Perceptual consequences of face viewpoint adaptation: Face viewpoint aftereffect, changes of differential sensitivity to face view, and their relationship

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Adaptation to a visual pattern can alter the sensitivities of neuronal populations encoding the pattern, which usually results in a visual aftereffect. However, the functional role of visual adaptation is still equivocal and its relation to visual aftereffect is largely unknown, especially for high-level visual adaptation. In this study, we took advantage of face view adaptation to investigate these issues. In the first experiment, we measured the angular tuning function of the face viewpoint aftereffect in F. Fang and S. He's (2005) study. As the adapting angle increased from 0° to 90°, the aftereffect magnitude increased quickly, peaked at 20°, and then gradually decreased. In the second experiment, the effects of face viewpoint adaptation on face view discrimination were measured. We found that face view discrimination around the adapting view improved but was impaired when the adapting view was about 30° away. These results suggest that the functional role of face viewpoint adaptation was not only to adjust the boundary of our perceptual categories but also to modulate the performance of our face view discrimination, highlighting the adaptive nature of face coding. Finally, we showed that a computational model proposed by C. W. G. Clifford, A. M. Wyatt, D. H. Arnold, S. T. Smith, and P. Wenderoth (2001) could account for these two phenomena and their relationship in terms of the changes of the tuning function of face view selective neurons.

Keywords: adaptation, aftereffect, discrimination, face, computational model

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Introduction

Prolonged exposure to a visual pattern can alter the tuning of neurons encoding that pattern, a phenomenon that was termed as adaptation and has been studied extensively. One of the main perceptual consequences of visual adaptation is that it usually biases the perception of a visual pattern presented subsequently. For example, after inspection of a clockwise tilted line for approximately 1 min, a vertical line appears to be tilted in the opposite direction (tilt aftereffect, Gibson & Radner, 1937). Aftereffects can be found after adaptation to nearly all simple sensory attributes such as contrast (Ross, Speed, & Morgan, 1993), orientation (Gibson & Radner, 1937), spatial frequency (Blakemore & Campbell, 1969), hue (Webster & Mollon, 1991), motion direction (Levinson &

& Heitger, 1988), while others have not (Maatanen & Koenderink, 1991). In the orientation domain, although the studies by Regan and Beverlay (1985) and Clifford, Wyatt, Arnold, Smith, and Wenderoth (2001) both reported a significant facilitation effect around the adapting orientation using a long-term adaptation paradigm, Dragoi, Sharma, Miller, and Sur (2002) reported the opposite effect (i.e., impairment) after a brief adaptation. With respect to motion direction, Phinney, Bowd, and Patterson (1997) reported a reduced discrimination threshold around the adapting direction using stereoscopic motion stimuli, while Hol and Treue (2001) reported no adaptation effect using moving random dot patterns. Psychophysical and electrophysiological studies (Bex, Bedinghan, & Hammett, 1999; Clifford & Wenderoth, 1999; Krekelberg et al., 2006) on speed adaptation found a slight enhancement of speed discrimination at the adapting speed, but Kristjansson (2001) observed a similar beneficial effect only when subjects adapted to first-order, not to second-order, motion. Evidence about adaptation effect on spatial frequency discrimination seems to be more consistent. Two studies (Greenlee & Thomas, 1992; Regan & Beverlay, 1983) both reported little or no effect on spatial frequency discrimination around the adapting frequency. Taken together, these studies suggest that the functional role of adaptation in low-level vision is still far from being established.

Adaptation influences not only low-level vision but also high-level vision. Recently, many studies have suggested that an adaptive neural coding mechanism was also employed by high-level vision such as face processing. For instance, adaptation to an expanded face causes a normal face to appear contracted, a phenomenon called the figural aftereffect (Webster & Maclin, 1999); the face viewpoint aftereffect shows that adaptation to a face side view could bias our percept of the face view direction opposite to the adapted direction (Bi, Su, Chen, & Fang, 2009; Fang & He, 2005; Fang, Ijichi, & He, 2007; Ryu & Chaudhuri, 2006). Similar aftereffects have also been documented in several other facial attributes, such as identity, gender, ethnicity, expression, and attractiveness (Leopold, O'Toole, Vetter, & Blanz, 2001; Ng, Ciaramitaro, Anstis, Boynton, & Fine, 2006; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & Maclin, 1999). These aftereffects demonstrate a perceptual shift in the categorical boundary for facial properties after adaptation.

Parallel to the adaptation studies in low-level vision, there are also extensive interests among researchers in whether face adaptation could affect face discrimination performance. So far, there is no empirical evidence supporting this claim that face adaptation can affect face discrimination performance. Rhodes, Maloney, Turner, and Ewing (2007) failed to find enhanced sensitivity to identity differences around the average face after adaptation. Other adaptation studies on gender and ethnicity coding (Ng, Boynton, & Fine, 2008) and expression coding (Pallett & Macleod, 2007) did not observe a reduced discrimination threshold after adaptation, either.

In the present study, we took advantage of face viewpoint adaptation to investigate the effects of visual adaptation on face view representation. Specifically, we attempted to address three questions: First, how does the magnitude of the face viewpoint aftereffect depend on the angular difference between the views of adapting and test stimuli? Second, how does face viewpoint adaptation affect subjects' face view discrimination ability? Third, what is the relationship between the face viewpoint aftereffect and the discrimination threshold changes after adaptation? Is it possible to predict discrimination threshold changes from the magnitude of the face viewpoint aftereffect?

We have several reasons for studying face viewpoint adaptation. First of all, a robust face viewpoint aftereffect can be induced by face viewpoint adaptation (Bi et al., 2009; Fang & He, 2005; Fang et al., 2007; Ryu & Chaudhuri, 2006). Second, in monkey electrophysiological studies, face view selective neurons have been well documented in the superior temporal sulcus (STS; De Souza, Eifuku, Tamura, Nishijo, & Ono, 2005; Perrett et al., 1991, 1985) and inferior temporal cortex (IT; Desimone, Albright, Gross, & Bruce, 1984). Their bell-shaped tuning curves are similar to the orientation-tuning curves in V1, though with a broader tuning bandwidth. Since orientation adaptation could affect orientation discrimination, we should have a better chance to reveal the effect of face viewpoint adaptation on face view discrimination than the effect of face identity adaptation on face identity discrimination. Note that identity has been suggested to be coded in a norm-based way in monkey IT (Leopold, Bondar, & Giese, 2006), rather than an exemplar-based way with bell-shaped tuning functions (Rhodes & Jeffery, 2006; Tsao & Freiwald, 2006). Third, the tuning curves of face view selective neurons have been quantitatively described, which helps us build a computational model to reveal the potential neural mechanisms underlying face viewpoint adaptation.

General methods

Subjects

Eight naive subjects (3 males and 5 females) participated in the first experiment, and five of them (3 males and 2 females) participated in the second experiment. They were right-handed, had normal or corrected-to-normal vision, and had no known neurological disorders. Ages ranged from 18 to 22 years. They gave written, informed consent in accordance with the procedures and protocols approved by the human subjects review committee of Peking University.

Apparatus and stimuli

Stimuli were presented on an IIYAMA HM204DT 22-inch monitor, with a spatial resolution of 1024 × 768 and a refresh rate of 100 Hz. Subjects viewed the stimuli from a distance of 57 cm. Their head position was stabilized using a chin rest and a headrest. The face stimuli were generated by projecting a 3D face model (FaceGen Modeller 3.1, http://www.facegen.com/) with variant in-depth rotation angles onto the monitor plane. The 3D face was the default average face in the software. No hair was rendered and the value of texture gamma correction was set to 2.

The perceived front view was determined for each subject by a method as described in Fang et al. (2007). The front view and the 3° and 6° side views (left and right) specified by FaceGen Modeller were briefly presented to subjects. They were asked to make a 2-alternative forced choice (2-AFC) to judge the viewing direction (left or right) of the face views. Psychometric values at the five views were fit by a cumulative Gaussian function. We interpolated to find the perceived front view, which was judged to be left tilted or right tilted at a 50% chance level. The perceived front view served as the initial position for variant in-depth rotations to generate different face side views. Indeed, the angle between the perceived front view and the front view specified by FaceGen Modeller was extremely small (0.0972° ± 0.0273°). All the face stimuli had the same identity and extended no more than 3° × 3°.

Experiment 1: Angular tuning function of the face viewpoint aftereffect

Stimuli and procedure

There were seven adaptation conditions. Subjects adapted to one of seven face views, including the front view (0°) and the 15°, 30°, 45°, 60°, 75°, and 90° side views. Five test stimuli were always the front view and the 3° and 6° side views (left and right). Each condition had five blocks. An adaptation block began with a 25-s pre-adaptation. After a 5-s topping-up adaptation and a 1-s blank interval, one of the five test stimuli was presented for 0.2 s and subjects were asked to make a 2-AFC judgment of the viewing direction of the test stimulus, either left or right (Figure 1A). In an adaptation block,

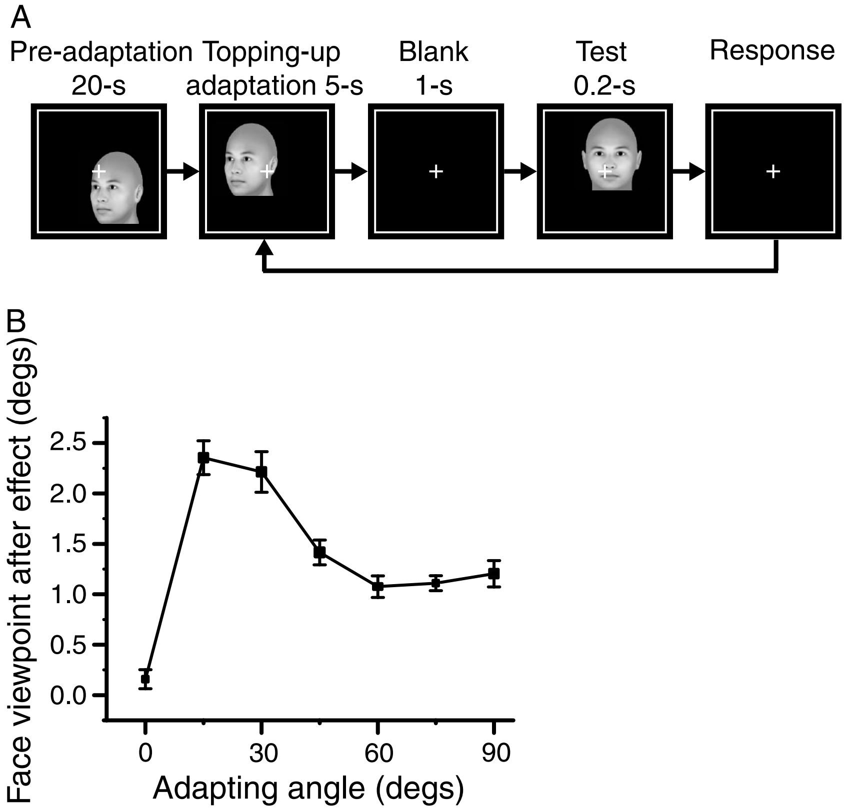

Figure 1. (A) Schematic description of the experimental procedure in Experiment 1. Following pre-adaptation and topping-up adaptation to a face view, a test stimulus around the front view was presented briefly. Subjects were asked to make a 2-alternative forced-choice (2-AFC) judgment of the viewing direction of the test stimulus, either left or right. (B) Magnitude of the face viewpoint aftereffect plotted as a function of adapting angle. Positive values denote a repulsive aftereffect. Error bars denote 1 *SEM* calculated across subjects.

each of the five test stimuli was presented 10 times, for a total of 50 stimulus presentations/trials and with a random sequence. The temporal order of a total of 35 (7×5) blocks was randomized across seven experimental conditions. Subjects were given one practice block for each experimental condition before the experiment. They were asked to take a rest of about 5 min between blocks.

To avoid local adaptation during the adaptation period, the adapting stimulus floated randomly within a $6° \times 6°$ area, whose center was coincident with the center of the monitor. The starting point of the adapting stimulus was randomly distributed in this $6° \times 6°$ area, and its floating velocity was 0.39°/s. The position of the test stimulus was also randomly distributed within the $6° \times 6°$ area. During the experimental period, a fixation point was placed in the center of the monitor and subjects were required to maintain fixation. To help subjects maintain their attention on the face stimulus during the adaptation phase, the floating of the adapting stimulus paused for 0.6 s about every 5 s and subjects were asked to detect the pause.

Preliminary data showed that there was a slight asymmetry of the face viewpoint aftereffect for individual subjects. For five subjects, the aftereffect magnitude after adaptation to right side views was slightly larger than that after adaptation to the corresponding left side views (e.g., right 30° vs. left 30°), while the asymmetry pattern was opposite for the other three subjects. Since we were interested in the characteristics of the angular tuning function of the face viewpoint aftereffect rather than the absolute value of the aftereffect magnitude, for the sake of simplicity, individual subjects adapted to either right or left side views to induce larger aftereffects in the main experiment.

Results

To measure the magnitude of the face viewpoint aftereffect, for each condition and subject, all of the data from the five blocks were pooled together for analysis. Consistent with previous studies (Bi et al., 2009; Fang & He, 2005; Fang et al., 2007; Ryu & Chaudhuri, 2006), after adaptation to the side views, the front view was often judged as facing away from the adapted viewing direction and even some of the test stimuli facing in the same direction as the adaptor were perceived as facing the direction opposite to that of the adaptor. Note that this front view was determined before adaptation. Using the same method in Fang et al. (2007), we found perceived front views after adaptation. The magnitude of the face viewpoint aftereffect was taken as the angle between the perceived front views obtained before and after adaptation.

The angular tuning function of the face viewpoint aftereffect averaged across eight subjects is shown in Figure 1B. As the adapting angle increased from 0° to 90°, the aftereffect magnitude increased quickly and then gradually decreased. This pattern was very consistent across subjects. A 5-order B-spline interpolation approach showed that the angular tuning function peaked at 20°. We performed one-sample t-tests to examine whether the aftereffect magnitude at each adapting angle was significantly larger than zero. Significant repulsive aftereffects were found after subjects adapted to all side views, even at the adapting angle of 90° (15°: $t(7) = 14.024$, $p < 0.001$; 30°: $t(7) = 11.019$, $p < 0.001$; 45°: $t(7) = 11.525$, $p < 0.001$; 60°: $t(7) = 10.059$, $p < 0.001$; 75°: $t(7) = 14.921$, $p < 0.001$; 90°: $t(7) = 9.21$, $p < 0.001$). These aftereffects were still significant at an alpha level corrected for doing seven t-tests (approximate 0.007). Not surprisingly, adaptation to the front view (0°) induced little aftereffect ($t(7) = 1.681$, $p = 0.137$).

Experiment 2: Effects of the face viewpoint aftereffect on face view discrimination

Stimuli and procedure

We attempted to measure face view discrimination thresholds before (baseline) and after adaptation to one of five face views, including the front view (0°) and the 15°, 30°, 60°, and 90° side views. Forty-one face views were pregenerated and served as test stimuli. Their view directions ranged from left 5° to right 5° by 0.25° steps. The experimental paradigm is shown in Figure 2A. An adaptation block began with a 25-s pre-adaptation. After a 5-s topping-up adaptation and a 1-s blank interval, the front view (0°) and a left or right $\theta°$ side view were each presented for 200 ms and separated by a 400-ms blank interval. The temporal order of the front view and the side view was randomized. Subjects were asked to make a 2-AFC judgment of the direction of the second face relative to the first face (left or right). The θ varied trial by trial and was controlled by a QUEST staircase (Watson & Pelli, 1983) to estimate subjects' face view discrimination threshold (82% correct). Each staircase consisted of 50 trials, with a fixed adaptor. Two subjects adapted to right side views, while the other three subjects adapted to left side views, consistent with Experiment 1. For the baseline condition, subjects performed the face view discrimination task without any adaptation. Each subject completed 8 staircases for each adaptation condition and the baseline condition. The temporal order of a total of 48 (6×8) staircases was randomized across six experimental conditions. Subjects were asked to take a rest of about 5 min between staircases.

Results

Figure 2B shows face view discrimination thresholds before adaptation (dashed line) and after adaptation to one of the five face views (solid line). We calculated the ratio of discrimination thresholds (post-adaptation/pre-adaptation) at each adapting angle, as an index of the adaptation effect on face view discrimination. The ratios averaged across five subjects were plotted as a function of adapting angle, which is shown in Figure 2C. Ratio values less than 1 indicate performance improvement in face view discrimination after adaptation, and those larger than 1 indicate an impairment.

After adaptation to the front view (0°), subjects' face view discrimination threshold significantly reduced ($t(4) = 2.717$, $p = 0.027$), which suggested a beneficial role of adaptation in discrimination performance around the adapting view. Although the improvement was small, it was consistent across five subjects. The significance of the improvement held even for three individual subjects (all $t(7) > 2.5$, $p < 0.02$). When the adapting view became more and more dissimilar to the test view, the facilitation effect disappeared and the adaptation effect manifested as an impairment. The impairment was maximal at the adapting angle of 30° ($t(4) = 8.327$, $p < 0.001$) and was also significant at the adapting angles of 15° ($t(4) = 6.363$, $p < 0.01$) and 60° ($t(4) = 4.725$, $p < 0.01$). However, when the adapting angle increased up to 90°, little adaptation effect was observed ($t(4) = 1.697$, $p = 0.165$).

Computational model

We designed a model inspired by Clifford et al. (2001) that aimed to reveal potential neural mechanisms underlying face viewpoint adaptation. Electrophysiological studies have shown that the effects of adaptation on neuronal tuning functions mainly manifest in three ways—response inhibition, bandwidth change, and preference shift (Dragoi et al., 2002; Kohn & Movshon, 2004; Krekelberg et al., 2006). Clifford, Wenderoth, and Spehar (2000) and Clifford et al. (2001) proposed a computational model suggesting that the orientation tilt aftereffect and several

to describe response inhibition, bandwidth change, and preference shift, respectively. $\alpha_\phi(\theta_0)$, $\beta_\phi(\theta_0)$, and $\theta_{0\phi}$ denote the peak response, bandwidth, and peak tuning of a model neuron (labeled by θ_0) after adapting to a ϕ degree face view, respectively. In these formulas, λ and σ control the magnitude and the range of response inhibition, respectively, σ_1 and σ_2 codetermine where the largest broadening occurs, μ controls the magnitude of broadening, γ controls the magnitude of preference shift, and σ_ϕ determines where the largest shift occurs.

The percept of face view direction is determined by the response of the model neuronal population, the vector sum of the individual neuronal responses (Pouget, Dayan, & Zemel, 2003). To compute the vector sum, each model neuron contributes a vector in the direction representing its preferred view direction with a length proportional to its response (Clifford et al., 2001). Without adaptation, the model produces a veridical estimate at all face view directions (Figure 3A). To simulate the adaptation effect on face view selective neurons, we first use one of the three ways or their combinations to adjust the tuning curves, then read out the perceived face view from the changed tuning curves with the method of population vector sum. The magnitude of predicted aftereffect is quantified as the difference between the perceived and the veridical front views. Using the method of least-squared error fitting, we search for the adjustment that could fit our measured aftereffect data optimally and parsimoniously.

We find that none of the three ways by itself can predict our aftereffect data. However, when we first inhibit the responses of the neurons responsive to face views around the adapting view ($\lambda = 0.35$, $\sigma = 20$), and then increase the bandwidth of the neurons with a preferred view away from the adapting view ($\sigma_1 = 100$, $\sigma_2 = 17$) (Figure 3B), the predicted aftereffect can precisely fit the face viewpoint aftereffect data (Figure 3C). Further manipulation of preference shift has a negligible effect on improving data fitting. These results suggest that face viewpoint adaptation might affect the tuning curve of face view selective neurons mainly through response inhibition around and bandwidth broadening away from the adapting view, which is similar to the effect of orientation adaptation on the tuning curve of orientation selective neurons (Clifford et al., 2001).

The second goal of our modeling is to examine if the changes in face view discrimination threshold after adaptation can be inferred from the angular tuning function of the face viewpoint aftereffect. It is straightforward to assume that the difference in the perceived direction between two face views could partially determine their discriminability (see Clifford et al., 2001). The predicted angular tuning function of the aftereffect is continuous and smooth and thus has good analytic properties. First, we add the magnitude of the aftereffect to the veridical angle between adaptor and test (Figure 3D, feint line) to obtain the perceived angle between them after adaptation (Figure 3D, bold line with symbols). Then, we calculate the slope of this perceived angle function (Figure 3D) and get the ratio of perceived differences (post-adaptation/pre-adaptation; Figure 3E). The ratio of face view discrimination thresholds (post-adaptation/pre-adaptation) predicted by perceived difference (Figure 3F) is the inverse of the ratio of perceived differences (post-adaptation/pre-adaptation). As shown in Figure 3F, although the model cannot predict the face view discrimination data (Figure 2B) precisely, the predicted ratios of face view discrimination thresholds capture certain important features of our data. First, discrimination performance improves around the adapting view. Second, discrimination performance is impaired at the adapting angle of 30°. Third, there is little adaptation effect at the adapting angle of 90°.

Discussion

We have demonstrated how the face viewpoint aftereffect varied as a function of the angle of adapting face view and showed that face viewpoint adaptation could affect subjects' performance of face view discrimination. The computational model suggests that face viewpoint adaptation might affect the tuning curves of face view selective neurons mainly through response inhibition around and bandwidth broadening away from the adapting view, resulting in the face viewpoint aftereffect. The model also shows that the changes of face view discrimination threshold after adaptation could be qualitatively explained by the perceived face view difference.

The angular tuning function of the face viewpoint aftereffect measured in Experiment 1 is partially similar to the angular tuning function of the orientation tilt aftereffect (Clifford et al., 2001). Both increased quickly, peaked at some angle, and then gradually decreased. This replicates our previous finding—adaptation to a 30° side view could induce a stronger aftereffect than adaptation to a 60° side view (Fang & He, 2005). For orientation adaptation, large adapting angles (i.e., 80°) could induce the attractive orientation tilt aftereffect. However, no attractive face viewpoint aftereffect was found after face view adaptation at large adapting angles (Wenderoth & Johnstone, 1987). Instead, substantial repulsive aftereffect was observed, even at the adapting angle of 90°. One possible explanation is that the tuning curve of face view selective neurons has a much broader bandwidth than that of orientation selective neurons (Perrett et al., 1991, 1985; Watkins & Berkley, 1974), leading to a wider range of response inhibition around the adapting view.

Our finding in Experiment 2 that face viewpoint adaptation could affect face view discrimination performance is of interest, given that no previous studies have reported subjects' altered discrimination ability after adaptation to other face attributes, such as identity (Rhodes et al., 2007), gender (Ng et al., 2008), and expression (Pallett & Macleod, 2007). Face viewpoint adaptation not only improved view discrimination around the adapting view but also impaired discrimination at face views about 30° away from the adapting view. This pattern is also partially similar to how orientation adaptation affects orientation discrimination, although the maximal impairment occurred for orientations about 10° away from the adapting orientation (Clifford et al., 2001). However, orientation adaptation is different from face viewpoint adaptation in that there was no adaptation effect on discrimination threshold with a large adapting angle (e.g., 90°). This finding confirms our hypothesis that face viewpoint adaptation is a promising place to begin looking at the functional advantage of adaptation in high-level vision. Previous studies (Ng et al., 2008; Rhodes et al., 2007) did not find such an effect with face identity adaptation. One possible reason is that face view and identity are coded in different ways in the visual cortex. Face view selective neurons have a bell-shaped tuning curve that is similar to the orientation-tuning curves in V1 (Perrett et al., 1991, 1985). However, identity has been suggested to be coded in a norm-based way in monkey IT (Leopold et al., 2006), rather than an exemplar-based way with bell-shaped tuning functions (Rhodes & Jeffery, 2006; Tsao & Freiwald, 2006).

It should be noted that the adaptation effects observed in Experiments 1 and 2 cannot be explained by low-level retinotopic adaptations. First, the positions of the adapting and test stimuli were randomized. Second, the adaptor was randomly drifting during pre-adaptation and topping-up adaptation. Third, there are some fundamental differences in adaptation effect as discussed above between face viewpoint adaptation and low-level feature (e.g., orientation and spatial frequency) adaptations. In the future, it would be interesting to investigate if the changes of face view discrimination performance after adaptation still occur when adapting and test faces have different identities. Such an experiment will not only help rule out the low-level adaptation explanation more convincingly but also clarify if the adaptation effect is identity-invariant (Fang et al., 2007).

Our modeling results demonstrate that Clifford et al.'s (2000, 2001) idea can be generalized to high-level face adaptation. In their model, neuronal tuning functions were manipulated in three ways: response inhibition, bandwidth change, and preference shift, which have been documented in low-level feature adaptations by previous single-unit studies (Dragoi et al., 2002; Kohn & Movshon, 2004; Krekelberg et al., 2006). We simply applied these manipulations into our modeling. Indeed, little is known about how high-level adaptation influences neuronal tuning functions to objects and faces. To the best of our knowledge, existing electrophysiological literature (Li, Miller, & Desimone, 1993; Liu, Murray, & Jagadeesh, 2009; Sawamura, Orban, & Vogels, 2006; Verhoef, Kayaert, Franko, Vangeneugden, & Vogels, 2008) completely focused on the effect of repetition suppression on IT neurons. In repetition suppression studies, an adapting stimulus was typically presented for a fraction of a second (Grill-Spector, Henson, & Martin, 2006), rather than tens of seconds in traditional adaptation studies. Thus, repetition suppression is also called brief adaptation by some researchers. It is the consensus of researchers that repetition suppression is characterized by inhibited neuronal responses to a test stimulus if the test stimulus shares some visual property with the adapting stimulus. Other than that, we know little about how repetition suppression influences neuronal responses. Hopefully, high-level adaptation effects could draw more attention from neurophysiologists in the future, whose work will be definitely helpful to verify our model.

It should be noted that, although our modeling results capture certain important features of the discrimination data, the model suggests a greater improvement around 0° and less impairment around 30° than the human data show. The lack of a quantitative match between the human data and the model suggests that the changes of face view discrimination thresholds after adaptation cannot be precisely inferred from the angular tuning function of the face viewpoint aftereffect. Some additional mechanisms need to be taken into account. For example, we assume that the sensitivities of the neuronal population to the first test view and the second test view are the same. Indeed, it is likely that the presentation of the first test view could have altered the sensitivities to the second test view, though we know little about this mechanism from neurophysiological literature. Future modeling studies should consider these issues for a better quantitative match. Nevertheless, we believe that Clifford's model is a simple and effective model to explain both low- and high-level adaptation effects in the visual cortex.

Adaptation is a fundamental property of the visual system. Its key function is to optimize the use of the limited dynamic range of neural responses for coding visual stimuli by calibrating coding mechanisms to the visual environment (Barlow, 1990; Clifford et al., 2000; Laughlin, 1989; Rhodes et al., 2007 proportional to the length of visual experience. For example, tens of hours of visual experience (e.g., perceptual learning) can dramatically improve our discrimination ability (Gilbert, Sigman, & Crist, 2001). However, the visual experience in the current study was only 25 s.

The work by Perrett et al. (1985) on the coding of face view direction suggests that eye gaze, face view, and body posture are encoded within the same system. The directions of face, gaze, and body are primary cues for conveying social attention and they have been the focus of a large body of "social attention" studies in recent years (Nummenmaa & Calder, 2009). Many psychophysical, single-unit recording and functional magnetic resonance imaging (fMRI) studies have been carried out to investigate the neural representations of the directions and have demonstrated their interaction at multiple levels (Bi et al., 2009; De Souza et al., 2005; Langton, 2000; Langton, Honeyman, & Tessler, 2004; Perrett, Hietanen, Oram, & Benson, 1992; Ricciardelli & Driver, 2008; Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009). For example, our recent study (Bi et al., 2009) showed that a gaze direction change in adapting face stimuli could induce a dramatic reduction in the magnitude of the face viewpoint aftereffect. In future studies, it would be interesting to manipulate the directions of face and gaze independently and examine the adaptation effects on the discrimination of face and gaze directions.

In summary, we have found that face viewpoint adaptation could not only bias our perception of face view direction but also alter our face view discrimination ability. We have also shown that the discrimination threshold changes could be inferred from the face viewpoint aftereffect. These results together suggest that the adaptive coding mechanism is employed in face view processing and provide new insights into the functional role of adaptation in high-level vision.

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References

Abbonizio, G., Langley, K., & Clifford, C. W. G. (2002). Contrast adaptation may enhance contrast discrimination. *Spatial Vision, 16,* 45–58. [PubMed]

Barlow, H. B. (1990). A theory about the functional role and synaptic mechanism of visual after-effects. In C. Blakemore (Ed.), *Vision: Coding and efficiency* (pp. 363–375). Cambridge, UK: Cambridge University Press.

Bex, P. J., Bedingham, S., & Hammett, S. T. (1999). Apparent speed and speed sensitivity during adaptation to motion. *Journal of Optical Society of America A, 16,* 2817–2814.

Bi, T., Su, J., Chen, J., & Fang, F. (2009). The role of gaze direction in face viewpoint aftereffect. *Vision Research, 49,* 2322–2327. [PubMed] [Article]

Blakemore, C., & Campbell, F. (1969). On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *The Journal of Physiology, 203,* 237–260. [PubMed] [Article]

Clifford, C. W. G., & Wenderoth, P. (1999). Adaptation to temporal modulation can enhance differential speed sensitivity. *Vision Research, 39,* 4324–4332. [PubMed] [Article]

Clifford, C. W. G., Wenderoth, P., & Spehar, B. (2000). A functional angle on some after-effects in cortical vision. *Proceedings of the Royal Society of London B: Biological Sciences, 267,* 1705–1710. [PubMed] [Article]

Clifford, C. W. G., Wyatt, A. M., Arnold, D. H., Smith, S. T., & Wenderoth, P. (2001). Orthogonal adaptation improves orientation discrimination. *Vision Research, 41,* 151–159. [PubMed] [Article]

Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience, 4,* 2051–2062. [PubMed] [Article]

De Souza, W. C., Eifuku, S., Tamura, R., Nishijo, H., & Ono, T. (2005). Differential characteristics of face neuron responses within the anterior superior temporal sulcus of macaques. *Journal of Neurophysiology, 94,* 1252–1266. [PubMed] [Article]

Dragoi, V., Sharma, J., Miller, E. K., & Sur, M. (2002). Dynamics of neuronal sensitivity in visual cortex and local feature discrimination. *Nature Neuroscience, 5,* 883–891. [PubMed]

Fang, F., & He, S. (2005). Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. *Neuron, 45,* 793–800. [PubMed]

Fang, F., Ijichi, K., & He, S. (2007). Transfer of the face viewpoint aftereffect from adaptation to different and inverted faces. *Journal of Vision, 7*(13):6, 1–9, http://journalofvision.org/7/13/6/, doi:10.1167/7.13.6. [PubMed] [Article]

Gibson, J. J., & Radner, M. (1937). Adaptation, aftereffect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology, 20,* 453–467.

Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron, 31,* 681–697. [PubMed]

Gilbert, C. D., & Wiesel, T. N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Research, 30,* 1689–1701. [PubMed] [Article]

Goldstein, A. G. (1957). Judgments of visual velocity as a function of length of observation time. *Journal of Experimental Psychology, 54,* 457–461. [PubMed]

Greenlee, M. W., & Heitger, F. (1988). The functional role of contrast adaptation. *Vision Research, 28,* 791–797. [PubMed]

Greenlee, M. W., & Thomas, J. P. (1992). Effect of pattern adaptation on spatial frequency discrimination. *Journal of the Optical Society of America A, 9,* 857–862. [PubMed]

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences, 10,* 14–23. [PubMed] [Article]

Hol, K., & Treue, S. (2001). Different populations of neurons contribute to the detection and discrimination of visual motion. *Vision Research, 41,* 685–689. [PubMed] [Article]

Kohn, A., & Movshon, J. A. (2004). Adaptation changes the direction tuning of macaque MT neurons. *Nature Neuroscience, 7,* 764–772. [PubMed]

Krekelberg, B., van Wezel, R. J., & Albright, T. D. (2006). Adaptation in macaque MT reduces perceived speed and improves speed discrimination. *Journal of Neurophysiology, 95,* 255–270. [PubMed] [Article]

Kristjansson, A. (2001). Increased sensitivity to speed changes during adaptation to first-order, but not second-order, motion. *Vision Research, 41,* 1825–1832. [PubMed] [Article]

Langton, S. R. H. (2000). The mutual influence of gaze in the macaque temporal cortex. *Experimental Brain Research, 86,* 159–173.

Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Head, A. S., & Milner, A. D. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London B: Biological Sciences, 223,* 293–317. [PubMed]

Phinney, R. E., Bowd, C., & Patterson, R. (1997). Direction-selective coding of stereoscopic (cyclopean) motion. *Vision Research, 37,* 865–869. [PubMed] [Article]

Pouget, A., Dayan, P., & Zemel, R. (2003). Inference and computation with population codes. *Annual Review of Neuroscience, 26,* 381–410. [PubMed]

Pouget, A., Zhang, K., Deneve, S., & Latham, P. E. (1998). Statistically efficient estimation using population coding. *Neural Computation, 10,* 373–401. [PubMed]