Broadly tuned, view-specific coding of face shape: Opposing figural aftereffects can be induced in different views ☆

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Abstract

Face aftereffects are sensitive to changes in viewpoint, suggesting view-specific face coding, yet are not entirely eliminated by changes in viewpoint, suggesting view-invariance. To determine whether broad view-tuning can account for these findings we measured the reduction of a figural face aftereffect induced in one view by concurrent adaptation to an opposite distortion in a second viewpoint, varying the angle between these views. To the degree that the same neural population codes both viewpoints, the opposing aftereffects should cancel. Cancellation increased monotonically as the angle between two adapting views decreased, consistent with broadly tuned, view-specific coding of face shape.
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1. Introduction

Our ability to recognize faces and objects across changes in viewpoint poses questions about the nature of the representations that support recognition. The degree to which the coding of faces and objects is view-invariant (e.g. Biederman & Bar, 1999; Biederman & Gerhardstein, 1995), view-specific (e.g. Hayward & Tarr, 1997; Tarr & Buelthoff, 1995) or a combination of both these kinds of coding (Hayward, 2003) is a central issue in face and object perception. Neurophysiological studies of monkeys have found evidence of both view-sensitive and view-invariant neural coding of faces (De Souza, Eifuku, Tamura, Nishijo, & Ono, 2005; Perrett et al., 1985; Perrett et al., 1991; Rolls, Baylis, Hasselmo, & Nalwa, 1989; Wang, Tanaka, & Tanifuji, 1996). Similarly, brain imaging studies have reported both

view-sensitivity and view-insensitivity in human face-sensitive brain regions (Chen, Kao, & Tyler, 2007; Fang, Murray, & He, 2007; Grill-Spector et al., 1999; Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005a, Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005b).

Face aftereffects have provided a new tool for investigating the representations underlying human perception of faces across different views (Leopold, O'Toole, Vetter, & Blanz, 2001; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & MacLin, 1999). Recent studies indicate that a variety of face aftereffects are view-sensitive (Benton, Jennings, & Chatting, 2006; Fang & He, 2005; Jeffery, Rhodes, & Busey, 2006; Jiang, Blanz, & O'Toole, 2006). For example, Jeffery et al. (2006) found that a figural face aftereffect (contracted or expanded distortion) induced in one viewpoint (3/4 left view) showed only limited transfer to other views (front, 3/4 right). Similarly, Jiang et al. (2006) and Benton et al. (2006) found that face identity aftereffects show only limited transfer across views. These results suggest that human neural coding of faces is view-specific.

While the sensitivity of these aftereffects to viewpoint suggests view-specific coding of faces, the small but signif-

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icant amount of transfer of aftereffects across views requires explanation. Benton et al. (2006) suggest the transfer may reflect the contribution of view-invariant populations. Jeffery et al. (2006) instead characterize the limited transfer as consistent with the broad view-tuning observed for view-specific face neurons in monkeys (De Souza et al., 2005; Eifuku, De Souza, Tamura, Nishijo, & Ono, 2004; Perrett, Hietanen, Oram, & Benson, 1992; Perrett et al., 1991; Perrett et al., 1985). When view-tuning is broad, the neural response is optimal to a particular view (view-specificity) but views close to the optimal view also elicit a response. The response decreases as the view increasingly diverges from the optimal view. Perrett et al. (1992, 1991) found that the average tuning width of the view-specific neurons in monkey STS was 60°, with responses halved for views rotated 60° from the optimal view. Their data also suggest that the tuning curves for different views overlap, with the overlap decreasing as views differ by a greater degree of rotation. If humans are similar to monkeys then some transfer of aftereffects could be expected when adapt and test views differ by less than 60°, as do the views used by Jeffery et al. (2006) and Jiang et al. (2006).

Consistent with broad view-tuning, Fang and He (2005) found that the size of their face view aftereffect reduced substantially when the difference in angle between adapt and test views was increased from 30° to 60°. Benton et al. (2006) have also shown that the face identity aftereffect decreases as the angle between adapt and test views increases. Most strikingly, Fang and colleagues

(2007) have shown that fMRI adaptation in human face sensitive brain regions (FFA and STS) diminished in a monotonic fashion as the test view was rotated away from the adapt view. If this relationship between the size of adaptation effects and the angular disparity between adapt and test view reflects the tuning properties of face neurons, rather than some contribution from view-invariant neurons, adaptation effects should be entirely eliminated when there is sufficient rotational difference between adapt and test views.

We investigated the view-specificity and the breadth of view-tuning for faces by measuring whether a figural, or face shape, aftereffect could be made contingent on viewpoint. Contingent aftereffects can be induced by adapting to paired visual attributes, as in the McCollough effect in which a color aftereffect is made contingent on grating orientation (McCollough, 1965). Similarly, figural face aftereffects can be made contingent on stimulus attributes such as contrast polarity and spatial frequency (Yamashita, Hardy, De Valois, & Webster, 2005), orientation (Rhodes et al., 2004), gender (Jaquet & Rhodes, in press; Little, DeBruine, & Jones, 2005) and race (Jaquet, Rhodes, & Hayward, in press-a; Jaquet, Rhodes, & Hayward, in press-b). However, contingent aftereffects can only be induced when distinct pools of neurons are adapted, otherwise the opposing aftereffects cancel (Rhodes et al., 2004; Yamashita et al., 2005). So, if two face viewpoints are coded by the same neurons, concurrently adapting to opposing distortions for the same duration should result
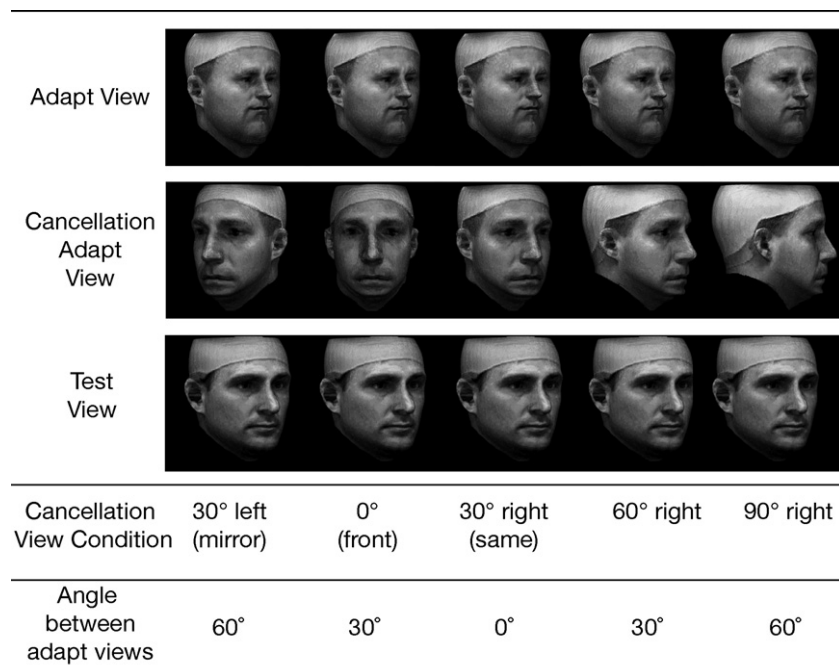

Cancellation View Condition	30° left (mirror)	0° (front)	30° right (same)	60° right	90° right
Angle between adapt views	60°	30°	0°	30°	60°

Fig. 1. An example of the adapting combinations. The top row shows an adapting face, which is always a contracted 30° right face. The second row shows faces in the cancellation views, all expanded but presented at views differing in 30° increments. The third row shows an undistorted face in the test view, which is always 30° right. Test faces are presented at varying distortion levels (see Fig. 2). The cancellation view condition name and the angular differences between the adapting views in each condition are shown below. The 30° right view is marked "same", to clearly indicate that both adapting views are the same in this condition. The 30° left view is marked "mirror", since mirror images of the 30° right views were used in this condition (see Method).

in no aftereffect. However, when distinct pools of neurons code two views it should be possible to induce aftereffects that are contingent on viewpoint, e.g. a contracted aftereffect in a right profile view and an expanded aftereffect in a front view. The size of these view-contingent aftereffects should not differ from those induced by separately adapting to a single distortion in each view. The degree to which the tuning curves for any two views overlap should therefore be reflected by the reduction in the size of the aftereffect (cancellation), relative to single view (simple) adaptation.

We measured the amount by which a 3D contracted figural aftereffect (Jeffery et al., 2006) induced in one view was reduced (cancelled) by concurrently adapting to an expanded distortion in a second viewpoint, to assess the view-specificity of face coding. We measured the reduction in a 'contracted' figural aftereffect for one face view, 30° right, due to adaptation to an opposing 'expanded' distortion in viewpoints to the left or right of this view. Participants adapted to contracted faces presented at a 30° right view, while concurrently adapting to expanded faces presented in either the same view or at a view rotated either side of this view, in 30° increments (cancellation views). The cancellation views were 90° right, 60° right, 30° right, 0°, 30° left and were varied between participants (see Fig. 1). An additional group of participants adapted only to contracted faces, presented at the 30° right view ("no cancellation view" condition). We measured the aftereffect by assessing each participant's perceptions of the "normality" of 30° right test faces (different identities to the adapting faces) that vary in their level of distortion, ranging from very contracted to very expanded. Participants rated the "normality" of the test faces both before and after adaptation. The size of the aftereffect was measured by taking the difference between the "most normal" distortion before and after adaptation. Cancellation of the aftereffect by the opposing distortion was measured by comparing the size of the aftereffect for each cancellation view condition to that found for the 'no cancellation view' condition. A significant reduction indicated that the aftereffect had been attenuated by the opposing aftereffect in the second view. A monotonic decrease in the size of aftereffect as the two adapt views converge would be consistent with broadly tuned, view-specific coding of face shape. Distinct coding of views, predicted for views separated by sufficient angular difference, would be suggested by an absence of cancellation. Test images were half the size of adapt images to rule out low-level retinotopic adaptation as the source of the effects.

2. Method

2.1. Participants

One hundred and fifty one (37 male) University of Western Australia undergraduate psychology students participated for course credit or payment. All participants had lived in either Australia or another Western country for at least 10 years.

2.2. Stimuli

Stimuli were constructed as described in Jeffery et al. (2006). Adapting and test faces were derived from 3D laser scan models (see Busey & Zaki, 2004 for details). To remove some surface artifacts, we morphed together pairs of faces to create 16 male Caucasian faces. To make the distortions the combined average of all the control points delineating the internal facial features in both x and y dimensions was calculated to estimate the center of each image. Each control point was then warped toward (contracted) or away from (expanded) the center in percentage increments of the distance between each point and the center. The warping was applied to the texture and structural (depth) maps, to emulate a three-dimensional warp, and then rendered using POV-Ray (Persistence of Vision Raytracer, 2003–2004). The distortions affected the internal face features but not the outer contour of the face or head shape. Test faces comprised 8 male faces at eleven distortion levels, ranging from 25% contracted (−25) to 25% expanded (−25, −15, −10, −6, −2, 0, 2, 6, 10, 15, 25, see Fig. 2). All were rotated 30° to the right.

Eight male faces, different individuals to the test faces, were used to create the adapting stimuli. Expanded 20% (+20) and contracted 25% (−25) versions were made of each individual at five different views: 0° (front) view, 30° right, 60° right, 90° right (right profile) and 30° left (a mirror image of the 30° right view, created by flipping the 30° right images around the vertical axis in Photoshop). See Fig. 1. Pilot testing showed that concurrently adapting to +20 and −25 distortions (randomly interleaved) in 30° right faces resulted in no net aftereffect in 30° right test faces, indicating that the strength of these distortion levels was approximately equal.

Faces were presented in colour on a black background on a 17 inch CRT monitor. Participants used a chin rest to maintain a viewing distance of 47 cm. Adapting faces were presented in a black rectangle measuring 15.8 cm wide by 15.0 cm high that subtended a visual angle of 19.1° × 18.1°. The height and width of the faces varied, within the rectangle, as a function of identity and angle of rotation, with a mean width of 11.4 cm ($SD = 1.0$) and a mean height of 13.1 cm ($SD = 0.5$), subtending a mean visual angle of 13.8° × 15.9°. Similarly, test faces were presented in a rectangle measuring 8.0 cm wide by 7.5 cm high that subtended a visual angle of 9.7° × 9.1°. The test faces had a mean width of 5.4 cm ($SD = 0.1$) and a mean height of 6.5 cm ($SD = 0.2$), subtending a mean visual angle of 6.6° × 7.9°.

2.3. Procedure

Participants were first exposed to the range of variation in "normality" in the stimulus set by viewing a sample of 32 faces presented at 30° right orientation, spanning the distortion levels. They were then asked to rate "how normal" each of the 88 test faces, 8 faces for each of the 11 distortion levels, looked, using a ten point scale ranging from 1-unusual to 10-normal. Each test face was shown for one second, surrounded by a box, with the instruction, "rate". The rating scale was then displayed and remained on the screen until the participant responded. Faces were presented in random order.

After the faces had been rated, 1 min of adaptation followed. Participants were randomly assigned to one of six Cancellation View conditions; "30° right (same view)", "60° right", "90° right", "0° (front)", "30° left (mirror)" or "no cancellation view (none)" (see Fig. 1). For all conditions except the "no cancellation view" condition, eight adapting faces (four at each view) were shown repeatedly, in random order, for 750 ms each, with a
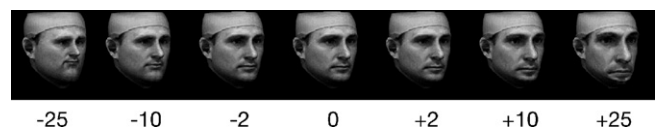

Fig. 2. Seven of the eleven distortion levels for a 30° right test face. Distortion level is shown below the figure.

200 ms interstimulus interval between each face. Four of these faces were contracted and presented at the 30° view and the other four were expanded faces presented at the cancellation view. In the "no cancellation view" condition, the presentation of adapting stimuli was identical to the other conditions but overall adaptation time was halved so that the duration of adaptation was equivalent to the amount of contracted adaptation in the other conditions. Participants saw four contracted 30° right faces, shown repeatedly, in random order, for 750 ms each, with a 200 ms interstimulus interval between each face, for a total of 30 s. The identities of the four contracted and four expanded adapting faces were varied between participants.

The 88 test faces were rated again for normality after adaptation. In all conditions, other than the "no cancellation view" condition, each test face was preceded by a six second top up adaptation period (cf., Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003) in which each of the eight adapting faces was presented once for 750 ms, in random order. In the "no cancellation view" condition, test faces were preceded by a 3 s top up period, equivalent to the amount of contracted top up in the other conditions. Four faces were presented once for 750 ms, in random order. Trials were divided into four equal blocks. The session took between 20 and 30 min to complete.

3. Results

The mean "normality" rating for each distortion level was calculated both before and after adaptation, for each participant. The "most normal" distortion before and after adaptation was measured by fitting third order polynomials to the means, plotted as a function of distortion level, and calculating the curve maxima, following Jeffery et al. (2006). The typical pattern of normality ratings is well described by these functions, as illustrated by fitted curves for two participants shown in Fig. 3. Typically, adaptation has a greater impact on the perceived normality of test faces featuring the adapting distortion than the opposite distortion, which is captured by a shift in the curve maximum (see Fig. 3a). This measure is also robust to overall increases (or decreases) in normal ratings that may not reflect adaptation induced changes (e.g. all test faces are rated as more normal on second viewing due to familiarity) (see Fig. 3b). Seven participants (3 male) were excluded from further analyses due to erratic response profiles with poor fits ($R^2 < .7$). This left 24 participants in each of the "0° (front)", "30° right (same)", "60° right" and "no cancellation view (none)" conditions, 25 participants in the "30° left (mirror)" condition and 23 in the "90° right" condition.

The size of the aftereffect was measured by calculating the shift in "most normal" distortion as a result of adaptation. After adapting to contracted faces the "most normal" distortion shifts to a more contracted distortion level (Jeffery et al., 2006; Rhodes et al., 2003). For each participant the most normal distortion (curve maximum) after adaptation was subtracted from the most normal distortion before adaptation. Two participants showed extreme shifts (deviating from both the overall mean and their respective condition means by more than three standard deviations) and were removed from further analysis.[1] The mean shifts for each condition are shown in Fig. 4.
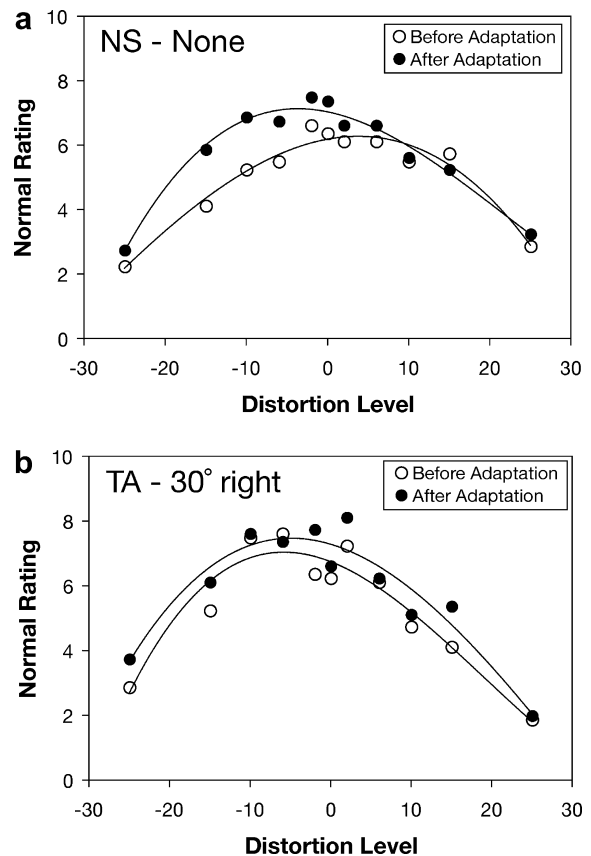

Fig. 3. Mean normal ratings, before and after adaptation, showing fitted 3rd order polynomial curves for two typical participants, (a) NS – "No Cancellation View" condition, Most normal distortion *before* adaptation = 3.79, $R^2 = 0.958$, Most normal distortion *after* adaptation = −3.64 $R^2 = 0.975$, (b) TA – "30° right (same)" condition, Most normal distortion *before* adaptation = −5.96, $R^2 = 0.920$, Most normal distortion *after* adaptation = −4.87, $R^2 = 0.914$.

The pattern of means shows that concurrently adapting to an opposing distortion generally decreased the size of the aftereffect, relative to when there was no opposing distortion ("no cancellation view (none)" condition, horizontal line on Fig. 4). However, the amount by which the aftereffect was reduced varied, depending on the rotational difference between the two adapting views. The largest reduction was observed when adapting to opposing distortions presented in the same view (30° right). Indeed, the size of this aftereffect did not differ from zero, $t(22) = 1.76$, $p = .092$, suggesting the opposing aftereffects cancelled out completely. Substantial but not complete cancellation was observed when adapting to an opposing distortion in views rotated 30° either side of the test view ("0° (front)" and "60° right" conditions). The size of the aftereffect was least affected by the opposing distortion when the adapting views diverged by 60° ("30° left (mirror)" and "90° right" conditions). This was most striking for the "90° right" condition, in which the aftereffect was almost the same size as when there was no opposing adaptation. Overall, the aftereffects show a monotonic decrease in size as the cancellation view is rotated closer to the adapt view.

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[1] One participant was removed from the "30° left (mirror)" condition and one from the "30° right (same)" condition.
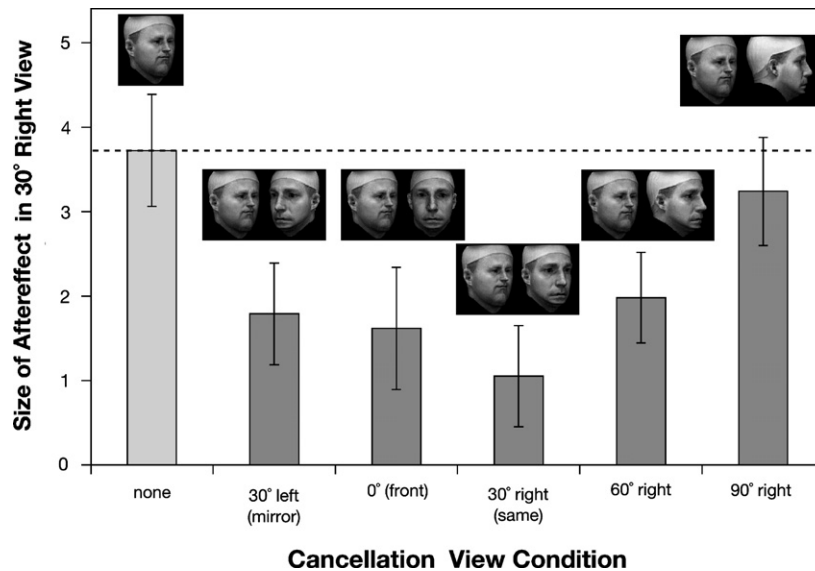
Fig. 4. Mean shift in the most normal distortion for 30° right test faces as a function of cancellation view condition. Error bars show one standard error either side of mean. The dashed horizontal line marks the mean for the "no cancellation view" (none) condition. Sample faces from both the adapting views are shown above each mean. The cancellation condition in which opposing distortions were presented in the same view is marked "same" and the cancellation condition in which the cancellation view was the mirror of the adapt view is marked "mirror".

A one way ANOVA confirmed a significant effect of adapting condition, $F(5, 136) = 2.64$, $p < .05$. To formally assess the reduction, or cancellation, of the aftereffect by the opposing distortion we compared the size of the aftereffect in the "no cancellation view (none)" condition to that obtained in each of the other conditions. The aftereffect was significantly reduced for all but one ("90° right") cancellation view, (one-tailed planned comparisons – all t's > 1.96, all p's < .05). The aftereffect for "90° right" was not significantly less than when there was no opposing distortion ("no cancellation view (none)"), $t(136) = 0.542$, $p = .30$.

Planned comparisons (one-tailed) were used to compare the size of the aftereffects among the conditions in which there was opposing adaptation to assess the decrease in the size of the aftereffect as the cancellation view was rotated closer to the test view. Examining the cancellation views to the *right* of the test view, the difference between the 90° right and 60° right conditions was marginally significant $t(136) = 1.41$, $p = .08$ and the difference between 90° right and 30° right (same) conditions was significant $t(136) = 2.42$, $p = .009$, but the difference between the 60° right and 30° right (same) view was not significant $t(136) = 1.04$, $p = .15$. For cancellation views to *left* of the test view, none of the pair-wise decreases in the size of the aftereffects were significant, all t's < 1, all p's > .2.

To more clearly illustrate the view-tuning suggested by the cancellation effects, Fig. 5 re-plots the data, transformed to percentage cancellation as a function of rotational difference between adapt views. The mean aftereffect for each condition was subtracted from the mean aftereffect for the "no cancellation view (none)" and then divided by the mean aftereffect for the "no cancellation
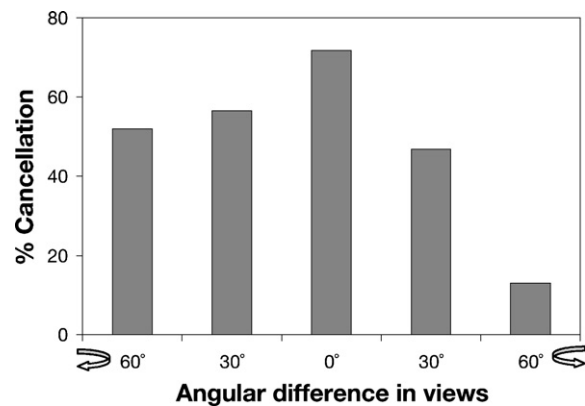

Fig. 5. The percent cancellation, relative to the "no cancellation view (none)" condition, as a function of the angular difference between the adapting views and the direction of rotation (cancellation view rotated to the left or right of the adapt view, as indicated by the arrows).

view (none)" and converted to a percentage. Peak cancellation, of 71%, occurred when adapting to opposing distortions in the same views with a decline in the amount of cancellation as the angle between the adapt views increases (see Fig. 5).

4. Discussion

The figural face aftereffect could be made contingent on face view when the views were sufficiently far apart but not when they were close to each other. Cancellation of opposing aftereffects was affected by the size of the angular difference between the adapting views. Opposing distortions presented in the same view resulted in complete cancellation (no net aftereffect) and significant cancellation also

occurred when cancellation views were 30° to the left or right of the adapt/test view. Significant recovery from cancellation was found when the adapting views differed by 60° (90° right and 30° right) and the size of this aftereffect was not significantly reduced by adapting to the opposing distortion in the 90° right view.[2] These results suggest distinct coding of face shape for 30° and 90° views and provide further evidence that face shape is coded in a view-specific manner. This view-specificity cannot be attributed to low-level, retinotopic coding, given the differing size of the adapt and test images, and suggests view-specificity in higher-level coding of faces, consistent with Fang et al.'s (2007) finding of face view fMRI adaptation in face-selective but not nonface-selective human visual brain regions.

The monotonic decrease in the size of the aftereffects as the adapting views with opposing distortions converge is consistent with broad view-tuning curves in which the neural response increases as the observed view approaches the neurons' preferred view (Fang et al., 2007; Perrett et al., 1991). For views differing by less than 60°, opposing figural face aftereffects significantly cancelled each other. These data are consistent with previous research suggesting broad view-tuning, of approximately 60°, for monkey face neurons (Perrett et al., 1991). The limited transfer of aftereffects across viewpoints differing by less than 60° observed in previous studies (Jeffery et al., 2006; Jiang et al., 2006) can be explained by the tuning breadth of view-specific neurons alone, without any contribution by view-invariant neurons.

While the amount of cancellation generally increased as angle between the adapting views decreased, significant cancellation was observed for the mirror view condition but not the 90° right view condition, even though the angle between the adapt views was the same in both conditions (60°). This may be due, in part, to the reduction in feature information available in the 90° view e.g. only one eye visible in the 90°. Lack of information about features and the horizontal relationship between them, e.g. distance between the eyes, could weaken the cancellation affect. However the distortions substantially affected the vertical relations between features and this information was available in profile views. Further, significant cancellation occurred for the 60° right condition, in which limited feature information was available e.g. only one eye visible (see Fig. 1). So the availability of differential feature information cannot entirely account for the lack of cancellation effects in the 90° right view condition, relative to the 30° left view. Another possibility is that the significant cancellation seen for the 30° left view may reflect the special relationship that mirror views have with each other. Mirror views of faces are recognised better than predicted by the difference in orientation from the original view (Troje & Bülthoff, 1996; Troje & Bülthoff, 1998; Vetter, Poggio, & Bülthoff, 1994) and both face-selective and object-selective cells have been found that respond well to both a view and its mirror view (De Souza et al., 2005; Logothetis, Pauls, & Poggio, 1995; Perrett et al., 1991). The cancellation effect we observed for 30° left views could therefore reflect common coding for mirror views. Common coding of mirror views is also suggested by our previous finding (Jeffery et al., 2006) that a figural aftereffect showed significant transfer across a 90° view change for mirror views (45° left and 45° right).

Our finding of view-specific but broadly tuned coding of face shape is consistent with hierarchical models of object-recognition in which the formation of view-specific representations are a necessary stage in achieving view-invariant perception (Riesenhuber & Poggio, 1999; Riesenhuber & Poggio, 2000; Tarr, 1999). Some view-based models propose that only a limited number of key views need be coded to achieve view-invariant recognition (e.g. Bülthoff & Edelman, 1992; Perrett, Oram, & Ashbridge, 1998; Vetter et al., 1994). Early monkey data also suggested that the majority of view-specific face neurons were tuned to a limited number of views, primarily the front view and profiles (Perrett et al., 1992; Perrett et al., 1991). It was conjectured that the broad view-tuning of these cells meant that face shape could be coded by neurons tuned only to these views (Perrett et al., 1992; Logothetis et al., 1995; Perrett et al., 1991). However, more recently clusters of neurons coding oblique face views (22.5° and 45°) have been found (De Souza et al., 2005; Eifuku et al., 2004; Wang et al., 1996). Our data are consistent with broadly tuned coding of a limited number of viewpoints in humans and suggest that there are neural populations that are tuned to profile views and further that these populations are distinct from those used to code 30° views. Our 30° view could be coded by neurons broadly tuned to a front view or to an oblique view, with the proviso that the tuning curve does not overlap with that for a profile view. Given the evidence that facial identity is coded relative to a norm (Leopold, Bondar, & Giese, 2006; Leopold et al., 2001; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Rhodes & Jeffery, 2006), view-specific norms, possibly for a limited number of key views, may be used to code facial identity.

The present study used unfamiliar faces to assess view-specificity in the coding of face shape. Recognition of familiar faces is more robust to changes in viewpoint than recognition of unfamiliar faces (Burton, Bruce, & Hancock, 1999; Hancock, Bruce, & Burton, 2000) suggesting that familiarity may influence the view-invariance of the underlying representations. Neural view-sensitivity in humans varies with the familiarity of the face (Eger, Schweinberger, Dolan, & Henson, 2005). However, the FFA shows view-sensitivity for both familiar and unfamiliar faces, with view-invariant familiarity effects found only in

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[2] The similar size of the aftereffects in the "no cancellation view" and "90° right" conditions also suggests that the difference in the adaptation period for the no cancellation view versus cancellation conditions did not impact the size of the aftereffect significantly. That is, continuous exposure to only one distortion for 30 s (no cancellation view) does not necessarily result in a larger aftereffect than 30 s exposure to one distortion accumulated over 60 s exposure to alternating distortions (all the cancellation conditions).

less face-specific brain areas (Pourtois et al., 2005a, 2005b). Pourtois et al. (2005b) suggest that familiarity may influence later stages of processing in which more abstract representations of identity are formed. Similarly Jiang, Blanz, and O'Toole (2007) have shown that increasing familiarity with a face results in greater transfer of identity aftereffects across views and suggest that this may reflect the strengthening of connections among view-specific populations.

In conclusion, cancellation of an aftereffect in one view by an opposing aftereffect in another view generally decreased as the angular difference between the adapt views increased, suggesting broadly tuned, view-specific coding of face shape.

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