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View-contingent aftereffects suggest joint coding of face shape and view

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Abstract. While it is well established that different neural populations code different face views, behavioural evidence that these neurons also code other aspects of face shape is equivocal. For example, previous studies have interpreted the partial transfer of face aftereffects across different viewpoints as evidence for either view-specific coding of face shape or that the locus of adaptation is in face-coding mechanisms that are relatively robust to changes in face view. Here we show that it is possible to simultaneously induce aftereffects in opposite directions for 3/4 and front views of upright faces with manipulated mouth position (experiment 1). For example, simultaneous adaptation to 3/4 views with raised mouth position and front views with lowered mouth position caused raised mouth position to appear more normal for 3/4 views of novel faces, but less normal for front views. View-contingent adaptation did not occur for inverted faces, however (experiment 2). Dissociable aftereffects for different views of upright faces, but not for different views of inverted faces, suggest that neurons that code face view can also code other aspects of face shape.

1 Introduction

Face recognition is relatively robust to changes in face view (ie faces learned from one viewpoint can typically be easily recognised from novel views; eg Bruce et al 1987), although recognition of faces from novel views is slightly poorer than that for learned views (eg Liu and Chaudhuri 2002). An important issue for our understanding of the mechanisms and processes that underpin face perception is the extent to which robust face recognition across views reflects the use of view-invariant representations of faces versus multiple view-specific representations of faces (Biederman and Bar 1999; Tarr and Bülthoff 1995). Indeed, Jeffery et al (2006) have emphasised the importance of establishing whether neurons that code face view also code other aspects of face shape (see also Benton et al 2006; Fang et al 2007).

fMRI (Grill-Spector et al 1999), electrophysiological (Perrett et al 1985, 1991; Wang et al 1996), and behavioural evidence (Fang and He 2005) demonstrate that different neural populations are broadly tuned to respond optimally to different face views. For example, view-specific face-selective cells in the monkey inferotemporal cortex have been reported, in addition to view-invariant face-selective cells (Perrett et al 1985, 1991; Wang et al 1996). View-specific neural populations have also been observed in humans in the lateral occipital cortex (Grill-Spector et al 1999). Most recently, Fang and He (2005) demonstrated that adaptation to faces shown in 3/4 views affects perceptions of the head orientation of these faces, but does not affect perceptions of the orientation of other (ie non-face) objects. This latter finding suggests that neurons coding face view do not code stimulus view more generally (Fang and He 2005). While there is therefore compelling evidence for view-specific face coding, it is unclear whether neurons coding face view also code other aspects of face shape. Indeed, some models of face processing propose that neurons that code head or gaze direction do not necessarily code fixed aspects of faces, such as identity and other relatively invariant aspects of face shape (eg Haxby et al 2000; but see also Calder and Young 2005).

Several recent studies have used visual adaptation paradigms to investigate coding of face shape with regard to viewpoint (Benton et al 2006; Jeffery et al 2006; Jiang et al 2006, 2007). These studies have all demonstrated significant face aftereffects when adapting and test faces were shown in different views, but have also found that these aftereffects are weaker than when adapting and test faces were shown in the same view (ie there was only partial transfer of face aftereffects across views). Jiang et al (2006) demonstrated that adaptation to a given identity induces aftereffects for the anti-face of the adapting stimulus when adapting and test faces are both shown in the same viewpoint (see also Leopold et al 2001) and also when the adapting and test faces are shown in different viewpoints (see also Jiang et al 2007). Aftereffects in the latter condition were smaller than when adapting and test views were matched, however. Similarly, Jeffery et al (2006) demonstrated that adaptation to faces with either compressed or expanded feature spacing induced significant aftereffects when the adapting and test faces were both shown in the same viewpoint and also when the adapting and test faces were shown in different viewpoints. Furthermore, using the identity aftereffect, Benton et al (2006) also found substantially reduced aftereffects when adapting and test face views were dissimilar. Both Benton et al (2006) and Jeffery et al (2006) emphasised the significant reduction in the magnitude of aftereffects when adapting and test face views were incongruent (ie different) and interpreted this as evidence that neurons coding face view also code other aspects of face shape. By contrast, Jiang et al (2006) interpreted the partial transfer of face aftereffects across views as evidence that face-coding mechanisms at the locus of adaptation are relatively robust to changes in view.

In a further and more recent study, Fang et al (2007) also used adaptation to test for joint coding of face shape and face view. Adaptation to a face viewed from one side (eg 30° to the left of centre) causes the perceived orientation of front views of this face to be biased away from the adapting view (ie to the right; Fang and He 2005). Fang et al (2007) found that this effect of adaptation to face view in upright faces generalises to judgments of novel upright faces, but is attenuated when the adapting and test faces are highly physically dissimilar (eg are different sexes). Fang et al (2007) interpreted these findings as evidence for joint coding of face view and face shape. Importantly, Fang et al (2007) also found that adaptation to face view did not generalise to judgments of inverted faces, however, implicating face-selective neurons that respond more to upright than to inverted faces in the joint coding of face view and face shape. Thus, the extent to which studies of face aftereffects show that neurons coding face view also code aspects of face shape remains somewhat controversial, with some studies arguing for joint coding of face view and face shape (Benton et al 2006; Fang et al 2007; Jeffery et al 2006), while others argue for view-invariant representations of faces (Jiang et al 2006, 2007).

In light of the above, in experiment 1 we tested if it is possible to simultaneously induce face aftereffects in opposite directions for different views (3/4-left and front) of upright faces. Previous studies showing that face aftereffects can be simultaneously induced in opposite directions for upright male and upright female faces (Bestelmeyer et al, 2008; Little et al 2005); upright human and upright macaque faces (Little et al 2008); upright infant and upright adult faces (Little et al 2008); upright White and upright East Asian faces (Jaquet et al 2007; Little et al 2008); and upright and inverted faces (Rhodes et al 2004) have been interpreted as evidence that dissociable mechanisms code face shape for these different types of faces. Thus, if it is possible to simultaneously induce face aftereffects in opposite directions for different views of faces, this would be evidence that neurons coding face view also code other aspects of face shape.

While it is well established that inverting faces reduces the extent to which configural processing associated with face perception occurs (Maurer et al 2002), some studies have found that face aftereffects are unaffected by inverting the adapting and test stimuli (for a review of these studies see Yamashita et al 2005). For example, Leopold et al (2001) found no effect of inversion for identity aftereffects. Recently, however, Yasuda et al (2006) found that contingent adaptation was weaker for inverted faces than for upright faces and interpreted this finding as evidence that contingent face aftereffects reflect adaptation of mechanisms for processing upright faces rather than adaptation of mechanisms for processing visual stimuli in general. An inversion effect was also reported in a recent fMRI study of face aftereffects (Yovel and Kanwisher 2005). Consequently, we tested for view-contingent adaptation for inverted faces in experiment 2. View-contingent adaptation to mouth position for upright faces (experiment 1), but not inverted faces (experiment 2), would suggest that neurons that code orientation of upright faces, rather than stimulus view more generally, can also code other aspects of face shape. Indeed, Fang et al (2007) have previously interpreted effects of inversion on face aftereffects as evidence that mechanisms for coding face view, rather than mechanisms for coding stimulus view more generally, underpin joint coding of face shape and face view.

2 Experiment 1

2.1 *Methods*

2.1.1 *Stimuli.* A total of 10 female faces with neutral expressions were randomly chosen from the Karolinska directed emotional faces (KDEF) image set (Lundqvist and Litton 1998). Front and 3/4-left views of each individual were selected.

First, we manufactured stimuli for the adaptation phase of the experiment by making a version of each face image in which the mouth position had been raised and a version of each face image in which the mouth position had been lowered. Computer graphic methods (see Tiddeman et al 2001) were used to transform the mouth position by +100% (to raise the mouth position) or −100% (to lower the mouth position) of the difference in position between an original composite female face and a version of this composite in which the *x-y* coordinates defining mouth position had been shifted upwards. This method ensures that the magnitude of the change in mouth position in the lowered mouth and raised mouth versions are identical. Examples of face images used in the adaptation phase are shown in figure 1.

For use in the pre-adaptation and post-adaptation tests, versions of these images that had been manipulated more subtly in mouth position were manufactured (ie mouth position was transformed by $\pm 50\%$) with the same procedure that was used to vary mouth position among the adapting faces. In order to assess face perceptions in pre-adaptation and post-adaptation tests, previous studies of face aftereffects have also used more subtle manipulations than those that had been applied to the faces shown in the adaptation phases (eg Little et al 2005). Images to be used in the pre-adaptation and post-adaptation phases of the experiment were resized to 80% of the size of the adapting faces to control for possible effects of low-level adaptation (following Bestelmeyer et al 2008; Jeffery et al 2006; Leopold et al 2001).

2.1.2 *Procedure.* The experiment consisted of three phases. First, participants completed an initial pre-adaptation test to assess their baseline perceptions of the normality of face images with raised and lowered mouth positions in front and 3/4-left views. Second, participants viewed a slide show consisting of either 3/4-left views of faces with raised mouth position and front views of faces with lowered mouth position (condition 1) or of 3/4-left views of faces with lowered mouth position and front views of faces with raised mouth position (condition 2). Finally, participants repeated the pre-adaptation test to test for a change in perceptions of the normality of these images.

Figure 1. Examples of face images shown in the adaptation phase. The top row shows 3/4-left and front views with mouth position lowered by 100%. The bottom row shows 3/4-left and front views with mouth position raised by 100%.

For the pre-adaptation test, fifty-four participants (thirty-four female; mean age = 22.87 years, SD = 7.27 years) were shown 2 individuals in 2 different viewpoints (ie 4 pairs of faces in total). The 2 different viewpoints were 3/4-left view and front view. Each pair of images depicted the same individual from the same viewpoint. One image in each pair had a raised mouth position and one a lowered mouth position. Participants were instructed to choose which face looked more normal: whether it looked 'slightly more normal', 'somewhat more normal', 'more normal', or 'much more normal'. Pairs of images were presented on a computer screen (each image 300×400 pixels) in a random order, and the side of the screen on which any particular image appeared was also randomised.

Immediately after making these judgments, participants completed an adaptation phase where they viewed 32 faces for 3 s each (totalling 96 s). These face images were of the 8 individuals whose images were not used in the pre-adaptation test. Each of the 8 individuals was shown twice in 3/4-left view and twice in front view. As mentioned previously, adapting images were presented at 80% of the size of test images. For twenty-seven participants, the 3/4-left views were presented with raised mouth and the front views were presented with lowered mouth (condition 1). For the other twenty-seven participants, the 3/4-left views were presented with lowered mouth and the front views were presented with raised mouth (condition 2). Images were presented in a random order. Participants were instructed to watch the faces closely during the adaptation phase. Immediately after this adaptation phase, the participants completed a post-adaptation test that was identical to the pre-adaptation test. Following previous studies of contingent face aftereffects (Bestelmeyer et al 2008; Little et al 2005, 2008), the pre-adaptation and post-adaptation tests were self-paced.

Full colour images were shown in both the adaptation and the test phases.

2.1.3 *Initial processing of data.* Responses on the forced-choice normality judgment task were coded as perceived strength of normality for the manipulation that was seen in conjunction with the 3/4-left view during the adaptation phase by means of the following scale: 0, 1, 2, 3 = manipulation that was seen in conjunction with the front view during the adaptation phase was perceived as 'much more normal' (= 0), 'more normal' (= 1), 'somewhat more normal' (= 2), or 'slightly more normal' (= 3) than the manipulation that was seen in conjunction with the 3/4-left view during the adaptation phase. 4, 5, 6, 7 = manipulation that was seen in conjunction with the 3/4-left view during the adaptation phase was perceived as 'slightly more normal' (= 4), 'somewhat more normal' (= 5), 'more normal' (= 6), or 'much more normal' (= 7) than the manipulation that was seen in conjunction with the front view during the adaptation phase.

Thus, if, for example, the 3/4-left views were seen with raised mouth position during the adaptation phase and front views were seen with lowered mouth position (condition 1), then judgments would be coded on a 0 to 7 scale as normality of raised mouth (eg lowered mouth judged as 'much more normal' than raised mouth = 0; raised mouth judged as 'much more normal' than lowered mouth = 7). By contrast, if the 3/4-left views were seen with lowered mouth position during the adaptation phase and front views were seen with raised mouth position (condition 2), then judgments would be coded on a 0 to 7 scale as normality of lowered mouth (eg raised mouth judged as 'much more normal' than lowered mouth = 0; lowered mouth judged as 'much more normal' than raised mouth = 7).

The average perceived normality of the manipulation that was seen in conjunction with the 3/4-left view during the adaptation phase was calculated separately for 3/4-left and front views at the pre-adaptation and post-adaptation tests. Finally, the average score for each viewpoint at pre-test was subtracted from the average score for each viewpoint at post-test in order to calculate the magnitude and direction of change in the perceived normality of the manipulation that was seen in conjunction with the 3/4-left view. Thus, positive scores reflected an increase in the perceived normality of the manipulation that was seen in conjunction with 3/4-left views during the adaptation phase, which is equivalent to the decrease in the perceived normality of the manipulation that was seen in conjunction with front views. Negative scores reflected a decrease in the perceived normality of the manipulation that was seen in conjunction with 3/4-left views during the adaptation phase, which is equivalent to the increase in the perceived normality of the manipulation that was seen in conjunction with front views.

Baseline data from the pre-adaptation tests are given in table 1.

2.2 *Results*

The magnitude and direction of change in the perceived normality of the manipulation that was seen in conjunction with 3/4-left views during the adaptation phase between the pre-adaptation and post-adaptation tests for each viewpoint were analysed with a mixed design ANOVA [within-subject factor: test face view (3/4-left, front); between-subject factor: adaptation condition (mouth raised in 3/4-left view and mouth lowered in front view; mouth lowered in 3/4-left view and mouth raised in front view)]. This analysis revealed the predicted significant main effect of test face view ($F_{1,52} = 5.01$, $p = 0.03$), whereby the perceived normality of the face manipulation seen in conjunction with the 3/4-left views during the adaptation phase was increased for judgments of 3/4-left views of novel faces following adaptation (mean = 0.22, SEM = 0.19), but was decreased for judgments of front views of novel faces (mean = −0.24, SEM = 0.18). There was no main effect of adaptation condition ($F_{1,52} = 0.10$, $p = 0.76$) and no interaction between test face view and adaptation condition ($F_{1,52} = 2.32$, $p = 0.13$).

Table 1. Mean scores from pre-adaptation and post-adaptation tests in experiment 1. Scores are perceived normality (on a 0–7 scale, chance = 3.5) of the manipulation seen in conjunction with the 3/4-left view.

Adaptation condition	Test phase	Mean for front view (SEM)	Mean for 3/4-left view (SEM)
Condition 1 3/4-left views with raised mouth, front views with lowered mouth	Pre-adaptation	3.11 (0.20)	2.91 (0.21)
Condition 2 3/4-left views with lowered mouth, front views with raised mouth	Pre-adaptation	4.02 (0.16)	3.94 (0.22)
Condition 1 3/4-left views with raised mouth, front views with lowered mouth	Post-adaptation	3.00 (0.20)	2.94 (0.23)
Condition 2 3/4-left views with lowered mouth, front views with raised mouth	Post-adaptation	3.69 (0.29)	4.39 (0.27)

3 Experiment 2

3.1 *Methods*

The methods and procedure used to test for view-contingent adaptation for inverted faces in experiment 2 were identical to those used to test for view-contingent adaptation for upright faces in experiment 1, except that all face images used in experiment 2 (both adapting and test images) had been inverted. Inverted images of 3/4-left views were also mirror-reversed around their central vertical axis, so that the mouth was on the left side of the image (as was the case for the upright images in experiment 1).

Sixty-one participants (thirty-four female; mean age = 23.77 years, SD = 8.52 years) took part in experiment 2. None of these participants had taken part in experiment 1. Thirty participants were simultaneously adapted to 3/4-left views with raised mouth and front views with lowered mouth (condition 1) and thirty-one participants were simultaneously adapted to 3/4-left views with lowered mouth and front views with raised mouth (condition 2). As in experiment 1, all participants had been randomly allocated to either condition 1 or condition 2 after completing identical pre-adaptation tests.

3.2 *Results*

Responses were processed and analysed as in experiment 1. Baseline data from the pre-adaptation tests are given in table 2.

ANOVA [within-subject factor: test face view (3/4-left, front); between-subject factor: adaptation condition (mouth raised in 3/4-left view and mouth lowered in front view; mouth lowered in 3/4-left view and mouth raised in front view)] revealed no significant effect of test face view ($F_{1,59} = 0.20$, $p = 0.66$) or adaptation condition ($F_{1,59} = 3.31$, $p = 0.07$). There was also no significant interaction between test face view and adaptation condition ($F_{1,59} = 2.59$, $p = 0.11$). Note that, although the main effect of adaptation condition approached significance ($p = 0.07$), this does not imply view-contingent adaptation since the effect of face view (which was significant in experiment 1) was not significant.

Table 2. Mean scores from pre-adaptation and post-adaptation tests in experiment 2. Scores are perceived normality (on a 0–7 scale, chance = 3.5) of the manipulation seen in conjunction with the 3/4-left view.

Adaptation condition	Test phase	Mean for front view (SEM)	Mean for 3/4-left view (SEM)
Condition 1 3/4-left views with raised mouth, front views with lowered mouth	Pre-adaptation	3.20 (0.23)	3.40 (0.24)
Condition 2 3/4-left views with lowered mouth, front views with raised mouth	Pre-adaptation	3.55 (0.21)	3.35 (0.21)
Condition 1 3/4-left views with raised mouth, front views with lowered mouth	Post-adaptation	3.63 (0.22)	3.47 (0.18)
Condition 2 3/4-left views with lowered mouth, front views with raised mouth	Post-adaptation	3.00 (0.20)	3.45 (0.16)

4 Discussion

Our findings show that it is possible to simultaneously induce aftereffects in opposite directions for 3/4-left and front views of upright faces (experiment 1). For example, simultaneously adapting participants to 3/4-left views of upright faces with raised mouth and front views of upright faces with lowered mouth (ie condition 1) caused novel 3/4-left views of upright faces with raised mouth to appear more normal, but caused novel front views of upright faces with raised mouth to appear less normal. Equivalently, simultaneously adapting participants to 3/4-left views of upright faces with lowered mouth and front views of upright faces with raised mouth (ie condition 2) caused novel 3/4-left views of upright faces with lowered mouth to appear more normal, but caused novel front views of upright faces with lowered mouth to appear less normal. That we were able to simultaneously induce face aftereffects in opposite directions for front and 3/4-left views of upright faces supports Jeffery et al's (2006), and Benton et al's (2006) proposal that, at the locus of adaptation, some neurons coding face view also code face shape (see also Fang et al 2007). By contrast with our findings for view-contingent aftereffects for upright faces (experiment 1), view-contingent aftereffects did not occur for inverted faces (experiment 2).

While our findings for view-contingent aftereffects in experiment 1 demonstrate that it is possible to dissociate aftereffects for two different views of upright faces with a contingent adaptation paradigm, it is important to note that generalisation across views occurs when participants are adapted to only one view (Jeffery et al 2006; Jiang et al 2006). These latter findings show that transfer of aftereffects across views certainly can occur. Indeed, together with such partial transfer of face aftereffects (Jeffery et al 2006; Jiang et al 2006), our findings for opposite aftereffects for different views of upright faces (experiment 1) suggest that, at the locus of adaptation, some neural populations that code face shape respond optimally, but not exclusively, to certain face views. That view-contingent aftereffects did not occur for inverted faces (experiment 2) suggests that view-contingent face aftereffects for upright faces reflect adaptation of mechanisms for coding the orientation of upright faces, rather than mechanisms for coding stimulus view more generally, and support the proposal that contingent face aftereffects are disrupted by inversion (Yasuda et al 2006). That inversion affected view-contingent aftereffects is also consistent with Fang et al (2007), who found that inverting faces disrupted the effect of adaptation to face view on perceptions of the orientation of these faces. Both our own findings and those of Fang et al (2007) implicate neurons that code upright faces in the joint coding of face view and face shape. It is intriguing that while viewpoint aftereffects (Fang et al 2007) and view-contingent aftereffects (our experiments) appear to be affected by inversion, other face aftereffects, such as identity aftereffects, are not (Leopold et al 2001). Identifying the circumstances under which inversion effects do and do not emerge for face aftereffects may shed light on the different mechanisms underpinning different types of face aftereffects.

The view-contingent aftereffects observed in experiment 1 appear to be somewhat smaller than those observed in other studies of contingent face aftereffects in which very similar methods were used (eg Bestelmeyer et al 2008; Little et al 2005, 2008). This difference in the magnitude of contingent aftereffects may be a consequence of the 1-D manipulation (vertical position of mouth either raised or lowered) causing interference across face views that would have biased against the view-contingent results reported in experiment 1. Indeed, given findings for partial transfer of face aftereffects across views, one would not necessarily expect view-contingent aftereffects to be equivalent in magnitude to contingent aftereffects for other (social) categories of faces for which no transfer across category appears to occur (eg sex—Little et al 2005). Following many previous studies of contingent adaptation (eg Bestelmeyer et al 2008; Jeffery et al 2006; Little et al 2008), we assessed the magnitude of face aftereffects using normality judgments. Further research is needed to investigate whether the view-contingent aftereffects we observed for normality judgments of upright faces also occur for identity judgments of faces.

Although our findings suggest that view-specific coding of face shape for unfamiliar upright faces can occur, further research is required to investigate how representations of individual faces change with increasing familiarity (Haxby et al 2000; Jiang et al 2007) so that familar individuals can be easily recognised from different viewpoints (Maurer et al 2002). One possibility is that familiarity increases the ease with which information from view-specific representations of individual faces can be integrated to support view-invariant recognition (Jiang et al 2007).

Indeed, Jiang et al (2007) have recently demonstrated that increasing familiarity with individual faces can increase the extent to which face aftereffects transfer across different face views. While such findings suggest the emergence of view-invariant representations of faces as their familiarity increases, our findings for view-contingent aftereffects for upright faces, together with those of other studies (eg Benton et al 2006; Fang et al 2007), point to joint coding of view and shape for unfamiliar faces.

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