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Cross-orientation transfer of adaptation for facial identity is asymmetric: A study using contrast-based recognition thresholds

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ABSTRACT

Recent studies suggest that adaptation effects for face shape and gender transfer from upright to inverted faces more than the reverse. We investigated whether a similar asymmetry occurred for face identity, using a recently developed adaptation method based on contrast-recognition thresholds. When adapting and test stimuli shared the same orientation, aftereffects were similar for upright and inverted faces. When orientation differed, there was significant transfer of aftereffects from upright adapting to inverted test faces, but none from inverted to upright faces. We show that asymmetric cross-orientation transfer of face aftereffects generalize across two distinct face adaptation paradigms: the previously used perceptual-bias methodology and the recently introduced contrast-threshold based adaptation paradigm. These results also represent a generalization from aftereffects for face shape and gender to aftereffects for face identity. While these results are consistent with the dual-mode hypothesis, they can also be accounted for by a single population of units of varying orientation selectivity.

1. Introduction

Humans are highly skilled at recognizing and discriminating between different faces, despite the structural complexity of and the high degree of similarity within this stimulus class. This ability may exceed that for recognizing other objects, and thus represents a form of perceptual expertise. The face-expert mechanism may develop over many years of childhood (Nelson, 2001; Taylor, Batty, & Itier, 2004). It is also postulated that because most faces are encountered in an upright orientation, orientation-selectivity is one of the emergent properties of this face expertise (Passarotti, Smith, DeLano, & Huang, 2007) that gives rise to the “face-inversion effect”, in which turning the stimulus upside-down impairs recognition and perceptual discrimination for faces more so than for other types of objects (Valentine, 1988; Yin, 1969).

While there are some accounts that attribute the face-inversion effect to quantitative differences in processing efficiency between upright and inverted stimuli (Sekuler, Gaspar, Gold, & Bennett, 2004), a longer standing view is that upright and inverted faces use qualitatively distinct perceptual mechanisms. This “dual-mode hypothesis” interprets the face-inversion effect as being due to the ability of upright faces alone to access a highly efficient face-expert mechanism, possibly involving configural or holistic forms of processing (Rhodes, Brake, & Atkinson, 1993). Inverted faces and other objects proceed instead by less efficient generic object recognition systems, which may rely more on part-based or feature-based processing (Bartlett & Searcy, 1993; Diamond & Carey, 1986).

Implicit in the dual-mode hypothesis is the assumption of separate perceptual representations for upright and inverted faces. Functional evidence for separate upright and inverted representations can be sought with behavioural adaptation techniques. In a study of orientation-contingent face aftereffects (Rhodes et al., 2004), subjects adapted to a stimulus consisting of two faces, one upright and one inverted, with each having opposite properties in shape (contracted versus expanded) or gender (male versus female). The fact that the resulting aftereffects depended on the orientation of the test face suggests that the upright and inverted faces seen during the adapting phase influenced separate neural representations of faces.

If multiple face representations exist, one important question is the degree of activation produced in each representation by different facial stimuli. In the case of orientation, this can be studied by examining the degree to which adaptation transfers between faces of different orientations. An early study of figural aftereffects for faces undergoing horizontal compression or expansion found similar aftereffects for upright and inverted faces when both the adapting and test faces had the same orientation, but reduced aftereffects when one was upright and the other inverted (Webster & MacLin,

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1999). More interestingly, a later study examining the same figural aftereffects showed an asymmetry in adaptation transfer, with an inverted adapting face producing much smaller aftereffects on an upright test face than the reverse (Watson & Clifford, 2003). Another study of gender aftereffects claimed a similar asymmetry in cross-orientation adaptation transfer (Watson & Clifford, 2006). However, interpreting the transfer results in this last study is complicated by the fact that the aftereffects for upright test faces were smaller than those for inverted test faces in general.

To clarify and further the study of cross-orientation adaptation transfer, we employed a novel adaptation method recently introduced by Oruc & Barton (2008, submitted for publication) and performed another investigation of upright and inverted face adaptation. Rather than probing perception of face shape or gender, we examined recognition of face identity, which is considered a key function of one specific face-processing stream in the fusiform and medial temporal cortices (Haxby, Hoffman, & Gobbini, 2000). Since both cognitive and neuroanatomic models of face processing suggest that distinct modules may serve the extraction of different types of facial dimensions like expression, gender, and identity (Bruce & Young, 1986; Haxby et al., 2000), an assertion that receives support from dissociations in prosopagnosic patients (Barton, 2003), it cannot be assumed *a priori* that behavioural effects seen in one dimension will generalize to other dimensions.

To perform this study we used an adaptation technique that differed from that used in the prior studies (Watson & Clifford, 2003, 2006; Webster & MacLin, 1999). They measured perceptual-shift aftereffects where adaptation to a particular facial attribute results in the observer being more likely to see the opposite attribute in an ambiguous test face. However, aftereffects can also be measured by changes in perceptual thresholds. Thus, prolonged adaptation to a stimulus often results in increased thresholds for perceiving or discriminating that stimulus (Blakemore & Campbell, 1969). Recently, we introduced a different face adaptation paradigm where the effect of face adaptation on recognition contrast thresholds for faces are measured (Oruc & Barton, 2008, submitted for publication). In this paradigm, a test face is briefly presented after which the observers are asked to indicate which face they saw from a limited set of options. The contrast of the test face is controlled by a psychophysical staircase to determine the lowest contrast observers are able to recognize faces at a set criterion performance level, i.e., recognition contrast threshold for faces. We have previously shown that prior adaptation to a face alters recognition contrast thresholds compared to no adaptation (i.e., blank adaptor). In addition, this effect differs based on whether the adapting face is the same or different identity as the test face, as well as based on the duration of the adapting period. Unlike techniques that examine perceptual-shift aftereffects, this contrast-based technique allows one to determine how adaptation changes responses for not only the adapted face but also responses for the un-adapted face. Furthermore, our prior study showed that the dynamics of these aftereffects for adapted and un-adapted faces were complex: while un-adapted faces showed a monotonic increase in recognition thresholds as the adaptation period lengthened, very brief periods of adaptation (20–200 ms) reduced the threshold for recognition of the adapted face, but longer periods elevated them. Initial facilitation and later suppression of the adapted representation have not generally been reported for low-level aftereffects, but rarely have such studies used adapting durations of 200 ms or less. However, other studies examining the effect of adapting duration have shown initial facilitation followed by suppression for word perception (Huber, Shiffrin, Lyle, & Ruys, 2001; Huber, Shiffrin, Quach, & Lyle, 2002) and three-dimensional structure, as explored with the Necker cube (Long, Toppino, & Mondin, 1992). Such results are consistent with a recent dynamic model of aftereffects that explains such complexities by incorporating multiple effects, including repetition facilitation, accommodation, and lateral inhibition (Huber & O'Reilly, 2003).

If multiple effects participate in adaptation, then it cannot be assumed *a priori* that all aftereffects for all adapting durations will show the same modulation by other factors such as orientation congruency. For this reason we measured thresholds following two different durations of adaptation—one at which facilitation for the same face is seen, and one at which suppression for the same face occurs, to determine if the cross-orientation adaptation transfers were similar despite a potential difference in mechanisms.

2. Methods

2.1. Participants

There were 11 subjects with normal or corrected-to-normal vision (six females, ages 18–49). There were data from four subjects for each of the four conditions; however, because of the durations involved, five subjects performed only one of the four conditions, and only three subjects performed more than one condition. The protocol was approved by the review boards of the University of British Columbia and Vancouver Hospital, and informed consent was obtained in accordance with the principles in the Declaration of Helsinki.

2.2. Apparatus and stimuli

A SONY Trinitron 17-in. GDM-G500 monitor displayed all stimuli at 1024 × 768 resolution and 100 Hz refresh rate. The stimuli were manipulated in Matlab (www.mathworks.com) and displayed via a Cambridge Research Systems VSG 2/3 card using the CRS VSG Toolbox for Matlab. Displays were gamma-corrected and average luminance was 35 cd/m^2.

Five Caucasian female faces with neutral expression were selected from the Karolinska Database of Emotional Faces (Lundqvist & Litton, 1998). These were the same faces used in a previous study (Oruc & Barton, 2008, submitted for publication), from which the data for the *upright-adaptor/upright-test* condition are taken. All face images were converted to grayscale, aligned vertically such that pupils were level, and centered horizontally by the tip of the nose. An oval aperture that concealed the facial contour and hairline was superimposed on the faces. This aperture was 283 × 400 pixels in size and subtended a 5.10 × 7.2° visual angle at the viewing distance of 99 cm. Inverted versions of faces were produced by rotating the images 180° in Adobe Illustrator (www.adobe.com).

Mean luminance and root-mean-squared (rms) contrast were made equal across all five facial images by scaling the luminance values inside the oval apertures. The mean luminance of the face templates was equal to the background luminance (outside the aperture), which was half of the maximum luminance, and rms contrast was 1. Adapting stimuli had a fixed rms contrast of 0.6.

2.3. Procedure

We measured contrast thresholds for face recognition in a five-alternative forced-choice (5-AFC) paradigm. At each trial, one of five possible faces was randomly chosen to be the test stimulus, and displayed for 150 ms. The subjects' task was to indicate which of the five faces they saw, using the computer keyboard. The contrast of each test face was controlled by a psychophysical staircase that ran for a fixed length of 40 trials and produced an estimate of threshold at 82% accuracy, using the QUEST procedure (Watson & Pelli, 1983) in Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

Each trial began with an adapting period during which one of the five faces or a blank screen was displayed. This was followed by a sequence of a white noise mask (50 ms), a fixation cross (150 ms), a blank screen (150 ms), the test face (150 ms), a blank screen again (150 ms), and finally the answer display, which remained until the subject entered their response (Fig. 1A). With six different adapting stimuli and five different test faces, there were 30 possible adaptor/test pairings. Five belong to the baseline condition (adaptor stimulus is a blank screen), five to the congruent condition (adaptor stimulus is the same face as the test face) and twenty to the incongruent condition (adaptor stimulus is a face that is different from the test face). Thirty randomly interleaved staircases measured the individual contrast thresholds for each of these 30 pairings. The adaptor/test pairs were then classified into three types according to their congruency in facial identity: *congruent*, where the adapting and test faces were the same identity, *incongruent*, where the adapting and test face were different identities, and *baseline*, where the adapting stimulus was a blank.

There were four conditions in the current experiment: (1) upright-adaptor/upright-test (UU), (2) upright-adaptor/inverted-test (UI), (3) inverted-adaptor/upright-test (IU), and (4) inverted-adaptor/inverted-test (II) (Fig. 1B). All four conditions were measured for two adaptation durations, 100 ms and 1600 ms. Our prior work established that recognition in the congruent condition is facilitated at brief adapting durations of 20–200 ms, but thresholds at

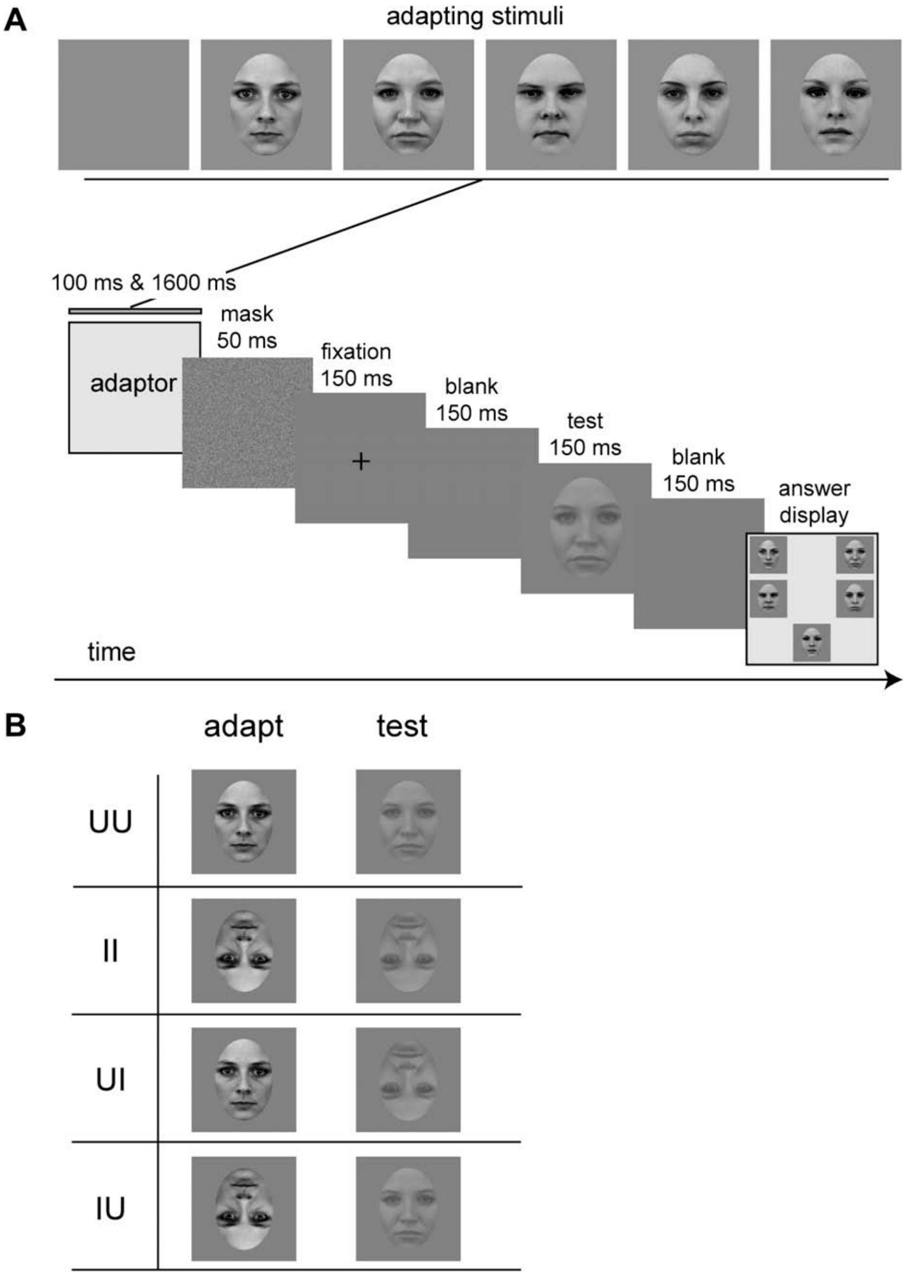

Fig. 1. Illustration of the experimental design. (A) Adapting stimuli were displayed for 100 ms (short duration) or 1600 ms (long duration) at high contrast. Blank adaptors were used to estimate baseline thresholds. This was followed by a 50 ms noise mask, 150 ms fixation cross, and 150 ms blank. A low-contrast test face was presented afterwards for 150 ms before subjects indicated which test face they saw, in a 5-AFC paradigm. Trials are further broken up into congruent (same adapting and test face, not shown) and incongruent (different adapting and test face, as shown) conditions. A total of five different Caucasian female face stimuli were used from the Karolinska face database. (B) Four conditions result from pairing adapting and test stimuli of two possible orientations (upright or inverted). The upright-adaptor, upright-test (UU) condition was the design used in our previous study (Oruc & Barton, 2008, submitted for publication). In the present study, we explored the remaining three conditions: upright/inverted (UI), inverted/upright (IU), and inverted/inverted (II).

long adapting durations (>1s) are substantially elevated (i.e., performance is worse) in both the congruent and incongruent conditions (Oruc & Barton, 2008, submitted for publication).

Adapting duration was fixed within a given block. Each subject completed two blocks, one for each adapting duration, in an order that was counterbalanced across all four subjects. Subjects were told to shift their gazes as they viewed the adaptor, especially during the 1600-ms adapting duration, in order to reduce the involvement of low-level aftereffects.

To familiarize them with the face stimuli, subjects first completed a training session for the faces in the test orientation they would see during that experimental block. The training session measured contrast thresholds for recognizing the faces in a 5-AFC paradigm identical to the experimental procedure, but with the adaptation period omitted. Each block of training included five interleaved staircases that measured individual contrast thresholds for each face. Five blocks of training were completed by each subject, with more blocks added if necessary, until their thresholds stabilized as determined by visual inspection of their learning curve.

2.4. Analysis

Post-adaptation changes in performance were quantified by *threshold change ratios*, computed as the ratio of the threshold for a given adapting/test pair to its corresponding baseline threshold. As a preliminary observation, these unadapted baseline thresholds were significantly lower for upright faces (0.015) than for inverted faces (0.025), confirmed by a one-way ANOVA ($F(1, 30) = 10.8$, $p < 0.01$). A ratio of 1 indicates the absence of any aftereffect. Ratios less than 1 indicate facilitation, and ratios larger than 1 indicate impairment of performance following adaptation. Since the threshold change ratio measure does not satisfy the normality requirements of standard statistical tests, we used non-parametric methods such as bootstrap confidence intervals and Friedman's non-parametric ANOVA for tests of significance. Indices of congruent and incongruent threshold changes were obtained by taking geometric averages of threshold change ratios of all congruent and incongruent pairs, respectively (Oruc & Barton, 2008, submitted for publication). The significance of threshold change ratios was determined with 95% bootstrap confidence intervals.

To quantify the size of the identity-selective component of the aftereffects for each adaptation duration, we calculated the differences between each subject's threshold change ratios for congruent and incongruent face-pairs. We first submitted these identity-selective aftereffects to a Friedman's non-parametric two-way ANOVA with orientation condition (UU, UI, IU, and II) and adapting duration (10 ms and 1600 ms) as the main factors. Next, we ran pair-wise comparison of aftereffect sizes across all experimental groups using a Wilcoxon rank-sum test. Last, we tested whether the identity-selective aftereffect of each orientation condition at each adapting duration was significant, using a Wilcoxon signed-rank test to determine if the aftereffect was larger than 0.

3. Results

As described previously (Oruc & Barton, 2008, submitted for publication), the *upright-adaptor/upright-test* (UU) condition showed facilitation of recognition of the adapted face (congruent pairs) after a brief 100 ms adaptation duration (95% bootstrap CI = [0.48, 0.90]), but elevation of thresholds for the adapted face after a longer adaptation of 1600 ms (95% bootstrap CI = [0.90, 1.63]) (Fig. 2A). Thresholds for un-adapted faces (incongruent pairs) were elevated more than those for adapted faces at both durations, indicating identity-selectivity of the effects of adaptation. For the incongruent condition, the 95% confidence intervals for threshold change at the short ([1.10, 1.30]) and long ([1.60, 1.95]) adapting durations both indicated significant elevation of thresholds.

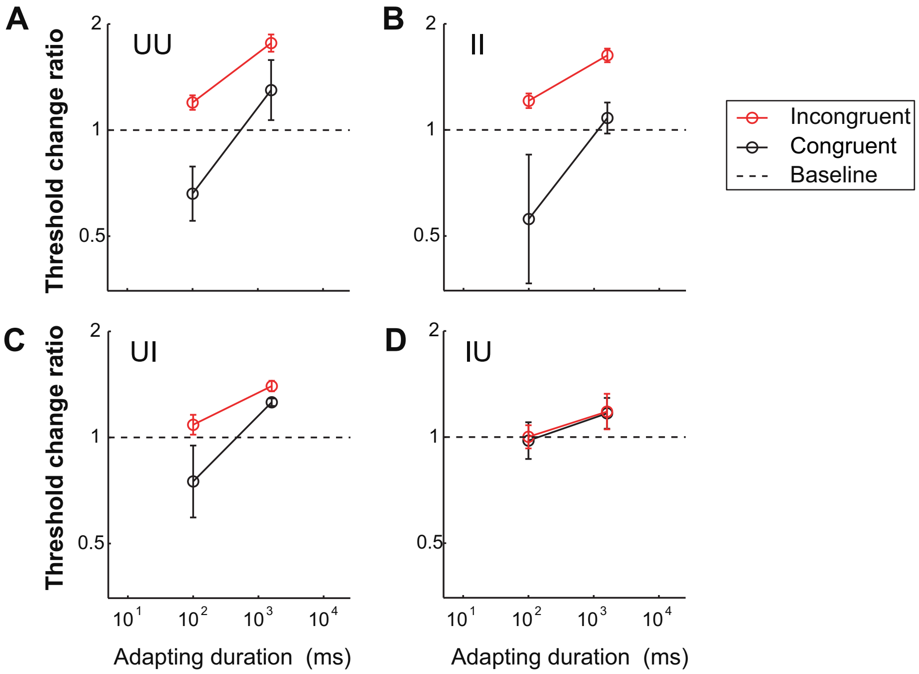

Fig. 2. Adaptation aftereffects for all four orientation conditions. In each panel face aftereffects are plotted as threshold change ratios for the congruent (solid black line) and the incongruent (solid red line) conditions at two adapting durations (100 ms and 1600 ms). Each data point presents the geometric averages across four subjects. Error bars represent 68% bootstrap confidence intervals. Baseline threshold elevation ratio (shown in dashed black line) is by definition 1. (A) Upright-adaptor, upright-test (UU) condition from our previous study (Oruc & Barton, 2008, submitted for publication); (B) upright-adaptor, inverted-test (UI); (C) inverted-adaptor, upright-test (IU); and (D) inverted-adaptor, inverted-test (II). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A very similar pattern of performance was seen for the *inverted-adaptor/inverted-test* (II) condition (Fig. 2B). Again, the data for congruent face-pairs were distinct from that for incongruent face-pairs, indicating identity-selectivity of the aftereffect. We also found significant facilitation for the congruent condition at brief adaptation (95% bootstrap CI = [0.25, 0.97]). At the long adapting duration, thresholds were elevated but did not significantly exceed the baseline (95% bootstrap CI = [0.82, 1.43]).

The data for cross-orientation adaptation transfer revealed an asymmetry. First, the *upright-adaptor/inverted-test* (UI) condition did show some transfer of adaptation (Fig. 2C). The pattern of effects on recognition thresholds at both short and long adaptation durations was similar to that seen for the UU and II conditions. There was facilitation for the congruent condition at the short adapting duration (95% bootstrap CI = [0.49, 0.99]) and thresholds were significantly elevated above the baseline at the long adapting duration (95% bootstrap CI = [1.20, 1.32]). As expected, incongruent thresholds were monotonically elevated with adapting duration: 95% bootstrap confidence intervals are [0.96, 1.16] at the short, and [1.31, 1.46] at the long adapting durations.

For the *inverted-adaptor/upright-test* (IU) condition, however, there was no evidence of any aftereffect at either short or long adapting durations and for either congruent or incongruent face-pairs (Fig. 2D). The 95% bootstrap confidence intervals (CI) of all four data points included 1, indicating no significant difference from the baseline measures without adapting faces (at short adapting duration, congruent = [0.85, 1.24], incongruent = [0.87, 1.15]; at long adapting duration congruent = [0.98, 1.42], incongruent = [0.88, 1.55]).

Friedman's non-parametric two-way ANOVA for the identity-selective aftereffect showed a main effect of orientation condition ($p < 0.01$), but not of adapting duration ($p = 0.67$) (Fig. 3). Pair-wise comparisons of aftereffect sizes with a Wilcoxon rank-sum test showed, first, no significant difference between the UU and II conditions at either adapting duration. Thus, identity aftereffects of similar magnitude are produced for both inverted and upright faces when adapting and test faces have the same orientation. Second, we can assess the efficiency of cross-orientation adaptation transfer by examining the effect on the test face of changing the orientation of the adapting face, since it is the test face that is probing the status of facial representations. A comparison of the UU and IU conditions showed a significant decline in adaptation magnitude with changing adaptor orientation at 100 ms ($p < .05$) and a trend toward the same at 1600 ms ($p < .08$). A comparison of the II and UI conditions showed consistent trends towards a decline with changing adaptor orientation at both 100 ms ($p < .08$) and 1600 ms ($p < .08$).

To determine if the size of the identity-selective aftereffect was significant for any condition, we used the Wilcoxon signed-rank test (Fig. 3). For the UU and II conditions, all identity-selective aftereffects were significant ($p < .05$) with the exception of a trend for the UU condition at 1600 ms ($p < .07$). For the cross-orientation conditions, there was a significant aftereffect ($p < .05$) at 1600 ms and a trend ($p < .07$) for the UI condition, but no significant aftereffects for the IU condition.

4. Discussion

Although we used a different adaptation paradigm and assessed a different dimension of face processing, our results parallel some of the findings reported in the few studies that have assessed the effect of orientation congruency between adapting and test faces.

First, when both adaptor and test faces have the same orientation, the magnitude of the aftereffect for inverted faces is equal to that for upright faces. The two previous studies of shape aftereffects also found this (Watson & Clifford, 2003; Webster & MacLin, 1999), although a study of gender aftereffects found that, if anything, the aftereffects for inverted faces were greater (Watson & Clifford, 2006). It was initially considered somewhat surprising that "the poorer recognition associated with inverted images did not result in a weaker figural aftereffect" (Webster & MacLin, 1999). However, since aftereffects are measured as relative rather than absolute changes in perception (i.e., perceptual-bias aftereffects are measured as a relative shift in perception, and our recognition-threshold aftereffects are indexed relative to an unadapted baseline), the magnitude of the aftereffect does not necessarily reflect the strength of the underlying activation or the richness of the underlying representation. Rather, this result simply indicates that a weak adapting stimulus can adapt a weak pattern of activity (the II condition) as capably as a strong adapting stimulus can adapt a strong pattern of activity (the UU condition). In our experiment, the difference in strength of upright versus inverted patterns of activity is probably better reflected by the unadapted baseline

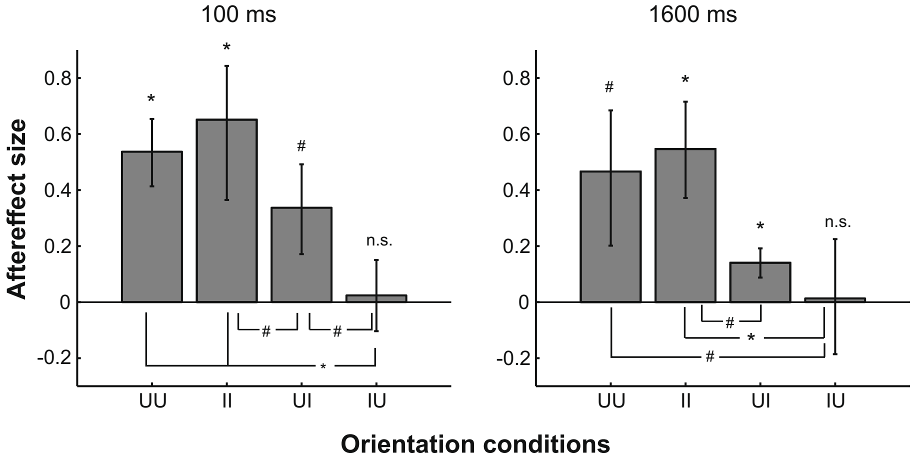

Fig. 3. Aftereffect sizes at all four orientation conditions. We define aftereffect size as the difference between the incongruent and congruent threshold change ratios at the two adapting durations. Aftereffect sizes at (A) the short (100 ms) adapting duration, and (B) the long (1600 ms) adapting duration are shown. Errorbars indicate 68% bootstrap confidence intervals. Aftereffects significantly larger than zero are marked with an asterisk placed above the data. Trends toward significant effects are marked with the number sign (#), and nonsignificant results are indicated with (n.s.). Results of pair-wise comparisons between the four orientation conditions are marked similarly along lines connecting the relevant pairs.

thresholds, which were significantly higher for inverted than for upright faces.

Second, we confirm that the conditions assessing cross-orientation transfer of adaptation show a significant asymmetry. While upright adapting faces were capable of generating an aftereffect in inverted test faces, inverted adapting faces did not create any aftereffect in upright test faces. These results are significant in showing that the effect on identity processing parallels the asymmetry in cross-orientation transfer of aftereffects reported for face shape (Watson & Clifford, 2003) and possibly gender (Watson & Clifford, 2006). In addition, we have shown that the cross-orientation transfer of aftereffects obtained using our novel contrast-based adaptation paradigm confirms those previously reported for perceptual-bias aftereffects (Watson & Clifford, 2003, 2006). This not only solidifies and strengthens the finding of asymmetry in cross-orientation transfer of face aftereffects, but also validates the relatively new adaptation paradigm we used as an effective tool for studying face perception.

Our results suggest that upright faces may not be quite as effective as inverted faces in adapting inverted test faces, which is consistent with one report on figural aftereffects (Webster & MacLin, 1999) and probably with another on gender aftereffects (Watson & Clifford, 2006). However, the data or figures in most of those reports also suggest some small transfer of adaptation from inverted to upright faces (Watson & Clifford, 2003, 2006; Webster & MacLin, 1999), as did another paper on viewpoint adaptation (Fang, Ijichi, & He, 2007), whereas we found none. The reason for this is not clear, but it may be that our more dramatic effect reflects the greater specificity of face-processing demands involved in making identity judgments.

As discussed in the introduction, previous reports of asymmetric cross-orientation transfer of adaptation have shown how these results can be interpreted in the framework of the dual-mode hypothesis (Watson & Clifford, 2003, 2006). If upright faces adapt both an orientation-selective expert face-processing mechanism and a generic part-based object-processing mechanism, then the latter will cause significant transfer of orientation from upright to inverted faces. If inverted faces adapt only the generic object-processing system, then minimal transfer of adaptation from inverted to upright faces will occur, if the vast majority of the aftereffect for upright faces is generated in the expert face-processing system.

If this interpretation is correct, then our results carry some additional implications. First, the fact that upright-to-inverted adaptation appears smaller in magnitude than inverted-to-inverted adaptation implies that the representations in the generic object-processing system also possess some orientation selectivity. This is not necessarily controversial, as even the earliest studies of the face-inversion effect did not claim that the perception of other objects shows no inversion effect, just that the effect for faces was greater (Yin, 1969, 1970). Also of relevance are observations that inversion affects the processing not just of holistic or configural information in faces but also of feature-based data (Endo, 1986; Malcolm, Leung, & Barton, 2005; Riesenhuber, Jarudi, Gilad, & Sinha, 2004; Yovel & Kanwisher, 2004). Second, the fact that no adaptation is transferred from inverted to upright faces implies that the upright face aftereffect is generated almost exclusively in the expert face-processing system. This too may be an expected consequence of some orientation selectivity in the generic object-processing system, if inverted faces have only a modest effect on upright representations within it.

Although these results are consistent with a dual-mode system, they do not in themselves constitute convincing evidence for its existence. As Watson and Clifford (2006) also pointed out, a similar pattern of findings could emerge from a single orientation-selective representation of faces that prefers upright stimuli. In such a system, adaptation with the strongly preferred stimulus (i.e. an upright face) would cause a considerable effect on both strong (upright) and weak (inverted) activation patterns in the test phase, whereas a weakly preferred stimulus (i.e. an inverted face) could still have a significant effect on weak (inverted) activation patterns in the test phase, but minimal or no effect on strong (upright) activation patterns. This would be consistent with assertions of a single shape-based mechanism for face-encoding (Riesenhuber et al., 2004) and quantitative rather than qualitative explanations of the face-inversion effect (Sekuler et al., 2004).

Another possibility would be a single face-space populated by neurons with varying orientation and viewpoint preferences, as described in neurophysiological studies of inferotemporal cortex (Perrett, Hietanen, Oram, & Benson, 1992; Tanaka, Saito, Fukuda, & Moriya, 1991). If cells preferring inverted faces were more broadly tuned for orientation than cells preferring upright faces, which could be one possible product of face expertise, asymmetric cross-orientation transfer of adaptation would be the result. While this explanation may superficially resemble the dual-mode hypothesis in that there are different units for upright and inverted faces, it does not demand that the cells preferring inverted faces and the cells preferring upright faces perform fundamentally distinct computations. This explanation also has the advantage of better accommodating findings concerning orientation-contingent face aftereffects. Although the initial report of orientation-contingent aftereffects interpreted the inferred existence of separate upright and inverted representations in a dual-mode framework (Rhodes et al., 2004), their data could just as easily be explained by a single mechanism with orientation-selective neurons. As well, recent data show orientation-contingent aftereffects with faces tilted 90° left versus right (Watson & Clifford, 2006): in this situation, there are no grounds for invoking qualitatively different mechanisms for the rightward orientation compared to the left.

Given these arguments, we suggest that while it is possible to interpret the data regarding both orientation-contingent aftereffects and asymmetric cross-orientation transfer in terms of the dual-mode hypothesis, these bodies of work do not constitute a definitive proof of this hypothesis. At present, these results can still be accounted for parsimoniously by orientation effects within a single representational system.

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