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# The Neural Correlates of the Face Attractiveness Aftereffect: A Functional Near-infrared Spectroscopy (fNIRS) Study

Genyue Fu<sup>1</sup>, Cathy Mondloch<sup>2</sup>, Xiao Pan Ding<sup>1</sup>, Lindsey Short<sup>2</sup>, Liping Sun<sup>1</sup>, and Kang Lee<sup>3,4</sup>

<sup>1</sup>Zhejiang Normal University, China

<sup>2</sup>Brock University, Canada

<sup>3</sup>University of Toronto, Canada

<sup>4</sup>University of California, San Diego, USA

# Abstract

Extensive behavioral evidence shows that our internal representation of faces, or face prototype, can be dynamically updated by immediate experience. This is illustrated by the robust attractiveness aftereffect phenomenon whereby originally unattractive faces become attractive after we are exposed to a set of unattractive faces. Although behavioral evidence suggests this effect to have a strong neural basis, limited neuroimaging evidence exists. Here we used functional near-infrared spectroscopy methodology (fNIRS) to bridge this gap. During the preadaptation trials, participants judged the attractiveness of three sets of faces: normal/undistorted faces, compressed faces (the internal features and distances between them were compressed), and expanded faces (the internal features and distances between them were stretched). Then, participants were shown extremely compressed faces for 5 minutes as adaptation stimuli, after which participants judged the same three sets of faces in post-adaptation trials. Behaviorally, after the adaptation trials, participants rated the compressed faces more attractive whereas they judged the other two sets of faces as less attractive, replicating the robust adaptation effect. fNIRS results showed that short-term exposure to compressed faces led to significant decreases in neural activity to all face types, but in a more extended network of cortical regions in the frontal and occipital cortexes for undistorted faces. Taken together, these findings suggest that the face attractiveness aftereffect mainly reflects changes in the neural representation of the face prototype in response to recent exposures to new face exemplars.

# Keywords

face processing; face perception; fNIRS; attractiveness aftereffects; norm-based

# **1. INTRODUCTION**

Extensive behavioral evidence suggests that we encode faces in a norm-based manner. According to this model, individual faces are represented in a multidimensional space, at the center of which is a prototype that represents the average of all faces previously encountered

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(Valentine, 1991). Face space comprises vectors that represent the dimensions (e.g., eye size; distance between nose and mouth) on which faces vary, and the location of each individual face represents how (e.g., larger or smaller eyes?) and how much (e.g., +1 or +2 SDs?) that face varies from the prototype. The location of a face in face space has important perceptual-cognitive implications. For example, the closer a face is to the center, the less distinctive it is and consequently the more difficult it is to recognize (Lee et al., 2000). However, the face is also perceived as more attractive and normal looking (e.g., Potter and Corneille, 2008; Valentine et al., 2004). The use of a prototype and reliance on norm-based coding has been implicated as an explanation for numerous perceptual phenomena such as the own-race recognition advantage (Valentine, 1991), the other-race categorization advantage (Ge et al., 2009), caricature effects (Lee et al., 2000), and aftereffects for numerous characteristics, including race, sex, and emotional expression (Webster et al., 2004).

Our face prototype is not static; rather, it is dynamically and constantly updated by experience (Rhodes et al., 2003). The attractiveness aftereffect phenomenon is an excellent example of the dynamics of our face prototype. This robust aftereffect can be observed in the following manner. First, individuals view and judge the attractiveness of three sets of faces: normal/undistorted faces, compressed faces (the internal features and distances between them are compressed), and expanded faces (the internal features and distances between them are expanded). Second, they view a set of adapter faces that have been severely distorted along one dimension (e.g., compressing the internal face features) for a short period of time (e.g., 2-5 minutes). Third, they view the three sets of faces that were previously shown prior to adaptation and judge the faces' attractiveness once more (see Figure 1(a)). It has been consistently shown that after adapting to the distorted faces, both adults and children judge undistorted faces previously rated as most normal and attractive less normal (e.g., more expanded) and thus less attractive than before. Also, they tend to judge the faces distorted in the opposite direction even more distorted and less attractive. In contrast, they judge similarly distorted (i.e., compressed) faces more normal and attractive than before (Anzures et al., 2009; Jeffery et al., 2010; Webster and MacLin, 1999; Short et al., 2011). Further, the magnitude of aftereffects is correlated with the strength of the adapter stimuli, with more extremely distorted adapters producing the strongest effects (e.g., Robbins et al., 2007).

Jeffery et al. (2010) proposed a two-pool opponent model to account for neural mechanisms underlying the aftereffects. According to this model, oppositely tuned neural populations respond maximally to the extreme values of each dimension in face space. The average value would be associated with equal response in these two neural pools. Adaptation is proposed to reduce the response of one pool (e.g., neurons maximally responsive to large eyes) thus shifting the point of equal responsiveness towards the adapting stimuli (see Figure 2), making previously average faces appear distorted in the opposite direction. For example, one population of neurons is maximally responsive to the extremely compressed face features whereas another population of neurons is maximally responsive to the extremely expanded face features. Because undistorted faces (those falling near the black dashed vertical line in Figure 2) activate approximately the same number of neurons in these two populations, they are judged more normal looking and attractive than expanded and compressed faces. In contrast, because the expanded and compressed faces activate one pool of neurons more than the other, they are judged with lower attractiveness ratings than the normal and undistorted faces (Figure 2). However, after being exposed to compressed face adapters, the neurons originally tuned to compressed faces become adapted and less responsive, whereas the neurons tuned to expanded faces are unchanged in responsiveness. As a result, the point of equal activation for both populations of neurons shifts towards the compressed end. Consequently, the compressed faces become more normal and attractive

than before, whereas the originally undistorted and expanded faces become more expanded and thus less attractive than before.

This model is consistent with findings from a single-cell recording study with monkeys (Freiwald et al., 2009) and a recent event-related potential (ERP) study with humans (Zheng et al., 2011) in which neural responses varied linearly with changes in individual features. However, although the ERP technique has an exquisite temporal resolution, it is poor in spatial resolution. Further, Zheng et al. (2011) did not specifically examine the aftereffect. Thus, little is currently known regarding the cortical activation patterns in humans during the figural face aftereffect and what cortical regions are involved. Perceptual aftereffects for low-level visual characteristics such as motion (Mather, 1980) and color (Hering, 1964) are presumed to reflect reduced neural activation in the lower visual cortex following repetitive stimulation (Ibbotson, 2005). However, there are reasons to believe that the face aftereffect may involve cortical regions higher up along the visual object processing pathways (Rhodes and Jeffery, 2006; Webster et al., 2004). Most notably, unlike the motion and color aftereffects, the face aftereffect is still observed when the adaptation faces differ from the test faces in physical size and orientation (Rhodes et al., 2003). Given that the aftereffect is observed most robustly with faces, it is reasonable to expect that changes in the core and extended face processing networks (Haxby et al., 2000) may be associated with the attractiveness aftereffect.

Additional evidence for the involvement of cortical regions higher up along the visual object processing pathways stems from recent fMRI studies examining high-level adaptation aftereffects in category representation. Repeated exposure to specific body shapes (e.g., thin versus fat bodies) is associated with neural adaptation in the fusiform body area and the right middle occipital gyrus (Hummel et al., 2012). Likewise, adaptation to face versus hand images leads to category-specific behavioral aftereffects when participants view ambiguous face/hand composites; these aftereffects are simultaneously reflected in greater signal reduction in the fusiform and occipital face areas (FFA and OFA) and in the extrastriate body area (EBA), for face and body adapters, respectively (Cziraki et al., 2010). In both cases, signal reduction was largest on trials in which an aftereffect (test stimulus was perceived as opposite category of the adapter) was observed. Furthermore, face identity and expression aftereffects are associated with changes in cortical activation in the anterior medial temporal region (Furl et al., 2007), though not in the fusiform or occipital gyri (Furl et al., 2007). Collectively, these studies suggest that both face- and body-specific aftereffects are mediated by activity in category-specific areas of the brain that are implicated in the later stages of the visual processing pathway.

Although the aforementioned fMRI studies provide evidence for the involvement of regions outside the lower visual cortex in face-specific aftereffects, no study to date has examined the cortical activation patterns in humans during the face attractiveness aftereffect and the underlying hemodynamic responses that occur following changes in attractiveness preferences as a function of shifts in the prototype. However, indirect neural evidence for the involvement of higher order cortical regions in the figural face aftereffect does exist. First, consistent with the norm-based coding model, neural activity is influenced by face distinctiveness. As face distinctiveness increases, the BOLD signals increase in the human fusiform face area (Loffler et al., 2005), the amplitude of the N250 on the posterior scalp sites—one of the electrophysiological signatures of face recognition—increases (Kaufman and Schweinberger, 2008; Zheng et al., 2012), as does single cell activity in the anterior inferotemporal cortex of macaque monkeys (Leopold et al., 2006). Second, neural activity in response to individual faces varies as a function of recent experience. Repeated exposure to same-identity faces reduces the BOLD signal in face-selective regions (Loffler et al., 2005; Mazard et al., 2006; Winston et al., 2004) and some studies have reported a reduction in the

amplitude of the N170 following repeated exposure to a face identity (Caharel et al., 2009; Jacques and Rossion, 2006) or when a face is preceded by a face versus voice adaptor (Kloth et al., 2010, but see Cooper et al., 2007). Third, neural responses in several regions of the putative extended network of face processing (Haxby et al., 2000) vary with facial attractiveness. The effects of attractiveness are widespread; activation in the orbital frontal and anterior cingulated cortices, ventral occipital regions, and the amygdala vary as a function of face attractiveness (Aharon et al., 2001; Chatterjee et al., 2009; Ishai, 2007; Liang et al., 2010; O'Doherty et al., 2003), with activity in some regions having a linear relationship and others having a nonlinear relationship with attractiveness.

Building on this indirect evidence, here we examined the cortical neural response patterns associated with the face attractiveness aftereffect. In the present study, participants first rated the attractiveness of undistorted, compressed, and expanded faces (Figure 1(a)). They were then adapted to compressed faces for 5 minutes, after which they rated the attractiveness of the three types of faces again. Throughout the procedure, we used nearinfrared spectroscopy (NIRS) methodology to collect neural responses. It should be noted that the current NIRS methodology has poor spatial resolution relative to MRI. Thus, NIRS methodology only allows for collecting cortical activation data as deep as 15-25 mm beneath the scalp. Despite this shortcoming, the NIRS system's portability and inaudibility make it possible for participants to view face stimuli in a more naturalistic manner. Also, due to the low cost and ease of use, NIRS methodology allows for data collection from a large number of participants in a timely manner. It is thus ideally suited for exploratory studies that identify cortical regions involved in certain perceptual and cognitive processes, which can later be examined in more depth and with higher spatial resolution using fMRI. In addition, because our NIRS equipment has a 10 Hz sampling rate, with the use of a slow event-related design, it is possible to obtain the actual time course of the neural activity for individual trials. Such data allow us to derive grand averaged event-related oxygenated hemoglobin ([oxy-Hb]) and deoxygenated hemoglobin ([deoxy-Hb]) signal changes for a particular event such that [oxy-Hb] and [deoxy-Hb] signal change latencies can be obtained.

For the behavioral data, we hypothesized that attractiveness ratings of compressed faces would increase and those of undistorted faces would decrease following adaptation. At the neural level, we first hypothesized that before adaptation, neural responsiveness to undistorted faces would be greater than that to both compressed and expanded faces as the undistorted faces, being more similar to the face prototype, are perceived as more attractive. Second, based on the two-pool neural model described above, we expected significant decreases in neural activity to all face categories following adaptation. This is because the two pools of neurons are involved in processing the three types of faces. Adaptation of one pool of neurons to the extremely compressed faces would reduce the overall reactivity to all faces as depicted by the red solid line in Figure 2. Third, after adaptation, we hypothesized that neural responsiveness to compressed faces and to the undistorted faces should be switched as the compressed faces are now perceived as more attractive whereas undistorted faces are now perceived as less attractive. Furthermore, we predicted that individual differences in the magnitude of neural responsiveness changes would correlate with the magnitude of behavioral aftereffects.

# 2. METHOD

#### 2.1 Participants

Forty Chinese undergraduates with no history of neurological or psychiatric disorders took part in this study (Mean age = 22.13, SD = 1.88, age range = 19-26 years; 22 male). All participants had normal or corrected-to-normal vision and were right-handed. The research was approved by the Zhejiang Normal University research ethics committee. All participants

provided informed consent prior to participating in the study and were debriefed after the experiment.

#### 2.2 Materials

Stimuli consisted of 20 faces (10 female) of Chinese undergraduate students. Ten of the 20 identities were used as test faces in the pre- and post-adaptation phases, and each test face had three types: undistorted, expanded (+40%), and compressed (-40%). Faces were distorted using the spherize function of Adobe Photoshop version CS4. The remaining 10 identities were used in the adaptation phase and were compressed by -60%.

All faces had a neutral expression, did not have facial hair, and were photographed in a forward-facing position. A light blue occluder was placed around each test face and a light green occluder was placed around each adapting face to conceal background information. Test faces were standardized such that the distance from hairline to chin was approximately 400 pixels, and adapting stimuli were standardized such that the distance from hairline to chin was approximately 300 pixels.

#### 2.3 Procedure

Participants were seated in front of a 17-inch LCD monitor at a distance of approximately 60 cm. Faces were presented using E-prime 2.0. The experiment included three phases: preadaptation, adaptation, and post-adaptation. In the pre-adaptation phase, the 30 test faces (3 versions of 10 identities) were randomly presented. Each trial consisted of a 2-second fixation cross followed by a test face that appeared for 3 seconds. After the presentation of each face, participants were asked to respond verbally according to a 7-point attractiveness scale (1 = *very ugly*, 7 = *very good-looking*) and were given 15 seconds to respond. The experimenter inputted participants' verbal responses into the computer before the next trial began.

After participants rated the 30 faces, the adaptation phase began. During the adaptation phase, 10 compressed faces (-60%) were randomly presented for 2 seconds each. These faces were different from the faces in the pre-adaptation trials. Each face was repeated 15 times; thus 150 images were presented randomly as adaptation stimuli.

Lastly, participants completed the post-adaptation trials. The procedure of the postadaptation phase was identical to the pre-adaptation phase except that 10 adaptation faces were presented as "top-up" stimuli before each test face appeared on the screen. These topup faces were the same faces shown during the adaptation phase and were used to maintain adaptation during the test phase (see Rhodes et al., 2003). Each of the 10 adapting top-up faces was randomly presented for 2 seconds each prior to the presentation of a test face. The same 30 faces were used in the post-adaptation phase as in the pre-adaptation phase. Similar to pre-adaptation trials, participants viewed a test face for 3 seconds and then verbally provided a 7-point attractiveness rating. Participants were given 15 seconds to respond before the next trial began.

# 2.4 Near-infrared spectroscopy (NIRS) data acquisition

A 48-channel continuous wave system (ETG-4000, Hitachi Medical Co., Japan) was used in the present study (though we only used 46 channels). The optodes of the NIRS machine were fixed using two  $6 \times 6$  cm<sup>2</sup> rubber arrays over the frontal areas and one  $6 \times 12$  cm<sup>2</sup> rubber array over the occipital cortex areas. The arrays were covered with a nylon-net to keep them attached to the head. The two arrays of 9 optodes, consisting of a pair of  $3 \times 3$ arrays with five light emitters and four detectors, and one array of 15 optodes, consisting of a pair of  $5 \times 3$  arrays with eight light emitters and seven detectors, were capable of measuring the relative concentrations of hemoglobin at 46 points (See Figure 3). The lowest optodes of the frontal areas were positioned along the Fp1-Fp2 line while the lowest optodes of the occipital areas were positioned along the O1-O2 line in accordance with the international 10-20 system for electroencephalography. The placements of the optodes in the dorsal bilateral frontal areas and occipital areas were based on our hypotheses derived from the existing related fMRI studies.

The inter-optode distance was 30 mm, which allowed for the measurement of neural activity approximately 15 mm beneath the scalp (Fukui et al., 2003). Optical data from individual channels were collected at 2 different wavelengths (695 and 830 nm) and analyzed using the modified Beer-Lambert Law for a highly scattering medium (Cope and Delpy, 1988). Changes in [oxy-Hb] signals were calculated in units of millimolar-millimeter (mM\*mm) (Maki et al., 1995). The sampling rate was set to 10Hz.

The placements of the optodes in the bilateral dorsal frontal areas were based on our hypotheses derived from the existing neuroimaging studies of facial attractiveness (Aharon et al., 2001; Chatterjee et al., 2009; Ishai, 2007; Liang et al., 2010; O'Doherty et al., 2003). To ensure optode placement consistency across participants, we placed the lowest optodes along the Fp1-Fp2 line in accordance with the international 10-20 system for electroencephalography. A 3D digitizer (EZT-DM401, Hitachi Medical Corporation, Japan) was then used to measure the exact spatial location of each optode in relation to the veridical landmarks of a participant's head (i.e., nasion, inion, Cz, the pre auricular points anterior to the left and right ears). Using the algorithms by Singh et al. (2005), we converted the 3D spatial location data obtained from the 3D digitizer to obtain the cortical positions of our NIRS channels on an estimated Montreal Neurological Institute coordinates (MNI) space with estimated probabilities of accurate localization. The NIRS channels covered a large swath of the posterior and frontal cortical sites.

#### 2.5 fNIRS data analysis

Because previous studies found that [oxy-Hb] has a better signal to noise ratio and is more sensitive than [deoxy-Hb] signals (Homae et al., 2007), we analyzed only the [oxy-Hb] signals. For each participant, we segmented event epochs from the time course data. Each event epoch consisted of a 2-second period prior to stimulus onset, 3 seconds of the stimulus period, 10 seconds of the recovery period, and a 2-second post-stimulus period.

**2.5.1 General linear model (GLM) analysis**—To explore the spatial correlates underlying the different trial types, the [oxy-Hb] data were analyzed using NIRS-SPM (Jang et al., 2009; Tak et al., 2011; Ye et al., 2009). For each participant, data were preprocessed to remove sources of noise and artifact (such as movement and heart rate) using a hemodynamic response function (hrf) filter and wavelet-MDL (minimum description length) detrending algorithm. To determine whether adaptation caused a decrease in neural response (i.e., the neural fatigue purported to underlie aftereffects) we used paired t-tests to compare [oxy-Hb] pre-versus post-adaptation at each channel. To determine whether differences in neural responses to undistorted versus compressed faces changed following adaptation, we analyzed difference scores [oxy-Hb undistorted – oxy-Hb compressed] both pre- and post-adaptation using paired t-tests. To confirm that any changes in difference scores were adaptation-specific we also analyzed difference scores for undistorted versus expanded faces.

**2.5.2 Correlational analyses between behavior and NIRS data**—Participants' behavioral aftereffects scores were measured by subtracting attractiveness ratings of post-adaptation faces (e.g., the post-adaptation undistorted faces) from those of pre-adaptation

faces (e.g., the pre-adaptation undistorted faces). Pearson correlation coefficients between the behavioral measures and NIRS data for each channel based on the results of the GLM analyses were calculated.

# 3. RESULTS

#### 3.1 Behavioral data

Participants were asked to evaluate the attractiveness of each face according to a 7-point scale (1=*very ugly*, 7=*very good-looking*). As shown in Table 1, participants' ratings of undistorted and expanded faces decreased following adaptation, but their ratings of compressed faces increased, consistent with the existing robust behavioral findings.

#### 3.2 NIRS results

In all analyses above, to avoid false discoveries, the FDR correction method was used with alpha=.05.

**3.2.1 Neural response difference before and after adaptation within each face type**—For the undistorted faces, as shown in Table 2, the neural responses were significantly reduced following adaptation in terms of [oxy-Hb] concentration change in several frontal and occipital areas: Channel 1 (BA6, the left superior frontal gyrus (SFG)), Channel 5 (BA46, the left middle frontal gyrus (MFG)), Channel 13 (BA46, the right inferior frontal gyrus (IFG)), Channel 14 (BA45, the right IFG), Channel 15 (BA46, the right MFG), Channel 18 (BA9, the right MFG), Channel 20 (BA9, the right MFG), Channel 26 (BA19, the left superior occipital gyrus (SOG)), and Channel 32 (BA19, the right SOG). In addition, the neural responses were significantly reduced following adaptation in terms of [deoxy-Hb] concentration change in Channel 33 (BA19, the right MOG).

Following adaptation, a significant decrease in [oxy-Hb] concentration was also observed for both expanded and compressed faces, although this change was limited to Channel 5 (BA46, the left MFG) for expanded faces and Channel 15 (BA46, the right MFG) for compressed faces. Also, the [deoxy-Hb] concentration decreased significantly in Channel 25 (BA7, the left angular gyrus) for compressed faces. In contrast, the [deoxy] concentration increased significantly in Channel 21 (BA9, the right MFG).

In addition to the GLM analyses, we also analyzed the peak latencies of the hemodynamic response functions under various conditions and found no significant effects. Figure 4 illustrates the typical time course of the pre- and post-adaptation [oxy-Hb] and [deoxy-Hb] changes of the face stimuli (in this case, channel 5 & channel 15).

#### 3.2.2 Neural response difference between face types before and after

**adaptation**—We contrasted the neural activities between the undistorted, compressed, and expanded faces before or after adaptation, respectively. In the pre-adaptation phase, undistorted faces elicited higher [oxy-Hb] changes than the compressed faces in Channel 26 (BA19, the left SOG) and expanded faces in frontal and occipital areas: Channel 15 (BA46, the right MFG), Channel 24 (BA6, the right precentral gyrus), and Channel 26 (BA19, the left SOG) (see Table 3). In the post-adaptation phase, undistorted faces continued to elicit higher [oxy-Hb] changes than expanded faces in Channel 45 (BA17, the right MOG), whereas compressed (adapter) faces elicited higher [oxy-Hb] than undistorted faces in Channel 8 (BA6, the left precentral gyrus).

We also analyzed the [deoxy-Hb] differences between the three types of faces before or after adaptation, respectively. In the pre-adaptation phase, undistorted faces elicited significantly

lower [deoxy-Hb] changes than the compressed faces in Channel 16 (BA45, the right IFG) and higher [deoxy-Hb] changes than the expanded faces in Channel 26 (BA26, the left SOG). In the post-adaptation phase, undistorted faces elicited significantly lower [deoxy-Hb] changes than expanded faces in Channel 41 (BA17, the right MOG), whereas undistorted faces elicited lower [deoxy-Hb] than compressed (adapter) faces in Channel 46 (BA18, the right MOG).

#### 3.3 The correlation between behavior and NIRS data

Pearson correlation analyses showed that the magnitude of the behavioral attractiveness aftereffect (post-adaptation minus pre-adaptation ratings) was not significantly correlated with the neural attractiveness aftereffect (i.e., the contrast [oxy-Hb] signals between postand pre-adaptation for either undistorted or expanded faces). However, the behavioral aftereffect score was significantly correlated with the neural aftereffect for the compressed (adapter) faces in Channel 13 (BA 46, the right IFG) (r=0.49, p<.001; Figure 5). The greater the change in attractiveness ratings of the originally unattractive compressed faces from the pre-adaptation period to the post-adaptation period, the greater the change in the beta value from the pre-adaptation period to the post-adaptation period, as the compressed faces were now perceived to be more normal and less distorted than before the adaptation.

# 4. DISCUSSION

The present study examined the neural correlates of the face attractiveness aftereffect. Several major findings were obtained. First, after participants saw extremely compressed faces for only 5 minutes, their attractiveness judgments were significantly altered. They judged the compressed faces more attractive than they did before adaptation. In contrast, they judged the undistorted and expanded faces less attractive than they did before adaptation. Second, GLM analyses of the fNIRS data showed that short-term exposure to extremely compressed faces led to significant decreases in [oxy-Hb] activity to undistorted faces in the extended network of cortical regions in the frontal and occipital cortexes. In contrast, significant decreases in [oxy-Hb] activity were observed only in the right middle frontal gyrus to the compressed faces and in the left middle frontal gyrus to the expanded faces. The greater involvement of cortical regions in the adaptation of the undistorted faces indicates that adaptation has the greatest impact on the neural representation of the normative face prototype. Third, patterns of relative [oxy-Hb] responses to undistorted versus compressed (adapted) faces were altered post adaptation. [oxy-Hb] activity was higher for undistorted than compressed (adapted) faces (left SOG) pre-adaptation but not post-adaptation. This shift in relative activity may contribute to the behavioral aftereffect. Conversely, compressed faces elicited higher [oxy-Hb] than undistorted faces in Channel 8 (left precentral gyrus) post-adaptation, but not pre-adaptation. Forth, the exposure to compressed faces led to significant changes of neural responses in terms of [deoxy] concentration mostly in the occipital cortex, and the patterns of relative [deoxy-Hb] changes to undistorted versus compressed (adapted) faces were altered post adaptation. Finally, we also found significant correlations between participants' changes in attractiveness ratings for the compressed faces and changes in the [oxy-Hb] activity in the right IFG. Below, we will discuss each of these major findings in turn.

First, our behavioral findings are consistent with a large body of evidence showing aftereffects in adults and children (Anzures et al., 2009; Jeffery et al., 2010; Robbins et al., 2007; Short et al., 2011; Webster and MacLin, 1999). Our robust behavioral evidence allows us to extend our understanding of how faces are represented by investigating the neural underpinnings. The present and existing behavioral findings collectively suggest that brief exposure to a set of "ugly" faces is sufficient to alter our criteria for facial attractiveness and

thus attest to the dynamic nature of our standard of beauty. More generally, as facial attractiveness has been strongly linked to the averageness of faces and proximity to the prototype (Langlois & Roggman, 1990; Rhodes & Tremewan, 1996), the behavioral attractiveness aftereffect also suggests that our representation of the norm may be dynamically updated according to immediate experience.

Second, our fNIRS data provide the first evidence of the neural underpinnings of face attractiveness aftereffects. Although past research has examined the neural underpinnings of high-level face aftereffects (e.g., Furl et al., 2007), our study is the first to examine such effects with regard to attractiveness preferences and associated changes in the prototype using the norm-based coding model. We consistently found that [oxy-Hb] activity decreased significantly for all three face types (compressed, undistorted, and expanded) post-adaptation when compared to pre-adaptation. These findings are consistent with the predictions of the two-pool opponent model proposed by Jeffery et al. (2010). As indicated by Figure 2, after adaptation, there should be a general reduction in neural activity due to neural fatigue.

It should be noted that we detected significant reductions in [oxy-Hb] activity at nine different channels for the normal/undistorted faces. The affected cortical regions span from the posterior, bilateral superior occipital gyri to the prefrontal cortex where many of the implicated areas are part of the extended face processing neural network. Also, these areas (e.g., the right IFG and MFG) have been specifically found to be associated with the judgment of attractiveness (Aharon et al., 2001; Chatterjee et al., 2009; Haxby et al., 2000; Ishai, 2007; Liang et al., 2010; O'Doherty et al., 2003). This is in strong contrast to the reduction in [oxy-Hb] activity that occurred in only one channel for the compressed faces (right MFG) and one for the expanded faces (left MFG). According to the two-pool opponent model (see Jeffrey et al., 2010), adaptation occurs because the pool of neurons that is most responsive to faces similar to the adapter faces (e.g., faces with compressed features) becomes fatigued. Our findings suggest that the extent of the impact that the adapting faces have on the two pools of neural populations may not be uniform and monotonic across the spectra of face space. Rather, the adapting faces may have greater impact on faces similar to the average face than faces distinctly different from the average. In other words, the neural system of face processing may be tightly tuned towards processing normal/undistorted faces and thus more neural resources are devoted towards discriminating them. This is adaptive because normal-looking faces are the faces we encounter more frequently than distinctive, abnormal-looking faces (Valentine, 1991). Thus, the number of cortical regions affected by adaptation may reflect the uneven distribution of neural resources devoted to processing normal-looking faces as opposed to unusual-looking faces.

Third, a comparison of relative [oxy-Hb] activity between undistorted and both compressed and expanded faces yielded further evidence in support of this explanation. The two-pool opponent model of norm-based coding (see Jeffery et al., 2010) attributes aftereffects to shifts in the relative firing rate of neural populations that fire maximally in response to opposite stimulus characteristics (e.g., small versus large eyes). The observed changes in relative [oxy-Hb] are consistent with this model, although it is puzzling that part of this shift was observed in Channel 8 (left precentral gyrus) and so this particular finding should be treated with caution. We note, though, that Hummel et al. (2012) also report adaptation effects in the left precentral gyrus, a finding for which they had no explanation. Future studies will need to establish the reliability and potential interpretations of this effect.

Forth, we found that results based on [deoxy-Hb] signals differed from those based on [oxy-Hb] signals. Some of the differences might possibly stem from the differential neural mechanisms associated with the [deoxy-Hb] vs. [oxy-Hb] signals. It has been reported that

in some circumstances these two types of signals may respond in opposite directions during neural activation (Cui et al., 2010). Indeed, we found such a case in the channel 41 and Channel 45 where we recorded signals from the right MOG. In the right MOG, [deoxy-Hb] signals of Channel 41 and the [oxy-Hb] signals of Channels 45 were significantly different between the post-adaptation undistorted faces minus the post-adaptation expanded faces, but directions of significance were opposite. Another possibility of differences in finding might be due to signal quality. It is well established that [oxy-Hb] signals are more sensitive to changes in cerebral blood flow than are [deoxy-Hb] signals and have a higher signal to noise ratio (Strangman et al.,2002). Perhaps for this reason, the majority of existing fNIRS studies have mainly reported results based on [oxy-Hb] signals rather than [deoxy-Hb] signals. In line with the existing findings, we also found fewer significant changes of neural responses in terms of [deoxy-Hb] concentration than [oxy-Hb] concentration before vs. after adaptation.

Finally, perhaps the strongest evidence concerning changes in neural responses to adaptation comes from our correlational analyses: individual differences in changes in the [oxy-Hb] response to the compressed faces were significantly correlated with individual differences in adaptation strength in Channel 13 (BA 46, the right IFG). More specifically, the greater the changes in the behavioral attractiveness aftereffect, the greater the changes in the neural attractiveness effect in terms of the [oxy-Hb] activity in the right IFG. This was because the compressed faces were now perceived to be more normal and less distorted than before adaptation. As the right IFG is consistently implicated in face attractiveness processing, this significant behavior-neural response correlation suggests that this area may be sensitive specifically to the extent of adaptation. If this possibility is true, different doses or strengths of adaptation should engender different levels of neural activity changes in this area, an issue that awaits future investigation.

Several caveats of the present study should be noted. First, the present study used only compressed faces as the adapting faces whereas existing behavioral studies have used different types of adapter faces (e.g., expanded faces). To ascertain the robustness of our neural findings, expanded faces should also be used as adapting stimuli. Also, the adapter faces should vary in strength so as to obtain a neural tuning function relative to the adapter face strength. Second, in the current study we investigated simple aftereffects but opposing aftereffects would provide a stronger test of the neural mechanisms. In opposing aftereffect studies, faces from two categories (e.g., upright/inverted; male/female) are distorted in opposite directions during adaptation and opposite shifts in normality/attractiveness judgments occur (e.g., Little et al., 2005; Rhodes et al., 2004). An opposing aftereffect paradigm would allow researchers to see whether, for example, [oxy-Hb] activity increases for compressed faces belonging to one category (e.g., male) but not for expanded faces from the other category (e.g., female). Third, due to the limitations of NIRS methodology, we were unable to investigate various important cortical and subcortical areas known to be involved in the processing of facial attractiveness, such as the fusiform gyrus and the amygdala (e.g., Liang et al., 2010). This limitation could be overcome with the use of fMRI methodology.

In summary, the present study used functional near-infrared spectroscopy methodology (fNIRS) to reveal for the first time the neural underpinnings of the face attractiveness aftereffect. We found that short-term exposure to compressed faces led to significant decreases in [oxy-Hb] activity to undistorted faces in an extended network of cortical regions in the frontal and occipital cortexes, many of which are known to be involved in the processing of facial attractiveness. In contrast, significant decreases in [oxy-Hb] activity were observed only in the right middle frontal gyrus to the compressed faces and in the left middle frontal gyrus to the expanded faces. These differential responses to the three sets of

faces suggest that the attractiveness face adaptation effect for the three sets of faces may have different neural bases consistent with the two-pool opponent model. The greater involvement of cortical regions in the adaptation of the undistorted faces suggests that adaptation may have the greatest impact on the normative face prototype. Taken together, the present findings suggest that the face attractiveness aftereffect mainly reflects the neural representation of the face prototype in response to recent exposure to new face exemplars.

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## **Highlights**

>We are the first to examine neural correlates of the face attractiveness aftereffect.

>Viewing distorted faces made them more, and normal faces less, attractive.

>[oxy-Hb] activities showed corresponding neural attractiveness aftereffect.

>This effect reflects the dynamic nature of cortical face representation.



#### Figure 1.

(a) A schematic diagram of the experiment (The experiment included three phases: the preadaptation phase, the adaptation phase and the post-adaptation phase); Figure 1(b). A schematic diagram of a trial.



#### Figure 2.

A representation of the two-pool opponent model and adaptation to compressed faces. The black lines represent neural responses pre-adaptation; the red lines represent neural responses post-adaptation. The intersection represents the perceived average.

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#### Figure 3.

The estimated cortical locations of the 46 NIRS channels: (a) the right frontal view of the brain; (b) the left frontal view of the brain; (c) the occipital view of the brain. The different colour codes represent the significant channels for the different face comparison conditions: • represents the significant results for the constrast between the pre-minus the post-adaptation undistorted faces; • represents the significant results for the contrast between the pre-minus the post-adaptation expanded faces; • represents the pre-minus the post-adaptation compressed faces; • represents the significant results for the contrast between the pre-adaptation represents undistorted faces minus expanded faces; • represents the significant results for the contrast between the significant results for the contrast between the pre-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the pre-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the pre-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the post-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the post-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the post-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the post-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the post-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the post-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the post-adaptation undistorted faces minus expanded faces; • represents the significant results for the contrast between the post



#### Figure 4.





#### Figure 5.

Scatterplot of the correlation between participants' behavioral aftereffect scores and NIRS data for the compressed faces. The y-axis represents the contrast beta value of [oxy-Hb] signals in Channel 13 between the pre-adaptation period minus the post-adaptation period and the x-axis represents the change in attractiveness ratings between the post-adaptation period minus the pre-adaptation period.

#### Table 1

## Mean attractiveness ratings (SD)

	Pre-adapt. faces	Post-adapt. faces	t(N=40)
Undistorted faces	3.87(.61)	3.64(.74)	2.25*
Expanded faces	3.53(.60)	3.12(.85)	3.903**
Compressed faces	2.95(.76)	3.52(.66)	-5.973**

\*Note: *p*< .05

\*\* p<.01.

#### Table 2

Paired t-test results (two-tailed) of the beta value of the hemodynamic activities

Ch	Estimated MNI		ANI	Brain area	Probability	Paired t-test		
	X	Y	Z			Oxy	Deoxy	
The	The pre-adaptation undistorted faces minus the post-adaptation undistorted faces							
Ch1	-57	30	7	Left IFG (BA45)	1	4.28***	NS	
Ch5	-32	59	25	Left MFG (BA46)	1	4.82***	NS	
Ch13	45	57	13	Right IFG (BA46)	.51	3.80***	NS	
Ch14	59	33	8	Right IFG (BA45)	1	3.32**	NS	
Ch15	34	58	27	Right MFG (BA46)	1	6.04***	NS	
Ch18	43	40	39	Right MFG (BA9)	1	3.50**	NS	
Ch20	28	40	51	Right MFG (BA9)	.67	4.04***	NS	
Ch26	-16	-82	54	Left SOG (BA19)	.51	2.91**	NS	
Ch32	21	-90	41	Right SOG (BA19)	.98	2.83**	NS	
Ch33	43	-80	40	Right MOG (BA19)	.54	NS	2.22*	
Th	The pre-adaptation expanded faces minus the post-adaptation expanded faces							
Ch5	-32	59	25	Left MFG (BA46)	1	3.32***	NS	
Ch21	48	21	49	Right MFG (BA9)	1	NS	-2.26*	
The pre-adaptation compressed faces minus the post-adaptation compressed faces								
Ch15	34	58	27	Right MFG (BA 46)	1	4.78***	NS	
Ch25	-35	-78	50	Left angular gyrus (BA7)	.82	NS	3.21**	

Note: *p*< .05

\*\* p<.01

\*\*\* p<.001, NS represents non-significant. The results are corrected by *FDR*<.05. Probability refers to the estimated probabilities of accurate localization

#### Table 3

Paired t-test results (two-tailed) of the beta value of the hemodynamic activity between the undistorted, compressed, and expanded faces before adaptation

Ch	Esti	mated M	INI	Brain area	Probability	Paired t-test	
	Х	Y	Z			Oxy	Deoxy
The pre-adaptation undistorted faces minus the pre-adaptation expanded faces							
Ch15	34	58	27	Right MFG (BA 46)	1	3.04*	NS
Ch24	51	1	56	Right precentral gyrus (BA 6)	.71	4.55**	NS
Ch26	-16	-82	54	Left SOG (BA 19)	.52	3.74*	2.20*
The pre-adaptation undistorted faces minus the pre-adaptation compressed faces							
Ch16	53	39	25	Right IFG (BA45)	.64	NS	-2.01*
Ch26	-16	-82	54	Left SOG (BA 19)	.52	3.78*	NS
The post-adaptation undistorted faces minus the post-adaptation expanded faces							
Ch41	21	-103	16	Right MOG (BA17)	.86	NS	-2.27*
Ch45	13	-107	5	Right MOG (BA 17)	.83	2.45*	NS
The post-adaptation undistorted faces minus the post-adaptation compressed faces							
Ch8	-60	-3	41	Left precentral gyrus (BA6)	.59	-2.49*	NS
Ch46	34	-99	2	Right MOG (BA18)	.94	NS	-3.09**

\*Note: *p*< .05

\*\* p<.01, NS represents non-significant. The results are corrected by *FDR*<.05. MOG represents middle occipital gyrus. Probability refers to the estimated probabilities of accurate localization.