Journal of Experimental Psychology:
Human Perception and Performance
2005, Vol. 31, No. 3, 420–437

0096-1523/05/$12.00 DOI: 10.1037/0096-1523.31.3.420

# Stimulus Selectivity of Figural Aftereffects for Faces

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Viewing a distorted face induces large aftereffects in the appearance of an undistorted face. The authors examined the processes underlying this adaptation by comparing how selective the aftereffects are for different dimensions of the images including size, spatial frequency content, contrast, and color. Face aftereffects had weaker selectivity for changes in the size, contrast, or color of the images and stronger selectivity for changes in contrast polarity or spatial frequency. This pattern could arise if the adaptation is contingent on the perceived similarity of the stimuli as faces. Consistent with this, changing contrast polarity or spatial frequency had larger effects on the perceived identity of a face, and aftereffects were also selective for different individual faces. These results suggest that part of the sensitivity changes underlying the adaptation may arise at visual levels closely associated with the representation of faces.

*Keywords:* face adaptation, face perception, face processing, selective aftereffects, figural aftereffects

Face recognition is among the most exquisite capacities of human form perception. We typically have little trouble identifying and discriminating familiar faces, even though as a class of objects human faces are highly similar to each other, and even though the image presented by the same individual can vary widely (e.g., because of changes in lighting, viewpoint, expression, or age). It is uncertain to what extent this ability is innate or develops through experience and to what extent it represents mechanisms specialized for faces versus a more generic potential for expert object recognition (Diamond & Carey, 1986; Farah, Wilson, Drain, & Tanaka, 1998; Gauthier & Tarr, 1997). Yet, in any case, it seems evident that humans normally possess a specialized capacity for face perception and that this involves specialized, high-level mechanisms in the visual system.

Evidence for these specialized mechanisms has been suggested by physiological, clinical, and behavioral approaches. For example, a number of studies have documented responses of neurons in the inferotemporal cortex that appear specifically responsive to faces (Desimone, 1991; Perrett, Mistlin, & Chitty, 1987), and neural imaging approaches have identified distinct cortical areas that are selectively activated during face perception (Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & MacDonald, 1992). Specific extrastriate areas important to face coding are also implied by the clinical deficit of prosopagnosia, in which patients show selective losses in face recognition (Farah, Wilson, Drain, & Tanaka, 1995). Finally, psychophysical tests have shown that faces tend to be processed in ways that are distinct from other classes of objects. For example, compared with other objects, faces appear much more difficult to recognize or discriminate when presented upside down (Yin, 1969) or contrast reversed as in a photographic negative (Galper, 1970). Inversion is thought to disrupt face recognition because it hinders the processing of configural information—and specifically the spatial relationships between facial features (Freire, Lee, & Symons, 2000). Psychophysical studies have also revealed that faces are processed holistically such that the perception and recognition of parts of the face are strongly influenced by the overall *face context* in which they appear. For example, individual facial features (such as the nose) are more accurately recognized when they are shown as part of the whole face (Tanaka & Farah, 1993); however, an image of half a face becomes less recognizable when it is combined with a half image of a different face (Young, Hellawell, & Hay, 1987). Such results suggest that face perception depends strongly on coding the overall configuration of the face rather than a piecemeal representation of its individual features (Maurer, Le Grand, & Mondloch, 2002; Peterson & Rhodes, 2003).

In the present study, we explored properties of configural coding in face perception by examining how face perception is altered by adaptation. Visual perception is constantly recalibrated by processes of adaptation that adjust to the stimuli people are currently exposed to, and these adjustments can strongly affect how stimuli look (Webster, 2003). The perceptual aftereffects of adaptation can reveal the stimulus dimensions that are important for a given perceptual task by revealing which aspects of the stimuli the visual system can adjust to. Webster and MacLin (1999) investigated adaptation aftereffects in face perception by measuring how the perceived configuration of a face was altered after observers were exposed to a distorted version of the face. The distortions were formed by locally expanding or contracting the image to form punched or pinched versions of the original face (see Figure 1).

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We thank Yoko Mizokami, Aaron Bilson, Jennifer Muskat, and Carrie Paras for their valuable time and assistance. This research was supported by National Eye Institute Grant EY10834 awarded to Michael A. Webster.

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Subjects first viewed the altered configurations for a few minutes and then physically adjusted the distortion in a test image until it appeared undistorted (i.e., like the original). Their study revealed pronounced negative aftereffects in the perceived configuration. For example, after viewing an expanded face, the original face appeared too contracted. To null this perceptual contraction, subjects therefore had to choose a test face that was physically moderately expanded. A contracted adapting stimulus induced the opposite aftereffect, causing the original face to appear too expanded (so that a physically contracted face was now perceptually undistorted). The results thus suggested that face perception can be strongly biased by even brief periods of adaptation. Moreover, strong adaptation effects occur for images defined by the natural variations characteristic of actual faces (e.g., the image distortions that distinguish individual identity or attributes such as gender; Leopold, O'Toole, Vetter, & Blanz, 2001; Webster, Kaping, Mizokami, & Duhamel, 2004). This means that the adaptation may play an important role in face perception under everyday viewing conditions.

Several lines of evidence suggest that face adaptation is altering sensitivity at a high level of perceptual encoding. First, Webster and MacLin (1999) found that the figural aftereffects for faces were asymmetric—adaptation to a distorted face strongly affected the appearance of the original face, yet adapting to the original had no effect on the distorted face. This asymmetry would not be predicted if adaptation were adjusting only to low-level features in the stimuli (e.g., to the separation between eyes), because in that case there is no reason to expect the original face to be special. Second, Zhao and Chubb (2001) and Leopold et al. (2001) found that the adaptation transferred across large changes in stimulus size, whereas Leopold et al. also found transfer across retinal position. Third, Rhodes, Jeffery, Watson, Clifford, and Nakayama (2003) and Watson and Clifford (2003) found that the aftereffects transfer across large changes in stimulus orientation (e.g., between faces presented 45° clockwise or counterclockwise from vertical). These results suggest that the adaptation is altering sensitivity at sites at which shape or configuration are represented more or less independently of absolute size or position, again implying that the adaptation is affecting configural and perhaps face-specific levels of processing. Consistent with this, the responses of face-selective neurons can be largely independent of stimulus size (Rolls & Baylis, 1986). However, countering these results is the finding that equally strong aftereffects are also observed when the faces are presented upside down. As noted, inverting the face is thought to disrupt configural encoding, and inversion effects are thus considered a hallmark of configural processing. The failure to observe an inversion effect in face adaptation therefore remains a puzzle and raises the question of what specifically the adaptation is adjusting to.

As the examples above illustrate, measurements of how adaptation generalizes across different face images—and which aspects of the images it is instead selective for—can provide important clues about how face information is represented at the level of the visual system at which the adaptation occurs. In the present study, we compared how the adaptation transfers across a range of different stimulus dimensions. The tuning of the aftereffects was evaluated with two different paradigms, one that tests for transfer across stimulus levels and a second that tests for selectivity between levels. In the first case, observers were adapted to a single face and then tested with a pair of different faces. For example, they might adapt to a red–expanded face and then make settings for a red face or a green face. This is a common paradigm in adaptation, and it allows one to evaluate how readily the adaptation can generalize across different stimuli. In the example, a nonse-

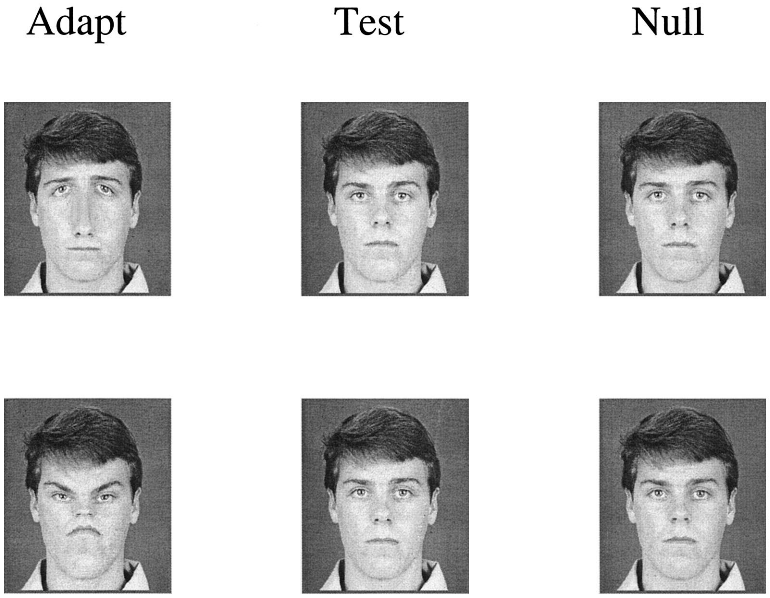

*Figure 1.* An example of the face images from the Matsumoto & Ekman (1988) set that were distorted, similar to the Webster & MacLin (1999) study. Adaptation to an expanded face causes the original test to appear too contracted. In order to null this perceptual contraction, subjects must choose an image that is physically expanded (top row). Contracted adapting faces induce the opposite aftereffect: The original appears too expanded and thus must be nulled by an image that is physically contracted (bottom row).

lective adaptation effect would be suggested if the aftereffects were identical for the red and green test faces, whereas a sensitivity change that was completely selective for the stimulus color would result in an aftereffect from the red adapt face only in the red test face. We also used a second procedure in which observers simultaneously adapted to two different stimuli and were then tested with stimuli defined by these differences. For example, they might adapt to a red–expanded face alternated in time with a green–contracted face and then rate the appearance of a red or green test face. The two adaptors were always distorted in opposite ways (i.e., one expanded and the other contracted) so that they should induce opposite aftereffects. This procedure is frequently used in tests of contingent adaptation (Stromeyer, 1978), for in this case any common aftereffects should cancel and directly reveal any selective sensitivity change by shifts of the opposite sign in the different test stimuli. For example, if the adapted mechanisms were insensitive to a color change, then the expanded and contracted adaptors should (if appropriately matched) have no net effect, whereas any selective aftereffects would result in opposite shifts in the appearance of the red and green test faces.

We used these tasks to compare the relative selectivity of the aftereffects for differences in both the color and form of the adapting and test stimuli. One goal of the present study was to determine whether the pattern of aftereffects for faces is better explained directly by the low-level changes in the stimulus or by how these changes alter the higher-level interpretations of the images. The image properties we tested are ones that have been widely used to characterize adaptation effects in simple visual patterns and include differences in mean color or contrast, contrast polarity, size, and spatial frequency. Traditionally, adaptation effects are interpreted in terms of visual channels directly tuned to encode the dimensions along which the stimuli are varied (Graham, 1989; Webster, 2003). For example, if a spatial aftereffect was selective for the color of the stimulus, then this could imply that the adapted channels were jointly tuned to both color and spatial pattern. Such contingent aftereffects have been widely studied and have revealed joint tuning for a variety of stimulus dimensions (Stromeyer, 1978). Our measurements test whether similar contingent aftereffects occur for complex spatial patterns like faces.

In contrast to the channel models that are common in studies of pattern adaptation, studies of face perception have instead focused on how the stimuli alter the perception of the images as faces. In particular, this approach has emphasized how a given manipulation alters featural versus configural processing of the images (Peterson & Rhodes, 2003). This provides a very different perspective for interpreting visual aftereffects. For example, changing the color of the face can be thought of as altering a facial feature. If the aftereffect is selective for this alteration, then this could imply that the feature of color is important in the mechanisms mediating face perception and that adaptation is altering sensitivity at the level of featural coding. Alternatively, scrambling the location of features or masking features with local noise are methods that have been used to isolate configural processing (McKone, Martini, & Nakayama, 2001; Tanaka & Farah, 1993). Selective aftereffects for manipulations that influence configuration could therefore be interpreted as revealing response changes at the level of configural encoding. Notably, there are a number of distinct ways in which changing the stimulus might change configural processing and thereby influence the adaptation (Maurer et al., 2002). For some manipulations (e.g., scrambling the parts), the stimulus is no longer perceived as a face at all. For others (e.g., inverting the image), the image is still seen as a face but observers lose the ability to distinguish the spatial relationships between the features (Thompson, 1980). Finally, manipulations might change the identity of a face by changing the features or their configuration. For example, a new individual could potentially be created by altering either the position or the shape of the eyes. The identity of the face may be represented relative to a prototypical reference face (Leopold et al., 2001), though the stimulus properties on which face prototypes depend remain elusive.

The stimulus changes we examined represent global changes in the image (e.g., in the average color or size of the face) and thus do not map in a simple way onto the distinction between a local feature (e.g., the shape of the nose) versus a global configuration. However, although each of the manipulations changes the lower level properties of the images and thus their features, they differ in the degree to which they alter facial configuration. For example, changing the size of the image has no effect on the configuration of the face, yet changing contrast polarity has a large effect. We tested whether these configural differences influence the pattern of adaptation, and we also evaluated this possibility by testing whether the adaptation is selective for images of actual faces. The results of these experiments may thus help to reveal the kinds of visual processes that are being adapted when we look at faces.

## Method

### *Subjects*

Subjects included two of the authors (JY and MW) and four additional observers (CP, JM, YM, and AB) who were unaware of the specific aims of the experiment. Except where noted, at least three of the naive observers were tested for each experiment. All had normal or corrected-to-normal vision acuity, and subjects in the color experiments were screened for normal color vision.

### *Stimuli*

Gray-scale face images were taken from the frontal view, neutral-expression face set of Matsumoto and Ekman (Matsumoto & Ekman, 1988). For most experiments, the images were shown at the full resolution of 512 × 512 pixels. The faces were locally distorted by expanding or contracting the original image along the vertical axis using the metric and procedures described by Webster and MacLin (1999). As in their study, the distortions were relative to a midpoint on the nose and weighted by a circular Gaussian envelope so that changes were largest near the center of the face and negligible near the outline of the head. By varying the magnitude of the distortion in small steps (from $\alpha = -1$ to $+1$ in .025 increments; see Webster & MacLin, 1999), an array of 80 images was created that varied in finely graded steps from fully contracted to fully expanded. A subset of images from this array is illustrated in Figure 2.

### *Procedure*

Images were presented on a Sony Trinitron color monitor controlled by a Cambridge Research Systems VSG graphics card (Rochester, England). The images subtended an angle of 4° and were displayed within a gray background of $\sim$20 cd/m$^2$ (close to the mean luminance of the face images). Subjects free viewed the images binocularly in a darkened room from a distance of 250 cm.

A daily session consisted of two neutral adaptation runs followed by four adaptation runs. In the neutral runs, the subject first adapted to a gray

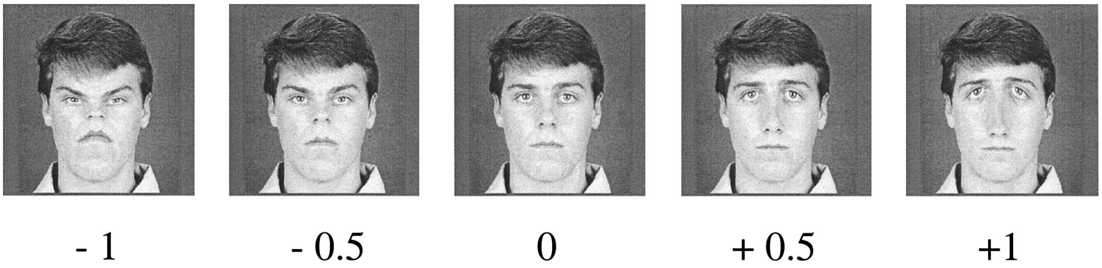

*Figure 2.* An example of the distortion array. The 81 images in the array varied from strongly contracted (−1) to strongly expanded (+1) along the vertical axis of the original image.

screen for 120 s and was then tested with distorted faces with the selected color (e.g., green) or form (e.g., low spatial frequency) properties that corresponded to specific adapting conditions. In the adaptation run, they instead made settings for the same stimuli after viewing distorted adapting images for 120 s. The neutral runs provided a baseline measure of which image from the face array looked least distorted to the observer, and the adaptation runs probed how this judgment was influenced by prior exposure to distorted images. In most of the figures below we plotted the differences between the pre- and postadaptation settings as a measure of the adaptation effect. To avoid crossover of the adaptation effects, each observer participated in only one session per day with a single adapting condition.

The subjects were presented with a single face for 1 s, and we measured the image that appeared the least distorted, after the initial adaptation period, by using a forced-choice response to indicate whether the face appeared "too expanded" or "too contracted." The test face was initially drawn from a random value within the image array and then varied over trials in two randomly interleaved staircases that converged on the subject's neutral point. Each successive trial was preceded by a further 6-s period of exposure to the adapting stimuli in order to maintain a constant state of adaptation. Settings were based on the average of the last six reversals from each of the two staircases. For unopposed adapting conditions, subjects were exposed to a single static adapting image (e.g., a red–expanded face), and for the opposing adaptation condition they viewed a pair of images alternated at a rate of one image per second (e.g., red–expanded face alternated with a green–contracted face). We have found previously that this alternation rate is fast relative to the integration time of the adaptation, so that during the test presentation observers are not simply adapted to the last presented image (Muskat, Paras, & Webster, 2000). In both the opposed and unopposed conditions, subjects made settings for two different test stimuli (e.g., a red test face and a green test face) that were randomly alternated across trials with each in two staircases.

## Experiment 1: Image Size

In the following experiments, we first evaluate the adaptation effects for individual dimensions and then assess their relative influence. In the first case, we examined how the aftereffects transferred across changes in the size of the adapting and test images, similar to the experiments reported by Zhao and Chubb (2001) and Leopold et al. (2001). Again, strong transfer is important because it implies that the adaptation alters sensitivity in processes that represent shape or configuration independent of the actual spatial location of the features making up the configuration, thus implying higher levels of visual coding. Alternatively, strong selectivity might instead imply sites of adaptation that are more directly tied to simple properties of the stimuli such as their retinal location. To test between these alternatives, we assessed the aftereffects for images that differed by a factor of 2 in relative size. Figure 3 illustrates how the cross adaptation between these images might lead to different aftereffects depending on the relative importance of featural versus configural information or, more precisely, on the position of local features versus the overall shape of the face. In this example, the large adapting image is contracted. However, because of the large size, the absolute distance between the eyes and mouth is still greater than it is in the small original image. If adaptation was displacing the perceived location of local features like the eyes and mouth or biasing featural properties like the size of the region defined by their separation, then the large contracted adaptor should be comparable to an expanded stimulus when aftereffects are measured with the small test, and thus should make the eyes and mouth in the small test appear closer together. Alternatively, if the adaptation depends on a configural property such as feature locations relative to the overall face size, then the large adaptor should instead cause the eyes and mouth in the small test to appear farther apart.

### Method

*Subjects.* Observers included author JY and three additional subjects.

*Stimuli and procedure.* Observers adapted to the gray-scale stimuli presented at a size of 4° (large) or 2° (small) in visual angle. They then adjusted the appearance of large or small test images by nulling any perceived distortions in the images using the staircase procedure. Settings were made for the test images after adapting to a single image (large or small) that was fully expanded or contracted, or after adaptation to the

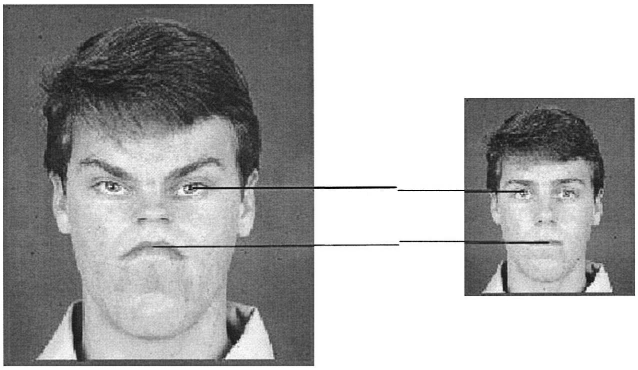

*Figure 3.* Large and small adapting images. Even when the features are contracted, a large adapting face has a greater distance between the eyes and mouth compared to the small neutral test face.

opposing pair of a large–contracted and small–expanded face or vice versa.

## Results

Figure 4 shows the magnitude of the aftereffects following adaptation to the different image sizes. Each row shows the settings for a different observer. As noted previously, the results are plotted as the change in the settings relative to the observer's preadapt settings. A value of 0 would imply an absence of a figural aftereffect. Instead, the settings are systematically biased following adaptation. Adapting to expanded faces shifted the neutral points toward positive values, which suggested that the adaptation caused the original image to appear too contracted (so that the stimulus required to null this aftereffect is physically expanded) whereas contracted adapting stimuli induced the opposite shifts. The results are thus similar to the aftereffects described by Webster and MacLin (1999).

The different columns in the figure compare the aftereffects for adaptation to either sized image alone (middle and right columns) or to the opposing distortions presented in the large and small faces (left column). In the former case there are large aftereffects of similar sign across the different test image sizes. That is, adaptation to either the large face or the small face had large effects on the appearance of both the large and the small test faces and biased their appearance in similar ways. (Control settings for two observers [not shown] showed that strong transfer persisted across the two sizes even when the images were filtered to remove all internal structure except the eyes and mouth. This rules out the possibility that subjects were adapting to distortions in the texture of the images rather than the facial configuration.) The aftereffects for size are thus consistent with the predictions for configural changes

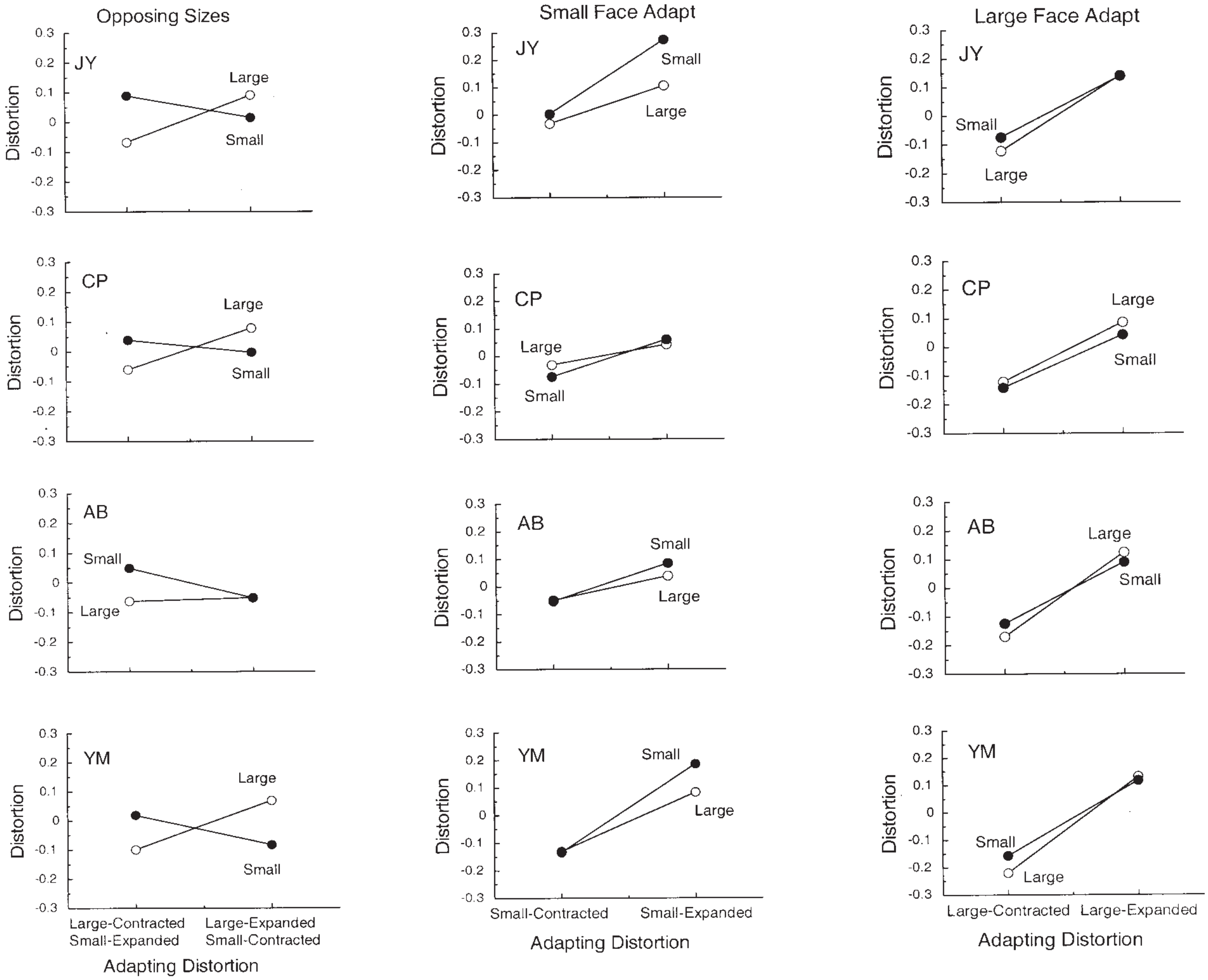

*Figure 4.* Adaptation aftereffects for small or large test faces. The magnitude of the aftereffect is given by the difference between the postadapt and preadapt null settings for the small (filled circles) or large (unfilled circles) test face. The four rows show these settings for four individual observers whose initials are shown in each panel. The left column plots the results for opposing adaptation to a small–expanded face alternated with a large–contracted face or vice versa. The middle column shows settings for nonopposing adaptation when observers viewed only the small face during adaptation. The right column shows settings following nonopposing adaptation to the large face.

in the stimuli rather than the predictions for distortions in the positions of the local features (see Figure 3) and replicate the results of Zhao and Chubb (2001) and Leopold et al. (2001).

The crossing curves in the left-hand panels of Figure 4 show that there is also selectivity for size in the aftereffects. Specifically, in the opposing condition opposite aftereffects were simultaneously induced in the appearance of the large and small test faces. For example, adaptation to the large–contracted face made the large test face appear expanded, and at the same time adaptation to the small–expanded face made the small face appear contracted. These results indicate that the adapted mechanisms are not completely insensitive to absolute stimulus size, which is a finding that is also consistent with the results of Zhao and Chubb (2001).

To better evaluate the role of stimulus size in the aftereffect, we calculated indices of selectivity from each observer's results (Hardy & De Valois, 2002). For the nonopposing adaptation conditions, the index was defined as

$$\text{Selectivity} = (\Delta A_s - \Delta A_d)/\Delta A_s,$$

in which $\Delta A_s$ equals the difference between the observer's settings for expanded and contracted adaptation when the adapt and test stimuli were the same (e.g., both large or both small), and $\Delta A_d$ equals the corresponding difference when the adapt and test stimuli differed (e.g., large test and small adapt or vice versa).

By this measure, a completely selective aftereffect would have a value of 1.0 (i.e., no aftereffect when the test and adapt differed), and a completely nonselective aftereffect would have a value of 0 (i.e., same aftereffect whether the adapt and test were the same or different). A value less than 0 would mean that adaptation was actually stronger when the adapt and test stimuli differed. For example, this could happen if a large adapting face had larger effects than a small adapting face on small test faces, perhaps because the large face adapted a larger visual area and thus a larger pool of mechanisms.

For the opposing adaptation, we used an unnormalized index based on only the difference in the null settings for each test face (small or large) following adaptation to an expansion or contraction in the corresponding adapting face (small or large). Thus, in this case: change in null setting equals the difference between the observer's settings for a small (large) test face when the small (large) adapting face was expanded or contracted.

Here again, positive values correspond to a selective aftereffect, a value of 0 corresponds to a nonselective effect, and negative values suggest that the different-adapt stimulus dominated over the same-adapt stimulus. The actual size of this difference is less easy to interpret because the opposing conditions do not provide a way to normalize for the overall magnitude of the aftereffect (and measurements of this magnitude from nonopposing conditions were collected for a different subset of observers and conditions). Nevertheless, we show below that the two measures lead to very similar interpretations about the selectivity for the different stimulus dimensions.

Figure 5 plots these indices for the individual observers. The top panel shows the size of the shifts in the nulls for opposing adaptation, and the bottom panel plots the indices derived from the results for the unopposed adaptation. In each case, the bar charts show the values for both the large and small stimuli and their mean. We evaluated these indices using within-subject analyses of variance (ANOVAs) based on the mean settings for each observer in each adapting and test condition. The opposing aftereffects were assessed with a two-way ANOVA comparing adapting condition (large–expanded and small–contracted vs. large–contracted and small–expanded) and test size (large vs. small); see Table 1. Main effects for the adapt condition and test size were not significant, which suggests that the two image sizes were equally potent under these conditions. On the other hand, the interaction was highly significant, which confirms that the aftereffects are selective for the relative size of the adapt and test images.

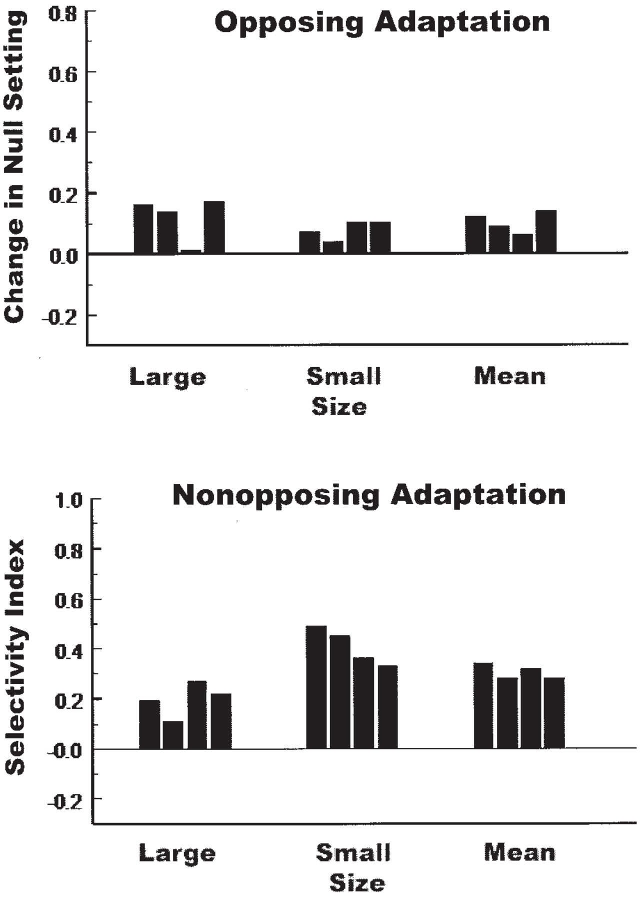

*Figure 5.* Estimates of the selectivity of the adaptation for the size differences in the images. Each bar shows the selectivity of the aftereffect measured for a single observer for the small or large images or the mean selectivity for both. The upper panel plots the size of the aftereffects for opposing adaptation as represented by the difference between the null settings for the expanded or contracted adapting conditions for either the small or large test. The lower panel plots the selectivity index for the nonopposing adaptation (see text).

For the nonopposing adaptation, the results also suggest partial selectivity for the two sizes (i.e., the indices are consistently greater than zero but less than one). Aftereffects for the nonopposing conditions were assessed by evaluating the observers' mean settings in a three-way ANOVA comparing adapt size (large vs. small), test size (large vs. small), and adapt distortion (expanded vs. contracted); see Table 2. In this case, there is a significant effect of the distortion (showing that significant figural aftereffects were indeed induced in the faces), and a significant effect of the adapt size. This is likely to reflect less selective adaptation following exposure to the large adapt faces, an asymmetry which was

Table 1
*Two-Way Within-Subject Analysis of Variance of the Mean Changes in the Null Settings for Large and Small Test Faces Following Adaptation to Opposing Distortions (Expanded vs. Contracted) in Large and Small Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt (large-expanded / small-contracted vs. large-contracted / small-expanded) | 1, 3 | 0.85 | *ns* |
| Test size (large vs. small) | 1, 3 | 1.86 | *ns* |
| Adapt vs. test size | 1, 3 | 33.8 | <.01 |

also reported by Zhao and Chubb (2001), and which was confirmed by comparing the indices for the large and small adapt conditions, $t(6) = -4.21$, $p < .01$. Note that in this ANOVA, the selectivity for size is tested by the three-way interaction between the factors. (This is because the two-way interaction between adapt and test size pools across the two distortion levels, which induce opposite aftereffects and thus cancel each other.) This interaction is again significant and thus again confirms selectivity for size even in the case of nonopposing adaptation. Finally, a significant interaction was also found between the adapt size and the adapting distortion, though the basis for this is unclear.

## Experiment 2: Spatial Frequency

The preceding results confirmed that adaptation could alter the appearance of faces even if they differed in stimulus size. In the next experiment, we examined a different form of scaling by testing the influence of the spatial frequency content of the stimuli, or the size of the spatial structure making up the images. Specifically, we examined whether a distortion presented at one frequency range (e.g., high) could produce aftereffects in images presented at different ranges (e.g., low). Lower level pattern adaptation effects can be strongly selective for spatial frequency, (Graham, 1989) yet it is unclear how filtering the images might influence adaptation in face processing. Previous studies have shown that medium spatial frequencies may be especially important for face recognition (Costen, Parker, & Craw, 1996; Gold, Bennett, & Sekuler, 1999; Nasanen, 1999), though some capacity for recognition persists even for images that are strongly blurred (Yip & Sinha, 2002). If filtering leaves the basic facial configuration intact, then we might expect little selectivity for frequency. On the other hand, if frequency was an important feature in the representation of faces, or if changing this feature also altered configural processing, then aftereffects might be strongly selective for this dimension.

### Method

*Subjects.* Observers included authors JY and MW and three additional subjects.

*Stimuli and procedure.* The gray-scale image arrays were filtered into different frequency ranges to form two new arrays that corresponded to a high-pass and low-pass image set. These had frequency ranges of 1–8 and 16–128 cycles per image (equal to 0.25–2 and 4–32 cycles per degree in the display; see Figure 6). The high- and low-frequency sets were thus each three octaves wide with one octave gap between them. For technical reasons the image size was reduced to 256 × 256 pixels. For this experiment, we therefore halved the viewing distance so that the displayed images still subtended 4°. Procedures were otherwise identical to Experiment 1.

### Results

The bar charts in Figure 7 again illustrate the aftereffects for each subject for both opposing and nonopposing adaptation. Compared to the effects of image size, aftereffects for the filtered images showed less transfer across the two frequency ranges. The indices varied widely for individual subjects, but averaged roughly 0.6 for the low- and high-frequency nonopposing conditions compared to a mean of 0.3 for the large and small size conditions, a difference which was significant, $t(16) = -3.35$, $p < .01$. There is also no evidence for an asymmetry between the selectivity for the low- and high-frequency images, $t(8) = -.83$, *ns*. Again, the effects of frequency were assessed with within-subject ANOVAs. Significant interactions for both opposing and nonopposing adaptation confirmed that the adaptation was selective for the spatial frequency content of the face images (Tables 3 and 4).

The clear selectivity for the frequency content of the stimuli could be because the low-pass and high-pass images adapted mechanisms tuned to different spatial frequencies, or because filtering the images altered other properties of the faces that the adaptation is selective for. We consider the latter possibility in Experiment 6.

## Experiment 3: Contrast Polarity

In the next three experiments, we kept the spatial properties of the images the same but varied the contrast or color of the faces. The present experiment assessed the influence of contrast polarity. Early visual mechanisms are known to include distinct on and off pathways encoding contrast increments and decrements, and figural aftereffects for simple two-dimensional patterns have been shown to be polarity-selective (Burton, Nagshineh, & Ruddock, 1977; De Valois, 1977). Sensitivity changes tied to this type of channel structure might therefore show strong selectivity for the sign of the image contrast. However, as noted earlier, in the case of faces, inverting the contrast strongly hinders recognition (Galper, 1970). This suggests that the mechanisms subserving face recognition are specialized for encoding positive contrast, perhaps because the inversion disrupts shape from shading cues or because of differential experience with positive contrast images (George et al., 1999). A figural aftereffect that was tied closely to the stage of

Table 2
*Three-Way Within-Subject Analysis of Variance of the Mean Changes in the Null Settings for Large and Small Test Faces Following Adaptation to Nonopposing Distortions in Large and Small Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt size (large vs. small) | 1, 3 | 17.8 | <.05 |
| Test size (large vs. small) | 1, 3 | 1.57 | *ns* |
| Adapt distortion (expanded vs. contracted) | 1, 3 | 49.2 | <.01 |
| Adapt Size × Test Size | 1, 3 | 5.60 | *ns* |
| Adapt Size × Adapt Distortion | 1, 3 | 10.58 | <.05 |
| Test Size × Adapt Distortion | 1, 3 | 1.68 | *ns* |
| Adapt Size × Test Size × Adapt Distortion | 1, 3 | 36.8 | <.01 |

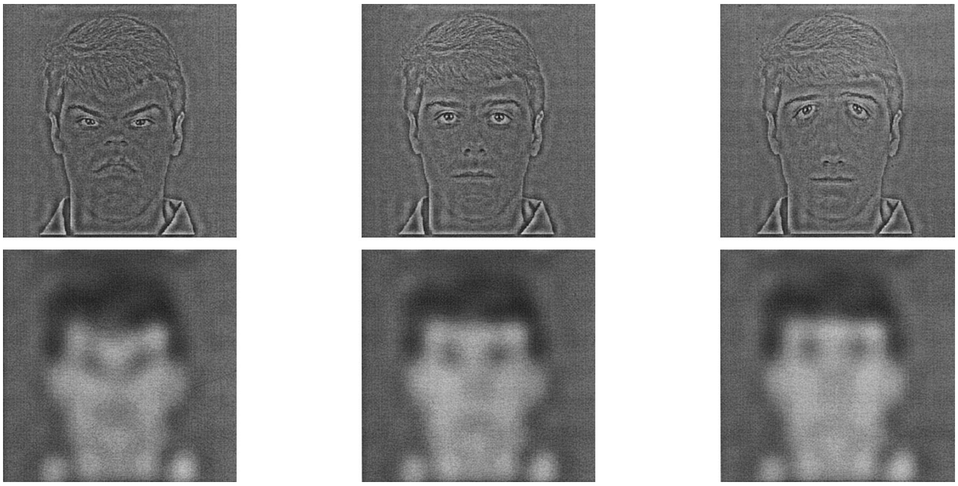

*Figure 6.* Examples of the highpass or lowpass filtered images used to measure selectivity for spatial frequency.

face recognition might therefore show asymmetric aftereffects for positive and negative contrast images. For example, the distortions might be more salient in the positive images, so that positive contrast adapting and test images might lead to larger aftereffects.

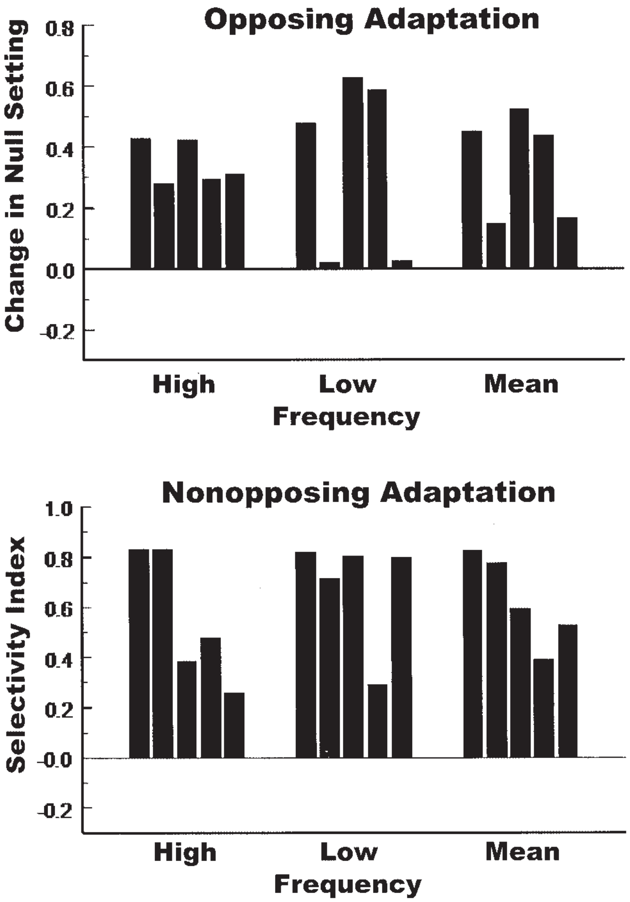

*Figure 7.* Estimates of selectivity of the aftereffects for the highpass and lowpass filtered images (see Figure 5 legend).

## Method

*Subjects.* Observers included authors JY and MW and three additional subjects.

*Stimuli and procedure.* Images from the array of distortions for the face in Figure 1 were shown as positive gray-scale images or with the contrasts inverted by inverting the pixel luminance values (relative to the image mean; Figure 8). Aftereffects were then assessed as before for both opposing adaptation to opposite distortions in the negative and positive images and simple adaptation to either the positive or negative distortion.

## Results

Figure 9 plots the pattern of the aftereffects following adaptation to the positive and negative faces. Opposing adaptation induced simultaneous shifts in opposite directions for the two types of images, thus resulting in changes in the null settings that were clearly selective for the adapting polarity (see Table 5). Thus, like spatial frequency and size, the adaptation aftereffect was also contingent on contrast polarity. Moderately strong selectivity is also suggested by the results for nonopposing adaptation, as again confirmed by a significant three-way interaction between adapt polarity, test polarity, and adapt distortion (see Table 6). In this case, adaptation to positive contrast showed more transfer to test images of negative contrast than vice versa, $t(8) = -3.09, p < .01$. This asymmetry may parallel the asymmetries in contrast coding in face recognition. However, like the previous reports for upside-

Table 3
*Two-Way Within-Subject Analysis of Variance of the Mean Changes in the Null Settings for Low- and High-Frequency Test Faces Following Adaptation to Opposing Distortions (Expanded vs. Contracted) in Low- and High-Frequency Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt (low-expanded / high-contracted vs. low-contracted / high-expanded) | 1, 4 | 0 | *ns* |
| Test frequency (low vs. high) | 1, 4 | 4.39 | *ns* |
| Adapt vs. test frequency | 1, 4 | 19.5 | <.05 |

Table 4
*Three-Way Within-Subject Analysis of Variance of the Mean Changes in the Null Settings for Low- and High-Frequency Test Faces Following Adaptation to Nonopposing Distortions in Low- and High-Frequency Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt frequency (low vs. high) | 1, 4 | 5.03 | NS |
| Test frequency (low vs. high) | 1, 4 | 0.09 | NS |
| Adapt distortion (expanded vs. contracted) | 1, 4 | 91.0 | <.001 |
| Adapt frequency × Test Frequency | 1, 4 | 0.84 | NS |
| Adapt frequency × Adapt Distortion | 1, 4 | 0.02 | NS |
| Test Frequency × Adapt Distortion | 1,4 | 2.71 | NS |
| Adapt Frequency × Test Frequency × Adapt Distortion | 1, 4 | 32.2 | <.01 |

down images, aftereffects were strong with the contrast-inverted stimuli.

## Experiment 4: Mean Contrast

We next compared the aftereffects for face images that had the same contrast polarity but differed in absolute contrast. These conditions were in part of interest because face-selective cells show responses that are largely invariant with contrast (Rolls & Baylis, 1986), and contrast adaptation shows a strong contrast dependence (Georgeson, 1985). We therefore again asked which pattern the face aftereffects might follow.

### Method

*Subjects.* Observers included authors JY and MW and three additional subjects.

*Stimuli and procedure.* High-contrast images were shown at the original contrast, and the low-contrast images were reduced to 10% of this value (see Figure 10). The same procedures were followed to assess the aftereffects after opposing adaptation to the two contrast levels or adaptation to each individual level.

### Results

Results for these conditions are shown in Figure 11. In this case, the aftereffects showed very little selectivity for the two stimulus levels. Mean shifts in the nulls for the opposing adaptation were near zero and thus nonselective (see Table 7). Moreover, the opposing adaptation this time showed a significant difference in the size of the aftereffects for the two contrast levels, $t(8) = 1.84$, $p = .05$. Specifically, in this case the indices for low contrast tend to be negative, which suggests that the low-contrast tests were biased more by the high-contrast adapting faces than the low-contrast ones. This asymmetry is also clearly evident when observers adapted to a single image. High-contrast adapting faces produced largely nonselective change in both high- and low-contrast tests, whereas low-contrast adaptors were more selective than their high-contrast counterparts, $t(8) = 6.05$, $p < .01$, presumably because they had only a weak influence on the high-contrast tests. As a result, the overall selectivity for contrast levels

*Figure 8.* Examples of the positive and negative contrast images used to measure selectivity for contrast polarity.

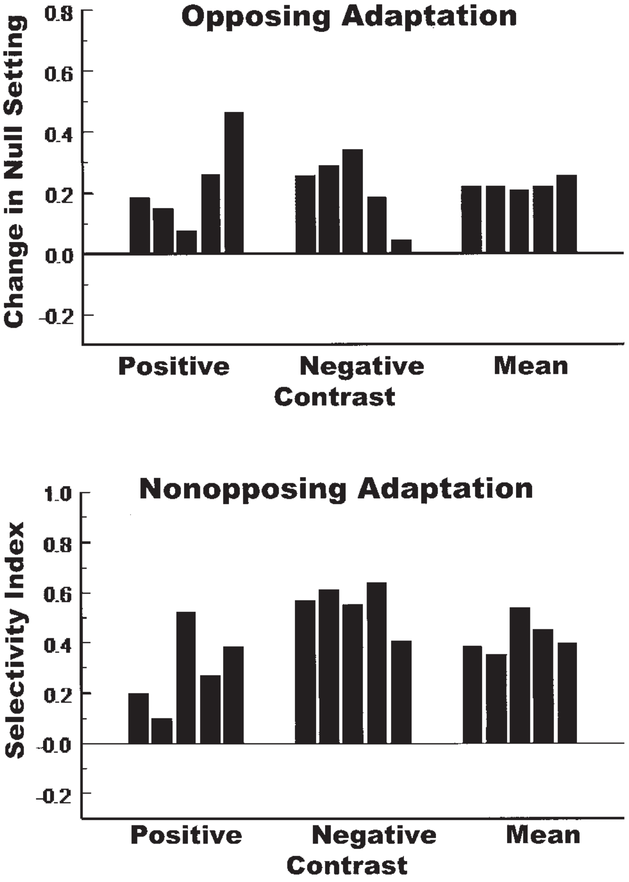

*Figure 9.* Estimates of the selectivity of the aftereffects for the positive and negative contrast images (see Figure 5 legend).

Table 5
*Two-Way Within-Subject Analysis of Variance of the Mean Changes in the Null Settings for Positive- and Negative-Polarity Test Faces Following Adaptation to Opposing Distortions (Expanded vs. Contracted) in Positive- and Negative-Polarity Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt (positive-expanded / negative-contracted vs. positive-contracted / negative-expanded) | 1, 4 | 2.06 | *ns* |
| Test polarity (positive vs. negative) | 1, 4 | 3.97 | *ns* |
| Adapt vs. test polarity | 1, 4 | 50.4 | <.01 |

Table 6
*Three-Way Within-Subjects Analysis of Variance of the Mean Changes in the Null Settings for Positive- and Negative-Polarity Test Faces Following Adaptation to Nonopposing Distortions in Positive- and Negative-Polarity Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt polarity (positive vs. negative) | 1, 4 | 7.10 | *ns* |
| Test polarity (positive vs. negative) | 1, 4 | 0.75 | *ns* |
| Adapt distortion (expanded vs. contracted) | 1, 4 | 21.9 | <.01 |
| Adapt Polarity × Test Polarity | 1, 4 | 10.7 | <.05 |
| Adapt Polarity × Adapt Distortion | 1, 4 | 0.88 | *ns* |
| Test Polarity × Adapt Distortion | 1, 4 | 2.51 | *ns* |
| Adapt Polarity × Test Polarity × Adapt Distortion | 1, 4 | 87.4 | <.001 |

was not significant (see Table 8). Thus, the results suggest that there is in fact little selectivity for contrast, and that aftereffects are stronger for higher contrast adaptation, which is a pattern that is similar for grating contrast (Georgeson, 1985).

## Experiment 5: Color

The final image property that we examined was stimulus color. In this case, the gray-scale images were replaced by images that again varied in luminance but differed in mean chromaticity. Orientation and size aftereffects for simple two-dimensional patterns such as gratings show selectivity for mean color (Hardy & De Valois, 2002), so that aftereffects for complex naturalistic images like faces might similarly show a contingency for color. On the other hand, shape-from-shading cues are largely restricted to luminance variations in the stimulus and thus are not carried by color (Cavanagh & LeClerc, 1989). Thus, aftereffects that were more tied to the three-dimensional interpretation of the patterns might be expected to show little dependence on color.

### *Method*

*Subjects.* Observers included authors JY and MW and three additional subjects. MW made settings only for opposing adaptation.

*Stimuli and procedure.* Selectivity for color was tested by opposing adaptation to pairs of distortions defined by red and green images. The red and green chromaticities were chosen from the monitor's phosphors. This provided the largest attainable color differences in the images, and thus should be the most likely to produce a measurable effect. These are also the colors typically used in studies of contingent color aftereffects like the McCollough effect, as described next (Stromeyer, 1978). The red and green images were equated for luminance by flicker-photometric matching between green and red faces presented in rapid alternation. Specifically, the red image was shown at the highest luminance available, and then observers adjusted the luminance of the green face in order to minimize luminance flicker between the red and green images.

*Figure 10.* Examples of the high- and low-contrast images used to measure selectivity for contrast level.

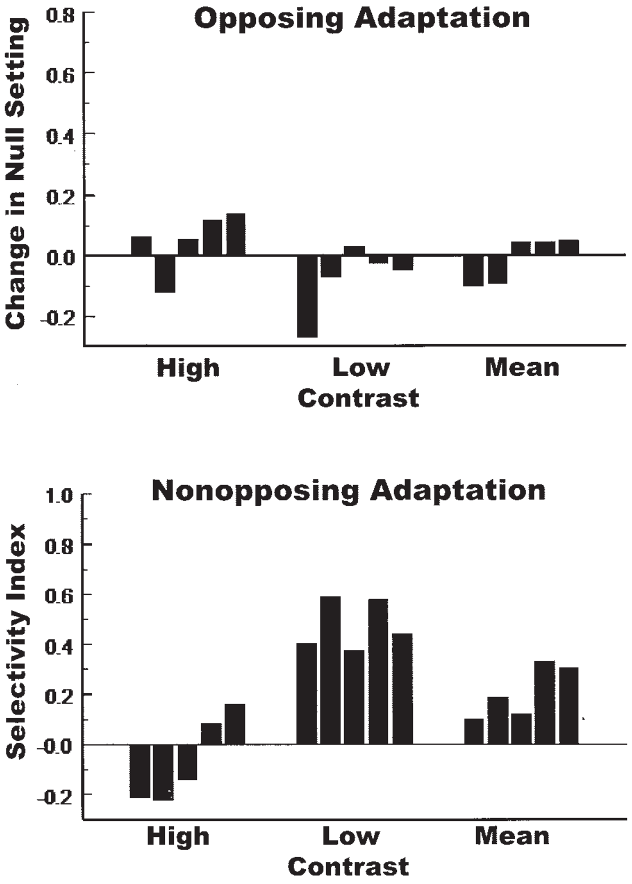

*Figure 11.* Estimates of the selectivity of the aftereffects for the high- and low-contrast images (see Figure 5 legend).

### *Results*

Opposing adaptation to the red–green face pairs produced little aftereffect in the appearance of the test faces (see Figure 12). Yet despite this, the interaction between adapt color and test color was significant, suggesting some degree of selectivity for color (see Table 9), and a significant three-way interaction was also found for the nonopposing conditions (see Table 10). Surprisingly, the non-

Table 7
*Two-Way Within-Subjects Analysis of Variance of the Mean Changes in the Null Settings for Low- and High-Contrast Test Faces Following Adaptation to Opposing Distortions (Expanded vs. Contracted) in Low- and High-Contrast Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt (low-expanded / high-contracted vs. low-contracted / high-expanded) | 1, 4 | 2.88 | *ns* |
| Test contrast (low vs. high) | 1, 4 | 0 | *ns* |
| Adapt vs. test contrast | 1, 4 | 0.01 | *ns* |

Table 8
*Three-Way Within-Subject Analysis of Variance of the Mean Changes in the Null Settings for Low- and High-Contrast Test Faces Following Adaptation to Nonopposing Distortions in Low- and High-Contrast Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt contrast (low vs. high) | 1, 4 | 5.31 | *ns* |
| Test contrast (low vs. high) | 1, 4 | 0.04 | *ns* |
| Adapt distortion (expanded vs. contracted) | 1, 4 | 15.4 | <.05 |
| Adapt Contrast × Test Contrast | 1, 4 | 0.27 | *ns* |
| Adapt Contrast × Adapt Distortion | 1, 4 | 7.75 | *ns* |
| Test Contrast × Adapt Distortion | 1, 4 | 1.93 | *ns* |
| Adapt Contrast × Test Contrast × Adapt Distortion | 1, 4 | 1.10 | *ns* |

opposing adaptation also showed a strong asymmetry—adaptation was more selective for the red faces than the green faces, $t(6) = 4.83, p < .01$. We are uncertain of the basis for this difference. The asymmetry parallels the difference between high-contrast and low-contrast images, and might thus reflect differences in the effective contrasts of the red and green images. Alternatively, it is at least conceivable that the difference is related to the possibility that red is a more plausible color of skin pigmentation. However, the red chromaticity far exceeded the chromaticities of skin, and we have no other evidence bearing on this possibility.

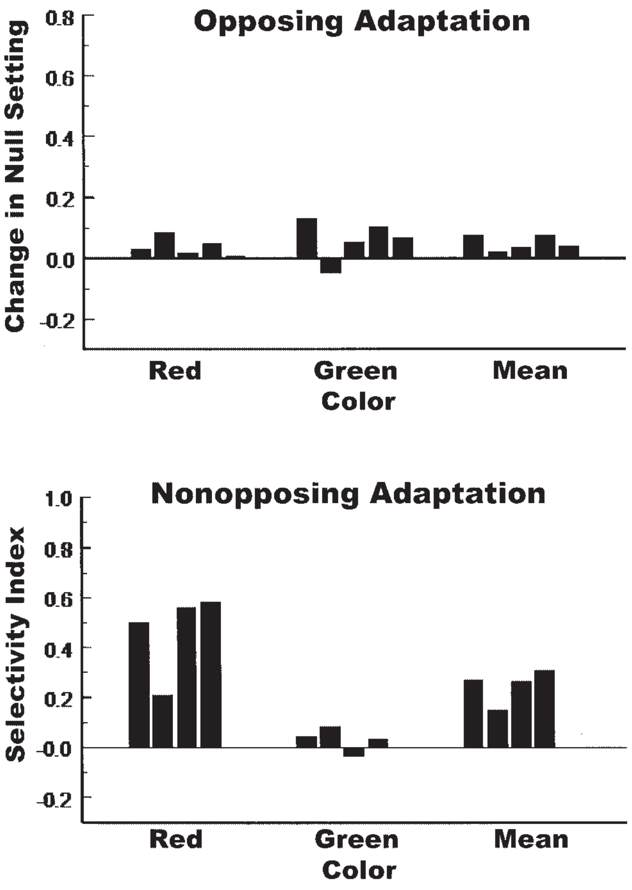

*Figure 12.* Estimates of the selectivity of the aftereffects for the red and green face images (see Figure 5 legend).

Table 9
*Two-Way Within-Subject Analysis of Variance of the Mean Changes in the Null Settings for Red and Green Test Faces Following Adaptation to Opposing Distortions (Expanded vs. Contracted) in Red and Green Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt (red-expanded / green-contracted vs. red-contracted / green-expanded) | 1, 4 | 0.53 | *ns* |
| Test color (red vs. green) | 1, 4 | 0.24 | *ns* |
| Adapt vs. test contrast | 1, 4 | 21.5 | <.05 |

The weak aftereffects for opposing color adaptation were further confirmed in control settings for three observers (not shown) who adapted to the colored images cropped into ovals. This was done to reduce the perception that the faces were gray-scale images viewed through a transparent color filter. However, the aftereffects for these conditions remained comparable to the full images. As a further test of the selectivity for color, we also tried to induce a converse aftereffect by asking whether the perceived color of a test face could be made contingent on the face's form. This experiment was similar to the paradigm used in the McCollough effect, in which observers are adapted to red–vertical bars alternated with green–horizontal bars (McCollough, 1965). After adaptation, a vertical achromatic grating appears tinged with green, and a horizontal test grating appears reddish. Thus, the McCollough effect reveals a negative color aftereffect that is contingent on the orientation of the adapting gratings, which implies a sensitivity change that is jointly selective for color and orientation. We therefore asked whether a color aftereffect in the gray-scale faces could be made contingent on the distortion in the adapting faces. Observers again adapted to an alternation between red–expanded and green–contracted faces or vice versa, but this time judged the perceived color of an expanded or contracted achromatic face. To maximize the chance of detecting a color aftereffect, the adaptation time was increased from 120 s to 600 s, a duration that is typical for studies of the McCollough effect. However, following this adaptation, no color biases were visible in the gray test images. Thus, for the conditions tested there was no evidence for a form-contingent color aftereffect in the face images. This result is consistent with the results for opposing adaptation of Figure 12 in showing only weak color selectivity in the figural aftereffects for faces.

Table 10
*Three-Way Within-Subject Analysis of Variance of the Mean Changes in the Null Settings for Red and Green Test Faces Following Adaptation to Nonopposing Distortions in Red and Green Adapting Faces*

| Source of variance | *df* | *F* | *p* |
|---|---|---|---|
| Adapt color (red vs. green) | 1, 3 | 0.32 | *ns* |
| Test color (red vs. green) | 1, 3 | 0.52 | *ns* |
| Adapt distortion (expanded vs. contracted) | 1, 3 | 53.1 | <.01 |
| Adapt Color × Test Color | 1, 3 | 0.89 | *ns* |
| Adapt Color × Adapt Distortion | 1, 3 | 0.38 | *ns* |
| Test Color × Adapt Distortion | 1, 3 | 10.1 | *ns* |
| Adapt Color × Test Color × Adapt Distortion | 1, 3 | 26.8 | <.05 |

## Experiment 6: Stimulus Selectivity and Subjective Similarity

Figure 13 replots the mean selectivity for each of the five stimulus dimensions that we examined. On the graphs, these dimensions have been ordered from least to greatest selectivity. This ordering is similar for both the opposing and the nonopposing adaptation, and in this case the size of the indices for the opposing adaptation can now be normalized by comparing them across the different conditions. The bar charts show that the aftereffects were more strongly contingent on spatial frequency differences and contrast polarity differences in the faces, whereas they showed relatively more transfer across differences in size and—strongly but asymmetrically—differences in color or mean contrast. Differences in mean selectivity across the five stimulus conditions were confirmed with a one-way ANOVA. The effect of adapting condition was significant for both opposing adaptation, $F(4, 19) = 12.66$, $p < .01$, and nonopposing adaptation, $F(4, 18) = 11.53$, $p < .01$. (This comparison must be qualified because it assumes that we tested comparable stimulus differences along each dimension, yet there is no simple way to equate differences, e.g., in size or color. However, in each case, these differences were large and very salient, and thus it is unlikely that the variations in selectivity are an artifact of the choice of stimulus levels.)

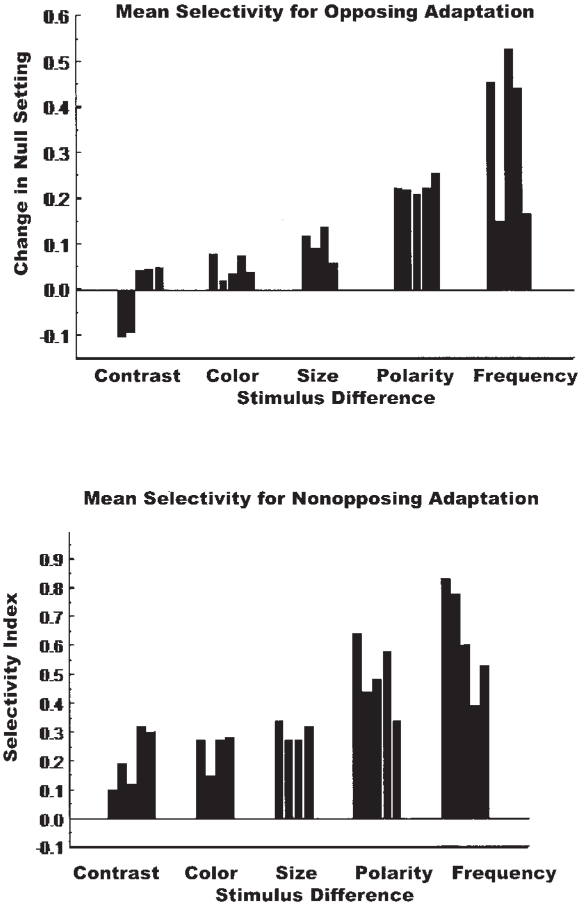

*Figure 13.* Mean selectivity compared for the different stimulus dimensions. Each bar represents the mean estimate for a single subject. Upper panel plots the difference in null settings for expanded or contracted adaptation in the opposing condition, and the lower panel plots selectivity estimated from the nonopposing adaptation settings. For both, the different stimulus dimensions have been ordered from least selective (mean contrast) to most selective (spatial frequency).

What pattern might the results for these different stimulus dimensions reflect? As we noted in the introduction, one possible interpretation is that each reveals a different low-level coding property of the adapted channels. By this account, the adaptation may be altering sensitivity in mechanisms that are tuned for spatial frequency and contrast polarity but less so for color, mean contrast, or size. However, an alternative possibility is that the adaptation is not directly varying with these stimulus dimensions, but only indirectly varying according to how these dimensions alter processes that might be important in face or object coding. For example, inspection of the images used in the different experiments suggests that changing the frequency or polarity of the images had comparatively larger effects on the perceived configural properties of the face. Thus, the degree of transfer in the adaptation may be related to the perceived similarity of the stimuli as faces, and not simply to physical differences in the low-level properties that we varied. That is, by this account, stimulus changes that preserved the perceived identity of the images may have resulted in stronger interactions during adaptation and thus less selectivity in the aftereffects. To explore this possibility, we examined how selectivity was related to the subjective similarity of the face images.

### *Method*

*Subjects.* Settings were made for four new naive observers who had not participated in the adaptation experiments.

*Stimuli and procedure.* Subjects viewed a display with two pairs of images. The top and bottom pair showed the two stimulus levels from different adapting dimensions (e.g., the undistorted red and green images on the top and the undistorted large and small images on the bottom). They were then asked to select the pair that appeared more similar as faces, and specifically, which pair appeared more like they had been photographed from the same original face. Ratings were made for each possible pairing of the five stimulus dimensions.

### *Results*

Table 11 shows the rank ordering of the five dimensions for each observer. A value of 1 indicates that the two faces for that stimulus pair appeared most similar (i.e., most often chosen over other pairs), and a value of 5 corresponded to least similar. The rankings show that the faces defined by different frequency bands or different contrast polarities appeared least similar, and the image pairs defined by differences in color, contrast, or size were similar. Table 11 also shows the mean selectivity of the adaptation effects for either opposing or nonopposing adaptation. There is good agreement between the rank orderings for all three measures. Thus, this is consistent with the possibility that the contingencies underlying the adaptation in part reflect the perceived similarity of the stimuli as faces.

## Experiment 7: Individual Faces

Such considerations led us in the final experiment to ask whether the adaptation could be selective for the stimulus properties that distinguish actual individuals. The physical differences by

Table 11
*Rank Ordering of the Stimulus Pairs Defined by Different Stimulus Dimensions*

| Observer and mean | Contrast | Color | Size | Polarity | Frequency |
|---|---|---|---|---|---|
| Observer 1 | 1 | 2 | 3 | 4 | 5 |
| Observer 2 | 2 | 3 | 1 | 4 | 5 |
| Observer 3 | 4 | 2 | 1 | 3 | 5 |
| Observer 4 | 2 | 2 | 4 | 4 | 4 |
| Mean | 2.1 | 2.1 | 2.25 | 3.75 | 4.75 |
| Mean null difference: opposing | −0.01 | 0.05 | 0.10 | 0.23 | 0.35 |
| Mean selectivity: nonopposing | 0.21 | 0.24 | 0.30 | 0.50 | 0.63 |

*Note.* 1 = *Most Similar* and 5 = *Least Similar Relative to the Other Pairs.* Mean ranks are compared with the mean selectivity for opposing and nonopposing adaptation to each stimulus dimension.

which we discriminate between faces are often subtle. An aftereffect that depended on general stimulus properties such as the overall expansion and contraction of the face might thus be expected to strongly transfer across individual faces. Evidence for this transfer was reported by Webster and MacLin (1999), who found that adapting to distortions in one face could strongly affect the appearance of other individuals (see also Leopold et al., 2001 and Rhodes et al., 2003). However, because they adapted to only a single face at a time, the presence of a selective component was not fully evaluated. To the extent that the adaptation is instead tapping a level that reflects the perceptual salience of individual differences, rather than their physical differences, aftereffects might show clear selectivity for individuals. To explore this, we examined to what extent the aftereffects could be made contingent on different individual faces.

### *Method*

*Subjects.* Observers included authors JY and MW and two additional subjects.

*Stimuli and procedure.* In order to assess the aftereffects for a set of faces that varied systematically in perceived similarity, observers first arranged a set of seven faces from the Matsumoto and Ekman (1988) set by ordering them from most similar to least similar relative to the face shown in Figure 1. Rankings by the subjects showed close agreement. From the ranked set, we then chose the face that was rated most like this face, least like it, and the intermediate image from the set. The four faces are shown in Figure 14 as faces A (original), B (most similar), C (intermediate similarity), and D (least similar). Each face was again distorted to form an array of test and adapting images. The observers adapted to opposing distortions in each of the six different possible pairs of faces, and then made settings for all four of the different test faces.

### *Results*

Figure 15 plots the aftereffects by showing the selectivity for each face pair with a separate bar chart for each subject. Again, for three of the subjects each bar represents the difference in the stimuli that appeared undistorted after adapting to the expanded or contracted face. Observer JM was instead tested for only a single distortion in each adapting face (expanded or contracted), and thus her shifts are plotted as the difference relative to the setting under neutral adaptation.

The filled bars in Figure 15 show the shifts in the settings for the two test faces that formed the pair of opposing adapting faces with each pair indicated along the *x*-axis. As before, positive selectivity for these faces means that they were biased consistent with the same-face adaptation even though the different-face adaptation was distorted in the opposite way. If there were no contingent adaptation, then the values should have a zero mean and be randomly distributed above or below this mean. Instead, only 1 of the 46 values is negative, a pattern that by a simple sign test is highly significant. Thus, these opposing face pairs show that the adaptation can be clearly selective for different individual faces.

The unfilled bars show the shifts in the two faces that were not part of the adapting pair (e.g., changes in the appearance of faces C and D after adapting to opposite distortions in A vs. B). The direction of these changes could follow either of the oppositely distorted adapting faces. The letter below each bar indicates which face in the adapting pair the test shifted with (and are left blank if the shift was less than one step of the image array). These labels again show that the settings for the opposing test faces (filled bars) almost always followed the same-face adaptation. For the remaining two faces, the pattern for which faces they follow is less obvious. However, if the adaptation was selective for the specific individual face, then we might expect the shifts in the settings for the two individuals that were part of the adapting pair to be larger than the shifts for the two that were not adapted to. Thus, comparing the aftereffects for the adapted versus not-adapted test faces provides another measure of selectivity. For observer JY, there was not a significant difference between the two pairs, $t(22) = .59$, *ns*, whereas the same-face shifts were larger for MW, $t(22) = 2.46$, $p < .05$; YM, $t(22) = 3.04$, $p < .01$; and JM, $t(18) = 5.91$, $p < .01$. Thus, this further suggests that the aftereffects are selective for whatever properties distinguish images of actual faces.

Figure 16 further examines the contingencies between all four faces by testing whether two faces were biased in a similar way across all of the different adapting conditions. The scatter plots compare the aftereffects for each of the six possible pairs of test images. In all but one case, the shifts are not significantly correlated, which indicated that the adaptation essentially affected the two faces independently. The exception is for faces B and C, which show a significant correlation ($r = .59$, $p < .05$). This suggests that these two faces tended to behave as similar test stimuli in the adaptation (though this is not evident in the settings for all three observers). As inspection of the images in Figure 14 suggests, it may be that faces B and C were perceptually the most similar pair and thus that the selectivity in the adaptation again paralleled the perceptual similarity of the stimuli. In any event, the present results show that the adaptation can be selective for differences in identity even though the images were very similar in terms of the low-level stimulus dimensions we varied.

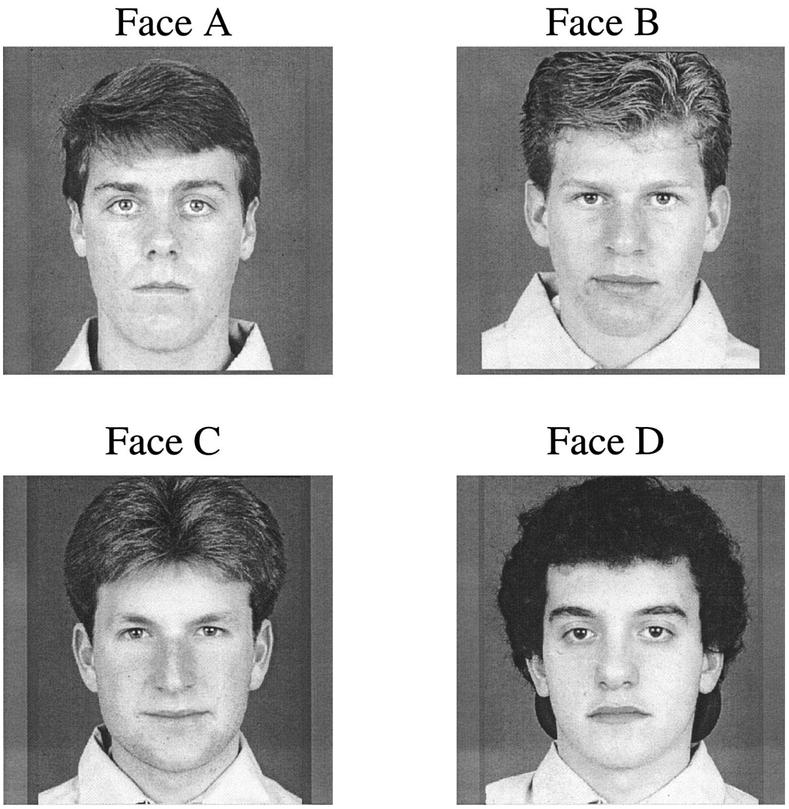

*Figure 14.* Faces used to test transfer of adaptation between different individual faces. Faces were ranked according to how similar they appeared to face A. Face B was ranked most similar, face D least similar, and face C was intermediate in similarity.

## Discussion

That the perception of faces can be easily biased by brief exposures to different faces suggests that the processes of face recognition may be highly susceptible to adaptation (Webster & MacLin, 1999). In this study we explored how these adjustments depend on the stimulus relationships between the adapt and test stimuli. Before evaluating these, it is important to note that adaptation occurs throughout the visual system (Webster, 2003). Thus, it is unreasonable to suppose that our face images do not lead to adaptation at early visual loci—from simple afterimages owing to local light adaptation to possible contrast and pattern-selective aftereffects owing to simple spatial or chromatic properties of the images. However, it remains of considerable interest to ask to what extent the aftereffects might also reflect higher-level properties of the images. With this in mind, we summarize and evaluate the results for each of the dimensions we examined in terms of both the image dimensions we varied and how those dimensions might influence face processing.

### *Form*

Our results replicate the reports of Zhao and Chubb (2001) and Leopold et al. (2001) in showing strong transfer across image size. In particular, we found that adaptation followed the perceived configuration of the faces even when the positions of local features predicted the opposite aftereffects. Simple figural aftereffects can be strongly dependent on the spatial location of features (Whitaker, McGraw, & Levi, 1997). That the face adaptation instead depends on configuration despite differences in size and position implies sensitivity changes in mechanisms that encode configural information. On the other hand, some selectivity was also observed for size (see also Zhao & Chubb, 2001). This could be because lower level mechanisms tuned to size were also adapted or because size itself is also a dimension that is represented at the level of configural processing.

In contrast to size, we found much weaker transfer across changes in spatial frequency. This might be predicted from low-level pattern aftereffects, which show strong selectivity for spatial frequency (Blakemore & Sutton, 1969). However, as we noted, an alternative is that bandpass filtering of the images altered their effective identity so that low-frequency and high-frequency images appeared to be drawn from different faces. This account is given some credence by our finding that aftereffects were selective for different individual faces. The present results do not allow us to discriminate between these alternatives, and it may in fact be that the sensitivity changes are selective at both levels, thus leading to the highly specific aftereffects we found for the high- and low-frequency bands.

### *Contrast*

Strong aftereffects were found for both positive and negative polarity-adapting stimuli, and these were also strongly selective

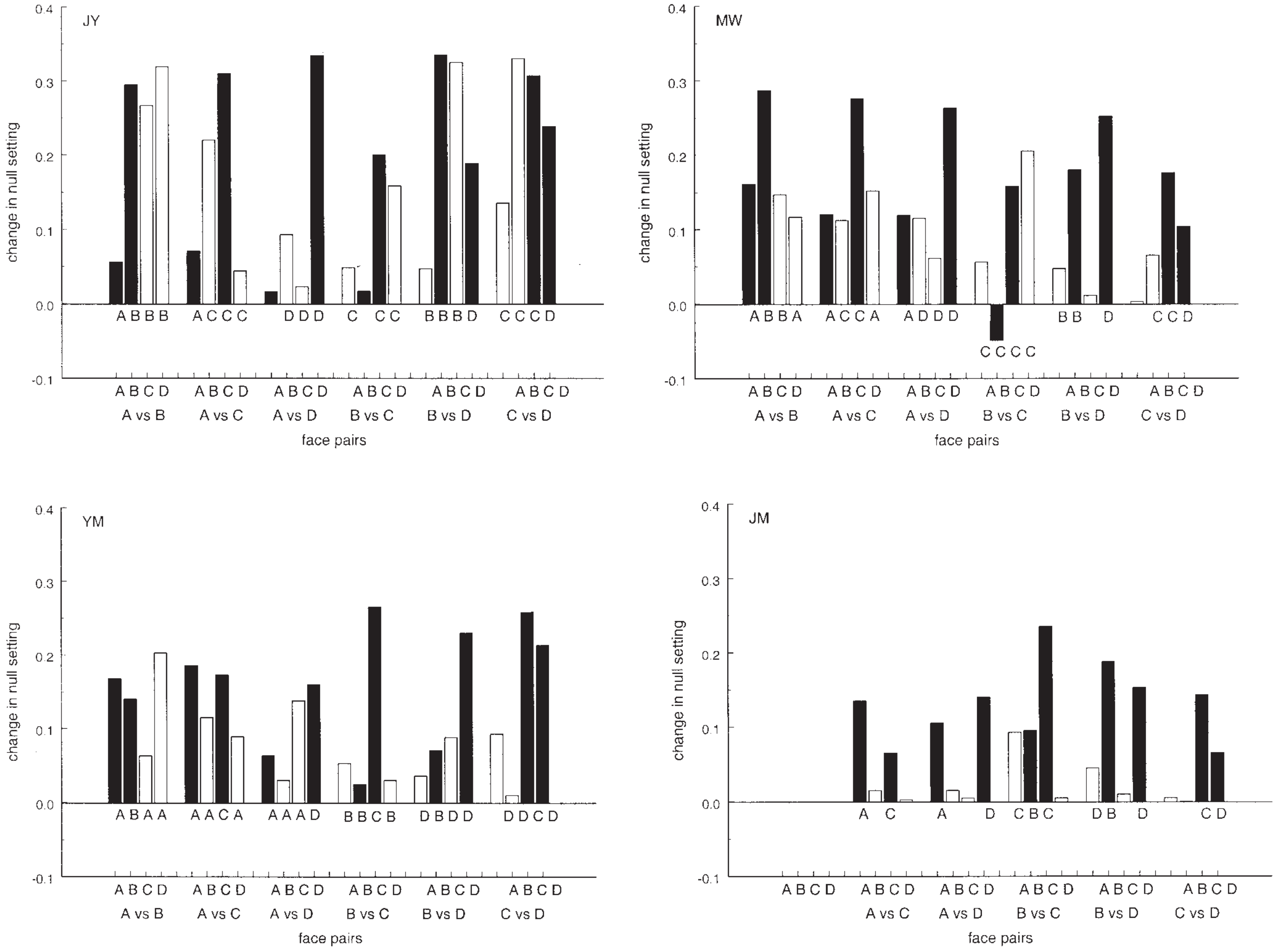

*Figure 15.* Selectivity of adaptation for distortions in different faces. The four panels plot the results for 4 observers. Filled bars show the change in settings for a single face (e.g., A or B) after adapting to opposing distortions in the same face and a different face (e.g., A vs. B). Unfilled bars show the shifts in the two remaining test faces (e.g., C and D) that were not part of the adapting pair. Each of the six adapting pairs is shown along the *x*-axis. Letters under each bar indicate which of the two opposing adapting faces the test face was more strongly biased by.

when observers adapted to opposing distortions presented in the positive and negative images. A recent study has also demonstrated analogous contingent aftereffects between upright and upside-down faces (Rhodes et al., 2004). The pronounced adaptation for contrast-reversed patterns is surprising in light of the poorer recognition for these images but is consistent with previous reports of strong and selective aftereffects for spatially inverted images (Leopold et al., 2001; Watson & Clifford, 2003; Webster & MacLin, 1999; Zhao & Chubb, 2001). As we noted, in this sense the aftereffects do not clearly implicate face-specific processing. That is, we might have expected distortions in inverted images to be less recognizable, and therefore these images might be less potent as adapting stimuli. However, to fully evaluate this possibility, it would be important to quantify the actual extent to which recognition is impaired in the inverted images, and then compare the aftereffects for perceptually equivalent distortions in the upright and inverted images. If aftereffects are strong for faces with inverted contrast or orientation, and if the adaptation strongly transfers across changes in size and orientation, then it is somewhat surprising that there is also strong selectivity between a face and its inverted image. One proposed explanation for this selectivity is that the positive and inverted faces adapt separate pools of face-specific and object-specific mechanisms (Rhodes et al., 2004). A further possibility is that inversion alters the identity of the face and thus is another example of an identity-specific aftereffect.

### Color

Recent studies have shown that color can play a significant role in face recognition, particularly when the images are spatially degraded (Tarr, Kersten, Cheng, & Rossion, 2001; Yip & Sinha, 2002) and may be an explicit property of object representations (Naor-Raz, Tarr, & Kersten, 2003). However, the aftereffects for faces showed only weak selectivity for color. Some influence of color might be expected from the color-contingent aftereffects

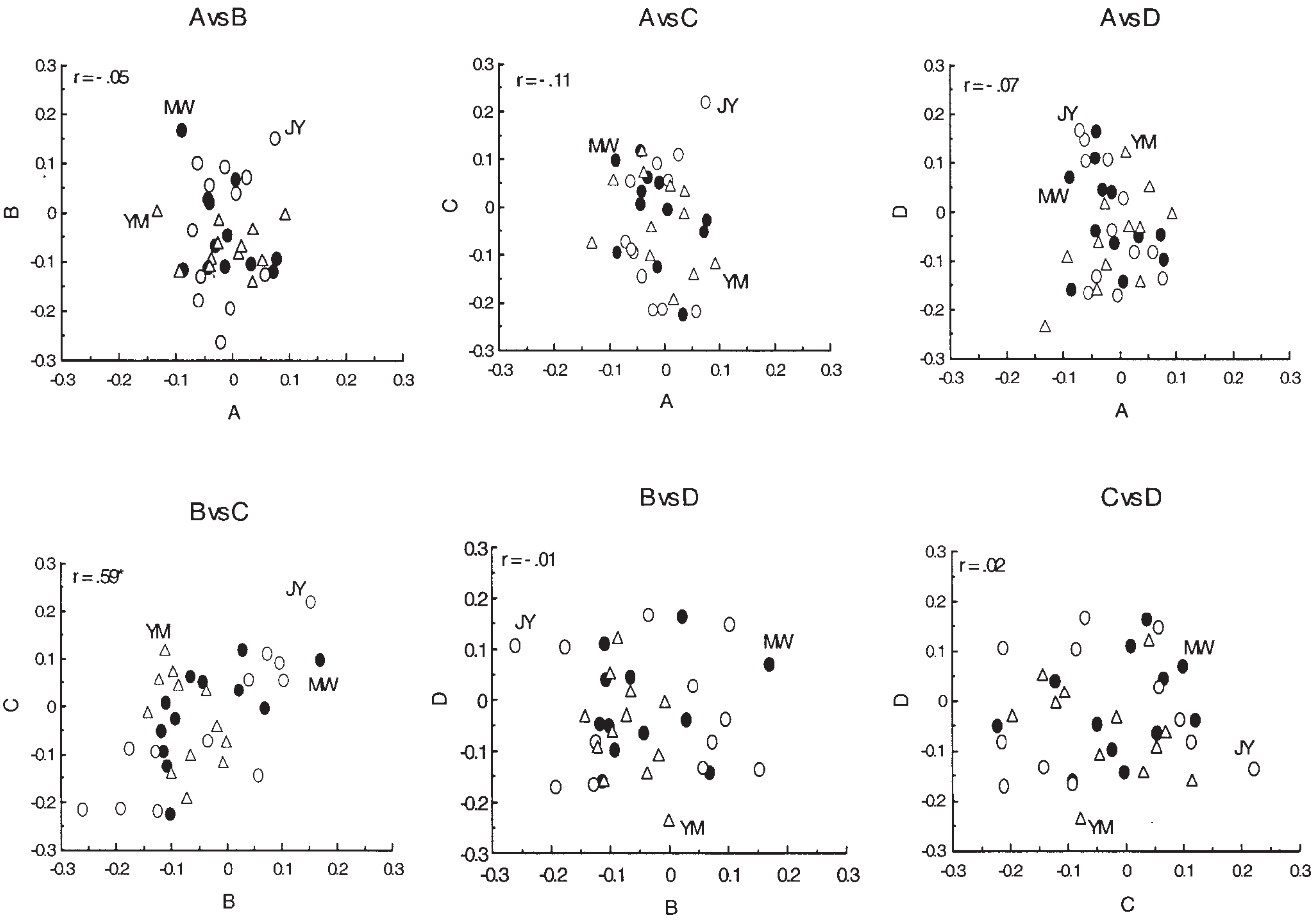

*Figure 16.* Scatterplots of the settings for different pairs of individual faces. Each point compares the shift in two different faces after adapting to a given face pair for observer JY (filled circles), MW (unfilled circles), and YM (triangles). Numbers in each panel give the correlation between the settings for each pair. This was significant only for pair B versus C.

found for simple grating patterns. Both orientation (Flanagan, Cavanagh, & Favreau, 1990) and spatial frequency (Hardy & De Valois, 2002) shifts following adaptation are selective for the color directions defining the patterns. In our case, color was introduced as a mean chromaticity change in the luminance-varying images. It is likely that much greater selectivity would be found if we instead compared luminance-varying versus isoluminant color-varying images, because these lead to independent sensitivity changes in contrast adaptation (Bradley, Switkes, & De Valois, 1988). It is also possible that the colors we used were ineffective because they were outside the gamut of natural variations in complexions. The stimuli we did use are analogous to the grating stimuli in McCollough effects. However, we were also unable to induce a color aftereffect in the faces that was contingent on the facial distortion. The extent to which McCollough-like effects can be observed for arbitrary spatial patterns (e.g., English text) remains unclear (Allan, Siegel, Collins, & MacQueen, 1989; Humphrey, Skowbo, Symons, Herbert, & Grant, 1994). The differences between our distortions were very large, and faces are arguably highly significant spatial patterns. Thus, it is not a priori obvious that they should fail to support a contingent color aftereffect. However, this failure could again arise if the color changes do not appreciably alter the perceived identity of the faces. It would be of interest to test this possibility by measuring whether color-contingent aftereffects become manifest when the two faces are drawn from different individuals.

### Facial Identity

The suggestion that face aftereffects are related to the identity of the face is motivated in part by our finding that the relative selectivity for the different stimulus dimensions parallels differences in the subjective similarity of the stimuli as faces. Thus, differences in mean contrast, color, or size showed stronger transfer across the stimulus levels, but differences across these levels did little to alter the recognizability of the face. Alternatively, changes in contrast polarity or spatial frequency were more selective and at the same time had larger effects on perceived similarity. Consistent with this, we also found that the adaptation was selective for actual differences between individual faces. Selective aftereffects for different individual faces have also been recently reported by Rhodes et al. (in press). Moreover, the aftereffects show selectivity for natural face attributes such as differences in gender and ethnicity (Ng, Kaping, Webster, Anstis, & Fine, 2003).

If the aftereffects are tuned for identity, it remains unclear which aspects of the image this depends on, for the featural and configural information that determine face recognition remains itself very poorly understood. For the stimuli we examined, the aftereffect depends on adapting to an image that has been distorted into a new configuration (and which also alters the shapes of features, e.g., by differentially contracting or expanding the nose). Thus, these configural (and featural) differences alone cannot be the basis for the selectivity. Yet the distorted faces remain perceptually similar in the way, for example, that an individual appears similar despite changes in expression. Presumably it is this similarity that allows the test and adapting images to interact. This is consistent with accounts of face processing that assume that the representation depends upon coding faces relative to a norm or prototype, and with the idea that these prototypes can be updated through new examples and thus biased by adaptation to a specific example (Hurlbert, 2001; Leopold et al., 2001; Rhodes et al., in press). The prototype for a face must be extracted from a set of distributed samples, for any given instance of the face is highly variable (Bruce, 1994; Solso & McCarthy, 1981). This raises the intriguing question of which images should contribute to the development or fine-tuning of a prototype, because these should be chosen only from the set of stimuli that fall within the appropriate category (Rosch, 1975). Clearly, a generic prototype for faces should be built on images that are in some way classified as a face. In the same way, the norm for a specific face or a specific attribute (such as gender) should in part be based on the subset of images that are admitted as possible examples of the relevant face or attribute. By this account, the distortions we introduced to measure the aftereffects are influencing both generic and identity-specific prototypes for faces. Generic norms are suggested because adaptation to one set of faces can strongly bias the appearance of a different set of faces (Rhodes et al., 2003; Webster et al., 2004; Webster & MacLin, 1999). (If the distortions were instead so extreme that they destroyed the impression that the adapting image was a face, then we might instead expect little aftereffect, or alternatively, aftereffects that were not tied to face coding.) However, because these distortions are also introduced into a specific face, the aftereffects for them may also reflect identity-specific aftereffects. Changes in color, mean contrast, or size may represent smaller deviations from the identity-specific prototype and thus allow stronger interactions between the adapt and test stimuli, whereas changes in frequency or contrast polarity may more readily transcend face-specific boundaries and consequently lead to weaker interactions. Finally, to the extent that the distortions themselves created new faces, the aftereffects we measured may have more strongly biased generic face norms. That is, the selectivity for identity (e.g., between actual face images) might be even stronger when the adapting distortions are weaker because the adapting faces might then be tied more closely to the specific face that was distorted.

Although this hypothesis remains tentative, it at least raises the possibility that the aftereffects for faces reflect adjustments in processes that are tied closely to face perception—and in particular, to processes that must allow us to differentiate between faces based on very small physical differences while allowing us to recognize the same face from physically very different images. As noted in the introduction, there is a wealth of evidence for mechanisms specialized for face coding, and it seems plausible to assume that these mechanisms can adapt—in the same way as other cortical processes—to adjust to the specific stimulus dimensions that they encode. Selectivity of the adaptation for the perceived similarity or identity of faces would be a natural consequence of adaptation at such sites.

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Received October 7, 2002
Revision received May 6, 2004
Accepted October 18, 2004 ■