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Face adaptation improves gender discrimination

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ABSTRACT

Adaptation to a visual pattern can alter the sensitivities of neuronal populations encoding the pattern. However, the functional roles of adaptation, especially in high-level vision, are still equivocal. In the present study, we performed three experiments to investigate if face gender adaptation could affect gender discrimination. Experiments 1 and 2 revealed that adapting to a male/female face could selectively enhance discrimination for male/female faces. Experiment 3 showed that the discrimination enhancement induced by face adaptation could transfer across a substantial change in three-dimensional face viewpoint. These results provide further evidence suggesting that, similar to low-level vision, adaptation in high-level vision could calibrate the visual system to current inputs of complex shapes (i.e. face) and improve discrimination at the adapted characteristic.

1. Introduction

Visual adaptation is the process by which the visual system alters its operation properties in response to changes in the environment (Clifford et al., 2007). For example, adapting (seconds of exposure) to a visual pattern can modify the tuning of neurons encoding that pattern. One perceptual consequence of visual adaptation is that it usually biases the perception of a visual pattern presented subsequently, which is called visual aftereffect. 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). Visual aftereffects could be utilized to infer selective neural sensitivities to various stimulus dimensions, from low-level stimulus features (Anstis & Moulden, 1970; Blakemore & Campbell, 1969; Kohler & Wallach, 1944) to mid-level surface and shape properties (Regan & Hamstra, 1992; Suzuki & Grabowecky, 2002; van Lier, Vergeer, & Anstis, 2009), to high-level object and face properties (Fang & He, 2005; Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Watson & Clifford, 2003; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & Maclin, 1999; Zhao & Chubb, 2001). Therefore, visual adaptation has often been dubbed the psychophysicist's microelectrode.

Another perceptual consequence of visual adaptation is visual sensitivity change. It has been proposed that a key function of visual adaptation 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, Wenderoth, & Spehar, 2000; Laughlin, 1989; Rhodes, Maloney, Turner, & Ewing, 2007). One possible consequence of the optimization is that the visual system could maintain good discrimination in that environment. Empirical evidence supporting this idea is mainly from low-level feature adaptations. For example, orientation discrimination around vertical improved after adaptation to a vertical grating (Clifford, Wyatt, Arnold, Smith, & Wenderoth, 2001; Regan & Beverlay, 1985). It has also been shown that adaptation could improve discrimination on contrast (Abbonizio, Langley, & Clifford, 2002; Greenlee & Heitger, 1988), motion direction (Phinney, Bowd, & Patterson, 1997) and speed (Bex, Bedingham, & Hammett, 1999; Clifford & Wenderoth, 1999; Krekelberg, van Wezel, & Albright, 2006).

Recently, there has been a growing interest in whether face adaptation could improve face discrimination. Although several experiments have been conducted to address this issue, evidence is equivocal and it is still difficult to draw a definite conclusion. Rhodes and colleagues (2007) failed to find enhanced sensitivity to identity differences around the average face after adaptation (but see Wilson, Loffler, & Wilkinson, 2002). Other adaptation studies on gender and ethnicity coding (Ng, Boynton, & Fine, 2008) and expression coding (Pallett & Macleod, 2006) did not observe a reduced discrimination threshold after adaptation either. However, two very recent studies showed that face adaptation could affect face discrimination. A study by Chen, Yang, Wang, and Fang (2010) examined the effects of face view adaptation on face view discrimination. They measured face view discrimination thresholds at a face front view before adaptation and after adapting to the face front view and face side views. They found that, adapting to the front view improved face view discrimination, whereas

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adapting to the 30° side view impaired discrimination. Similarly, Rhodes, Watson, Jeffery, and Clifford (2010) discovered that 5 min of adaptation to an average Asian or Caucasian face reduced identification thresholds for faces from the adapted relative to the unadapted race.

In this study, we performed three experiments to test whether visual adaptation can improve gender discrimination. In the first and the second experiments, subjects adapted to male, female and gender-neutral faces, and then gender discrimination thresholds were measured for female faces (Experiment 1) and male faces (Experiment 2). If the re-calibration theory of adaptation (Barlow, 1990) can be applied to high-level vision, face adaptation should enhance discrimination around the adapted state. Specifically, adapting to a male/female face should reduce discrimination thresholds for male/female faces. In the third experiment, we tested whether the discrimination enhancement induced by face adaptation could be generalized to a different face view. Subjects adapted to the front view and the 30° side view of female faces, and then gender discrimination thresholds were measured for the front view of female faces.

2. Methods

2.1. Participants

A total of 36 undergraduates (15 male and 21 female) from Peking University participated in the study, 12 for each of the three experiments. They were right-handed with reported normal or corrected-to-normal vision and had no known neurological or visual disorders. Their ages ranged from 19 to 23. They gave written, informed consent in accordance with the procedures and protocols approved by the human subjects review committee of Peking University.

2.2. Apparatus and stimuli

Stimuli were presented on an IIYAMA HM204DT 22 in. 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.

Three pairs of faces were generated by FaceGen Modeller 3.1 (http://www.facegen.com/). Two pairs were Asian faces and one pair Caucasian faces. In each pair, one face was fully female and the other fully male. Fully female/male faces were determined by setting the gender slider position to 100% female/male in FaceGen Modeller 3.1. We then morphed between faces in each pair using Morpher 3.1 (http://www.asahi-net.or.jp) to generate a symmetrical continuum of 101 images (morphs) that represented gradual transition from fully male face to fully female face in steps of 1 (that is, gender strength ranged from 0 to 100. See also Rotshtein, Henson, Treves, Driver, & Dolan, 2005). Three morph continua used in this study are showed in Fig. 1. For each continuum, the mean luminance and the root-mean-square (RMS) contrast of all morphs were equalized.

2.3. Experimental procedure

In Experiment 1, we attempted to measure gender discrimination thresholds at the gender strength of 80 without adaptation and after adaptation to faces with gender strengths of 20, 50 and 80. Note that the adapting faces with gender strengths of 20, 50 and 80 were male, gender-neutral and female faces respectively. The adaptation paradigm is shown in Fig. 2A. An adaptation staircase began with a 25 s pre-adaptation. After a 5 s topping-up adaptation and a 1 s blank interval, two test faces with gender strengths of 80 and 80 ± θ were each presented for 200 ms and separated by a 400 ms blank interval. The temporal order of these two test faces was randomized. Subjects were asked to make a two-alternative forced-choice (2-AFC) judgment, indicating whether the second test face was more male or more female, relative to the first test face. The θ varied trial by trial and was controlled by a QUEST staircase (Watson & Pelli, 1983) to estimate subjects' gender discrimination threshold (75% correct). The adapting and the test faces were from the same morph continuum. Each staircase consisted of 50 trials, with a fixed adaptor. To avoid local adaptation during the adaptation period, the adapting face floated randomly within a $6° \times 6°$ area as indicated by the white frame in Fig. 2A, whose center was coincident with the center of the monitor. The starting point of the adapting face was randomly distributed in this $6° \times 6°$ area, and its floating velocity was 0.39°/s. The positions of the test faces were also randomly distributed within the $6° \times 6°$ area. Throughout the experiment, a fixation point was placed at 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 face paused for 0.6 s about every 5 s and subjects were asked to detect the pause by pressing a button. For the no adaptation condition, subjects performed the same gender discrimination task without any adaptation.

Each subject participated in four daily sessions and completed one staircase for each adaptation condition (at the gender strengths of 20, 50 and 80) and the no adaptation condition in a daily session. The temporal order of the four staircases in a session was randomized. Subjects were asked to take a rest of at least 5 min between staircases to avoid carry-over effects. Twelve subjects were randomly assigned to three groups, with four subjects in one group. Each group of subjects were tested with one morph continuum.

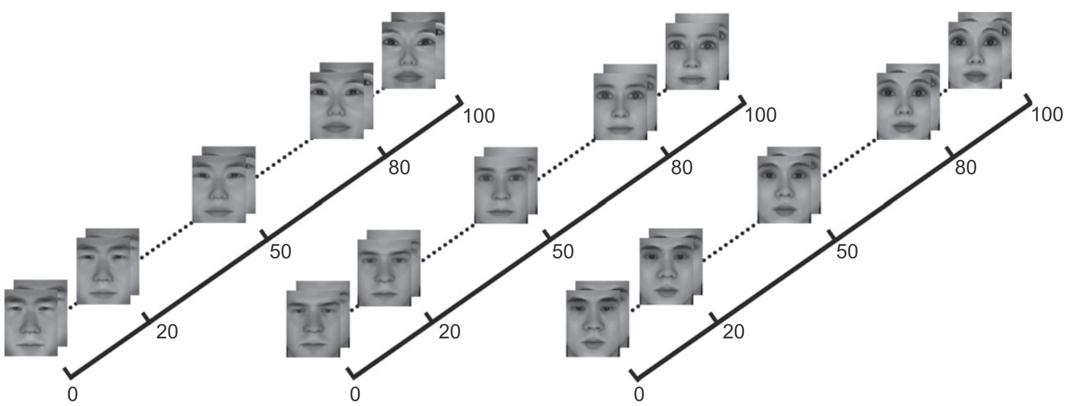

Fig. 1. Gender morph continua from fully female (0) to fully male (100).

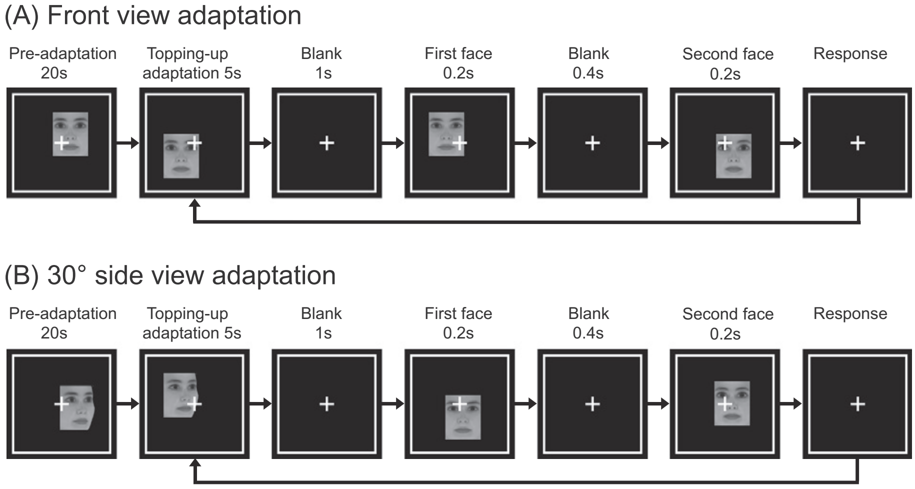

Fig. 2. Schematic description of experimental procedures. Following pre-adaptation and topping-up adaptation to a face, two test faces with slightly different gender strengths were presented sequentially. Subjects were asked to judge whether the second test face was more male or more female, relative to the first test face. They adapted to a front view in Experiments 1 and 2 (A) and a 30° side view in Experiment 3 (B).

In Experiment 2, we attempted to measure gender discrimination thresholds at the gender strength of 20 without adaptation and after adaptation to faces with gender strengths of 20, 50 and 80. The experimental procedure was identical to that in Experiment 1. In Experiments 1 and 2, all adapting and test faces were face front views.

In Experiment 3, we measured gender discrimination thresholds at the gender strength of 80 without adaptation and after adaptation to a front face view and a 30° face side view (Fig. 2B). The 30° side view were generated by projecting a 3D face model with a 30° in-depth rotation angle onto the monitor plane. These two adapting faces had the same identity and had a gender strength of 80. Test faces were around the front face view. Similar to the experimental procedure in Experiments 1 and 2, each subject participated in four daily sessions and completed one staircase for each adaptation condition (front view and 30° side view) and the no adaptation condition in a daily session. The temporal order of the three staircases in a session was randomized. Subjects were asked to take a rest of at least 5 min between staircases to avoid carry-over effects. Twelve subjects were randomly assigned to three groups, with four subjects in one group. Each group of subjects were tested with one morph continuum.

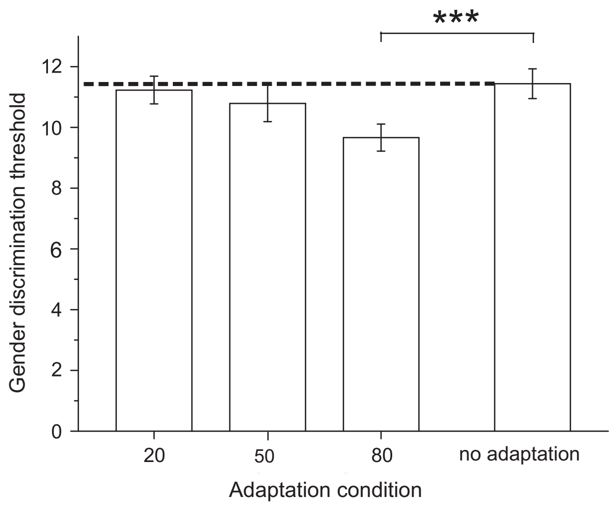

Fig. 3. Gender discrimination thresholds at the gender strength of 80 without adaptation and after adaptation to faces with gender strengths of 20, 50 and 80. Asterisks indicate a statistically significant difference between adaptation conditions ($^{***}p < 0.001$). Error bars denote 1 SEM calculated across subjects.

3. Results

Experiment 1 measured the effects of adaptation to male, female and gender-neutral faces on gender discrimination for female faces. Gender discrimination thresholds in these three adaptation conditions are shown in Fig. 3, along with the threshold measured without adaptation. A repeated-measures analysis of variance (ANOVA) of discrimination threshold was performed with adaptation condition as a within-subject factor. The main effect of adaptation condition was significant ($F(3, 36) = 6.965$, $p = 0.001$). We run planned t-tests to compare discrimination thresholds between face adaptation conditions and no adaptation condition. Relative to the gender discrimination thresholds without any adaptation, subjects' discrimination thresholds for female faces significantly reduced after adapting to a female face ($t(11) = 6.426$, $p < 0.001$), but not after adapting to a male face ($t(11) = 0.6$, $p = 0.561$) or a gender-neutral face ($t(11) = 1.65$, $p = 0.127$). Although the reduction was not large (15.4%), it was quite consistent across subjects. We further run planned t-tests to compare discrimination thresholds between different adaptation conditions. The thresholds after female face adaptation were (marginally) significantly lower than those after male face adaptation ($t(11) = 4.144$, $p = 0.002$) and gender-neutral face adaptation ($t(11) = 2.13$, $p = 0.057$).

Experiment 2 measured the effects of adaptation to male, female and gender-neutral faces on gender discrimination for male faces. Fig. 4 shows gender discrimination thresholds after adaptation and without adaptation. Similar to Experiment 1, a repeated-measures ANOVA of discrimination threshold showed a significant main effect of adaptation condition ($F(3, 36) = 6.67$, $p = 0.001$). Planned t-tests showed that, relative to the gender discrimination thresholds without any adaptation, subjects' discrimination thresholds for male faces significantly reduced after adapting to a male face ($t(11) = 6.559$, $p < 0.001$), but not after adapting to a female face ($t(11) = 1.331$, $p = 0.21$) or a gender-neutral face ($t(11) = 1.472$, $p = 0.169$). Note that the reduction (11.2%) was also quite consistent across subjects. We further run planned t-tests to compare discrimination thresholds between different adaptation conditions. The thresholds after male face adaptation were significantly lower than those after female face adaptation

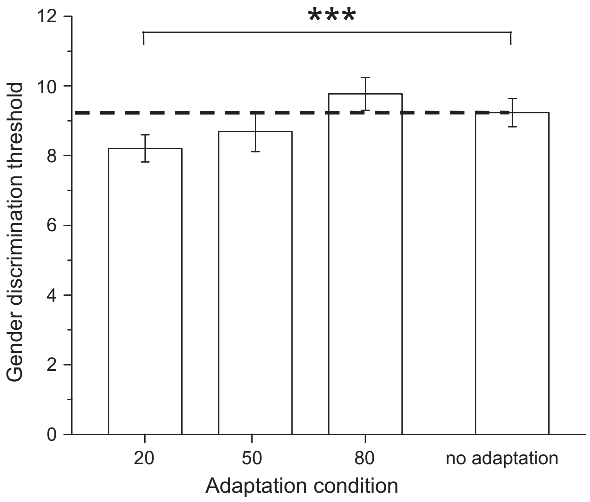

Fig. 4. Gender discrimination thresholds at the gender strength of 20 without adaptation and after adaptation to faces with gender strengths of 20, 50 and 80. Asterisks indicate a statistically significant difference between adaptation conditions ($^{***}p < 0.001$). Error bars denote 1 SEM calculated across subjects.

($t(11) = 3.951$, $p = 0.002$). Although the thresholds after gender-neutral face adaptation were higher than those after male face adaptation, their difference was not significant ($t(11) = 1.245$, $p = 0.239$).

We also analyzed the data in Experiments 1 and 2 all together by reverse-coding the data in Experiment 2. As expected, a repeated-measures ANOVA of discrimination threshold showed a highly significant main effect of adaptation condition ($F(3, 72) = 12.622$, $p < 0.001$).

Results in Experiments 1 and 2 demonstrated a beneficial role of adaptation in gender discrimination performance only at the adapted gender strength. Experiment 3 examined if the adaptation benefit could generalize to a different face view. Fig. 5 shows gender discrimination thresholds for female faces without adaptation and after adaptation to the front view and the 30° side view of a female face. A repeated-measures ANOVA of discrimination threshold showed a significant main effect of adaptation condition ($F(2, 24) = 29.317$, $p < 0.001$). Planned t-tests showed that, relative

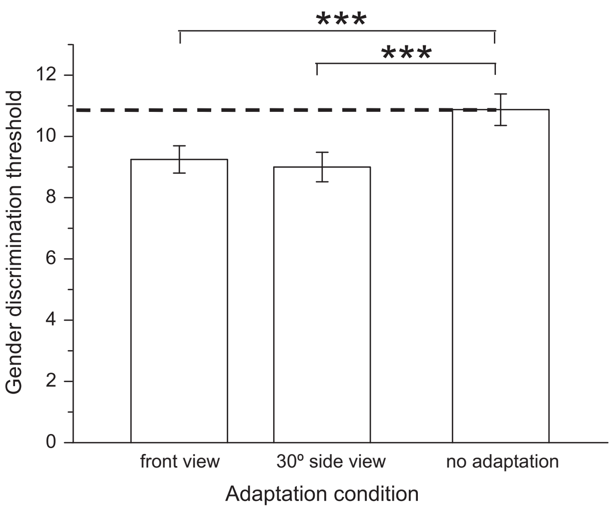

Fig. 5. Gender discrimination thresholds at the gender strength of 80 without adaptation and after adaptation to a face front view and a 30° face side view with a gender strength of 80. Asterisks indicate a statistically significant difference between adaptation conditions ($^{***}p < 0.001$). Error bars denote 1 SEM calculated across subjects.

to the gender discrimination thresholds without any adaptation, subjects' discrimination thresholds significantly reduced after adapting to both the front view ($t(11) = 6.627$, $p < 0.001$) and the 30° side view ($t(11) = 5.334$, $p < 0.001$). But there was no significant difference between the thresholds in these two adaptation conditions ($t(11) = 1.483$, $p = 0.166$). Threshold reductions after adapting to the front view and the 30° side view were 14.7% and 16.8% respectively.

4. Discussion

Three experiments were carried out to examine if face adaptation could improve gender discrimination. Experiments 1 and 2 revealed that adapting to a male/female face could selectively enhance discrimination for male/female faces. Experiment 3 showed that the discrimination enhancement induced by adaptation could be generalized to a different face view. These results demonstrated that, similar to low-level vision, adaptation in high-level vision could calibrate the visual system to current inputs of complex shapes (i.e. face) and improve discrimination at the adapted characteristic. It should be emphasized here that, since adapting and test faces were always from the same morph continuum, our adaptation effect is an identity-based gender adaptation rather than a general gender adaptation that could be generalized across multiple individuals of the same gender.

Face gender aftereffect was first described by Webster and colleagues (2004), which showed that, after adapting to female/male faces for a few minutes, observes perceived a gender-neutral face as male/female. This aftereffect suggests that a functional role of face adaptation is to adjust the boundary of our perceptual categories. Ng and colleagues (2008) investigated whether this adaptation has perceptual consequences beyond the boundary shift by measuring the effects of adaptation on RSVP, spatial search, and discrimination tasks. They did not find any discernable effect on performance for any of these tasks. In the current study, we measured adaptation effects only with a discrimination task. The reason why they failed to find adaptation effects is hard to ascertain since their study differed from ours in many respects. Here, we discuss two potentially important factors. One factor is attention. In their study, subjects passively viewed adapting faces. But in our study, subjects maintained their attention on adapting faces by doing a detection task (see Section 2). It is likely that subjects in our study allocated more attentional resource to adapting faces than their study. A functional magnetic resonance imaging (fMRI) study (Wojciulik, Kanwisher, & Driver, 1998) has shown that attending to faces could increase blood oxygen level-dependent (BOLD) signals in face-selective areas in human visual cortex by three times. Also, attention has a profound effect on visual adaptation, as demonstrated by many psychophysical and brain imaging studies (Fang, Boyaci, & Kersten, 2009; Murray & Wojciulik, 2004; Yeh, Chen, De Valois, & De Valois, 1996). The other factor is the difference in performance measure. We used an adaptive staircase to measure discrimination thresholds with and without adaptation. In Ng et al.'s study, the method of constant stimuli was used. Only a limited number of pairs of faces were presented to subjects for a 2-AFC discrimination task. However, the task might be too difficult to reveal adaptation effects since the gender strength differences in the face pairs were small and the average percent correct was only 58% (Experiment 4C).

It should be admitted that the performance improvement after face gender adaptation is small, which is comparable to the improvements after orientation adaptation (Clifford et al., 2001) and face view adaptation (Chen et al., 2010). Even such a small improvement can be considered as a functional benefit because the amount of improvement is usually 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 (Bi, Chen, Weng, He, & Fang, in press; Fahle & Poggio, 2002). However, the visual experience in the current study was only 25 s.

Experiment 3 demonstrated that the gender discrimination improvement induced by adaption could be generalized to a different face view, which resonates with the finding that face identity aftereffect could transfer across a substantial change in three-dimensional viewpoint (Jiang, Blanz, & O'Toole, 2006). In monkey's high-level visual areas, view-depend and view-independent face neurons mixed together (Booth & Rolls, 1998; Perrett, Hietanen, Oram, & Benson, 1992). Psychophysical adaptation studies provide evidence for both view-dependent and view-independent codings of face identity in the human visual system (Jeffery, Rhodes, & Busey, 2006; Jiang, Blanz, & O'Toole, 2006; Welling et al., 2009). It has been suggested that view-independent representation (recognition) is achieved by using a hierarchy of neural mechanisms with view-dependent responses (Riesenhuber & Poggio, 2002). Our finding suggests that face gender adaptation took place (at least partially) at the level of view-independent face representation. Meanwhile, it also provides further evidence to rule out low-level adaptation as an explanation of the performance improvement.

In this study, we measured discrimination threshold reductions not only when the adapting face was identical to the test face, but also when they were different in gender strength. Results in Experiments 1 and 2 show the same pattern. That is, significant reductions were observed only when the adapting and the test faces were identical. When the adapting and the test faces became more and more dissimilar, discrimination threshold reductions gradually diminished. This pattern is different from the effects of orientation adaptation (Clifford et al., 2001) and face view adaptation (Chen et al., 2010). For these two kinds of adaptations, discrimination thresholds after adaptation also reduced significantly when adapting and test stimuli were identical. However, when adapting and test stimuli differed moderately, discrimination thresholds increased and subjects' performance was impaired. One possible reason for this difference is that, in the visual cortex, face gender is coded in a different way from face view and orientation. Both face view selective neurons and orientation selective neurons have a bell-shaped tuning function responsive to a specific face view or orientation (Perrett et al., 1992), whereas identity (e.g. gender) has been suggested to be coded in a norm-based way in monkey inferotemporal (IT) cortex (Leopold, Bondar, & Giese, 2006).

Although our data provide a clear demonstration that face adaptation can improve gender discrimination, the precise mechanisms underlying the improvement remain uncertain. A possible mechanism is that adaptation to a female/male face could temporarily bias the generic norm towards the adapted gender, which might improve discrimination (Rhodes et al., 2010). Wilson and colleagues (2002) found that the discrimination threshold for face sets around the average (norm) face was lower than that for face sets far from the average face (but see also Rhodes et al., 2007), which is consistent with the neurophysiological finding that IT neurons were most often tuned around the average face (Leopold et al., 2006). In the future, complementary to psychophysical studies, more single-unit and brain imaging studies are needed to carry out to obtain a full understanding of the mechanisms of face adaptation. Indeed, we know little about how adaptation influences neuronal tuning functions to faces (and objects) in the high-level visual cortex.

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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.

Anstis, S. M., & Moulden, B. P. (1970). Aftereffect of seen movement: Evidence for peripheral and central components. *Quarterly Journal of Experimental Psychology, 22*, 222–229.

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*. Cambridge: 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 American A, 16*, 2817–2824.

Bi, T., Chen, N., Weng, Q., He, D., & Fang, F. (in press). Learning to discriminate face views. *Journal of Neurophysiology*.

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

Booth, M. C. A., & Rolls, E. T. (1998). View-invariant representations of familiar objects by neurons in the inferior temporal visual cortex. *Cerebral Cortex, 8*, 510–523.

Chen, J., Yang, H., Wang, A., & Fang, F. (2010). Perceptual consequences of face viewpoint adaptation: Face viewpoint aftereffect, changes of differential sensitivity to face view, and their relationship. *Journal of Vision, 10*(3):12, 1–11.

Clifford, C. W. G., Webster, M. A., Stanley, G. B., Stocker, A. A., Kohn, A., Sharpee, T. O., et al. (2007). Visual adaptation: Neural, psychological and computation aspects. *Vision Research, 47*, 3125–3131.

Clifford, C. W. G., & Wenderoth, P. (1999). Adaptation to temporal modulation can enhance differential speed sensitivity. *Vision Research, 40*, 4324–4332.

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.

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.

Fahle, M., & Poggio, T. (2002). *Perceptual learning*. Cambridge, MA: The MIT Press.

Fang, F., Boyaci, H., & Kersten, D. (2009). Border ownership selectivity in human early visual cortex and its modulation by attention. *Journal of Neuroscience, 29*, 460–465.

Fang, F., & He, S. (2005). Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. *Neuron, 45*(5), 793–800.

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

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

Jeffery, L., Rhodes, G., & Busey, T. (2006). View-specific coding of face shape. *Psychological Science, 17*, 501–505.

Jiang, F., Blanz, V., & O'Toole, A. J. (2006). Probing the visual representation of faces with adaptation: A view from the other side of the mean. *Psychological Science, 17*, 493–500.

Kohler, W., & Wallach, H. (1944). Figural aftereffects: An investigation of visual processes. *Proceedings of the American Philosophical Society, 88*, 269–357.

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.

Laughlin, S. B. (1989). Coding efficiency and design in visual processing. In D. G. Stavenga & R. C. Hardie (Eds.), *Facets of vision* (pp. 213–234). Berlin: Springer.

Leopold, D. A., Bondar, I. V., & Giese, M. A. (2006). Norm-based face encoding by single neurons in the monkey inferotemporal cortex. *Nature, 442*, 572–575.

Leopold, D., O'Toole, A., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience, 4*(1), 89–94.

Murray, S. O., & Wojciulik, E. (2004). Attention increases neural selectivity in the human lateral occipital complex. *Nature Neuroscience, 7*, 70–74.

Ng, M., Boynton, G. M., & Fine, I. (2008). Face adaptation does not improve performance on search or discrimination tasks. *Journal of Vision, 8*(1):1, 1–20.

Pallett, P. M., & MacLeod, D. I. A. (2006). Inefficient discrimination of natural stimuli: Faces (abstract). *Journal of Vision, 6*(13), 59.

Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society B, 335*, 23–30.

Phinney, R. E., Bowd, C., & Patterson, R. (1997). Direction-selective coding of stereoscopic (cyclopean) motion. *Vision Research, 37*(7), 865–869.

Regan, D., & Beverlay, K. L. (1985). Postadaptation orientation discrimination. *Journal of the Optical Society of America A, 2*, 147–155.

Regan, D., & Hamstra, S. J. (1992). Shape discrimination and the judgment of perfect symmetry: Dissociation of shape from size. *Vision Research, 32*, 1845–1864.

Rhodes, G., Jeffery, L., Watson, T. L., Clifford, C. W. G., & Nakayama, K. (2003). Fitting the mind to the world: Face adaptation and attractiveness aftereffects. *Psychological Science, 14*, 558–566.

Rhodes, G., Maloney, L. T., Turner, J., & Ewing, L. (2007). Adaptive face coding and discrimination around the average face. *Vision Research, 47*, 974–989.

Rhodes, G., Watson, T. L., Jeffery, L., & Clifford, C. W. G. (2010). Perceptual adaptation helps us identify faces. *Vision Research, 50*, 963–968.

Riesenhuber, M., & Poggio, T. (2002). Neural mechanisms of object recognition. *Current Opinion in Neurobiology, 12*, 162–168.

Rotshtein, P., Henson, R. N. A., Treves, A., Driver, J., & Dolan, R. (2005). Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. *Nature Neuroscience, 8*, 107–113.

Suzuki, S., & Grabowecky, M. (2002). Evidence for perceptual "trapping" and adaptation in multistable binocular rivalry. *Neuron, 36*, 143–157.

van Lier, R., Vergeer, M., & Anstis, S. (2009). Filling-in afterimage colors between the lines. *Current Biology, 19*, R323–R324.

Watson, T. L., & Clifford, C. W. G. (2003). Pulling faces: An investigation of the face-distortion aftereffect. *Perception, 32*, 1109–1116.

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics, 33*, 113–120.

Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature, 428*, 557–561.

Webster, M. A., & Maclin, L. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review, 6*, 647–653.

Welling, L. L. M., Jones, B. C., Bestelmeyer, P. E. G., DeBruine, L. M., Little, A. C., & Conway, C. A. (2009). View-contingent aftereffects suggest joint coding of face shape and view. *Perception, 38*, 133–141.

Wilson, H. R., Loffler, G., & Wilkinson, F. (2002). Synthetic faces, face cubes, and the geometry of face space. *Vision Research, 42*, 2909–2923.

Wojciulik, E., Kanwisher, N., & Driver, J. (1998). Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *Journal of Neurophysiology, 79*, 1574–1578.

Yeh, S. L., Chen, I. P., De Valois, K. K., & De Valois, R. L. (1996). Figural aftereffects and spatial attention. *Journal of Experimental Psychology: Human Perception and Performance, 22*, 446–460.

Zhao, L., & Chubb, C. (2001). The size-tuning of the face distortion aftereffect. *Vision Research, 41*, 2979–2994.