

Global face distortion aftereffects tap face-specific and shape-generic processes

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Face aftereffects are commonly used to investigate the mechanisms underlying face processing, based on the assumption that they tap processes involved specifically with face-level coding (e.g., face space). However, face aftereffects could potentially arise from many levels of the visual system, and recent research has shown that one figural aftereffect (eye height) has both face-level and shape-generic components. Another very widely used figural manipulation is global face distortion. Here we investigate whether a global face distortion aftereffect (vertical compression) transfers to nonface stimuli, and if so, to what extent. Arguing for a mid- or high-level shape-generic component to our face aftereffect, we found significant face-to-object transfer even after minimizing retinotopic components. Arguing for an additional face-specific component, we found, first, that face-to-face aftereffects were significantly larger than face-to-object aftereffects and second, that this occurred only when the adaptor face was whole and intact rather than scrambled. Our results argue that global face distortion aftereffects are a useful tool for investigating face-space but that, to do so unambiguously, requires developing methods to minimize or account for the shape-generic contribution.

Keywords: face perception, face aftereffects, figural aftereffects, face specific, shape generic

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Introduction

Face aftereffects are commonly used in face recognition literature as a tool to investigate the mechanisms and processes underlying face perception. A widespread assumption underlying their use is that the aftereffects arise from processes which are specifically involved with face perception, rather than those associated with coding of simple form parameters or generic representations of object shape. This assumption is revealed, for example, in the common idea that face aftereffect results are informative about the nature of coding in a high-level face space (Valentine, 1991) in which individual face structure is coded as a deviation from the average face (e.g., Leopold, O'Toole, Vetter, & Blanz, 2001; Nishimura, Doyle, Humphreys, & Behrmann, 2010; Palermo, Rivolta, Wilson, & Jeffery, 2011; Rhodes & Jeffery, 2006; Robbins, McKone, & Edwards, 2007; Susilo, McKone, & Edwards, 2010b).

However, prolonged viewing of a face will adapt cells throughout the visual form processing hierarchy. Therefore, logically, face aftereffects could potentially arise from various stages of visual processing (Figure 1), not just face-level processes, an issue raised by several previous authors (e.g., Dennett, McKone, Edwards, & Susilo, *in press*; O'Leary & McMahon, 1991; Rhodes & Leopold, 2011; Susilo, McKone, & Edwards, 2010a; Watson & Clifford, 2003; Webster & MacLeod, 2011; Webster & MacLin, 1999; Yamashita, Hardy, De Valois, & Webster, 2005; Zhao & Chubb, 2001).

Generally, researchers minimize the contributions of the retinotopically-mapped lower-level visual areas (Figure 1) by changing the size and/or retinal position of stimuli between adapt and test. The fact that face aftereffects normally survive changes in size and/or retinal position (Afraz & Cavanagh, 2009; Zhao & Chubb, 2001) argues for an origin of the surviving component in higher-level visual areas (cf. tilt aftereffects, which are strongly position-specific; Bell &

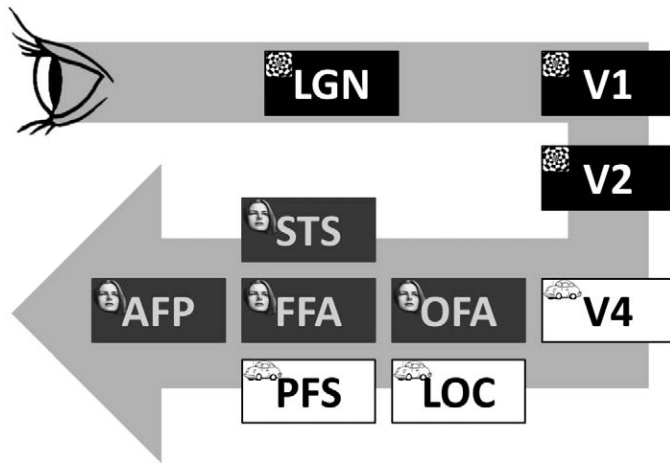


Figure 1. Areas that could potentially contribute to face distortion aftereffects. *Early visual areas* (checkerboard pattern) are retinotopically mapped and thus will contribute only where the size and/or retinal position of stimuli are held constant between adapt and test conditions. With size/position change, later areas in the visual form processing hierarchy that may potentially contribute to face aftereffects include: areas that show *face selectivity* (indicated with a face); plus other *shape-generic* areas (indicated with a car), namely intermediate- or high-level areas that are not selective for faces and respond to simple forms, object parts, or whole complex objects. It is also possible there are additional (not shown) contributions of general *memory areas* (e.g., hippocampal regions), given evidence that face aftereffects can sometimes be very long lasting (e.g., a week in Carbon & Ditye, 2011; although note that some aspects of memory could also perhaps arise within face-selective areas, similar to long-term repetition priming within face areas, e.g., the FFA, Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005).

Kingdom, 2009). However, this does not necessarily mean that face aftereffects primarily reflect the activity of face-specific processes. Rather, any post-retinotopic visual areas might potentially contribute. If contributions from nonface processing are noticeable in magnitude, or if the contribution of face-level processes is small enough, then this could complicate interpretation of aftereffect results and potentially limit their usefulness as a tool for investigating high-level coding.

In the post-retinotopic cortex, multiple regions have properties that imply they could plausibly contribute to face aftereffects. Such areas (Figure 1) include (a) *intermediate-level form processing areas* such as V4 (Ghose & Ts’O, 1997; Müller, Wilke, & Leopold, 2009; Pasupathy & Connor, 2002); (b) *object-generic processing areas* such as the lateral occipital complex (LOC; Grill-Spector, Kourtzi, & Kanwisher, 2001; Malach et al., 1995) and the posterior fusiform (PFS; Grill-Spector, 2009; Kim, Biederman, Lescroart, & Hayworth, 2009; Panis, Wagemans, & Op de Beeck, 2011; Pyles & Grossman, 2009; Taylor & Downing, 2011); and (c) several *areas which show face selectivity*¹, such

as the occipital face area (OFA; Fox, Moon, Iaria, & Barton, 2009; Kovács, Cziraki, Vidnyánszky, Schweinberger, & Greenlee, 2008; Pitcher, Walsh, Yovel, & Duchaine, 2007), the fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997; Kovács et al., 2008), the superior temporal sulcus (STS; Fox et al., 2009; Rolls, 2007; Tsao, Moeller, & Freiwald, 2008), and the anterior face patch (AFP; Rajimehr, Young, & Tootell, 2009; Tsao et al., 2008). Behaviorally, it is established that post-retinotopic aftereffects can occur for basic shapes (e.g., line curvature, Gibson, 1933; elongation of ellipses, Regan & Hamstra, 1992; elongation of T-shapes, Susilo et al., 2010a), suggesting potential for intermediate or object-general contributions to face aftereffects, given that these types of basic shapes are present within natural faces. Therefore, to be able to draw direct conclusions for face-level coding from a set of face aftereffect results, it would be necessary to know that the aftereffect derives entirely or almost so from *face-specific processes* (i.e., c) and very little or not at all from *shape-generic processes* (i.e., a and/or b).

Further complicating matters, there are several different types of face aftereffects, and these might potentially vary in the degree to which they tap face-specific processes. Examples include face identity aftereffects (Leopold et al., 2001; Rhodes & Jeffery, 2006), in which adaptation to one face (e.g., Ted) biases perception of an average face toward the hypothetical opposite face in face-space (i.e., anti-Ted) and various types of face figural aftereffects (Rhodes et al., 2004; Webster & MacLin, 1999), in which adaptation to faces consistently distorted in one direction (e.g., expanded; or eyes shifted-up) causes an undistorted face to be perceived as distorted in the opposite direction (e.g., contracted; or eyes shifted-down). For most face aftereffects, there has been little systematic investigation into the relative contributions of face-specific versus shape-generic processes.

For the identity aftereffect, there have been no studies testing the extent of any shape-generic contribution, but there is at least evidence of a face-level component. Specifically, the identity aftereffect is approximately 40% smaller for inverted faces than for upright faces (Rhodes, Evangelista, & Jeffery, 2009). There is also an association between the upright identity aftereffect and face recognition ability in developmental prosopagnosia (Palermo et al., 2011). And identity aftereffects are larger between opposite pairs in face-space (Ted and anti-Ted) than non-opposite pairs (Ted and anti-Jim) that are equally perceptual dissimilar (Rhodes & Jeffery, 2006). This indicates a face-level contribution: Anti-Ted is the true opposite of Ted only in a high-level space that codes whole-face structure (and not in other possible spaces that code general form attributes, e.g., convexity/concavity in V4; Müller et al., 2009).

Turning to figural aftereffects, previous studies have examined only one type, namely the eye-height aftereffect. Results imply this aftereffect has both face-specific and shape-generic components. Arguing for some face-level component, the aftereffect is 40% smaller for inverted faces than for upright faces (Susilo et al., 2010a), and also individual differences in upright aftereffect magnitude correlate positively with face, but not object, recognition ability in the normal population (Dennett et al., *in press*). Further, Susilo et al. (2010a) investigated transfer of aftereffects between faces and T-shapes, which captured the basic shape change of the eye-height manipulation (i.e., up and down movement of the horizontal bar formed by the eyes in the T-shaped region of eyes-nose-mouth). For inverted faces, the face-to-T (adapt-to-test) aftereffect was 100% of the face-to-face aftereffect (implying the inverted eye-height aftereffect was purely shape-generic with no face-level component). For upright stimuli, however, the face-to-T transfer was only 45% of the face-to-face eye-height aftereffect, indicating that (a) 55% of the upright aftereffect magnitude had a face-specific origin and (b) there was also a substantial (45%) shape-generic component.

Importantly, the finding that the face eye-height aftereffect is approximately half face-specific and half shape-generic does not necessarily mean that all types of figural face aftereffects would have a significant face-level component. Here, we provide the first investigation of the most commonly used type of figural

distortion, namely *global face distortion*. There are several variations (Figure 2), which include radial expansion/contraction of the face (e.g., Burkhardt et al., 2010; Jaquet, Rhodes, & Hayward, 2008; Palermo et al., 2011; Rhodes et al., 2004; Susilo et al., 2011), horizontal/vertical compression/stretching of the middle segment of the face (e.g., Watson & Clifford, 2003; Webster & MacLin, 1999; Zhao & Chubb, 2001), and horizontal/vertical compression/stretching of the entire face (e.g., Hole, 2011; O’Leary & McMahon, 1991).

Unlike face identity or eye height, global shape distortions can be applied to practically any class of object and are therefore potentially the least intrinsic to faces of all of the face aftereffects. That is, if different types of face aftereffects do vary in terms of the relative contributions of face-specific and shape-generic processes, then global face distortion aftereffects might be expected to have the smallest face-level contributions. Indeed, a possible finding of a weak face-level component is suggested by evidence that developmental prosopagnosics do not show impairment in aftereffects when the manipulation is a global distortion (radial expansion/contraction; Palermo et al., 2011). Thus, by exploring a global distortion manipulation in the present article, our results should establish a lower bound for the contribution of face-specific mechanisms to face aftereffects. If we find a significant face-specific contribution for even a manipulation which has nothing intrinsically face-like about it, this would suggest that all other shape aftereffects for faces also have some meaningful face-level contribution.

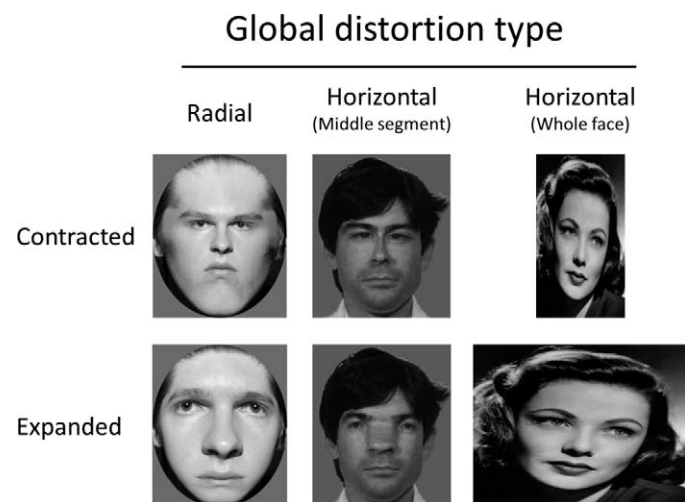


Figure 2. Variations of global face distortions commonly used in previous studies. Radial expansion/contraction as used by Rhodes et al. (2004); middle segment compression/stretching as used by Webster and MacLin (1999; images reproduced with permission from Watson & Clifford, 2003); and whole-face compression/stretching as used by Hole (2011) and O’Leary and McMahon (1991; original image taken from: http://commons.wikimedia.org/wiki/Gene_Tierney).

General design of our studies

We investigated the relative contributions of face-specific and shape-generic processes to global face distortion aftereffects by testing the extent to which these aftereffects transfer to nonface objects. The logic of all adaptation transfer studies (e.g., Fang & He, 2005; Jeffery, Rhodes, & Busey, 2006; McCollough, 1965; Regan & Hamstra, 1992; Susilo et al., 2010a) is that an aftereffect which transfers from an adaptor of one condition to a test stimulus of another condition reflects the activity of neural mechanisms which are common to both. In the present context, this corresponds to measuring the extent to which a face adaptor is adapting only neural mechanisms specific to faces (*face-specific component*, measured as the aftereffect for *adapt-face-test-face* minus the aftereffect for *adapt-face-test-object*) and the extent to which it is adapting neural mechanisms shared by faces and other objects (i.e., *shape generic component*, measured by the difference between the *adapt-face-test-object aftereffect* and zero).

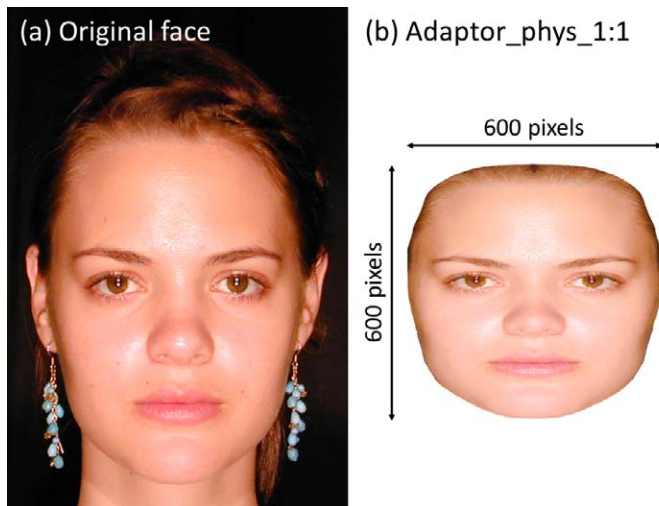


Figure 3. Making of the adaptor used in [Experiment 1](#). Starting from (a) an original photograph of a natural face, we (b) removed the hair and vertically compressed the face region to make the adaptor with physically 1:1 external contour.

Our adaptation experiments used a vertically compressed face as the adaptor (see [Figure 3](#)). The experiments then tested transfer of adaptation to four conditions ([Figure 4](#)) varying in similarity to the adaptor face: a face of the same identity as the adaptor shown in the original aperture style (outer contour tracking the face edge, *face_same*); a different-identity

face in a circular aperture (*face_diff*); a clock face, which has the same circular aperture and complex internal elements but different elements and structure from a human face (*clock*); and a plain circle with no internal elements (*circle*)². Based on the direction of the distortion of the adaptor face (i.e., vertically compressed), an aftereffect would correspond to test stimuli appearing distorted in the opposite direction (i.e., vertically expanded).

If our vertically compressed adaptor elicited aftereffects for test faces but not for nonface test stimuli, then this would argue that these aftereffects originate entirely from face-specific mechanisms. If equal-sized aftereffects are observed for both face and nonface test stimuli, then this would argue for an entirely shape-generic origin of the aftereffects. If the adaptor elicits significant aftereffects for nonface test stimuli and the aftereffects for faces are larger than those for nonface test stimuli, this would argue that global face distortion aftereffects originate partially in face-level processes and partially in shape-generic processes.

We chose vertical compression as our global manipulation because it allowed us to test aftereffect transfer to even very simple test shapes (i.e., the circle); other global manipulations such as radial expansion/contraction can be applied only to more complex objects that contain internal structure. However, at the same time, we wished to assess aftereffects arising from distortion of the face region, rather than from distortion of the external contour of the stimulus,

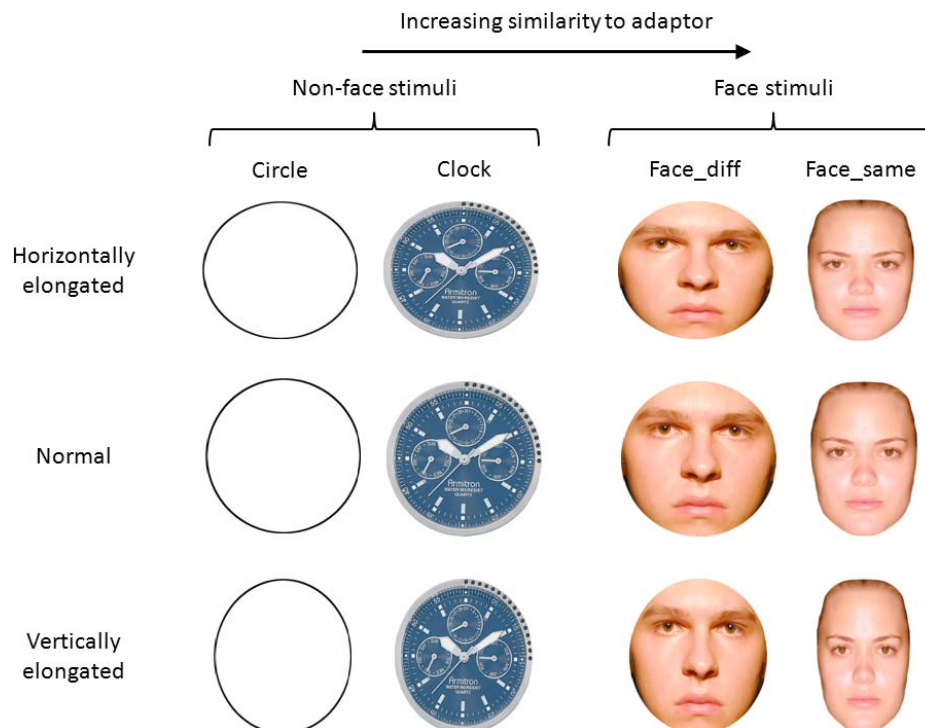


Figure 4. Test stimuli for which transfer of adaptation was measured in [Experiments 1](#) and [4](#).

elongation of which is already known to produce opposite-direction aftereffects that transfer to different shapes (e.g., adapting to a horizontally elongated circle causes a square to look vertically elongated; Regan & Hamstra, 1992). This was because most previous studies which have used global aftereffects maintained a consistent external contour for adaptor and test stimuli (e.g., see Figure 2a and 2b), meaning that external contour aftereffects did not contribute to the perceived face aftereffects.

The structure of our paper is as follows. Experiments 1 and 4 are the adaptation experiments which we used to investigate our central theoretical question concerning the degree to which global face distortion aftereffects tap face-level and shape-generic processes. Experiments 2 and 3 assessed participants' subjective percept of the outer contours of the adaptors used in Experiments 1 and 4.

Experiment 1: Transfer of aftereffects with physically 1:1 adaptor

In Experiment 1, we tested the aftereffect magnitude for our test stimuli (face_same, face_diff, clock, circle) following adaptation to our adaptor face compressed vertically such that the aspect ratio of the outer contour was physically 1:1 (Figure 3b). The experiment used separate pre- and postadaptation phases, with a two minute adaptation phase in between and brief top-up adaptors in the postadaptation phase (Figure 5). Several methods were used to avoid low-level retinotopic contributions to the aftereffects: There was a size change between adaptor and test stimuli, participants were able to move their head freely and were instructed to move their eyes around the face rather than fixate during the two minute adaptor phase, and during postadaptation the top-up adaptors and test stimuli were presented in different screen positions.

Method

Participants

Six students of the Australian National University (two female) completed two 45-minute sessions, separated by at least 24 hours. All were either Caucasian ($n = 5$) or had very high Caucasian exposure (one Caucasian parent and raised in Australia, $n = 1$). All were experienced psychometric observers. One was the first author (HWD). All except HWD were naïve to the purpose of the study and received \$10. All experiments reported in this paper were approved by the Human

Research Ethics Committee of the Australian National University, and all participants gave informed consent.

Apparatus

All experiments reported in this paper were presented on an eMac computer with a 40-cm CRT screen at 1152×864 resolution using PsyScope X software (Cohen, MacWhinney, Flatt, & Provost, 1993). All stimuli were viewed at approximately 60 cm (without a chinrest).

Stimuli

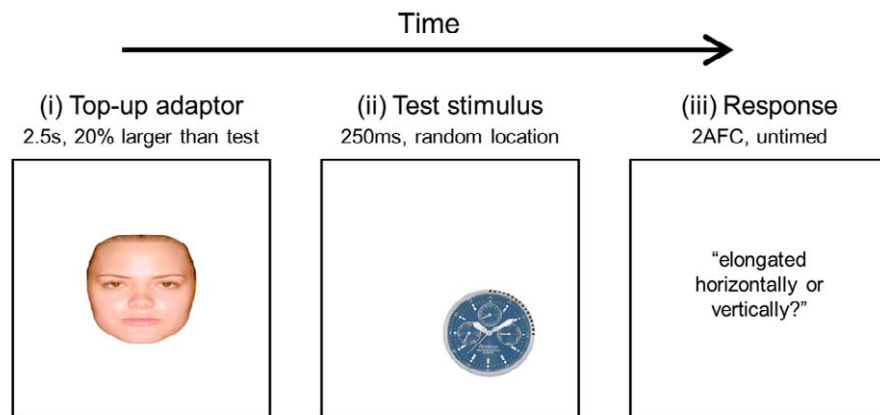
The adaptor (adaptor_phys_1:1; see Figure 3b) was made from a natural color photograph of a young adult female in front view with a neutral expression (Figure 3a). The photograph had had the hair cropped out and was then distorted by vertical compression so that the outer contour had a 1:1 aspect ratio. Its dimensions were 600×600 pixels (visual angle $16.1^\circ \times 16.1^\circ$).

The test stimuli were as shown in Figure 4: the same-identity female face, a different-identity male face in circular aperture, a clock face, and a circle. Each was made up in 15 evenly-spaced levels of distortion (*stimulus level*) with the undistorted stimulus at the center of each continuum. The step size between stimulus levels was equal in size for all four stimulus classes, namely an eight pixel change in one dimension. This step size was chosen to be approximately twice the smallest difference in elongation ratio shown to be discriminable by humans (for ellipses and rectangles; Regan & Hamstra, 1992). For the face_same stimulus, the undistorted dimensions were 450×652 pixels (visual angle $12.1^\circ \times 17.4^\circ$), and the far ends of this continuum had dimensions as follows: 394×652 pixels (maximum vertical elongation; visual angle $10.6^\circ \times 17.4^\circ$) and 450×596 pixels (maximum horizontal elongation; visual angle $12.1^\circ \times 16.0^\circ$). Dimensions of the undistorted circle, clock, and face_diff stimuli were 500×500 pixels (visual angle $13.4^\circ \times 13.4^\circ$), and the far ends of these continua had dimensions as follows: 444×500 pixels (maximum vertical elongation; visual angle $11.9^\circ \times 13.4^\circ$) and 500×444 pixels (maximum horizontal elongation; visual angle $13.4^\circ \times 11.9^\circ$).

Procedure for Session 1

The baseline phase presented test stimuli without adaptation. Test stimuli were presented in random order, with items from the four different classes of test stimuli interleaved. The baseline phase comprised 300 trials (four stimulus classes, each with 15 distortion levels and five presentations of each combination of these conditions). The procedure on each trial was:

(a) Post-adaptation trial with non-face test stimulus



(b) Post-adaptation trial with face test stimulus

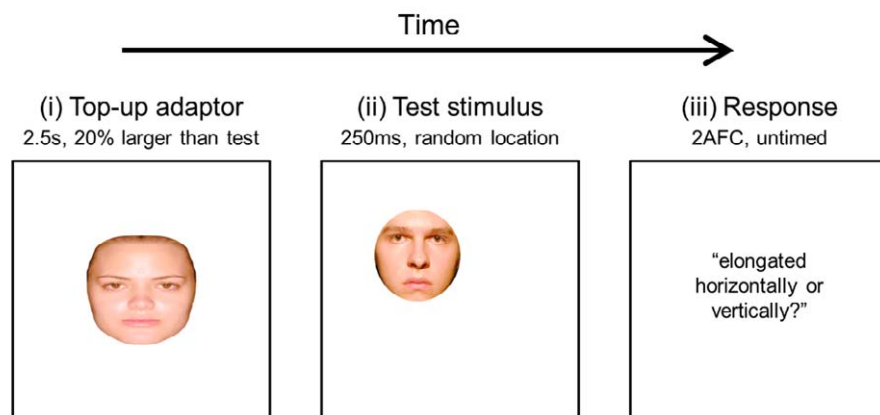


Figure 5. Procedure of the adaptation task (Experiments 1 and 4), showing trials from the postadaptation phase including top-up adaptors before each test item. For Experiment 1, the adaptor was always the intact face adaptor with physically 1:1 aspect ratio of external contour (adaptor_phys_1:1).

fixation cross (500 ms), test stimulus (250 ms), interstimulus interval (ISI) (100 ms), untimed two alternative forced-choice (2AFC) response (“Did that image appear to be elongated vertically or horizontally?”), ISI (250 ms). The test item appeared randomly in one of four locations on the screen, each centered 9.5° from the screen’s center. This baseline phase was preceded by 30 practice trials using the same procedure.

In the adaptation phase, participants viewed the adaptor face for two seconds. They were instructed to keep looking at the adaptor for the duration of the phase without fixating on any one point on the adaptor, but rather by scanning the face.

The postadaptation phase was the same as the baseline phase, except that each test stimulus was preceded by a 2.5 s top-up adaptor, presented centrally,

and a 250 ms ISI. Participants were able to move their eyes to the adaptor and test face locations.

Procedure for Session 2

This was identical to Session 1, except that a practice phase was not used for Session 2. Data were combined across sessions.

Curve fitting and extraction of aftereffect scores

Sigmoid-type psychometric functions³ were fitted to each participant’s pre- and postadaptation data using MATLAB in order to determine the stimulus level which observers perceived as being undistorted (i.e., the point of subjective equality, PSE, at which the stimulus

was chosen to be vertically elongated on 50% of occasions) before and after adaptation. Aftereffect magnitudes were calculated as the shift in this stimulus perceived as normal—that is, the difference between pre- and postadaptation PSEs ($PSE_{\text{post}} - PSE_{\text{pre}}$). A positive aftereffect score reflects a shift in the direction predicted if an aftereffect is present (i.e., PSE shifts toward the adaptor, corresponding to the original normal stimulus being perceived as more vertically elongated than before adaptation).

Fit quality was evaluated at the stage of preliminary data screening and used to exclude any individual aftereffect scores for which the component PSEs had low reliability. Reliability of each individual's aftereffect scores is dependent on the average of the R^2 values associated with the pre- and postadaptation fits. Aftereffect scores were calculated for each session separately, given previous evidence that baseline PSE varies across session (Susilo et al., 2010b; presumably reflecting exposure to slightly different faces in the natural environment in the period before each session). Prior to exclusion, there were 48 curves to fit (six participants, who each completed two sessions, with each session containing four test stimulus conditions). Shift scores associated with poor average fits ($R^2 < .5$ for average of pre- and post- within a session) were excluded from subsequent analyses (four instances). After these exclusions, the quality of the average fits was high (44 remaining shift scores, median $R^2 = .929$, minimum = .568, maximum = .990).

In cases where a participant had good fits in both sessions, the shift scores from the two sessions were averaged. In cases where a participant had a good fit for a certain condition only in one session, then the single-session shift score was used. In one instance, a participant's data for both sessions of the face_same

condition produced poor fits and therefore no shift score was available. See Table 1 for the final participant numbers in each condition.

Both here and in Experiment 4, some of our theoretical questions required combining two stimulus conditions together (e.g., the two face conditions). For subjects with a missing score on one of the conditions (due to bad fit), we used as the average measure their shift score from the one contributing condition for which they had an acceptable fit. We took this approach, rather than simply deleting the participant from all conditions, to maximize statistical power (e.g., it allowed all participants to be included in other tests).

Results

Figure 6 shows aftereffect scores averaged across the six participants (baseline and adapted PSEs are shown in Table 1). Our first theoretical question was whether there was a shape-generic component to the face aftereffect. A shape-generic component predicts significant face-to-object transfer; that is, that there should be a significant aftereffect observed for the circle and/or clock test stimuli (noting that the adaptor was always a face). This was observed. Aftereffects were significantly greater than zero for both classes of object stimuli: circle, $t(5) = 11.72$, $p < 0.001$, $d = 4.79$, clock, $t(5) = 7.55$, $p < 0.001$, $d = 3.08$ (and also for both types of test faces, $ps < 0.01$).

Our second theoretical question was whether—in addition to the shape generic component—there was also a face-specific component. A face-specific component predicts that the face-to-face aftereffect should be larger than the face-to-object aftereffect. This was observed. Considering the two face conditions first,

| | Circle | | Clock | | Face_diff | | Face_same | |
|--|--------|------|-------|------|-----------|------|-----------|-------|
| | Pre | Post | Pre | Post | Pre | Post | Pre | Post |
| Experiment 1: Adaptor_phys_1:1 | | | | | | | | |
| <i>M</i> | 7.29 | 8.99 | 7.54 | 9.38 | 4.91 | 8.27 | 9.77 | 15.78 |
| <i>SD</i> | 1.26 | 1.16 | 1.08 | .83 | 1.18 | 1.72 | 1.65 | 2.66 |
| <i>n</i> | 6 | 6 | 6 | 6 | 6 | 6 | 5 | 5 |
| Experiment 4: Adaptor_perc_1:1_intact | | | | | | | | |
| <i>M</i> | 5.72 | 7.48 | 5.84 | 6.96 | 3.76 | 8.23 | 7.92 | 14.24 |
| <i>SD</i> | 1.87 | 1.19 | 2.49 | 2.08 | 2.72 | 2.23 | 2.29 | 6.64 |
| <i>n</i> | 16 | 16 | 17 | 17 | 17 | 17 | 16 | 16 |
| Experiment 4: Adaptor_perc_1:1_scrambled | | | | | | | | |
| <i>M</i> | 5.95 | 7.00 | 4.50 | 5.82 | 3.55 | 6.14 | 9.44 | 11.70 |
| <i>SD</i> | 1.06 | .84 | 1.61 | .43 | 2.35 | 2.89 | 2.58 | 2.81 |
| <i>n</i> | 13 | 13 | 12 | 12 | 13 | 13 | 11 | 11 |

Table 1. PSEs (stimulus level perceived as most normal) pre- and postadaptation, averaged across participants in all adaptation experiments. Stimulus Level 1 was the most vertically elongated, and Stimulus Level 15 was the most horizontally elongated. Each unit of change in stimulus level was equal to eight pixels change on one dimension.

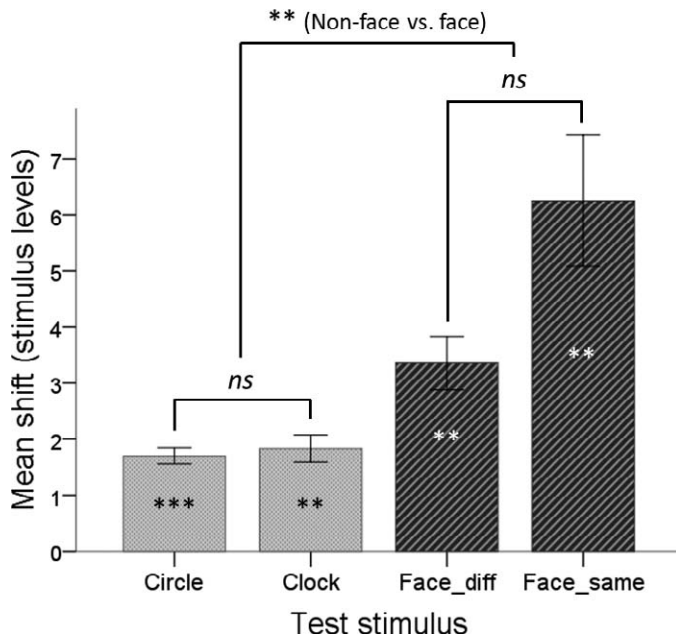


Figure 6. Aftereffect scores (change in stimulus level perceived as most normal) for Experiment 1, following adaptation to a vertically compressed face with physically 1:1 external contour. Results show significant transfer of aftereffects to nonface test stimuli (circle, clock; significance levels inside bars indicate comparison of aftereffect magnitude to zero) and significantly larger face-to-face aftereffects (face_diff + face_same) than face-to-object aftereffects (circle + clock). Error bars show ± 1 SEM; these are appropriate for the comparison of each bar to zero (note that the within-subjects error term for comparing face_same with face_diff was larger, accounting for the nonsignificant difference between these two conditions). *** $p < 0.001$; ** $p < 0.01$; ns $p > 0.05$.

there was a trend towards the aftereffect being larger for the same-identity face than for the different-identity face, but the difference between the two face conditions was not significant, $t(4) = 1.77$, $p = 0.15$, $d = .79$. The two classes of nonface stimuli also did not differ (circle vs. clock, $t(5) < 1$, $d = .19$). Therefore, we compared the average of the two face conditions to the average of the two nonface conditions. The aftereffect for the faces was significantly greater than for the objects, $t(5) = 4.29$, $p = 0.008$, $d = 1.75$.

We also compared just the different-identity face (i.e., face-to-different-face transfer) to the average of the objects. The former aftereffect was significantly larger, $t(5) = 3.68$, $p = 0.01$, $d = 1.50$. This argues for a component to the aftereffect that arises from face-level coding that generalizes across identity and sex. (It also shows that the differences in aftereffect magnitude we observed between face and nonface objects cannot be attributed purely to the circular outer contour of the nonface objects acting as a point of reference because face_diff also had a circular outer contour.)

Discussion

Our results show transfer of global face distortion aftereffects to nonface stimuli, consistent with the predictions of a shape-generic component to the aftereffects. Our results also show significantly smaller aftereffects for nonface test stimuli than for face test stimuli, consistent with the predictions of a significant face-specific component—despite the fact that manipulations involving distortions of global form could potentially be applied to almost any class of object, and therefore might not necessarily have been expected to tap face-level processes. Thus, our results suggest the presence of both shape-generic and face-specific components.

At this stage, however, there are two caveats on the suggestion that our results might reflect the presence of both shape-generic and face-specific aftereffect components. The first concerns the conclusion that there is a face-level component. Our finding that aftereffects were larger for test faces than for test objects is consistent with this interpretation, but also has an alternative possible explanation. This is that, even when the face is different in identity to the adaptor, there is still a greater physical difference between face adaptor and nonface test stimuli than between face adaptor and face test stimuli (i.e., in the component shapes, curves, and local attributes). It could be that the greater adaptation in face than object conditions reflects midlevel stages of the visual system responding to this greater shared similarity, rather than reflecting an origin in face-level coding. Experiment 4 addresses this issue by adding a scrambled face adaptor (containing the same midlevel shape distortion as the intact face, but without the face structure).

The second concerns the conclusion that there is a shape-generic component to the aftereffect that derives from adaptation to the distortion of the internal (face) region of the stimulus. To be confident that the significant face-to-object transfer derives from this source, we would need to be certain that the aftereffect could not be arising from an aftereffect to the external contour of the adaptor: if the latter were the case, the fact that the adaptor was a face (rather than containing any other internal shape) would be irrelevant, and our significant face-to-object transfer would in fact be contour-to-object or contour-to-contour transfer. In the present experiment, we aimed to avoid contour-based transfer by giving the adaptor a physically 1:1 ratio of external contour. This method is the correct one if it is the physical aspect ratio of the stimulus which drives elongation-of-contour aftereffects. However, there is also a possibility that perceived contour elongation could produce aftereffects.⁴ This is potentially relevant to our study because previous research has shown that vertically stretching or compressing the internal regions of a face inside an ellipse can affect the

perceived shape of the outer contour of the ellipse (Lee & Freire, 1999). The findings of Lee and Freire would suggest that, because our internal face region was vertically compressed, our physically 1:1 adaptor might have been perceived as having a horizontally distorted outer contour. This is of concern because the outer contour would then be (perceptually) distorted in the same direction as the face, thus potentially producing the same direction of aftereffect as we observed (i.e., circles and clocks appearing more vertically elongated after adaptation). To address this issue, we begin [Experiment 2](#) by testing whether or not the outer contour of the [Experiment 1](#) adaptor was actually perceived as having a 1:1 aspect ratio (i.e., matching its physical aspect ratio of 1:1).

Experiment 2: Percept of outer contour of the physically 1:1 adaptor

[Experiment 2](#) aimed to assess whether the adaptor used in the first experiment (adaptor_phys_1:1) was perceived as having a non-1:1 aspect ratio of external contour. To do so, we asked observers to compare our adaptor face with a series of face silhouettes which varied in aspect ratio of the contour. These silhouettes—with no internal structure—would not induce any illusion similar to that reported by Lee and Freire (1999). We should therefore expect the silhouette outer contours to be perceived veridically. If adaptor_phys_1:1 was perceived veridically (i.e., as having a 1:1 aspect ratio), we should expect participants to match it to a silhouette with a 1:1 aspect ratio. However, if the outer contour of adaptor_phys_1:1 was being misperceived (e.g., as horizontally elongated), then we should expect participants to match it with an elongated silhouette.

Method

Participants

Seven students of the Australian National University (ANU) (four female) completed the five minute experiment. Four were East Asian and three were Caucasian. (Note there were no race differences in results.) Three were experienced psychometric observers, including the first author (HWD). All except HWD were naïve as to the purposes of the experiment, and two (including HWD) had also participated in [Experiment 1](#). The experiment took only five minutes per participant, and so was included in sessions testing other studies not reported here, for which participants received course credit or payment.

Stimuli

Stimuli were adaptor_phys_1:1 (as used in [Experiment 1](#) except resized to 400×400 pixels, $10.7^\circ \times 10.7^\circ$) and seven face silhouettes which varied in evenly-spaced increments from 395 horizontal \times 405 vertical pixels (aspect ratio = .98:1, vertically elongated, $10.6^\circ \times 10.9^\circ$) to 425×375 pixels (1.13:1, horizontally elongated, $11.4^\circ \times 10.1^\circ$, see [Figure 7a](#)). We tested more silhouettes with aspect ratios larger than 1:1 than smaller because both the Lee and Freire (1999) results and pilot testing suggested the adaptor from [Experiment 1](#) would be perceived as having a horizontally elongated contour.

Procedure

On each trial, adaptor_phys_1:1 was presented simultaneously with one of the seven face silhouettes until there was a response. For each of these stimulus pairs, the two stimuli were positioned obliquely from one another (see [Figure 7b](#)) so that direct comparisons of height and width were not possible. Participants responded to the question, “Compared to the outline of the face, does the outline of the silhouette appear to be elongated vertically or horizontally?” ISI to the next trial was 250 ms. There were 70 trials (10 trials per silhouette stimulus level), presented in random order.


Curve fitting

Sigmoid-type psychometric functions were fitted to the data for each participant, plotting the proportion of times each test silhouette was perceived as more horizontally elongated than adaptor_phys_1:1 as a function of silhouette physical aspect ratio. The PSE was the silhouette which the participant perceived as perceptually matching the outer contour of adaptor_phys_1:1. The R^2 values associated with the fits were high (median = .983, minimum = .962, maximum = .996).

Results

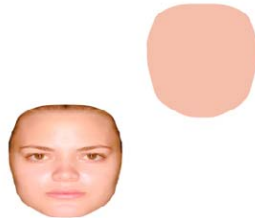
[Figure 7d](#) shows the mean psychometric function (i.e., averaged across participants), illustrating that the silhouette stimulus perceived as matching adaptor_phys_1:1 (i.e., producing 50% “silhouette more horizontal than adaptor” responses) was not 1:1 in aspect ratio, but instead horizontally elongated (415×385 pixels, corresponding to a horizontal:vertical aspect ratio of 1.08:1). There was little variation in the PSE value across participants ($SD = .01$). The difference between the perceived dimensions of the adaptor outer contour ($M = 1.08$) and its physical dimensions (1.00) was highly

(a) Sample test silhouettes from Experiments Two and Three

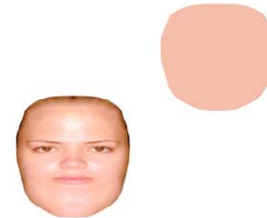


| | | | | | | | | | |
|---------------------|-----|-----|-----|-----|------|------|------|------|------|
| Width (pixels): | 385 | 390 | 395 | 400 | 405 | 410 | 415 | 420 | 425 |
| Height (pixels): | 415 | 410 | 405 | 400 | 395 | 390 | 385 | 380 | 375 |
| Aspect ratio (W/H): | .93 | .95 | .98 | 1 | 1.03 | 1.05 | 1.08 | 1.11 | 1.13 |

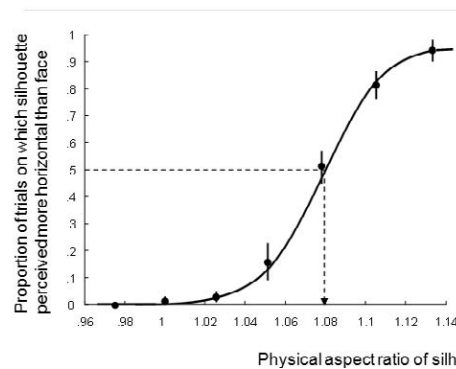
(b) Experiment Two screenshot



(c) Experiment Three screenshot



(d) Experiment Two results (Adaptor_phys_1:1)



(e) Experiment Three results (Adaptor_perc_1:1)

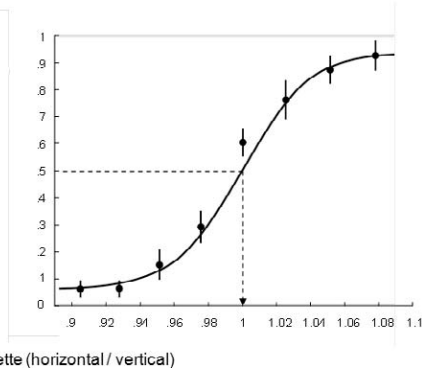


Figure 7. Experiments 2 and 3 tested participants' percept of the outer contours of adaptor_phys_1:1 and adaptor_perc_1:1, respectively. Participants compared each adaptor to a series of test silhouettes (a), each time indicating whether they thought that the outer contour of the silhouette looked elongated vertically or horizontally in comparison to the outer contour of the face adaptor. Stimuli were positioned obliquely from one another (b, c) so that direct comparisons of height and width were not possible. Results for Experiments 2 (d) and 3 (e) plot a psychometric curve averaged across participants and show that adaptor_phys_1:1 was perceived as having an external contour aspect ratio of 1.08:1 (horizontal:vertical) and adaptor_perc_1:1 as having a 1:1 external contour. Notes: Error bars are ± 1 SEM.

significant, $t(6) = 15.92$, $p < 0.001$, $d = 6.02$ (one-sample two-tailed t test comparing the PSE to 1.00).

Discussion

Our results show that despite the outer contour of the adaptor used in Experiment 1 having a physically 1:1 aspect ratio, participants actually misperceived the outer contour as being horizontally elongated (consistent with the direction predicted from the Lee and Freire illusion). Given that the perceived direction of contour elongation is horizontal (i.e., in the same direction as the elongation

of the face region itself), we cannot rule out the possibility that the aftereffects for nonface stimuli which we observed in Experiment 1 may have arisen from the adaptation to the percept of a horizontally elongated outer contour, as opposed to showing a genuine shape-generic contribution to global face distortion aftereffects. Therefore, we needed to test whether aftereffects for nonface stimuli would still be observed when we used a face adaptor with a perceptually 1:1 outer contour. To do so, we created a new adaptor stimulus which pilot testing suggested was perceived as having an outer contour with 1:1 aspect ratio, a result confirmed formally in Experiment 3.

Experiment 3: Development of perceptually 1:1 adaptor

Our new face adaptor stimulus (`adaptor_perc_1:1`; Figure 8a) had an external contour with a physical aspect ratio of 1:1.08 (horizontal:vertical). A further point to note about this adaptor is that we made the internal face region more vertically compressed than in the original adaptor (see Figure 8 vs. Figure 3). The reason for this was to maximize the size of aftereffects in the final experiment and thus provide the most opportunity to observe differences in aftereffect magnitude between conditions.

Experiment 3 provided empirical confirmation that the outer contour was perceived as 1:1.

Method

Nine students of the ANU (five female, eight Caucasian, one East Asian) participated. These included the first author (HWD), plus eight new naïve participants who also participated in Experiment 4 during the same session.

The procedure for Experiment 3 was identical to Experiment 2 on all except two points. First, the old adaptor face (`adaptor_phys_1:1`) was replaced with the new adaptor (`adaptor_perc_1:1`) and second, the range of test values (i.e., aspect ratios) of the silhouettes was adjusted (to suit the new adaptor) based on pilot testing. The R^2 values for the curve fits were high (across the nine participants, median = .952, minimum = .578, maximum = .998).

Results

Results (Figure 7e) confirmed that the new 1:1.08 adaptor perceptually matched the 1:1 silhouette. That is, the silhouette chosen as best matching the face contour had a mean aspect ratio of 1.00:1 (mean PSE = 1.00), with very high agreement across participants ($SD = .02$).

Experiment 4: Transfer of aftereffects with perceptually 1:1 adaptor

Regarding testing for a shape-generic component of our vertical compression aftereffect, Experiment 2 showed that participants perceived the outer contour of `adaptor_phys_1:1` as being horizontally elongated. It

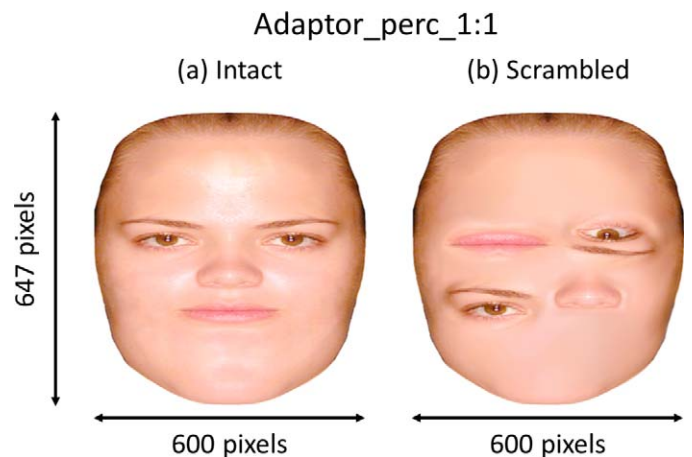


Figure 8. Adaptor stimuli used in Experiment 4. Adaptors had a vertically compressed face region and an outer contour that is perceptually 1:1 and physically slightly vertically elongated (i.e., 1:1.08 horizontal:vertical). (a) The intact version was the stimulus used in Experiment 3. (b) The scrambled version has the internal face features compressed by the same amount as the intact version.

is not known whether aspect ratio aftereffects are driven primarily by the physical or perceived aspect ratio, but it is possible that the aftereffects for nonface test stimuli we observed in Experiment 1 may have been due to the fact that participants perceived the outer contour of `adaptor_phys_1:1` as horizontally elongated. Therefore, in Experiment 4, we tested whether significant aftereffects would still be observed for nonface objects—thus indicating the presence of a shape-generic component—when the outer contour of the adaptor face was perceived as having a 1:1 aspect ratio (i.e., `adaptor_perc_1:1`, Figure 8a).

Regarding testing for a face-specific component, we also added a scrambled face version of the adaptor (Figure 8b). This was identical to the intact version, except that the internal features of the face (eyes, mouth, and nose) were rearranged, breaking the first-order configuration of the face. In Experiment 1, the apparent evidence for a face-specific component (i.e., face-to-face aftereffect greater than face-to-object) might potentially have been due to the fact that the clock and circle stimuli were less similar in terms of midlevel form components to the adaptor face than were the face test stimuli. Using both intact and scrambled adaptors allowed us to rule out this hypothesis because there would be no meaningful differences between the intact and scrambled adaptors from the perspective of shape-generic mechanisms (i.e., both contain the same degree of shape change to features such as eyes and mouth).

If our global face distortion aftereffect taps only shape-generic processes, we should expect to see

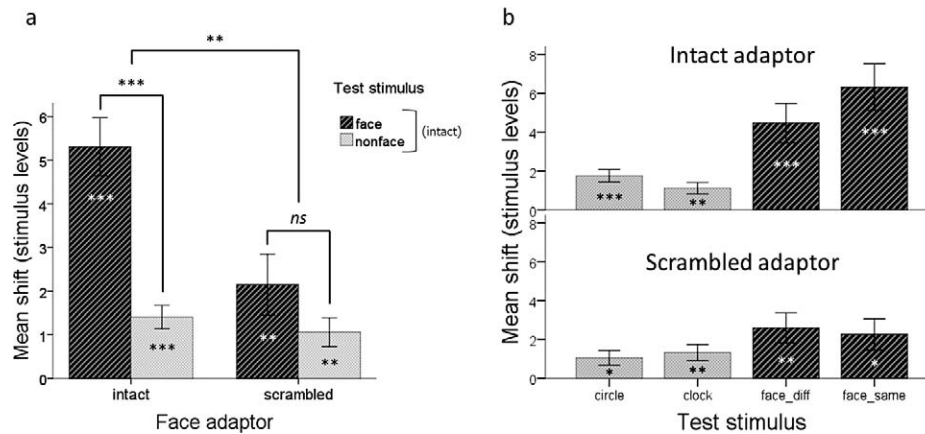


Figure 9. Results of Experiment 4. Larger aftereffects for face test stimuli than nonface test stimuli, but only when the face adaptor was intact. Notes: Error bars are ± 1 SEM. *ns* $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

equivalent sized aftereffects for face test stimuli from the intact and scrambled face adaptors. However, if face-specific processes are also tapped, then the predictions are of a two-way interaction between adaptor type (intact vs. scrambled) and test class (faces vs. objects), such that we find (a) the intact face adaptor produces greater aftereffects on faces than objects and this difference is reduced for the scrambled adaptor and (b) face test stimuli show larger aftereffects following adaptation to the intact face adaptor than the scrambled face adaptor. It should also be noted that such a pattern of results would support particularly a face-specific level that codes *whole face structure*; it is possible that there also exists a face-specific stage of coding that represents only isolated face parts (the OFA is more responsive to faces than objects, yet appears responsive to individual face features rather than overall structure; Liu, Harris, & Kanwisher, 2009; Pitcher, Walsh, & Duchaine, 2011), and face-specific adaptation in this type of mechanism would not contribute to a finding of larger aftereffects from the intact than scrambled face adaptor.

Method

Participants and design

Thirty students of the ANU (19 female) completed one 45 minute session in exchange for \$10 or first-year psychology course credit. These were either Caucasian ($n = 28$) or had very high Caucasian exposure (one Caucasian parent and raised in Australia, $n = 2$). All were naïve to the purposes of the experiment. Eight also participated in Experiment 3; the remainder were new. Adaptor type was manipulated between-subjects, with 17 participants in the intact adaptor condition and 13 in the scrambled adaptor condition.

Stimuli and procedure

The intact and scrambled face adaptors both had a horizontal:vertical outer contour ratio of 1:1.08. The intact adaptor was the stimulus used in Experiment 3 (adaptor_perc_1:1; see Figure 8a). The scrambled adaptor (Figure 8b) was identical in external contour and in the amount of compression of the internal face region—the only difference was that the internal features (eyes, nose, and mouth) were rearranged, breaking the first-order configuration of the face.

Test stimuli (circle, clock, face_one, face_two) were identical to Experiment 1. The procedure was the same as for Experiment 1, except that each participant completed only one session, with the shift scores calculated from this single session.

Curve fitting

PSEs and shift scores were obtained for each participant using the method described in Experiment 1. Shift scores associated with poor fits (average of pre- and post- $R^2 < .5$) were excluded from subsequent analyses (five instances). Prior to exclusion, there were 120 shift scores (30 participants each completed four test stimulus conditions). After exclusions, the quality of the average fits was high ($N = 115$, median $R^2 = .895$, minimum = .632, maximum = .989) and the final numbers in each condition are shown in Table 1.

Results

Figure 9 shows the mean aftereffect scores for each condition (see Table 1 for baseline and adapted PSEs). We first tested the predictions of a shape-generic component. Results replicated Experiment 1, showing significant face-to-object transfer for the intact face adaptor condition: That is, the intact face adaptor

produced significant aftereffects for circle, $t(15) = 5.51$, $p < 0.001$, $d = 1.38$, and clock, $t(16) = 3.71$, $p = 0.002$, $d = .90$ (as well as for face_same and face_diff, $ps < 0.001$). An additional prediction in the present experiment is that a shape-generic component should produce face-to-object transfer in the scrambled face adaptor condition. This was also observed, with significant aftereffects for circle, $t(12) = 2.78$, $p = 0.017$, $d = .77$ and clock, $t(11) = 3.12$, $p = 0.01$, $d = .90$ (as well as face_same and face_diff, $ps < 0.05$).

We then tested the predictions of a face-specific component. We again collapsed the two face test stimuli together and the two nonface stimuli together, as supported by no significant differences in aftereffect magnitude (face_same vs. face_diff for intact⁵ adaptor, $t(15) < 1$, $d = .24$; face_same vs. face_diff for scrambled adaptor, $t(11) < 1$, $d = .02$; circle vs. clock for intact adaptor, $t(15) = 2.05$, $p = 0.06$, $d = .51$; circle vs. clock for scrambled adaptor, $t(11) < 1$, $d = .02$). Analysis on the collapsed means (shown in Figure 9a) then supported the predictions of a face-specific component, namely that the face-to-face aftereffect should be larger than face-to-object transfer following the intact face adaptor, but this difference should be reduced for the scrambled face adaptor. Figure 9a reveals an interaction taking this predicted form. A two-way analysis of variance revealed this interaction between test stimulus (face vs. nonface) and adaptor type (intact vs. scrambled) was significant, $F(1, 28) = 8.97$, $p = 0.006$, $\eta^2 = .24$. Follow-up tests showed that, for the intact adaptor, aftereffects were significantly larger for test faces than objects, $t(16) = 5.47$, $p < 0.0001$, $d = 1.33$. In contrast, for the scrambled adaptor, there was no significant difference between test faces and objects, $t(12) = 2.06$, $p = 0.06$, $d = .57$.

We also conducted additional tests to examine the two-way interaction, comparing the conditions the other way around. Results showed that aftereffects were significantly larger following the intact face adaptor than the scrambled face adaptor for face test stimuli, $t(28) = 3.24$, $p = 0.003$, $d = 1.19$, but not for object test stimuli, $t(28) < 1$, $d = .31$.

Discussion

Results of Experiment 4 have confirmed the presence of both shape-generic and face-specific contributions to the vertical compression face aftereffect. Considering first the evidence for a shape-generic component, we replicated the findings from Experiment 1—significant face-to-object transfer—despite the change to an adaptor with a perceptually 1:1 external contour. Thus, together, the results of our two adaptation experiments unambiguously demonstrate that the source of the face-

to-object transfer is indeed the shape distortion of the face (internal) region of the adaptor. The present results rule out an external contour origin deriving from the perceived contour (i.e., face-to-object transfer was present despite a perceptually 1:1 contour). Aftereffects arising from the physical external contour are ruled out by the results of Experiment 1 (face-to-object transfer was found despite a physically 1:1 contour) and also by the present experiment, where it is worth noting that the physical distortion present in the adaptor's external contour (slightly vertically elongated), would have predicted an aftereffect in the opposite direction to that actually observed; that is, the observed aftereffect (normal objects appeared slightly vertically elongated) was in the direction predicted by the distortion direction of the face region (vertically compressed) not the distortion direction of the external contour (vertically elongated).

Considering evidence for a face-specific component, Experiment 4 found larger aftereffects for face test stimuli than nonface test stimuli (replicating Experiment 1), but only when the face adaptor was intact—not scrambled—and also showed that the aftereffect for face test items was substantially larger following the intact face rather than the scrambled face adaptor. These findings argue that a substantial component of the compression aftereffect can be attributed to adaptation of processes which are selective for whole intact faces; that is, to a face-level of coding that represents the whole face structure, not basic shapes, and also not to face-level coding of independent face parts.

General discussion

We found that the vertical compression face distortion aftereffect transfers to nonface test stimuli, arguing that the aftereffect arose partially from shape-generic processes sensitive to the distorted face region. However, we also found that the aftereffect was substantially larger when both adapt and test stimuli were faces and when the adaptor face was intact, which argues that the aftereffect also had a substantial face-level component.

Our results provide the first direct evidence that aftereffects for global distortions of face shape tap face-level processes. While another type of figural aftereffect has previously been shown to have a strong face-level component (approximately half of the aftereffect magnitude, Susilo et al., 2010a), the manipulation in that study—eye height—was rather closely tied to face structure. Our results for a global face distortion are important because global form distortions can be applied to practically any class of object. If one were to classify all of the different types of face aftereffect manipulations along a continuum ranging from most

intrinsic to faces to least intrinsic to faces, global form distortions such as the one we used in the present paper would very likely fall at the least intrinsic end of the continuum. Given that our results show that even an aftereffect at the least intrinsic end of the continuum taps face-selective processes, this strongly suggests that most other aftereffect manipulations in common use will also tap face-level processes.

Multiple sources of face aftereffects within the visual system

Our results support the view that face aftereffects derive from the combined output of several stages of visual processing (Susilo et al., 2010a; Yamashita et al., 2005; Zhao & Chubb, 2001). When adaptors and test stimuli are presented in the same size and position, this can include contributions from low-level vision (e.g., a field of local oriented line detectors; Dickinson, Almeida, Bell, & Badcock, 2010). In the more usual circumstance in which test stimuli are presented at a different size and/or retinal position than adaptor stimuli, our present results and those of Susilo et al. (2010a) show both a face-specific component and a significant nonretinotopic shape-generic component of figural face aftereffects.

What specific cortical regions might contribute to our present aftereffects? Regarding the face-specific component, there are several candidate regions that show face-selectivity: OFA, FFA, STS, and the anterior face patch. These areas show reduced responses to repeated stimuli (fMR-adaptation, repetition priming, e.g., Eger, Schyns, & Kleinschmidt, 2004; Fox et al., 2009; Henson, Shallice, & Dolan, 2000; Kouider, Eger, Dolan, & Henson, 2009; Xu, Yue, Lescroart, Biederman, & Kim, 2009). Making the reasonable presumption that response reductions also occur on a finer scale and can therefore affect the balance of population response from different cell subtypes within these regions, this argues these regions have the potential to produce perceptual aftereffects. Our results do not discriminate between origin in these various areas, beyond the fact that the substantial component selective for whole intact faces is unlikely to be coming from the OFA (which several studies have suggested is likely to be involved in representing face parts, Liu et al., 2009; Pitcher et al., 2011) and more likely to be coming from the other regions (e.g., the FFA, which is sensitive to the structure of whole intact faces, Schiltz & Rossion, 2006).

Turning to the origin of the shape-generic component, this again could include multiple areas within intermediate- and/or high-level vision. Macaque V4 and inferotemporal cortex has been demonstrated via single-unit recording to code basic form parameters

such as direction of curvature, elongation, and taper (Kayaert, Biederman, Op de Beeck, & Vogels, 2005; Pasupathy & Connor, 2001)—all of which are properties affected by our face compression manipulation. Other plausible areas include LOC and PFS. In human fMRI these regions demonstrate shape-generic responses (i.e., respond to other complex objects as strongly as to faces), and show reduced responses to repeated stimuli (e.g., Ewbank, Schluppeck, & Andrews, 2005; Kim et al., 2009; Pourtois, Schwartz, Spiridon, Martuzzi, & Vuilleumier, 2009; Pyles & Grossman, 2009).

An apparent conflict with developmental prosopagnosia results?

In apparent contrast to our present conclusion of a high-level face component, evidence from one neuropsychological study (Palermo et al., 2011) could be taken to question whether global face distortion aftereffects tap high-level face processes in showing impaired face identity aftereffects in developmental prosopagnosia (DP), but normal aftereffects for radial expansion/contraction. However, we can see at least two potential explanations for why these DPs show normal global face aftereffects.

First, it could be that, while global face distortion aftereffects do have a face-level component, this is comparatively smaller than for face identity aftereffects. If this is the case, it could make it more difficult to pick up a deficit in DP using global distortions than using the identity distortion without a large sample size.

Second, it might be that—in these subjects—the perceptual mechanisms which encode the dimensions of faces may not be the source of their poor face recognition, but instead there may be weak connectivity to face areas at later stages of the visual hierarchy. Evidence from both single cell recordings and fMRI suggests that mechanisms which encode dimensions of faces (e.g., mouth size, distance between eyes) are located in the posterior temporal lobe (Freiwald, Tsao, & Livingstone, 2009; Loffler, Yourganov, Wilkinson, & Wilson, 2005). And evidence from diffusion tensor imaging shows weaker forward connections to the anterior face regions in DPs (Thomas et al., 2009), suggesting the possibility that deficits in recognition ability in many DPs may not actually be a result of impaired perceptual coding, but instead in forward connectivity.

Using face aftereffects to draw inferences about face level processes

An assumption present in much of the current literature is that the properties of figural aftereffects

can be used as a direct tool to inform us about the properties of high-level face coding. As examples, figural aftereffects specifically from global distortions have been used to draw theoretical inferences about the development of norm-based face-space coding in children (Jeffery et al., 2010), the status of face-space coding in clinical populations (e.g., autism spectrum disorder; Pellicano, Jeffery, Burr, & Rhodes, 2007), the tuning of face-level neurons to face viewpoint (Jeffery et al., 2006), independent face norms for own and other-race faces (Jaquet et al., 2008), and viewpoint-independent, person-specific representations at the level of either face recognition units or person identity nodes (Hole, 2011).

Our results are consistent with those of Susilo et al. (2010a) in showing that figural face aftereffects do tap face-level coding, but at the same time do not arise purely from the face level. When an aftereffect reflects adaptation of both face-selective *and* shape-generic mechanisms, then inferences about face-selective mechanisms based on aftereffect results become potentially problematic, as it is not clear whether the aftereffects reflect the properties of one or both mechanisms. If the aim is to discover the properties of face-level coding, it would then be necessary to take additional steps in order to minimize the contribution of shape-generic processes.

How might this be accomplished? Some authors have argued that using identity aftereffects might tap face-space more directly than figural aftereffects (e.g., Leopold et al., 2001; Palermo et al., 2011; Rhodes & Jeffery, 2006). However, there is no guarantee that identity aftereffects have no shape-generic component. Manipulation of face identity invariably involves changes to various intermediate-level form parameters (e.g., curvature, concavity, color, etc.), and therefore some degree of adaptation would be expected in mechanisms which encode these parameters. Thus, while we are sympathetic to the idea that identity aftereffects might have the largest face-specific proportion of all face aftereffects, use of the identity aftereffect does not, in or by itself, fully solve the problem.

We therefore suggest that, in future research, more attention needs to be directed to the question of how to isolate the face-specific component of face aftereffects from the shape-generic component. One general method might be to measure the basic face aftereffect and also the aftereffect in the same subject for some control condition that assesses the shape-generic component, and then calculating a difference score to remove the shape-generic component while retaining the face-specific component. Suitable control conditions to subtract⁶ could include inverted faces, scrambled faces, or a condition measuring transfer of aftereffects from faces to matched nonface objects. (Although note that selecting a matched nonface object

is not always easy—e.g., there is no nonface object class to which the face identity manipulation can be applied—see discussion of Susilo et al., 2010a.)

We also note that, with the faces-minus-control approach, it might no longer be necessary to change the size or position between adaptor and test. Changing stimulus size removes low-level retinotopic components but will actually also remove some of the high-level components as well. Some degree of size- and position-specificity is maintained throughout intermediate- and high-levels cortical areas (DiCarlo & Maunsell, 2003; Kravitz, Kriegeskorte, & Baker, 2010; Yue, Cassidy, Devaney, Holt, & Tootell, 2011). For example, the fusiform face area—an important cortical locus of face processing (Kanwisher & Yovel, 2006)—shows sensitivity to the size and retinal position of stimuli (Yue et al., 2011). Moreover, in monkey inferotemporal cortex, those cells which show greater selectivity for stimulus type also tend to show greater sensitivity to retinal position (Zoccolan, Kouh, Poggio, & DiCarlo, 2007). This suggests that minimizing retinotopic aftereffect contributions might also reduce the strength of stimulus-selective (e.g., potentially face-level) contributions. Using a faces-minus-control approach without size or position change could potentially minimize contributions from low-level vision just as effectively as changing stimulus size between adaptation and test conditions, while also allowing retention of any aftereffect components which originate in face-level mechanisms that are sensitive to stimulus size.

In conclusion, our results argue that figural face aftereffects do have a valuable role to play as tools for investigating high-level face coding, in that they have a strong face-level component. At the same time, however, our results also argue that automatic attribution of face aftereffects to properties of high-level face coding (e.g., face-space) should be avoided. Instead, the field needs to address the challenge of developing methods that facilitate minimizing or avoiding the shape-generic component of face aftereffects, and thus isolating their true face-level component.

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Footnotes

¹ This face-selectivity (i.e., response two to three times greater for faces than other complex objects) is widely agreed upon in comparison to novices in the object domain (i.e., where participants have no special expertise in within-class discrimination of exemplars within the category, as in the present study). Concerning the rarer situation of experts in the object domain, there has been controversy regarding whether face selectivity still holds (e.g., Gauthier, Skudlarski, Gore, & Anderson, 2000; vs McKone, Kanwisher, & Duchaine, 2007). Current evidence suggests object expertise increases blood oxygen level dependent responses generically throughout the cortex, most likely via enhanced attention, rather having any specific association with face areas (e.g., all studies report greater increases outside face areas than in face areas and only 4 of 13 studies report significant increase in the FFA; for a review of 11 studies, see McKone & Robbins, 2011, p. 164; and two more recent studies, Brants, Wagemans, & Op de Beeck, 2011; Harel, Gilaie-Dotan, Malach, & Bentin, 2010).

² Note that we expected no problems to arise from the fact that there is strong pre-existing knowledge of the normal shape of circles and clocks. Previous studies have shown that adaptation can shift perception of perfect circularity (Regan & Hamstra, 1992; Suzuki & Cavanagh, 1998), indicating that the preknowledge does not fix or anchor perception of these stimuli.

³ The formula used to fit psychometric functions was: $y = (1 + \exp\{-[x - \text{beta}(1)] * \text{beta}(2)\})^{-1}$.

⁴ We know of no studies investigating whether this actually occurs. However, adaptation to illusory contours can elicit tilt aftereffects (Bockisch, 1998; Paradiso, Shimojo, & Nakayama, 1989; Smith & Over, 1975), and evidence from functional magnetic resonance imaging has shown that adaptation to illusory contours can occur at various levels of the visual hierarchy, including higher-level visual areas (Montasser-Kouhsari, Landy, Heeger, & Larsson, 2007)—meaning that the possibility of high-level perceptual aftereffects arising in response to perceived distortion of stimulus outer contour cannot be ruled out.

⁵ Note we are not claiming that real differences in aftereffect magnitude between same- and different-identity do not exist. Previous studies have found differences (e.g., Hole, 2011; Webster & MacLin, 1999), and our data suggest a potential difference that might be detected with increased statistical power (i.e., both Experiments 1 and 4 show a trend toward larger aftereffects for face_same than for face_diff for intact face adaptors).

⁶ Note that, in suggesting subtraction as the specific method, we are assuming the researcher is using a group design where the aim is to compare condition

means. Given recent evidence that there are also individual differences in aftereffect magnitude (Dennett et al., in press), other researchers may be interested in correlational designs. Under those circumstances, researchers have sometimes used subtraction but also a linear regression approach can be used (e.g., see supplementary materials of Wang, Li, Fang, Tian, & Liu, 2012), by saving the residuals from an analysis in which the control aftereffect measure is used to predict the face aftereffect.

References

- Afraz, A., & Cavanagh, P. (2009). The gender-specific face aftereffect is based in retinotopic not spatio-topical coordinates across several natural image transformations. *Journal of Vision*, 9(10), 1–17, <http://www.journalofvision.org/content/9/10/10>, doi:10.1167/9.10.10. [PubMed] [Article]
- Bell, J., & Kingdom, F. A. A. (2009). Global contour shapes are coded differently from their local components. *Vision Research*, 49(13), 1702–1710, doi:10.1016/j.visres.2009.04.012.
- Bockisch, C. J. (1998). Orientation discrimination and tilt aftereffects with luminance and illusory contours. *Vision Research*, 39(4), 765–776, doi:10.1016/S0042-6989(98)00129-1.
- Brants, M., Wagemans, J., & Op de Beeck, H. P. (2011). Activation of fusiform face area by Greebles is related to face similarity but not expertise. *Journal of Cognitive Neuroscience*, 23(12), 3949–3958, doi:10.1162/jocn_a_00072.
- Burkhardt, A., Blaha, L. M., Jurs, B. S., Rhodes, G., Jeffery, L., Wyatte, D. et al. (2010). Adaptation modulates the electrophysiological substrates of perceived facial distortion: Support for opponent coding. *Neuropsychologia*, 48(13), 3743–3756, doi:10.1016/j.neuropsychologia.2010.08.016.
- Carbon, C.-C., & Ditye, T. (2011). Sustained effects of adaptation on the perception of familiar faces. *Journal of Experimental Psychology: Human Perception & Performance*, 37(3), 615–625, doi:10.1037/a0019949.
- Cohen, J. D., MacWhinney, B., Flatt, M., & Provost, J. (1993). PsyScope: An interactive graphic system for designing and controlling experiments in the psychology laboratory using Macintosh computers. *Behavior Research Methods*, 25(2), 257–271, doi:10.3758/BF03204507.
- Dennett, H. W., McKone, E., Edwards, M., & Susilo, T. (in press). Face aftereffects predict individual

- differences in face recognition. *Psychological Science*.
- DiCarlo, J. J., & Maunsell, J. H. R. (2003). Anterior inferotemporal neurons of monkeys engaged in object recognition can be highly sensitive to object retinal position. *Journal of Neurophysiology*, *89*(6), 3264–3278, doi:10.1152/jn.00358.2002.
- Dickinson, J. E., Almeida, R. A., Bell, J., & Badcock, D. R. (2010). Global shape aftereffects have a local substrate: A tilt aftereffect field. *Journal of Vision*, *10*(13):20, 1–12, <http://www.journalofvision.org/content/10/3/20>, doi:10.1167/10.13.5. [PubMed] [Article]
- Eger, E., Schyns, P. G., & Kleinschmidt, A. (2004). Scale invariant adaptation in fusiform face-responsive regions. *NeuroImage*, *22*(1), 232–242, doi:10.1016/j.neuroimage.2003.12.028.
- Ewbank, M. P., Schluppeck, D., & Andrews, T. J. (2005). fMR-adaptation reveals a distributed representation of inanimate objects and places in human visual cortex. *NeuroImage*, *28*(1), 268–279, doi:10.1016/j.neuroimage.2005.06.036.
- Fang, F., & He, S. (2005). Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. *Neuron*, *45*(5), 793–800, doi:10.1016/j.neuron.2005.01.037.
- Fox, C. J., Moon, S. Y., Iaria, G., & Barton, J. J. S. (2009). The correlates of subjective perception of identity and expression in the face network: An fMRI adaptation study. *NeuroImage*, *44*(2), 569–580, doi:10.1016/j.neuroimage.2008.09.011.
- Freiwald, W. A., Tsao, D. Y., & Livingstone, M. S. (2009). A face feature space in the macaque temporal lobe. *Nature Neuroscience*, *12*(9), 1187–1196, doi:10.1038/nn.2363.
- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*(2), 191–197.
- Ghose, G. M., & Ts’O, D. Y. (1997). Form processing modules in primate area V4. *Journal of Neurophysiology*, *77*(4), 2191–2196.
- Gibson, J. J. (1933). Adaptation, after-effect and contrast in the perception of curved lines. *Journal of Experimental Psychology*, *16*(1), 1–31, doi:10.1037/h0074626.
- Grill-Spector, K. (2009). What has fMRI taught us about object recognition?. In S. Dickinson, A. Leonardis, B. Schiele, & M. J. Tarr (Eds.), *Object categorization: Computer and human vision perspectives* (pp. 102–128). Cambridge, MA: Cambridge University Press.
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*(10–11), 1409–1422.
- Harel, A., Gilaie-Dotan, S., Malach, R., & Bentin, S. (2010). Top-down engagement modulates the neural expressions of visual expertise. *Cerebral Cortex*, *20*(10), 2304–2318, doi:10.1093/cercor/bhp316.
- Henson, R. N. A., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, *287*(5456), 1269–1272, doi:10.1126/science.287.5456.1269.
- Hole, G. (2011). Identity-specific face adaptation effects: Evidence for abstractive face representations. *Cognition*, *119*(2), 216–228, doi:10.1016/j.cognition.2011.01.011.
- Jaquet, E., Rhodes, G., & Hayward, W. G. (2008). Race-contingent aftereffects suggest distinct perceptual norms for different race faces. *Visual Cognition*, *16*(6), 734–753, doi:10.1080/13506280701350647.
- Jeffery, L., McKone, E., Haynes, R., Firth, E., Pellicano, E., & Rhodes, G. (2010). Four-to-six-year-old children use norm-based coding in face-space. *Journal of Vision*, *10*(5):18, 1–19, <http://www.journalofvision.org/content/10/5/18>, doi:10.1167/10.5.18. [PubMed] [Article]
- Jeffery, L., Rhodes, G., & Busey, T. (2006). View-specific coding of face shape. *Psychological Science*, *17*(6), 501–505, doi:10.1111/j.1467-9280.2006.01735.x.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, *17*(11), 4302–4311.
- Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2109–2128, doi:10.1098/rstb.2006.1934.
- Kayaert, G., Biederman, I., Op de Beeck, H. P., & Vogels, R. (2005). Tuning for shape dimensions in macaque inferior temporal cortex. *European Journal of Neuroscience*, *22*, 212–224, doi:10.1111/j.1460-9568.2005.04202.x.
- Kim, J. G., Biederman, I., Lescroart, M. D., & Hayworth, K. J. (2009). Adaptation to objects in the lateral occipital complex (LOC): Shape or semantics? *Vision Research*, *49*(18), 2297–2305, doi:10.1016/j.visres.2009.06.020.
- Kouider, S., Eger, E., Dolan, R., & Henson, R. N. A. (2009). Activity in face-responsive brain regions is modulated by invisible, attended faces: Evidence

- from masked priming. *Cerebral Cortex*, 19(1), 13–23, doi:10.1093/cercor/bhn048.
- Kovács, G., Cziraki, C., Vidnyánszky, Z., Schweinberger, S. R., & Greenlee, M. W. (2008). Position-specific and position-invariant face aftereffects reflect the adaptation of different cortical areas. *NeuroImage*, 43(1), 156–164.
- Kravitz, D. J., Kriegeskorte, N., & Baker, C. I. (2010). High-level visual object representations are constrained by position. *Cerebral Cortex*, 20(12), 2916–2925, doi:10.1093/cercor/bhq042.
- Lee, K., & Freire, A. (1999). Effects of face configuration change on shape perception: A new illusion. *Perception*, 28(10), 1217–1226.
- Leopold, D. A., O’Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience*, 4(1), 89–94, doi:10.1038/82947.
- Liu, J., Harris, A., & Kanwisher, N. (2009). Perception of face parts and face configurations: An fMRI study. *Journal of Cognitive Neuroscience*, 22(1), 203–211, doi:10.1162/jocn.2009.21203.
- Loffler, G., Yourganov, G., Wilkinson, F., & Wilson, H. R. (2005). fMRI evidence for the neural representation of faces. *Nature Neuroscience*, 8(10), 1386–1390, doi:10.1038/nn1538.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A. et al. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences*, 92(18), 8135–8139.
- McCollough, C. (1965). Color adaptation of edge-detectors in the human visual system. *Science*, 149(3688), 1115–1116, doi:10.1126/science.149.3688.1115.
- McKone, E., Kanwisher, N., & Duchaine, B. C. (2007). Can generic expertise explain special processing for faces? *Trends in Cognitive Sciences*, 11(1), 8–15.
- McKone, E., & Robbins, R. (2011). Are faces special?. In A. J. Calder, G. Rhodes, M. H. Johnson, & J. V. Haxby (Eds.), *The Oxford handbook of face perception* (pp. 149–176). Oxford, UK: Oxford University Press.
- Montaser-Kouhsari, L., Landy, M. S., Heeger, D. J., & Larsson, J. (2007). Orientation-selective adaptation to illusory contours in human visual cortex. *The Journal of Neuroscience*, 27(9), 2186–2195, doi:10.1523/jneurosci.4173-06.2007.
- Müller, K.-M., Wilke, M., & Leopold, D. A. (2009). Visual adaptation to convexity in macaque area V4. *Neuroscience*, 161, 655–662.
- Nishimura, M., Doyle, J., Humphreys, K., & Behrmann, M. (2010). Probing the face-space of individuals with prosopagnosia. *Neuropsychologia*, 48(6), 1828–1841, doi:10.1016/j.neuropsychologia.2010.03.007.
- O’Leary, A., & McMahan, M. (1991). Adaptation to form distortion of a familiar shape. *Perception & Psychophysics*, 49(4):328–332, doi:10.3758/BF03205988.
- Palermo, R., Rivolta, D., Wilson, C. E., & Jeffery, L. (2011). Adaptive face space coding in congenital prosopagnosia: Typical figural aftereffects but abnormal identity aftereffects. *Neuropsychologia*, 49(14), 3801–3812, doi:10.1016/j.neuropsychologia.2011.09.039.
- Panis, S., Wagemans, J., & Op de Beeck, H. P. (2011). Dynamic norm-based encoding for unfamiliar shapes in human visual cortex. *Journal of Cognitive Neuroscience*, 23(7), 1829–1843, doi:10.1162/jocn.2010.21559.
- Paradiso, M. A., Shimojo, S., & Nakayama, K. (1989). Subjective contours, tilt aftereffects, and visual cortical organization. *Vision Research*, 29(9), 1205–1213, doi:10.1016/0042-6989(89)90066-7.
- Pasupathy, A., & Connor, C. E. (2001). Shape representation in area V4: Position-specific tuning for boundary conformation. *Journal of Neurophysiology*, 86(5), 2505–2519.
- Pasupathy, A., & Connor, C. E. (2002). Population coding of shape in area V4. *Nature Neuroscience*, 5(12), 1332–1338, doi:10.1038/972.
- Pellicano, E., Jeffery, L., Burr, D., & Rhodes, G. (2007). Abnormal adaptive face-coding mechanisms in children with autism spectrum disorder. *Current Biology*, 17(17), 1508–1512, doi:10.1016/j.cub.2007.07.065.
- Pitcher, D., Walsh, V., & Duchaine, B. (2011). The role of the occipital face area in the cortical face perception network. *Experimental Brain Research*, 209(4), 481–493, doi:10.1007/s00221-011-2579-1.
- Pitcher, D., Walsh, V., Yovel, G., & Duchaine, B. (2007). TMS evidence for the involvement of the right occipital face area in early face processing. *Current Biology*, 17(18), 1568–1573.
- Pourtois, G., Schwartz, S., Seghier, M. L., Lazeyras, F., & Vuilleumier, P. (2005). View-independent coding of face identity in frontal and temporal cortices is modulated by familiarity: An event-related fMRI study. *NeuroImage*, 24(4), 1214–1224, doi:10.1016/j.neuroimage.2004.10.038.
- Pourtois, G., Schwartz, S., Spiridon, M., Martuzzi, R., & Vuilleumier, P. (2009). Object representations for multiple visual categories overlap in lateral occip-

- ital and medial fusiform cortex. *Cerebral Cortex*, 19(8), 1806–1819, doi:10.1093/cercor/bhn210.
- Pyles, J. A., & Grossman, E. D. (2009). Neural adaptation for novel objects during dynamic articulation. *Neuropsychologia*, 47(5), 1261–1268, doi:10.1016/j.neuropsychologia.2009.01.006.
- Rajimehr, R., Young, J. C., & Tootell, R. B. H. (2009). An anterior temporal face patch in human cortex, predicted by macaque maps. *Proceedings of the National Academy of Sciences*, 106(6), 1995–2000, doi:10.1073/pnas.0807304106.
- Regan, D., & Hamstra, S. J. (1992). Shape discrimination and the judgement of perfect symmetry: Dissociation of shape from size. *Vision Research*, 32(10), 1845–1864, doi:10.1016/0042-6989(92)90046-L.
- Rhodes, G., Evangelista, E., & Jeffery, L. (2009). Orientation-sensitivity of face identity aftereffects. *Vision Research*, 49(19), 2379–2385, doi:10.1016/j.visres.2009.07.010.
- Rhodes, G., & Jeffery, L. (2006). Adaptive norm-based coding of facial identity. *Vision Research*, 46(18), 2977–2987, doi:10.1016/j.visres.2006.03.002.
- Rhodes, G., Jeffery, L., Watson, T. L., Jaquet, E., Winkler, C., & Clifford, C. W. G. (2004). Orientation-contingent face aftereffects and implications for face-coding mechanisms. *Current Biology*, 14(23), 2119–2123, doi:10.1016/j.cub.2004.11.053.
- Rhodes, G., & Leopold, D. A. (2011). Adaptive norm-based coding of face identity. In A. J. Calder, G. Rhodes, M. H. Johnson, & J. V. Haxby (Eds.), *The Oxford handbook of face perception* (pp. 263–286). Oxford, UK: Oxford University Press.
- Robbins, R., McKone, E., & Edwards, M. (2007). Aftereffects for face attributes with different natural variability: Adapter position effects and neural models. *Journal of Experimental Psychology: Human Perception & Performance*, 33(3), 570–592, doi:10.1037/0096-1523.33.3.570.
- Rolls, E. T. (2007). The representation of information about faces in the temporal and frontal lobes. *Neuropsychologia*, 45(1), 124–143, doi:10.1016/j.neuropsychologia.2006.04.019.
- Schiltz, C., & Rossion, B. (2006). Faces are represented holistically in the human occipito-temporal cortex. *NeuroImage*, 32(3), 1385–1394.
- Smith, A. T., & Over, R. (1975). Tilt aftereffects with subjective contours. *Nature*, 257(5527), 581–582, doi:10.1038/257581a0.
- Susilo, T., McKone, E., Dennett, H. W., Darke, H., Palermo, R., Hall, A. et al. (2011). Face recognition impairments despite normal holistic processing and face space coding: Evidence from a case of developmental prosopagnosia. *Cognitive Neuropsychology*, 27(8), 636–664, doi:10.1080/02643294.2011.613372.
- Susilo, T., McKone, E., & Edwards, M. (2010a). Solving the upside-down puzzle: Why do upright and inverted face aftereffects look alike? *Journal of Vision*, 10(13):1, 1–16, <http://www.journalofvision.org/content/10/13/1>, doi:10.1167/10.13.1. [PubMed] [Article]
- Susilo, T., McKone, E., & Edwards, M. (2010b). What shape are the neural response functions underlying opponent coding in face space? A psychophysical investigation. *Vision Research*, 50(3), 300–314, doi:10.1016/j.visres.2009.11.016.
- Suzuki, S., & Cavanagh, P. (1998). A shape-contrast effect for briefly presented stimuli. *Journal of Experimental Psychology: Human Perception & Performance*, 24(5), 1315–1341, doi:10.1037/0096-1523.24.5.1315.
- Taylor, J. C., & Downing, P. E. (2011). Division of labor between lateral and ventral extrastriate representations of faces, bodies, and objects. *Journal of Cognitive Neuroscience*, 23(12), 4122–4137, doi:10.1162/jocn_a_00091.
- Thomas, C., Avidan, G., Humphreys, K., Jung, K.-j., Gao, F., & Behrmann, M. (2009). Reduced structural connectivity in ventral visual cortex in congenital prosopagnosia. *Nature Neuroscience*, 12(1), 29–31.
- Tsao, D. Y., Moeller, S., & Freiwald, W. A. (2008). Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences*, 105(49), 19514–19519, doi:10.1073/pnas.0809662105.
- Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion, and race in face recognition. *The Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, 43(2), 161–204, doi:10.1080/14640749108400966.
- Wang, R., Li, J., Fang, H., Tian, M., & Liu, J. (2012). Individual differences in holistic processing predict face recognition ability. *Psychological Science*, 23(2), 169–177, doi:10.1177/0956797611420575.
- Watson, T. L., & Clifford, C. W. G. (2003). Pulling faces: An investigation of the face-distortion aftereffect. *Perception*, 32(9), 1109–1116, doi:10.1068/p5082.
- Webster, M. A., & MacLeod, D. I. A. (2011). Visual adaptation and face perception. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1571), 1702–1725, doi:10.1098/rstb.2010.0360.
- Webster, M. A., & MacLin, O. H. (1999). Figural

- aftereffects in the perception of faces. *Psychonomic Bulletin & Review*, 6(4), 647–653, doi:10.3758/BF03212974.
- Xu, X., Yue, X., Lescroart, M. D., Biederman, I., & Kim, J. G. (2009). Adaptation in the fusiform face area (FFA): Image or person? *Vision Research*, 49(23), 2800–2807, doi:10.1016/j.visres.2009.08.021.
- Yamashita, J. A., Hardy, J. L., De Valois, K. K., & Webster, M. A. (2005). Stimulus selectivity of figural aftereffects for faces. *Journal of Experimental Psychology: Human Perception & Performance*, 31(3), 420–437, doi:10.1037/0096-1523.31.3.420.
- Yue, X., Cassidy, B. S., Devaney, K. J., Holt, D. J., & Tootell, R. B. H. (2011). Lower-level stimulus features strongly influence responses in the fusiform face area. *Cerebral Cortex*, 21(1), 35–47, doi:10.1093/cercor/bhq050.
- Zhao, L., & Chubb, C. (2001). The size-tuning of the face-distortion after-effect. *Vision Research*, 41(23), 2979–2994, doi:10.1016/S0042-6989(01)00202-4.
- Zoccolan, D., Kouh, M., Poggio, T., & DiCarlo, J. J. (2007). Trade-off between object selectivity and tolerance in monkey inferotemporal cortex. *Journal of Neuroscience*, 27(45), 12292–12307, doi:10.1523/jneurosci.1897-07.2007.