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Face Aftereffects Predict Individual Differences in Face Recognition Ability

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Abstract

Face aftereffects are widely studied on the assumption that they provide a useful tool for investigating face-space coding of identity. However, a long-standing issue concerns the extent to which face aftereffects originate in face-level processes as opposed to earlier stages of visual processing. For example, some recent studies failed to find atypical face aftereffects in individuals with clinically poor face recognition. We show that in individuals within the normal range of face recognition abilities, there is an association between face memory ability and a figural face aftereffect that is argued to reflect the steepness of broadband-opponent neural response functions in underlying face-space. We further show that this correlation arises from face-level processing, by reporting results of tests of nonface memory and nonface aftereffects. We conclude that face aftereffects can tap high-level face-space, and that face-space coding differs in quality between individuals and contributes to face recognition ability.

Keywords

face perception, individual differences, cognitive ability, visual memory, performance

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Most humans have a remarkable ability to recognize faces, although there are surprisingly large individual differences in this ability (Bowles et al., 2009; Wilmer et al., 2010). In the study reported here, we investigated whether these individual differences might be partially attributable to the quality of face-space coding (Fig. 1), as measured using figural face aftereffects (Fig. 2a). It has been argued that face-space facilitates individuation of faces (Valentine, 1991), and the widespread investigation of face aftereffects is based on the common assumption that they reflect face-space coding (Leopold, O'Toole, Vetter, & Blanz, 2001; Nishimura, Doyle, Humphreys, & Behrmann, 2010; Rhodes & Jeffery, 2006; Robbins, McKone, & Edwards, 2007; Webster & MacLin, 1999). If these assumptions are correct, there should be a relationship between face aftereffects and face recognition ability, because of their common origin in face-space coding.

However, the degree to which face aftereffects originate in face-level coding has been a long-standing issue in the literature (Rhodes & Leopold, 2011; Webster & MacLin, 1999). Several studies have shown that face aftereffects can partly originate in low- and mid-level stages of the visual stream (Afraz & Cavanagh, 2008; Dickinson, Almeida, Bell, & Badcock, 2010; Susilo, McKone, & Edwards, 2010a). Moreover, two studies failed to show that face aftereffects are related to face recognition ability: These studies found normal face aftereffects in individuals who could not recognize faces because of their developmental prosopagnosia (DP; $N = 6$ in Nishimura et al., 2010; $N = 1$ in Susilo et al., 2011).[1] If face aftereffects arise even partly from face-space processes, and face-space is important for face recognition, then how could such individuals exhibit normal face aftereffects? We see two possibilities, both of which informed the design of our present study.

First, although face-space is likely coded in posterior face areas (Freiwald, Tsao, & Livingstone, 2009; Loffler, Yourganov, Wilkinson, & Wilson, 2005), the problem in some individuals with DP appears to be not in these areas but instead in weak connections from these areas to anterior face areas (Thomas et al., 2009). This means that failure to find abnormal aftereffects in individuals with DP does not rule out an association between face-space coding and face recognition within the normal population, in whom the forward connections are

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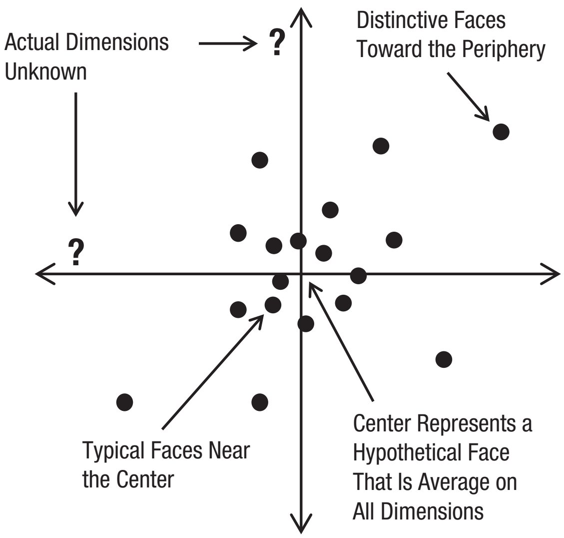

Fig. 1. Face-space coding. Each individual face is coded as a point in a multidimensional perceptual space that has dimensions corresponding to attributes that vary across faces and that has the average face at the center (Valentine, 1991). Face aftereffects are commonly interpreted as arising from a shift in the location of this average.

intact. Thus, in the present study, we tested only individuals in the normal range of face recognition ability.

Second, certain types of face aftereffects might be more effective at capturing face-space processes than others. A group analysis of 14 individuals with DP (Palermo, Rivolta, Wilson, & Jeffery, 2011) revealed a normal-sized aftereffect for a *figural* manipulation in which an expanded-face adaptor causes a different undistorted face to appear contracted, but an impaired aftereffect for an *identity* manipulation, in which adaptation to one person's face (e.g., "Dan") causes the average face to be perceived as resembling an individual opposite to the adaptor face on all face attributes (i.e., "anti-Dan"). Palermo et al. accounted for this difference by proposing that the identity aftereffect taps face-specific processes to a greater extent than does the more shape-generic expansion-contraction aftereffect. Thus, in the present study, we tested participants using a particular type of figural aftereffect (manipulation of eye height; Fig. 2a) that has previously been shown to have a substantial face-specific component (Susilo et al., 2010a).

Our basic question was whether, within the normal range, face recognition ability as measured using the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006) correlates with the magnitude of the eye-height aftereffect. Researchers (Nishimura et al., 2010; Palermo et al., 2011; Pellicano, Jeffery, Burr, & Rhodes, 2007) have implicitly assumed that the direction of the correlation should be positive—that is, that poorer face-space coding (in clinical conditions) should be associated with a smaller aftereffect. However, there has been no explicit rationale given for assuming this direction. We chose to study the eye-height aftereffect because recent evidence regarding its neural coding provides an empirical rationale for a positive correlation (Susilo, McKone, & Edwards, 2010b).

The relevant neural coding properties (Fig. 3) are broadband-opponent (two-pool) coding and linear response functions. In opponent coding (a neural implementation of norm-based coding), one pool of cells responds maximally to one end of the attribute dimension (e.g., low eyes), whereas the other responds maximally to the opposite end (e.g., high eyes). (Note that the low-eye and high-eye pools should be thought of not as pools of eye-height detectors, but rather as slices through each neuron's multidimensional response profile; individual face cells respond

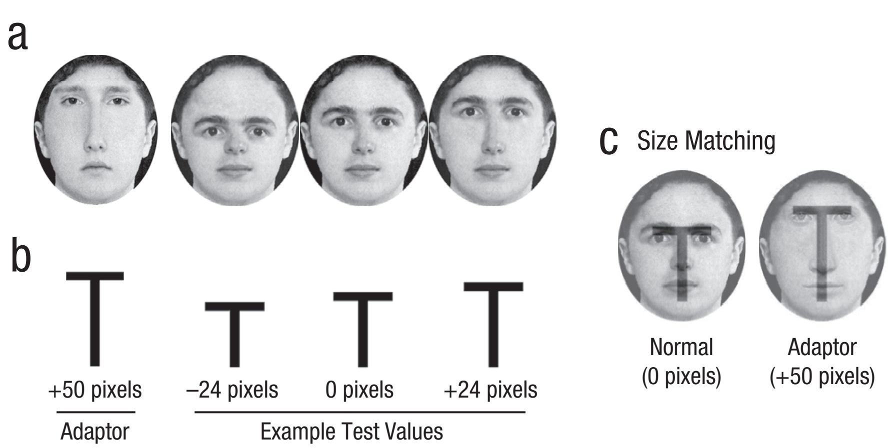

Fig. 2. The eye-height and T-shape aftereffects. In the eye-height aftereffect (a), adaptation to a distorted face in which the eyes are higher than in the original face (the +50-pixel deviation we used in our adaptors is shown here) makes the eyes in test faces (including the undistorted face with 0-pixel deviation) appear to be lower than they appeared before adaptation. In the T-shape aftereffect (b), adaptation to a T-shape with the horizontal bar shifted upward (the +50-pixel deviation we used in our adaptors is shown here) makes the bar in test T-shapes appear to be lower than it appeared before adaptation (Susilo, McKone, & Edwards, 2010a). In our study, the T-shapes used as stimuli for measuring the T-shape aftereffect were matched in size to the T-shaped region of the faces used to measure the eye-height aftereffect (c).

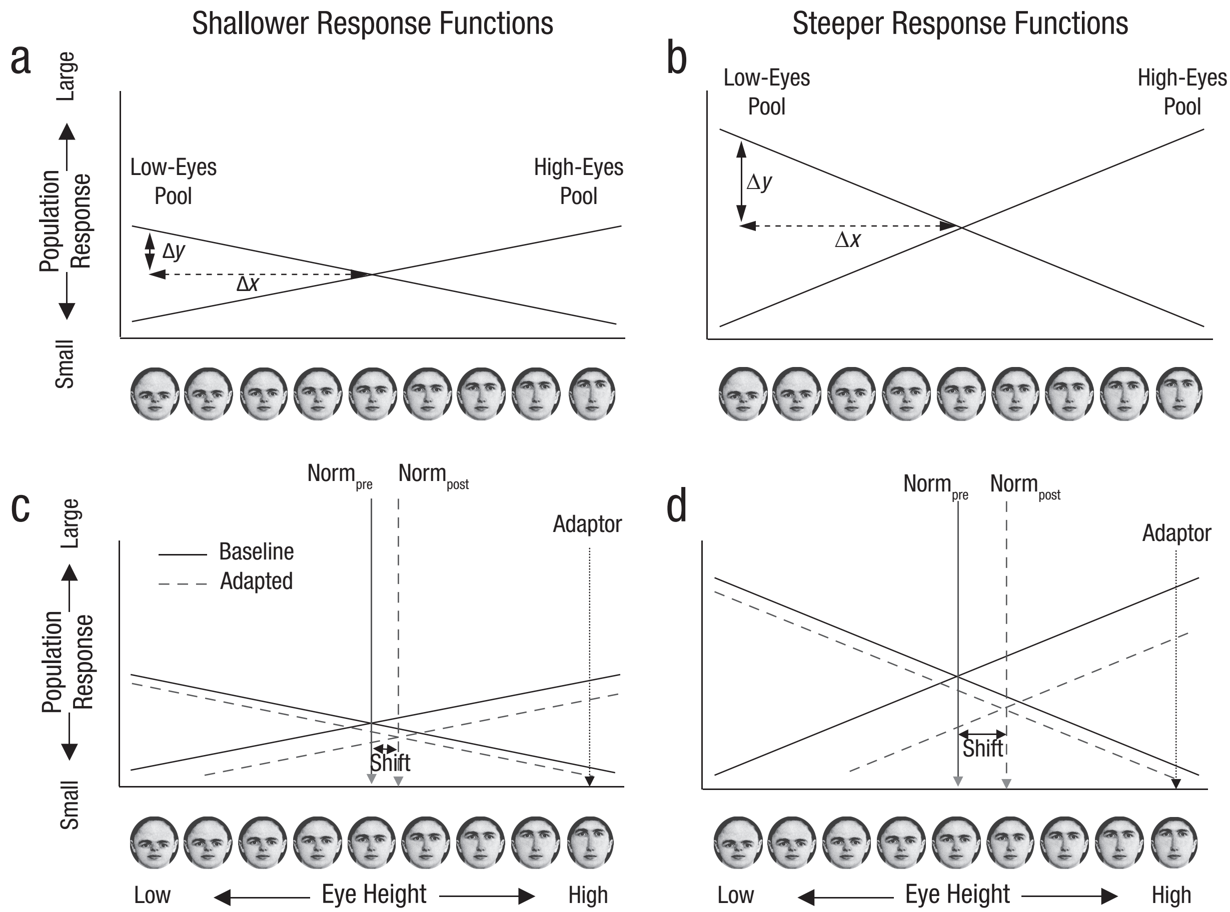

Fig. 3. Basis of the prediction that better face recognition should be positively correlated with larger eye-height aftereffects. Eye height is coded by the comparative activation of two pools of neurons (each with linear response): one that responds maximally to low eyes and one that responds maximally to high eyes. The eye height that elicits equal responses in the two pools would be perceived as normal or average. As illustrated in (a) and (b), steeper response functions of these pools mean that a unit change in eye height (Δx) would elicit a greater change in the population response (Δy). Thus, steeper response functions should yield better discrimination of eye height. As illustrated in (c) and (d), postadaptation responses (dashed lines) are lowered relative to preadaptation responses (solid lines) in proportion to the preadaptation response (Maddess, McCourt, Blakeslee, & Cunningham, 1988; Movshon & Lennie, 1979); this means that adapting to any eye height except for the norm would cause differential adaptation in the two pools, and hence cause the face perceived as normal before adaptation (Norm_{pre}) to shift toward the adaptor after adaptation (Norm_{post}). Steep functions would cause a larger shift than shallow functions because the initial difference in response between the two pools would be larger for steeper functions. Thus, steeper response functions predict both better discrimination of eye height and a larger eye-height aftereffect, and there should therefore be a positive correlation between face discriminability and the magnitude of the aftereffect.

to several face attributes; Freiwald et al., 2009.) Linear opponent coding is supported by neurophysiological evidence, which has revealed face-selective cells in monkeys with linear ramp-shaped response functions for many face attributes (Freiwald et al., 2009). Psychophysical evidence also supports this type of coding specifically for eye height (Robbins et al., 2007; Susilo et al., 2010b); moreover, the response functions remain linear across the full range of eye heights up to eyes approaching the hairline (Susilo et al., 2010b).

Together, these properties predict a positive correlation between the size of the aftereffect and ability to recognize faces, because both the aftereffect and discrimination ability derive from the slope of the individual's response functions. Steeper response functions should yield better face recognition because steeper slopes produce better discrimination of a unit change in eye height (Figs. 3a and 3b); steeper response functions also should yield larger eye-height aftereffects because the eye height perceived as normal will shift more after adaptation (Figs. 3c and 3d). Further, the linearity across the full range of eye heights (Susilo et al., 2010b) means that one can test for the predicted correlation using only one eye-height distortion in the adaptors. We used adaptors with very high eyes (Fig. 2a) because in broadband-opponent coding, adaptors furthest from the norm elicit the largest aftereffects (Fig. 3), and thus maximize the potential to observe individual differences in aftereffect magnitude.

We included two nonface control tasks in our study. The first was memory for cars (Cambridge Car Memory Test, or CCMT; Dennett et al., 2012). The second was a task measuring a T-shape aftereffect (Fig. 2b; Susilo et al., 2010a). The

T-shape task was designed to capture the shape-generic component of the eye-height manipulation by using a letter *T* matched to the T-shaped region of the face formed by the eyes, nose, and mouth. These control tasks allowed us to assess the extent to which any correlation between face aftereffects and face recognition arose specifically from face-level coding.

Method

Participants

Participants received course credit or were paid $30. To ensure that we were not testing individuals with prosopagnosia, we excluded 7 participants with CFMT scores in the lowest 5% of the population (using norms from 248 young adult Australians; McKone et al., 2011). We excluded an additional 5 participants whose data from the adaptation tasks had poor psychometric fits (see the section on curve fitting), as well as 2 participants who were extreme univariate outliers ($z > 3.32$) on the adaptation tasks. The final sample consisted of 78 participants (48 female, 30 male; ages 18–45 years, $M = 20.69$, $SD = 5.34$). All either were Caucasian ($n = 75$) or had very high Caucasian exposure (i.e., had one Caucasian parent and were raised in Australia; $n = 3$).

Tasks

For the CFMT, the method was as described in Duchaine and Nakayama (2006). Briefly, participants learned six Caucasian male faces—each in three views, to encourage face rather than image learning. Participants later discriminated these targets from similar-looking distractor faces (untimed three-alternative, forced-choice task, with simultaneous presentation of the faces; Fig. 4a). The CFMT has good psychometric properties and produces large individual differences (Bowles et al., 2009; Wilmer et al., 2010).

For the face eye-height adaptation task, the method was as in Susilo et al. (2010a, 2010b). In the preadaptation phase (348 trials), participants viewed faces that varied in eye height (29 levels ranging from –24 pixels to +24 pixels; negative numbers indicate eyes shifted down from the unaltered "zero" face, and positive numbers indicate eyes shifted up from the unaltered face; Fig. 2a). Participants indicated whether the eyes

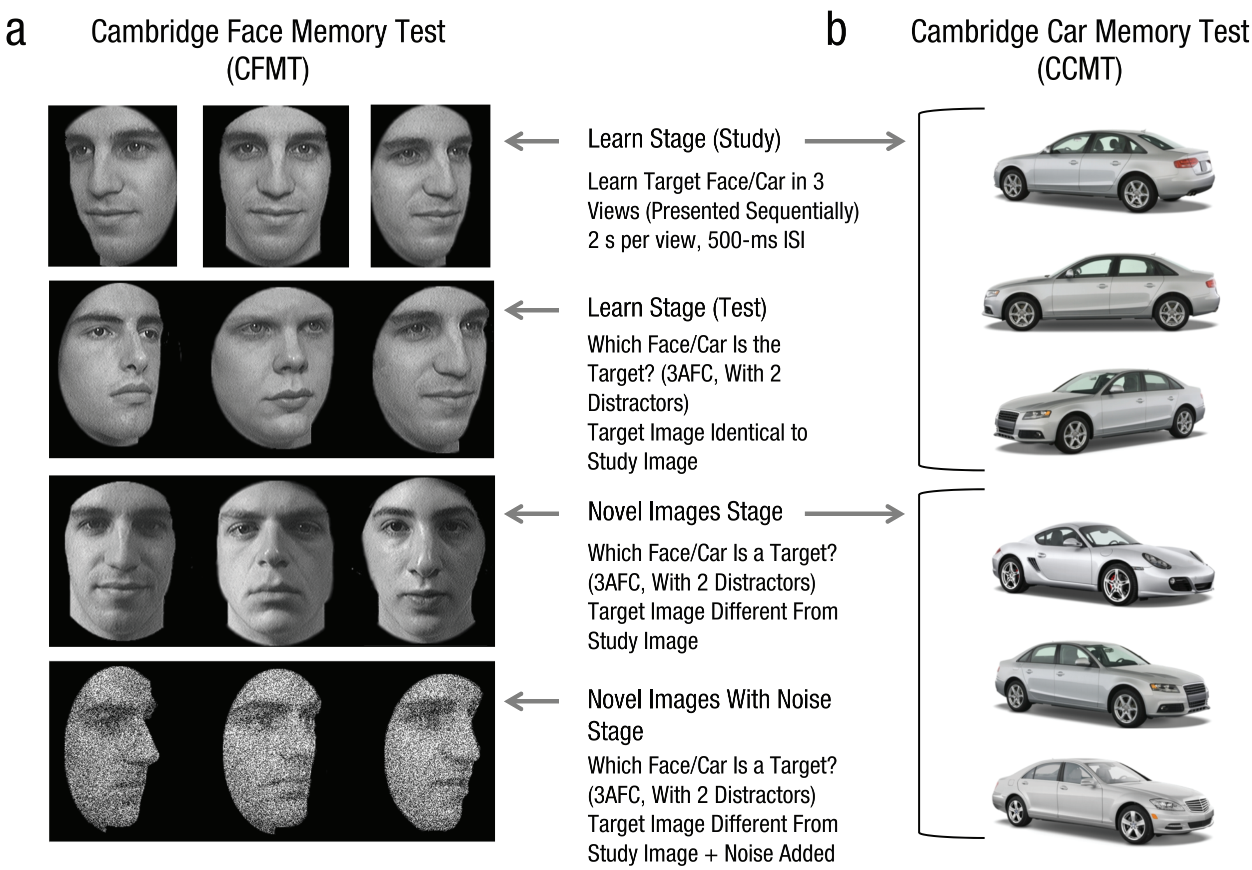

Fig. 4. Illustration of (a) the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006) and (b) the Cambridge Car Memory Test (CCMT; Dennett et al., 2012). These tests are very similar, differing only in the stimulus category. For the CFMT, the figure illustrates three stages: Learn (including study and test trials), Novel Images, and Novel Images With Noise. For the CCMT, the figure illustrates only the Learn stage (study trial) and Novel Images stage. In the Learn stage, participants learn target faces or cars and are tested on recognition of images identical to the learned targets; in the Novel Images and Novel Images With Noise stages, participants are tested on recognition of targets in novel views, novel lighting, or both. 3AFC = three-alternative forced choice; ISI = interstimulus interval.

were "high" or "low" relative to their idea of a normal face. The postadaptation phase was the same except that each test face was preceded by a 4,000-ms adaptor face with an eye height of +50 pixels (Fig. 2a). Adaptor faces were smaller than test faces, to minimize contributions to the aftereffect from retinotopic low-level vision.

For the CCMT, the method was as described in Dennett et al. (2012). The CCMT has the same structure, format, and scoring as the CFMT, but the stimuli are cars instead of faces (Fig. 4b).

For the T-shape adaptation task, the method was as in Susilo et al. (2010a). This task matched the eye-height adaptation task in method, except that the adaptors and test stimuli were T-shapes, matched in size to the T-shaped eyes-nose-mouth region of the faces in the face-height task (Fig. 2c).

Curve fitting and calculation of aftereffects (eye-height and T-shape tasks)

Psychometric functions were fitted to the data from the adaptation tasks (details in Susilo et al., 2010b) to determine the point of subjective equality (PSE; see Fig. 5 for an example), that is, the eye height or T-shape that each observer perceived as being most normal, before and after adaptation. Observers with poor fits ($R^2 < .8$ averaged across the pre- and postadaptation phases, resulting in an unreliable shift score) were excluded. For the 78 participants in the final sample, the mean R^2 across all face fits was .92 (SD = .04), and the mean R^2 across all T-shape fits was .91 (SD = .05).

Aftereffect magnitude was calculated as the difference (in pixels) between each participant's postadaptation PSE and his or her preadaptation PSE (postadaptation minus preadaptation), expressed as a percentage of the distance of the adaptor from the participant's preadaptation norm (Fig. 5). This measure was used because there were individual differences in the preadaptation norm: Although the mean preadaptation PSEs were close to zero, there was noticeable spread around the means (see the standard deviations in Table 1).

Results

Table 1 shows that, as required for individual differences studies (Wilmer, 2008), all tasks had high reliability, means well away from ceiling and floor, and large standard deviations (i.e., wide spread of scores). All tasks also had scores that were normally distributed (Kolmogorov-Smirnov tests, all ps > .05). There were no multivariate outliers. For all correlations reported in this section, N was equal to 78.

The first key finding was that face aftereffects correlated with face recognition abilities, in the predicted direction: There was a significant positive correlation between the magnitude of the eye-height aftereffect and face memory (Fig. 6).

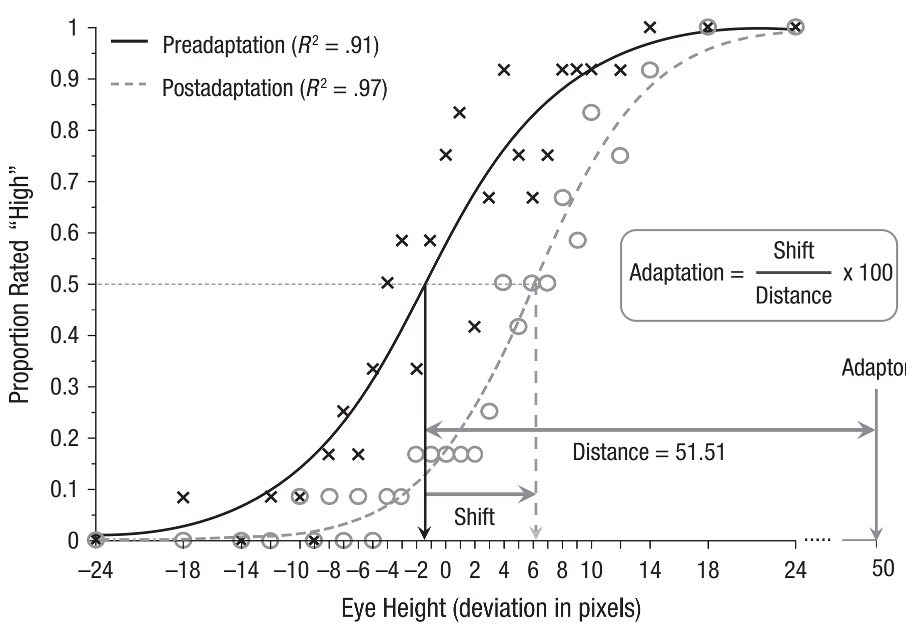

Fig. 5. Example of curve fitting and calculation of the eye-height aftereffect for a participant. The graph shows the proportion of faces that the participant rated as having "high" eyes as a function of eye height (deviation from the undistorted face; positive = up, negative = down). From the psychometric curves fitted to each participant's data, the locations of the preadaptation norm (solid black arrow) and the postadaptation norm (dashed arrow) were determined. Adaptation was calculated as the shift in the norm divided by the distance between the preadaptation norm and the adaptor face, multiplied by 100. As illustrated by this example, the distance of the adaptor from the preadaptation norm was not exactly 50 pixels for every participant, because of individual variation in the preadaptation norm.

Table 1. Descriptive Statistics for All Variables (N = 78)

Variable	Reliability	Mean	*SD*	Minimum	Maximum
Eye-height task: preadaptation PSE	.93	−0.18	3.73	−10.66	15.07
Eye-height task: postadaptation PSE	.96	3.98	5.19	−7.75	19.07
T-shape task: preadaptation PSE	.91	−6.66	4.15	−18.86	1.80
T-shape task: postadaptation PSE	.96	−1.64	5.46	−20.86	11.30
Eye-height aftereffect	.86	8.31	7.60	−6.30	33.40
T-shape aftereffect	.89	8.76	8.13	−11.10	30.60
CFMT	.85	79.02	10.95	58.33	100.00
CCMT	.83	74.25	11.36	47.22	98.61

Note: Points of subjective equality (PSEs) are expressed as the deviation (in number of pixels) from the zero (undistorted) face or T-shape. Eye-height and T-shape aftereffects are expressed as the shift in PSE as a percentage of the distance to the adaptor from the preadaptation norm. Results for the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006) and Cambridge Car Memory Test (CCMT; Dennett et al., 2012) are reported as the percentage correct, out of 72 trials. For these two tests, the reported reliabilities are Cronbach's alphas; all other reliabilities are Spearman-Brown corrected split-half correlations. CFMT scores in this table should not be used as test norms because individuals in the lowest-scoring 5% of the population have been excluded.

The second key finding was that this correlation was specific to faces. If it arose from shape-generic processes—for example, if individuals with larger face aftereffects simply had better memory, and larger aftereffects, for all shapes—scores for all tasks should have correlated positively with each other. This was not the case.

First, despite the strong physical similarity of the T-shape manipulation to the eye-height manipulation, the two aftereffects were uncorrelated, r = –.02, p = .90, 95% confidence interval (CI): [–.24, .21]. Thus, it was not the case that some participants were generically "more adaptable" than others. Second, the face aftereffect was uncorrelated with car memory

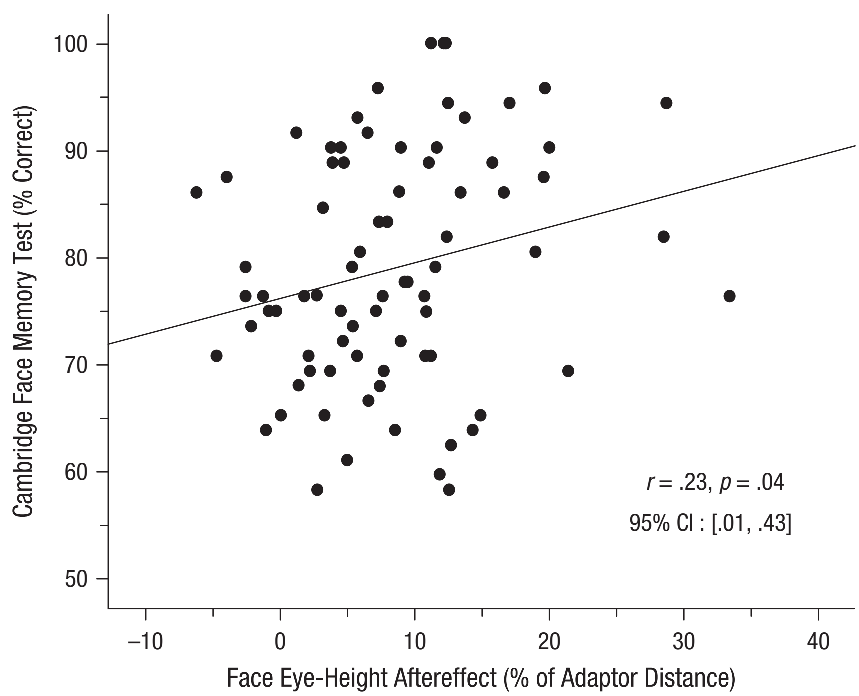

Fig. 6. Scatter plot (with best-fitting regression line) illustrating the Pearson correlation (r) between face recognition ability, as measured using the Cambridge Face Memory Test (Duchaine & Nakayama, 2006), and the magnitude of the face eye-height aftereffect. 95% CI = 95% confidence interval on the correlation value.

(CCMT), $r = .04$, $p = .76$, 95% CI: [–.19, .26]. This shows that the face aftereffect did not predict within-class object recognition memory generally, but predicted only face memory. Third, although there was a significant correlation between the T-shape aftereffect and face memory (CFMT), $r = –.25$, $p = .03$, 95% CI: [–.45, –.03], this correlation was negative, which means it cannot provide a shape-generic explanation for the positive association between magnitude of the face aftereffect and face memory. Finally, multiple regression revealed that the face aftereffect was a predictor of unique variance in face memory (CFMT). When the two nonface variables were added as predictors in the model, the negative relationship between magnitude of the T-shape aftereffect and CFMT was reduced to nonsignificance, $\beta = –0.16$, $t(74) = 1.58$, $p = .12$, and a significant relationship between car memory and face memory was revealed, $\beta = 0.39$, $t(74) = 3.81$, $p < .001$. Crucially, however, addition of these variables had no effect on the relationship between magnitude of the face aftereffect and CFMT, $\beta = 0.21$, $t(74) = 2.13$, $p = .04$ (cf. $r = .23$ for the simple bivariate correlation). These multiple regression results show that there was some overlap in CFMT variance explained by the two nonface tasks (T-shape aftereffect and CCMT), and that the variance in CFMT performance explained by the face aftereffect did not overlap with that explained by either of the nonface tasks.

Discussion

These results provide the first empirical evidence that individual differences in the quality of face-space coding exist, and that these contribute to individual differences in face recognition ability. The results support continued use of face aftereffects as a tool to investigate face-space. They further indicate that a figural (not just identity) face aftereffect can tap face-space (cf. Palermo et al., 2011). Finally, these results support a key prediction of a broadband-opponent (two-pool) face-space, namely, that steeper neural response functions should be associated with better face recognition ability.

Note that our results do not imply that all face aftereffects can necessarily be used as a tool to investigate face-space. Rather, several factors will affect the correlation between face aftereffects and face recognition. First, only face aftereffects that have a significant face-level component are suitable for investigating face-space. For eye height, the aftereffect has been argued to derive approximately 50% from face-level processes and 50% from shape-generic processes (Susilo et al., 2010a). Other types of figural aftereffects, however, might have a smaller face-level component, and would therefore be expected to have weaker relationships with face recognition ability. This may explain results showing normal expansion-contraction aftereffects in individuals with DP (Palermo et al., 2011).

Second, it may be that the correlation with face recognition depends on a direct link between aftereffect size and the slope of neural response functions in face-space. Linear functions allow use of a single adaptor value to measure response slope (Fig. 3), and there is evidence supporting linearity of eye-height coding (Susilo et al., 2010b). However, little is known about the shape of neural response functions underlying neural coding of other face attributes, and some findings suggest nonlinearity (Dakin & Omigie, 2009; Tanaka & Corneille, 2007; Wilson, Loffler, & Wilkinson, 2002; for discussion, see Susilo et al., 2010b). In the case of nonlinear functions, the aftereffect for a single adaptor value would not necessarily be related to discriminability—which would vary across the continuum—and thus the aftereffect would not necessarily correlate with face recognition.

Third, correlations between face aftereffects and face recognition might be masked if individual differences in preadaptation baseline are ignored. Theoretically, the link between aftereffect size and the slope of an individual's neural response functions requires that the deviation of the adaptor be measured from that individual's preadaptation norm, which was not zero pixels for all participants in our study. Ignoring individual differences in the distance of the adaptor from the norm would therefore potentially reduce statistical power by adding noise to any correlation.[2] Note that the traditional approach of calculating aftereffects as raw shift scores (postadaptation PSE minus preadaptation PSE) remains valid for group studies that average across participants (i.e., average adaptor distance = 50 pixels in our study).

Finally, the correlation between face aftereffects and recognition ability could plausibly have a non-face-space contribution. In our study, face aftereffects were dissociated from general visual memory and from nonface aftereffects, which ruled out the possibility that general attentional factors played a role in the correlation between face aftereffects and face recognition. However, there could perhaps be individual differences in *face-specific* attentional strategies. For example, if some individuals pay greater attention to the mouth than to the eyes, relative to other individuals, this might result in their exhibiting smaller eye-height aftereffects and—if the eyes are more diagnostic than the mouth—poorer face recognition.[3] (Note, however, that no current evidence suggests that region-specific attention influences magnitude of the aftereffect.)

What additional factors might contribute to individual differences in face recognition? Although our results indicate that face-space tuning for eye height is important for face recognition ability, the observed correlation ($r = .23$) was well below the upper bound ($r = .86$, calculated as the square root of the product of the internal reliabilities of the two tasks). Thus, considerable variance must be accounted for by other factors, such as the following.

Within face-space, quality of coding for face attributes other than eye height (e.g., mouth width, cheek shape) would also be expected to contribute to face recognition ability. Our finding that aftereffects for eye height alone correlate significantly with face recognition suggests that the steepness of neural functions for eye height might generalize to other face attributes; that is, an individual with more sensitive coding for one face-space attribute might also have more sensitive coding for others.

Beyond face-space, individual differences in holistic processing (Wang, Li, Fang, Tian, & Liu, 2012) and general visual memory (Dennett et al., 2012; Wilmer et al., 2010) may also contribute to face recognition ability. We found that the CCMT and face aftereffects explained nonoverlapping variance in the CFMT, which suggests that general visual memory contributes to face recognition independently of face-space coding. Indeed, holistic processing, general visual memory, and face-space coding might all contribute independently to face recognition ability.

Acknowledgments

Jess Irons tested some participants.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Notes

1. Children with autism spectrum disorder (ASD), who also sometimes show poor face memory, do show reduced face aftereffects (Pellicano, Jeffery, Burr, & Rhodes, 2007). However, it is difficult to rule out the possibility that these children apply reduced attention to the adapting faces as a result of the lack of social interest that characterizes ASD, and attention affects the size of face aftereffects (Moradi, Koch, & Shimojo, 2005; Rhodes et al., 2011).
2. In the present study, incorrectly assuming that adaptor distance was +50 pixels for all participants made little difference to the absolute r value, but resulted in the correlation becoming only marginally significant, $r = .22$, $p = .05$, 95% CI: [0, .42].
3. We thank Mike Webster for this idea.

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