is independent and generalizable across facial identity exists. Deduction about the second neural representation relates to the observation that much larger aftereffects were generated by images of the same person than images of a different person. Our balanced design (see Experimental procedure) ensured that the same facial images were used in the same-image conditions and the different-person conditions, both for adaptation and for probes. The pairing of the adapting stimuli and probe images, not the images themselves, generated the same-image or different-person conditions. Thus differences in the aftereffect cannot be attributed to differences in the intensity of emotion in different images, but is a result of the pairing in that particular condition. The larger aftereffects with the same-image condition therefore suggest that there is a second neural representation of facial expression that is not independent of facial identity.

One possibility we considered was that this second identity-dependent component of the heightened aftereffect of the same-image condition was simply the result of adaptation to low-level image properties. We addressed this issue in the second experiment by using the same-person/different-image condition. Our results demonstrated an aftereffect generated by the same-person/different-image stimuli which was equal in magnitude to the aftereffect generated by the same-image condition (Fig. 3). Thus the identity-dependent component of adaptation seen in the
same-image condition may relate to a visual representation of expression specific to the individual portrayed, which generalizes over variations in that expression by that individual. Due to the balanced design across subjects of this experiment with regards to the stimuli used for adaptation and the stimuli used for probing the aftereffect, the results again cannot be attributed to variations in the intensity of expression within the different images.

While it is true that in the same-person/different-image condition the physical difference between adapting stimuli and probe image is smaller than in the different-person conditions we posit that the aftereffect seen here is not the result of an aftereffect based on low-level image properties, but is the result of a neural representation which codes for both identity and expression (identity-dependent expression). An aftereffect to low-level features could operate on two levels, retinal and cortical. Retinal adaptation to local luminance values can be ruled out as subjects were not instructed to maintain steady fixation on one point. Cortical low-level adaptation cannot be entirely excluded: for example, given the residual similarity between the two images of the same face used, adaptation to the orientation of local features may in some degree contribute to the magnitude of the identity-dependent adaptation effect. However, there are other lines of evidence that support the hypothesis of a higher level identity-dependent representation of expression. First, the existence of an identity-dependent representation of expression is also suggested by studies showing interference effects from variations in identity on the speed of classification of expression (Schweinberger and Soukup, 1998; Baudouin et al., 2002; Ganel et al., 2004). Second, a recent study reported that expression can enhance identity recognition in familiar faces, suggesting there may be prototypical expressions linked with particular identities (Kaufmann and Schweinberger, 2004). Also, a principle component analysis study found a large degree of overlap between components which are important

Fig. 4 – A schematic diagram illustrating the two proposed representations of facial expression. Low-level image properties (bottom box) are processed and emerge as an identity-dependent representation of expression (middle pictures). Downstream of this representation of expression, which is linked to identity, is a general ‘visual semantic’ (i.e., identity-independent) representation of expression that is not specific to identity, but represents an abstract representation of that facial expression (top black and white figures; left = happy, right = angry) (note: the faces pictured here are taken from the authors’ collection, while actual experimental stimuli were taken from the Karolinska Database of Emotional Faces).
for expression discrimination and those which are important for identity discrimination (Calder et al., 2001). This study also showed that identity discriminations could still be made when using only the components which were selected for expression discriminations and vice versa (Calder et al., 2001). Thus there is a degree of overlap in the information used for these two types of facial discriminations, which would be expected if there were neural representations that processed expression in an identity-dependent manner, or identity in an expression-dependent manner.

The potential existence of a visual system designed to include both identity-dependent and identity-independent representations of faces has precedence in monkey studies of viewpoint variation (Perrett et al., 1991). These show two distinct neural populations that respond to faces in specific angles of view: (i) neurons that respond to a particular angle of view but only for a specific identity; and (ii) neurons that respond to a particular angle of view irrespective of identity (Perrett et al., 1991). Furthermore, populations that generalize responses for one stimulus property across other stimulus properties are often portrayed in neural models as a second hierarchical layer that receives converging input from a first layer whose responses also vary with those other properties. Thus, for example, a layer that encodes identity across variations in view point may receive converging input from a layer that encodes identity seen from specific viewpoints (Rosen, 2003). In Fig. 4, we speculate that our two neural populations might be arranged in a similar fashion, with a population that encodes expression across variations in identity receiving converging input from a population that encodes expression seen in specific individual faces.

Our additional conditions explored the properties of the visual semantic representation that is responsible for the portion of the aftereffect that generalizes across identity, as revealed by the different-person condition. There was a trend to an aftereffect from visual/non-facial stimuli. Whether this was related to expressions on the dog’s faces can be debated. Given the small residual aftereffects with these stimuli, it is not possible to exclude the possibility that the visual semantic representations involved in the different-person condition consists of both a face-semantic and a more modest, more general visual semantic for emotion beyond that for human faces.

We found no convincing evidence of cross-modal adaptation from auditory perception or from verbal semantic information. Viewing an emotional word or listening to a prosodic sentence did not affect expression judgment on an ambiguous face. This would suggest that all of the face adaptation effects we found for expression are related to visual processing. However, some caution is required with this conclusion, as the intensity of emotion perceived in the verbal stimuli was weaker than that perceived in the face stimuli. This emotional intensity explanation for the lack of an aftereffect cannot be extended to the auditory condition, as these stimuli were seen as more emotionally intense than the face stimuli. Therefore, despite reports that the superior temporal sulcus is considered a multi-modal region of cortex, combining both visual and auditory information (Sekiyama et al., 2003), our results fail to show integration of emotional information across modalities in the neural representations affected by adaptation. Similar failures to find cross-modal effects on face perception have been reported in a study that showed that visual distractors reduced a facial identity aftereffect while auditory distracters had no such influence (Moradi et al., 2005).

Cross-modal aftereffects likely occur at a point of emotional experience and integration rather than perceptual processing. Emotional integration of faces and voices has been demonstrated with fMRI, reportedly occurring in the right amygdala for negative emotions (fear), and the left superior temporal gyrus for positive emotions (happiness) (Pourtois et al., 2005). Other studies have linked emotional experience to activity in frontal and subcortical structures (Phan et al., 2002; Wicker et al., 2003; Yip et al., 2004), sites downstream of the superior temporal sulcus, which is generally accepted to be the site of facial expression recognition (Allison et al., 2000; Haxby et al., 2000). Failure of the auditory condition to generate aftereffects in our paradigm may suggest that the neural representations that can be adapted by this method are restricted to visually responsive populations in extra-striate cortex.

What are the possible neuroanatomic correlates of the different neural representations of expression which our probe stimuli revealed in the present study? A recent event-related fMRI study examined adaptation to both facial identity and expression (Winston et al., 2004). Adaptation to identity but not expression was found in the fusiform face area, and adaptation to expression but not identity was found in the middle portion of the superior temporal sulcus. In the posterior portion of the superior temporal sulcus there were large adaptation effects to identity and a smaller adaptation effect to expression. The authors concluded that the posterior superior temporal sulcus and the fusiform face area encoded identity, while expression was encoded more anteriorly than previously believed, in the middle superior temporal sulcus (Winston et al., 2004). Our results suggest a possible alternate explanation. Our finding of a neural representation of expression that is specific to facial identity, would predict a neural population that shows adaptation effects for both identity and expression, much as they reported for the posterior superior temporal sulcus. On the other hand, the finding of a visual semantic representation which generalizes across facial identities would predict a neural population that shows adaptation effects for expression but not identity, as they reported for the middle superior temporal sulcus. Thus the functional segregation reported in this fMRI study (Winston et al., 2004) may offer a tantalizing parallel with the behavioral data we report. Further investigations are desirable to address our proposal, that there are distinct identity-dependent and general visual semantic (identity-dependent) neural representations of face expression, and our speculation that these may reside in segregated neural populations within the superior temporal sulcus.

4. Experimental procedures

4.1. Subjects

Thirty-eight subjects (23 female) participated in the entire study. All subjects spoke English and did not understand
German. In the first experiment twenty-seven subjects (16 female; age = 30.63 years, SD = 10.24 years) were randomly assigned to one of the three possible expression pairs, while CJF participated in all three of the expression pairs in experiment 1, giving 10 subjects for each of the three expression pairs used in the first experiment. Other than CJF all subjects were naive to the purpose of the experiment, and CJF’s results did not differ from the group data. In the second experiment ten different naive subjects (7 female; age = 25.5 years, SD = 4.88 years) participated. All 38 subjects had normal or corrected-to-normal vision, and were able to clearly identify facial expressions and read on-screen text at the testing distance used (57 cm). The protocol was approved by the institutional review boards of Vancouver General Hospital and the University of British Columbia, and all subjects gave informed consent in accordance with the declaration of Helsinki.

4.2. Stimuli, experiment 1

Facial stimuli were obtained from the Karolinska Database of Emotional Faces (KDEF) (Lundqvist and Litton, 1998). Research of facial expression suggests six fundamental facial expressions that are reliably recognized across cultures, which are anger, fear, happiness, sadness, surprise, and disgust (Ekman et al., 1969; Ekman and Friesen, 1971). The Karolinska series includes 2 pictures of each individual displaying these six facial expressions. Four individuals were chosen, two female and two male. Two versions of the tests were created, with each version consisting of one of the male and one of the female faces as probe stimuli. For each individual the six facial expressions were paired to create three distinct expression pairs (angry/afraid, happy/sad, disgust/surprise). These pairings were based on a previously reported 3-dimensional model of human emotion (Plutchik’s solid) (Strongman, 1978). This model places anger and fear as opposite emotions, as well as happy and sad. Disgust and surprise are not placed as opposite emotions but are spatially removed from each other within the model. Since opposite emotions are not universally defined or recognized the present examination of aftereffects is different than aftereffects of stimuli with absolute opposites (i.e., color, tilt, etc.).

For the stimuli used as probes of the aftereffect, we created morphs across the three expression pairs for each Karolinska face, using Fantamorph 3.0 (www.fantamorph.com). Twenty-one images were produced for each morph series, with each picture representing a 5% step within the morph series (i.e., 0/100, 5/95, 10/90... 100/0). The thirteen images ranging from 20/80 to 80/20% were used as ambiguous probe stimuli in the final experiment. All facial images were presented in the center of the screen and spanned a distance of 8.6° horizontally and 11.8° vertically.

Before making judgments on these ambiguous probe stimuli, subjects were first exposed to adapting stimuli (varied by condition) for 5 s. For the same-image condition, the same faces used to generate the morph series were used as adapting stimuli for that particular series. For the different-person conditions, the faces used to generate the morph series in one version of the test were used as adapting faces for judgments on the morph series in the other version of the test. Thus in the different-person/same gender condition, the second of the two females was used as the adapting stimulus for the morphed probe stimuli created from the first female, and vice versa. In the different-person/different gender condition, one of the males was used as the adapting image for one of the female morphed probes, and the other male for the other female probes. This two-version balanced design ensured that an equal number of all the faces were used as adapting stimuli, and the multiple face series were used equally frequently as probes for aftereffects across these three different adapting conditions.

For the verbal condition, word stimuli consisted of the adjective form of the expression (Angry, Afraid, Happy, Sad, Disgusted, and Surprised) in all capital letters, created using Microsoft PowerPoint (www.microsoft.com). These images were re-sized to span the same horizontal distance (8.6°) as the facial images, and placed in the center of the screen. The letters themselves spanned 1.8° vertically.

4.3. Stimuli, experiment 2

This experiment also used the Karolinska faces (Lundqvist and Litton, 1998), but this time only those images representing anger and fear. For the probe stimuli, we used one of the female and one of the male morph series created for angry/afraid in the first experiment, and also generated another morphed series using the alternate images of the same expression for these two individuals. This was needed to create a balanced design between same-image and same-person/different-image conditions.

The probe stimuli for half of the subjects were the morph series used in the angry/afraid tests in the first experiment. For the other half of the subjects the probes were the morph series created from the alternate images of the same people from the Karolinska series. For adapting stimuli the same-image condition again used the same faces that generated the morph series used as probe stimuli in that subject. The same-person/different-image condition used the Karolinska faces that were morphed to generate the alternate morph series, which was not used as a probe in that subject. Thus, across all subjects, each Karolinska face was used with the same frequency as adapting stimuli in the same-image and same-person/different-image conditions, and each morph series was used equally frequently as a probe for the aftereffect.

The visual/non-facial condition used the images of Darwin’s dogs, obtained from the Internet, which were initially drawn by Charles Darwin as a standard representation of a dog displaying anger or fear (Darwin, 1899). These images were presented in the middle of the screen and spanned a distance of 10° horizontally and 6.8° vertically.

The auditory condition used audio files from a battery of emotional sounds that had been rated on a seven-point scale for emotional intensity (http://pascal.kgw.tu-berlin.de/emodb). The selected files ranged from ratings of 5.15 to 6.52. These sound files were German, semantically non-emotional sentences which were read with emotional prosody. Three to four of these audio files were linked to create a composite audio file, which lasted 5 s and contained both male and female voices.
4.4. Ratings

All Angry and Afraid adapting stimuli were rated by 6 participants (2 female) who had not been previously exposed to these stimuli. Subjects rated the stimuli on a 10-point scale (i.e., 1 to 10) and were asked how angry or how afraid the stimuli were.

4.5. Apparatus

All experiments were designed and run using SuperLab 1.71 software (www.cedrus.com). The first experiment was run on a G5 PowerMac with a 20” widescreen display. The second experiment was run on a G4 PowerBook with a 17” widescreen display. Audio files were presented with Sennheiser HD500 headphones. These headphones were large full ear-cup headphones which reduced external noises that would interfere with perception of the auditory stimuli.

4.6. Procedure

Subjects were told that they would be shown a series of faces and that they would have to state which of two possible facial expressions was depicted in each face. They were shown examples of the two (unmorphed) expressions and asked to name the expressions, which they all correctly identified. Next, they saw an example of a morphed image and were told that the faces they would be judging were mixtures of the two expressions, and that they should make their best guess at the displayed facial expression.

Subjects were randomly assigned to one of two versions of the test (each version having both one female probe series and one male probe series), and to one of the expression pairs. Each subject first completed a practice session for the expression pair being tested. The 13 morphed images of the 2 experimental faces (1 male and 1 female) were randomly presented 4 times each, for a total of 104 trials, without any adapting stimulus. Each face was on the screen for 300 ms, and was followed by a screen with a large question mark. This question mark remained until the subject indicated, with a key press, which expression they saw (two-alternative forced-choice decision). Following their decision there was a 500-ms inter-trial interval consisting of a blank screen.

Following the practice condition the experiment began. This consisted of 4 blocks, each with a different adapting condition (i.e., for the first experiment, these conditions were same-image, different-person/same-gender, different-person/different-gender, and verbal). The order of these blocks was randomized for each subject. In each block a trial consisted of a 5-s presentation of the adapting stimulus (Fig. 1), which represented one of the two expressions used to create that particular morph series (i.e., for same-image condition in the angry/afraid subtest, this would be either the angry face or the afraid face used to create the morphed series). The adapting stimulus was followed by a 50-ms mask (a random arrangement of black and white pixels) to reduce apparent motion effects in the following probe, and then a 300-ms probe image to measure the aftereffect, which was one of the morphed faces (Leopold et al., 2001). A question mark then appeared on the screen and remained until the participant indicated which of the two expressions they saw in the probe image, using a key press. After their decision a 500-ms blank screen served as the inter-trial interval. Subjects were asked to attend to the adapting stimulus, but not to make a judgment about this stimulus. Following each subtest there was a short rest break, before the next subtest began.

Each trial was seen only once. With thirteen degrees of morphing, two different probe series (one male and one female), and two different adapting stimuli (i.e., angry adapting stimulus and afraid adapting stimulus) this created 52 trials for each of the four adapting conditions, and hence 208 trials for each subject.

4.7. Analysis

For each adapting condition, we calculated the proportion of responses that were given for one of the choices (e.g., how many times they responded ‘afraid’). One score was for adaptation after one of the emotions (e.g., the angry adapting stimulus) and another score for adaptation after viewing the other emotion (e.g., the afraid adapting stimulus). The subtraction between these two values gave the difference score, which represents the magnitude of the adaptation effect for that particular adaptation condition.

All statistical analyses were run on SPSS 13.0 software (www.spss.com), and significance levels for all tests were set at p<0.05. In the first experiment, we used a univariate ANOVA with the difference score as the dependent measure. Emotional axis (3 levels), Adapting Condition (4 levels), Test version (2 levels) and Gender of the Probe Face (2 levels) served as predictors within the General Linear Model. Significant main effects were followed up with post hoc Bonferroni comparisons with correction for multiple comparisons. A priori two-tailed Student’s t-tests were run on each adaptation condition to determine whether that condition resulted in a significant aftereffect.

In the second experiment a univariate ANOVA was also run with the difference score as the dependent measure, and Adapting Condition (4 levels), Test Version (2 levels) and Gender of the Probe Face (2 levels) as the predictors. Significant main effects were followed up with post hoc Bonferroni comparisons with correction for multiple comparisons. A priori t-tests were performed as described above.

Independent samples t-tests were used to compare the same-image conditions from experiments 1 and 2, the different-person condition of experiment 1 with the visual/non-facial condition of experiment 2, as well as for the ratings of emotional intensity in all adapting stimuli.

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REFERENCES