PAPER

The Influence of a Low-Level Color or Figure Adaptation on a High-Level Face Perception

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SUMMARY  Visual adaptation is a universal phenomenon associated with human visual system. This adaptation affects not only the perception of low-level visual systems processing color, motion, and orientation, but also the perception of high-level visual systems processing complex visual patterns, such as facial identity and expression. Although it remains unclear for the mutual interaction mechanism between systems at different levels, this issue is the key to understand the hierarchical neural coding and computation mechanism. Thus, we examined whether the low-level adaptation influences on the high-level aftereffect by means of cross-level adaptation paradigm (i.e. color, figure adaptation versus facial identity adaptation). We measured the identity aftereffects within the real face test images on real face, color chip and figure adapting conditions. The cross-level mutual influence was evaluated by the aftereffect size among different adapting conditions. The results suggest that the adaptation to color and figure contributes to the high-level facial identity aftereffect. Besides, the real face adaptation obtained the significantly stronger effect than the color chip or the figure adaptation. Our results reveal the possibility of cross-level adaptation propagation and implicitly indicate a high-level holistic facial neural representation. Based on these results, we discussed the theoretical implication of cross-level adaptation propagation for understanding the hierarchical sensory neural systems.

key words: human visual system, low level neural representation, high-level neural representation, adaptation paradigm, face perception

1. Introduction

Adaptation illustrates that recent sensory experience would influence perception and response properties of visual neurons, which is a common characteristic in the human visual system. For instance, an observer adapts to a moving visual stimulus for a minute and then looks at stationary stimulus, the stationary stimulus seems to move slightly opposite to the direction of the original stimulus, which is called motion aftereffect induced by the adaptation. The reason for this aftereffect is that visual adaptation can isolate and/or temporarily reduce the contribution of specific neural populations [1] and thus bias the human perception. Based on this characteristic, adaptation could influence the perception of the low-level visual properties including color [2], motion [3], [4], and orientation [5], [6].

Human visual neural system is organized hierarchically [7] from neural systems in the lower level cortex processing the primary visual property of object (color, form, motion and so on) [8] to systems in the higher level cortex processing the complex output such as face perception [9]–[15]. Previous studies consistently found that the lateral fusiform gyrus is a critical area for the processing of the invariant aspects of face such as identity recognition [9]–[12], and the superior temporal sulcus (STS) is associated with the perception of changeable aspects of face such as gaze direction [9], [13], mouth movements [14], and expression perception [13], [15]. These observations suggest that several high-level cortex areas contribute to the key functions of face perception.

Recently, adaptation was also found to influence the process of complex visual patterns in the high-level visual system, such as facial identity [16], [17], expression [18], [19], attractiveness [20] and facial distortion [21], [22]. For instance, the selective adaptation to a specific facial dimension can bias the human perception to the opposite direction on this dimension. As far as facial identity is concerned, within a series of ambiguous faces morphing between two facial identities, adaptation to one identity will distort the perception of an observer to facilitate perceiving the ambiguous images as the other identity.

The possibility of adaptation at different levels of visual system raises the question whether the low-level adaptation could influence the high-level perception. Little is known about this issue, to the best of our knowledge. Only one very recent study [23] investigated whether low-level curve adaptation affects high-level facial expression judgment. This issue is however crucial to theoretically understand neural coding and computation mechanism, the better understanding for cross-level adaptation interaction will illuminate cross-hierarchy neural response transmission mechanism and implicate how the visual system integrates the complex stimuli from basic visual property. Also, tracking the effects of adaptation in cross-level system is increasingly important for interpreting imaging studies to use adaptation as a tool to assign computations to distinct cortical regions [24], [25].

In order to explore theoretical implication for this issue, we intend to investigate the relationship between low-level adaptation and high-level face perception by using cross-level adaptation paradigm, with adapting and test stimuli at
different end of neural hierarchy.

2. Purpose of the Research

There are two purposes in this study: 1) we examine whether the adaptation to the lower-level visual property can contribute to the high-level aftereffect. The adaptation propagations along two neural routes were investigated, respectively. One is from color system to facial identity system (Experiment 1), the other is from figure system to facial identity system (Experiment 2). In experiment 1, the aftereffects were measured within the real face while adapted by real face or color chip. Difference in aftereffect size was used to evaluate the influence from low-level color system to high-level facial identity system. In experiment 2, we examine whether figure adaptation can contribute to the facial identity system, we adapted subjects by real face and face profile without inter facial components, and measured aftereffects in the real face. Similarly, the aftereffect difference was used to estimate the contribution from the figure system to the facial identity system.

2) We also expect that our result can implicate how face is coded in the high-level visual system. We take a novel experiment paradigm to allow only one dimension to influence facial identity aftereffect. For example, in the experiment 1, only a facial color can be used to identify a face. Because two kinds of adapting stimuli, real faces and color chips, are the same in terms of RGB color values, two adapting conditions would generate approximately identical contribution to the identity aftereffect from low-level neural representation. Thus, if there is still the significant aftereffect difference between these two adapting conditions, this difference can only be attributed to the face high-level neural representation.

3. General Method

3.1 Subjects

Subjects were 5 Japanese undergraduate students with normal or corrected-to-normal vision acuity and normal color vision. Each subject participated in both of two experiments. In consideration of assuring the accuracy of subject’s response, it is crucial in these two experiments to keep every participant naïve to the experimental goal. Because once the subjects learn that the adapting face would bias the perception to the opposite direction within the series of test images, this knowledge will influence the subject’s decision in cognitive level rather than perceptual level [16].

Two ways were used to avoid this situation. Firstly, all subjects were interviewed to ensure naïve on adaptation paradigm before the participation. The second way was similar with that used by Leopold et al. [16]. The subjects were presented with some extra, unanalyzed trials in which some irrelevant adapting stimuli of color chips, grey figures and real faces was shown. This way was used to avoid subject associating the adapting stimuli with test facial images.

3.2 Apparatus

The images were presented on 19 inch LCD (DELL Monitor, Model 1905FP) controlled by the computer (DELL Xeon 2.8 GHz and NVIDIA Quadro FX 1400), with the vertical refresh rate adjusted to 85 Hz and the spatial resolution set to 1024*768 pixels. Subjects were instructed to view the monitor from the distance of 50 cm, the visual stimuli was shown in the center of screen and subtended a visual angle of approximately 12 degree (horizontally) by 15 degree (vertically) in this distance. All the experiments were run on Matlab platform with Cogent Psychophysics Toolbox extensions [26].

3.3 Procedure

Because the two faces with different colors or figures are of the identical face, in order to prevent the subjects from being confused, we firstly instructed the subjects to imagine that these two faces are of the twins and the facial color (Experiment 1) or figure (Experiment 2) can be used to identify them. Then, before each main session, the two face images that would be used in this session were simultaneously shown side by side in the screen and the subjects were instructed to memorize these two faces and the corresponding buttons for response. A short validation session of 8 trials was performed to examine whether the subject make the correct association between the response and face by using the 0%, 30%, 70%, 100% strength of face images (See Fig. 1a.2 and Fig. 1b.2). This validation session will be repeated until subjects succeeded to reach the 100% correct ratio. In this way, it ensures that the subjects could remember the faces and identify them correctly. All subjects learned the adaptation task through the oral instruction and the short practice session.

In each trial, the adapting image and test image were sequentially presented in the center of the screen. After the presentation of test image, the subjects were instructed to perform a two-alternative forced choice (2-AFC) task by pressing one button to classify the presented image into one of two categories (i.e., between two different identities). Feedback for pressing each button was given after each trial to confirm subject’s button response. The durations of adapting stimuli and test stimuli were determined to 4000 and 200 ms, respectively, without interval between adaptation and test stage (See Fig. 2). This paradigm was expected to produce the stronger aftereffect. For the relationship between facial aftereffect size and adaptation time configuration, see [27].

The subject was instructed to attend to the stimuli but no specific fixation point was given. For the role of visual attention to modulate the identity aftereffect, see [28]. The reason of not giving the fixation point is to prevent the subject overly attending to the local facial feature (for example, nose, eye) near to the fixation point and generate the unpredictable influence on the identity aftereffect of the whole
Fig. 1 (a) Stimuli in experiment 1. (a.1) Real faces and color chips as adapting stimuli in the experiment 1. (a.2) The ambiguous test face series morphed between whitish skin face and brownish skin face.

(b) Stimuli in experiment 2. (b.1) Real faces and figures as adapting stimuli in the experiment 2. (b.2) The ambiguous test face series morphed between narrow proportion face and wide proportion face. The numbers across the bottom in (a.2) or (b.2) illustrates the color strength or proportion strength, which indicated how far the face fell between the two originals (The images of 0% and 100% were not used as the test images) along the array.

Fig. 2 Illustration of visual adaptation paradigm and experimental procedure.
There are four adapting conditions in two experiments; color adapting condition and real face adapting condition used in the experiment 1 and figure adapting condition and real face adapting condition in the experiment 2. Each adapting condition included two adapting images and only one image was presented in one trial. Nine images in nine strength level were used as the test and 20 trials was performed in each strength level, thus resulting in a total of 1440 trials for each subject in these two experiments (20 (trials) * 9 (test level) * 2 (adapting images) * 2 (adapting conditions) * 2 (experiments)) = 1440 trials, practice trials and unanalyzed trials were not included). Each subject finished all these trials in 12 sessions, with each session including 120 trials and lasting for 30 minutes. The short period of each session prevented the subjects becoming too tired to lose the attention to the adapting stimuli, which will impoverish the effect of adaptation.

3.4 Criteria for Constructing the Stimuli

Numerous facial dimensions (nose, mouth, jaw, even hair line) will influence the identity perception and further affect the identity aftereffect. Thus, it is crucial for our experiments to exclude influence from other facial dimensions regardless of skin color (experiment 1) or face profile (experiment 2). Otherwise, we can not distinguish which neural representation would be responsible for aftereffect difference in various adapting conditions.

Three criteria were defined for these experiments to avoid this confusing situation. 1) Two adapting faces for tests should share the identical face configuration except facial color in experiment 1 and face profile in experiment 2 to exclude influence on identity aftereffect from the other facial dimension. 2) One adapting face and one adapting stimuli only share the same color or face profile. 3) All adapting and test stimuli share spatial location at the retinal to activate the same neural representation in the low-level visual cortex area.

4. Experiment 1: Adaptation Propagation from Color System to Identity System

4.1 Stimuli for Experiment 1

The face stimulus of frontal-view in the experiment 1 was selected from ALEIX face database [29]. We converted the image face to the size of 340*500 with grey background ((x, y) = (0.33, 0.36), L = 27 cd/m^2). The most of neck and clothing area were excluded but hair and jaw contour were included as shown in the Fig. 1a. Then, we constructed two faces with different skin colors from this image person using FaceFilter studio version 2.0 [30], as one face having a whitish skin (Referred to “W. Face”) and the other face having a brownish skin (Referred to “B. Face”). Then, we sampled two colors from these two faces to construct the corresponding adapting whitish color chip (Referred to “W. Color”, (x, y) = (0.41, 0.38), L = 90 cd/m^2) and brownish color chip (Referred to “B. Color”, (x, y) = (0.52, 0.40), L = 40 cd/m^2). The color chips were constructed as the same size with the face image frame. The two real faces with different skin color and two color chips served as the adapting stimuli of the real face adapting condition and color chip adapting condition, respectively (See Fig. 1a.1).

We morphed the ambiguous image series between these two faces (“W. Face” and “B. Face”) using Fantamorph version 3.0 [32], with the series of images from 30% to 70% in terms of skin color serving as test stimuli (See Fig. 1a.2). This series of ambiguous images was used to measure the corresponding aftereffect in both face adapting condition and color chip adapting condition.

4.2 Data Analysis

In order to index aftereffect size, we firstly determined the response proportion that were given for one of two choices at each test level (e.g., how many times does the subject response “B. Face”) for each subject as shown in Fig. 3a. The adaptation effect in each test level is calculated by subtracting the response proportion adapted after one face (e.g. “W. Face”) from the response proportion adapted after the other face (e.g. “B. Face”) at this test level. The aftereffect size for each adapting condition was determined by averaging the difference of response proportion of all test levels in five subjects for this condition.

We used the paired-samples t-test in SPSS software version 13.0 to perform the statistical test and the significance level was set at p < 0.01. In all statistical tests, the response proportion of every subject served as the statistical variables and the sample capacity for each adapting condition was 45 (9 level * 5 subjects = 45, df = 44).

4.3 Result

Before the further analysis, we examined whether there was a reasonable fit among the responses of the subjects. The response proportions of each subject were compared with those of each of the other four subjects in each adapting condition. Statistical comparisons were performed by means of the paired-samples t-test, with the differences of response proportions obtained from two adapting images at each test level for two subjects in that adapting condition serving as the paired variables. A subject’s responses were defined as low fit if they were significantly different from those of the other four subjects in a given adapting condition. It is initially expected that the low fit data would be excluded from the further analysis. Fortunately, we did not find the case matched to this point, thus, all data of subjects were used in the further analysis.

Both two adapting conditions produced measurable aftereffect (See Fig. 3b) with statistical significance. As expected, in the face adapting condition, the possibility of reporting one face (e.g., “W. Face”) in the ambiguous faces was increased if the subjects were adapted to the other face.
There is a significant aftereffect on face adapting condition or not. We employed the identical adaptation paradigm and experimental procedure in experiment 1.

5. Experiment 2: Adaptation Propagation from Figure System to Identity System

In experiment 1, we found that the low-level color adaptation can contribute to the high-level facial identity aftereffect. Here, we further examined whether the figure adaptation can contribute to the facial identity aftereffect or not. We employed the identical adaptation paradigm and experimental procedure in experiment 1.

5.1 Stimuli for Experiment 2

We have constructed two faces with different facial proportions from the same face used in the experiment 1 by the FaceFilter studio version 2.0 [30], with one profile having narrow proportion (Referred to “N. P. Face”) and the other version having wide facial proportion (Referred to “W. P. Face”). Then, we generate two grey face profiles (“N. P. Figure” and “W. P. Figure”) without internal facial component using Adobe Photoshop CS [31]. To avoid the color contrast effect at the border for figure stimuli, we used white background ((x, y) = (0.32, 0.35), L = 132 cd/m²) for these figure stimuli. These two faces and profiles served as the adapting stimuli in the face adapting condition and figure adapting condition, respectively (See Fig. 1b.1). Finally, we construct the ambiguous test image series by morphing between “N. P. Face” and “W. P. Face” (See Fig. 1b.2), using FantaMorph version 3.0 [32].

5.2 Result

The identical method to the experiment 1 was adopted to calculate the response proportion and corresponding aftereffect size. We obtained the similar data pattern as the experiment 1 as shown in Fig. 4.

Two adapting conditions generated measurable identity aftereffect (See Fig. 4a) with statistical significance. In the face adapting condition, the aftereffect size is 29.5% (S.E.M. = 5.7%), which indicates the bias of subjects’ perception by the adaptation (t44 = 8.150, p < 0.0001). There is also a significant aftereffect (t44 = 3.4, p < 0.001) in the figure adapting condition with the aftereffect size of 9.6% (S.E.M. = 5.8%), which suggests that the adaptation to the grey figure can also contribute to high-level identity aftereffect, implicating propagation from the figure system to the identity system.

We further compared the aftereffect size between these two conditions. There is a significant aftereffect difference between the face adapting condition and the figure adapting condition (t44 = 5.595, p < 0.0001) by paired-samples
Fig. 4  Results for experiment 2. (a) The Response proportion as the function of facial proportion (W. P. Face: Adapted by wide proportion face, N. P. Face: Adapted by narrow proportion face, W. P. Figure: Adapted by wide proportion figure, N. P. Figure: Adapted by narrow proportion figure). The data fitted with logistic functions averaged in all five subjects. (b) The aftereffect size corresponding to two different adapting conditions. Error bars denote S.E.M. and the asterisk (*p < 0.01) indicates the statistical significance.

6. Discussion

6.1 Result Evaluations

In the first experiment, the adaptation effect by the real face was significantly stronger than that by the color chip. It may be argued that this observation is likely due to the fact that a certain face part in the test images would weaken the adaptation effect by color chip, rather than the additional adaptation to high-level face neural representation by face stimuli. For example, the hair area is black and occupies a relatively large area in the stimuli (See Fig. 1a); it is possible that the hair area would weaken the adaptation effect by color stimuli, to some extent.

Thus, we performed a control experiment with the other five subjects to investigate this possibility. The real face and color chip adapting conditions were repeated using facial stimuli without hair area as the adapting stimuli and test. The results show no significant differences between the control experiment and the previous experiment in both adapting conditions. The aftereffect size for real face and color chip adapting conditions in the control experiment was 32.4% (S.E.M = 6.3%) and 13.2% (S.E.M = 2.3%), which is not significantly different from that in the real face adapting condition ($t_{44} = 0.080, p = 0.937$) and the color chip adapting condition ($t_{44} = 1.222, p = 0.228$) in the previous experiment. These observations suggest that the difference of adaptation effect between color stimuli and real face can not be attributed to hair area.

Additionally, it is also of interest whether the other color stimuli can produce the adaptation effect on the real face as the color chip. We performed a pilot experiment to measure the identity aftereffect with a house pattern and a glass pattern [33] as adapting stimuli. The results show significant adaptation effects on the real test faces by the house pattern and the glass pattern. Also, the adaptation effects by these patterns were significantly weaker than those by the real face. These two observations are somehow consistent with the adaptation by the color chip.

However, the adaptation effect by the house pattern was stronger than that by the color chip and the glass pattern. Although we cannot make further predictions regarding this issue based on the pilot observation, this result may provide a possibility that the adaptation effect by the normal object on real faces would vary in terms of the category of meaningful objects. This issue suggests an interesting inquiry in the future.

Additionally, we are also interested to know whether the other kinds of color stimuli can produce the stronger adaptation effect on the real face than the color chip, we performed a pilot experiment to measure the identity aftereffect with a house pattern and a glass pattern as adapting stimuli. The results show the significant adaptation effects on the real test faces by the house pattern and the glass pattern. Also, the adaptation effects by these patterns were significantly weaker than that by the real face. These two observations are somehow consistent with the adaptation by the color chip.

6.2 Scientific Findings

There are two major findings in these experiments: 1) The

The glass pattern are randomized dot arrays that produce the perception of a global pattern, it is an effective tool for psychophysicists to investigate how the information in the low-level visual system is converted to a global pattern responses in the higher level visual system.
adaptation to color and figure can contribute to the high-level facial identity aftereffect. It indicates that adaptation effects can propagate from neural systems in the lower visual areas (e.g., V1, V2, V4 for processing color) to a distributed face recognition system (maybe Fusiform Face Area, See [10],[15]) and from figure systems (e.g. in IT area) to the face recognition system. 2) Although both of adaptations by isolated facial dimensions (skin color or facial profile figure) and by whole faces generate significant facial identity aftereffect, the aftereffect size of latter is much stronger than that of isolated facial dimensions. What neural mechanism would be responsible for these two observations? We intend to discuss possible explanations for these two observations in terms of their theoretical implication for understanding the high-level facial neural presentation and the propagation of adaptation effect along hierarchies in human visual system.

Several previous behavioral researches [34]–[37] suggest a specific holistic strategy in face recognition. It means that face is represented as the whole rather than isolated parts (facial frame, eye, mouth, nose and so on). This holistic hypothesis primarily comes from the following two lines of evidences. One is composite face effect [34], [35] and the other is effect of configuration context [36], [37]. Concerning to composite face effect, if the stimulus face is separated into two parts along the horizontal midline, with the upper part showing one person and the lower part showing another person, the subjects will spend longer to identify the image person in the case that these two halves are aligned to construct a composite face than in the case that two halves are misaligned to construct a non-composite face. The effect of configuration context illustrates that a subject will obtain the higher recognition performance when facial components are shown in the whole face context than when the facial component are shown in isolation. These two line evidences indicate a holistic neural representation in the high visual cortex that will respond the unique collection of feature to identify the certain face.

The observations in this study could be implicitly interpreted by this hypothesized holistic neural representation. In conditions of adaptation to the isolated facial dimensions such as color and figure, only the perception system directly related to these visual properties will be adapted. Then, the adaptation contributions will be propagated to the high-level face neural representation system to produce aftereffects in the test stage. In contrast, when we use the whole face as the adapting stimuli, besides these isolated visual properties were adapted, the high-level holistic facial neural representation will also be adapted and thus produce the much stronger aftereffect.

One may ask whether there is a possibility that color chip or grey figure directly adapts the high-level face neural representation and generate the corresponding identity aftereffect, rather than the effect propagation of adaptation from the low-level system to high-level face system. Because skin color and face profile have holistic attribution in contrast to other facial dimensions and possibly provide a more fundamental reference in the integration by the metric way (About the neural coding of face in metric way, see [38]). In our sense, it seems unreasonable for a pure color chip to directly influence the high-level face neural representation. Because the color is not a specific visual element of face, it is widely involved in various different tasks of visual perception even in the case that RGB value of the color chip approximates that in the face. The direct influence from the color chip on the high-level face system disrupts the hierarchically coding mechanism of human visual system and do not fit the efficient coding principle of the brain. Also, to the best of our knowledge, we do not find any evidence for direct influence from the color chip stimuli on the high-level face perception system in previous literatures. Thus, we infer that the identity aftereffect by the color chip is effect propagation of adaptation from the low-level color system to the high-level face system.

As far as the figure adapting condition is concerned, the situation becomes slightly complicated. The grey figure is to some extend similar with face profile, it appears that the figure may possibly activate the high-level neural representation and generate the adaptation effect. We reason that if the grey figures can directly adapted the high-level face system, the aftereffect size in the figure adapting condition may differentiate that in the color chip adapting condition. However, we do not observe the significant difference of after-effect size between color chip adapting condition and grey figures adapting condition. Thus, although we can not make the explicit prediction about this issue, we tend to hypothesize that identity aftereffect by the grey figure is also the effect propagation of adaptation from the figure system to the high-level face system. We expect the explicit physiological evidence in the future to emerge to clarify this issue. This issue can be investigated by using the single cell recording technology [39] or functional magnetic resonance imaging (fMRI) adaptation paradigm [40]. The fMRI adaptation refers to the observation that repeated presentations of a visual stimulus will cause lower blood-oxygen-level dependent (BOLD) responses than presentations of novel stimuli. It is convenient by these two technologies to examine whether the neurons in the face-responsive cortex could selectively respond to the grey figure that is similar with the face profile, or whether the grey figure can activate the face-responsive cortex or not. The better understanding to this issue helps to address to what extend the identity aftereffect is generated by the high-level face neural representation and to what extend it is a effect propagation from the low-level system.

We expect our result to be able to implicate the neural coding mechanism for the hypothesized facial neural representation. Here we discuss two appealing neural coding mechanism, a grand-mother cells coding mechanism and a population coding mechanism. The grand-mother cell coding theory [41], [42] holds that the face is coded by the small amount of grand-mother cells. Each grand-mother cell will generate the same neural response for feature collections of a certain facial identity. This hypothesis, however, con-
fects to our result. Psychometric curves in our experiments show the shape of logarithmic function, however, for a single grand-mother neuron, it is difficult to exhibit this kind of output. This kind of decision cells is expected to be fitted to the discrete function instead, that is with about 0% of response proportion for lower strength image and 100% for the higher strength image exceeding the threshold.

Concerning to population coding mechanism [43], [44], it suggests that the face is coded by the certain pattern of neural activities over population of neurons. Our result can be interpreted by this mechanism. However, it will depend on the coding strategy and the layer of population neural representation to account for the observation. Thus, we can not make further detailed hypothesis only from our results and current literatures. It is clearly important for physiology and psychological studies to provide a more intensive evidence to clear this issue.

7. Conclusion

We found the adaptation propagation between color system or figure recognition system and facial identity system. The findings provide further insight into neural representation of hierarchy in human visual system and implicate the high-level neural representation for the face. Our results have the theoretical implications for understanding human sensory neural system.

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