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, McKeone, & 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, & Badecock, 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 with clinically poor face recognition because of their developmental prosopagnosia (DP; N = 6 in Nishimura et al., 2010; N = 1 in Susilo et al., 2011). 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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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...
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...
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 $p$s > .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).
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.
allow use of a single adaptor value to measure response slope of neural response functions in face-space. Linear functions depend on a direct link between aftereffect size and the slope of an individual’s neural response functions for eye height (Susilo et al., 2010b). Other types of figural aftereffects, however, might 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.

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 (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 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.

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.

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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.

**References**


Face Aftereffects Predict Face Recognition


