How distinct is the coding of face identity and expression? Evidence for some common dimensions in face space

Gillian Rhodes[1], Stephen Pond[1], Nichola Burton[1], Nadine Kloth[1], Linda Jeffery[1], Jason Bell[1], Louise Ewing[1,2], Andrew J. Calder[1,3] & Romina Palermo[1]

Word Count: 7438 (excl refs)

[1]ARC Centre of Excellence in Cognition and its Disorders, School of Psychology, University of Western Australia, Crawley, WA6009, Australia

[2]Department of Psychological Sciences, Birkbeck, University of London, London, UK

[3]MRC Cognition and Brain Sciences Unit, Cambridge, UK

Please address correspondence to:
Professor Gillian Rhodes
School of Psychology
University of Western Australia
35 Stirling Highway, Crawley, WA 6009
AUSTRALIA
phone: +61-8-6488-3251
fax: +61-8-6488-1006
email: gillian.rhodes@uwa.edu.au

Keywords: face perception, face aftereffects, adaptive coding, face recognition

Running Head: Face coding

Abstract

Traditional models of face perception emphasize distinct routes for processing face identity and expression. These models have been highly influential in guiding neural and behavioural research on the mechanisms of face perception. However, it is becoming clear that specialised brain areas for coding identity and expression may respond to both attributes and that identity and expression perception can interact. Here we use perceptual aftereffects to demonstrate the existence of dimensions in perceptual face space that code both identity and expression, further challenging the traditional view. Specifically, we find a significant positive association between face identity aftereffects and expression aftereffects, which dissociates from face (gaze) and non-face (tilt) aftereffects. Importantly, individual variation in the adaptive calibration of these common dimensions significantly predicts ability to recognize both identity and expression. These results highlight the role of common dimensions in our ability to recognize identity and expression, and show why the high-level visual processing of these attributes is not entirely distinct.

1. Introduction

There is a long-standing debate about whether face identity and expression are processed in distinct visual pathways or whether a shared perceptual representation underlies coding of both attributes. Early models proposed that identity, which requires the coding of invariant aspects of faces, and expression, which requires the coding of changeable aspects of faces, are processed in functionally and neurally distinct visual pathways (Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000, 2002). These highly influential models were motivated by the existence of dissociable deficits in recognizing identity and expression, and by distinct neural correlates in visual cortical areas for these attributes.

However, others have challenged the idea of independent pathways, noting that dissociations between deficits need not arise at a perceptual level and that the selectivity of neurons and neural areas for these attributes is far from complete (for reviews see Calder, 2011; Calder & Young, 2005). For example, the Fusiform Face Area (FFA), which codes identity, and the posterior Superior Temporal Sulcus (pSTS), which codes expression, are actually sensitive to perceived changes in both attributes (Fox, Moon, Iaria, & Barton, 2009). In addition, parts of the ventral fusiform gyrus near the FFA respond rapidly (within 120 ms) to both dynamic expressions and static aspects of faces such as identity (Kawasaki et al., 2012). These rapid responses seem consistent with some shared feed-forward visual processing of identity and expression, although it is difficult to rule out feedback from post-perceptual emotion processing areas. Thus, this evidence for shared processing is equivocal.

Behavioural evidence, mostly from classification studies, also challenges the independent processing of identity and expression. Initial studies reported that changes in identity affected expression judgments, but not vice versa (Schweinberger, Burton, & Kelly, 1999; Schweinberger & Soukup, 1998). This unidirectional influence has also been reported using a visual adaptation paradigm, with changes in identity reducing expression aftereffects (Ellamil, Susskind, & Anderson, 2008; Fox & Barton, 2007; Skinner & Benton, 2012), but not vice versa (Fox, Oruc, & Barton, 2008). However, when discriminability of expression and identity is well matched, both directions of influence have been reported in a variety of paradigms (e.g., Fitousi & Wenger, 2013; Ganel & Goshen-Gottstein, 2004; Wang, Fu, Johnston, & Yan, 2013; Yankouskaya, Booth, & Humphreys, 2012). Assuming that these effects reflect perceptual rather than post-perceptual analysis, then they challenge the independent visual processing of identity and expression. Some support for this assumption comes from evidence that interactions occur in visual adaptation studies (e.g., Fox et al., 2008), which tap perceptual processing, and for upright but not inverted faces (which do not engage face-coding mechanisms very effectively) (Yankouskaya et al., 2012). Finally, recent work on individual differences also fails to support independent visual processing of identity and expression, with a positive correlations observed between identity and expression recognition (Palermo, O'Connor, Davis, Irons, & McKone, 2013).

Taken together these findings may suggest common, rather than distinct, visual processing of identity and expression. But what might common coding mean? One proposal, motivated by impaired holistic processing of both identity and expression in developmental prosopagnosia, is that there is a common processing stage of holistic coding for both attributes (Palermo, O'Connor, et al., 2013; Palermo et al., 2011) (but see Calder, Young, Keane, & Dean, 2000 for evidence of independent holistic processing of identity and expression in neurotypical adults). On this view representations of identity and expression would share a common holistic format (Calder, Burton, Miller, Young, & Akamatsu, 2001). It remains unclear, however, whether the same actual representations are used for identity and expression, or whether there are distinct holistic representations for each attribute. Distinct representations are certainly possible in principle, as distinct image components are able to support accurate discrimination (using linear discriminant analysis) of identity and expression (Calder et al., 2001).

Here we ask whether there is a common perceptual representation underlying the perception of identity and expression. By a common representation, we mean one that contains dimensions used to code both identity and expression (common dimensions), as well as dimensions that are selective for identity or expression (see Fig 22.5 in Calder, 2011). Principal Components Analysis (PCA) of face images has demonstrated that common image components (cf dimensions) can in principle support the discrimination of identity and expression (Calder, 2011; Calder et al., 2001). However, it is not yet known whether such dimensions exist in human face space.

Our first goal here is to determine whether high-level face space contains any common dimensions that code both identity and expression. If we find that they do, then a second goal is to determine whether adaptive coding of such dimensions contributes to our ability to recognize faces and their expressions. There is increasing evidence that adaptive coding of face dimensions, indexed by face aftereffects, is important for face expertise. Adaptation of identity-related dimensions is linked to identity recognition ability (Dennett, McKone, Edwards, & Susilo, 2012; Rhodes, Jeffery, Taylor, Hayward, & Ewing, 2014) and adaptation of expression-related dimensions is linked to expression recognition ability (Palermo et al., 2015; Palermo, Jeffery, et al., 2013). Therefore, if any common dimensions contribute to coding both identity and expression, then adaptation of those dimensions should be linked to our ability to recognize both attributes.

We used a novel approach that examines individual differences in perceptual aftereffects. Aftereffects are widely used to investigate visual representations and coding mechanisms for faces and other stimuli (Clifford & Rhodes, 2005; Rhodes & Leopold, 2011; Webster, 2011), and have been dubbed the psychologist's microelectrode (Frisby, 1980). They occur when exposure (adaptation) to a stimulus alters neural processing and changes the perception of a subsequently viewed stimulus, as in the classic waterfall illusion when stationary objects appear to move upwards after viewing a downward-flowing waterfall (Mather, Verstraten, & Anstis, 1998). More generally, aftereffects reflect the adaptive updating of perceptual dimensions by experience. This updating helps to dynamically calibrate coding mechanisms to perceptual inputs, and plays an important functional role in perception (Clifford & Rhodes, 2005; Rhodes & Leopold, 2011; Webster & MacLeod, 2011).

We measured face identity and expression aftereffects in a large group of adults. If there are common dimensions that code both identity and expression, then we should find a positive association between these aftereffects, reflecting adaptation of those dimensions. Of course there could be other reasons for such an association, so we measured two other aftereffects with a view to ruling out plausible alternative accounts. We measured gaze aftereffects to test for a broader face adaptability factor, perhaps reflecting individual differences in attention to faces (Rhodes et al., 2011). We measured tilt aftereffects to test for a more general adaptability factor unrelated to face adaptation. Such a factor could reflect either genuine individual differences in perceptual plasticity or perhaps just differences in attention to adapting stimuli. If identity and expression aftereffects correlate with each other, but not with gaze or tilt aftereffects, then we could rule out differences in these other factors as the cause of the link. We used a size change between adapt and test stimuli to minimize the contribution of lower-level, retinotopic adaptation to the aftereffects.

To test whether adaptation of common dimensions is linked to our ability to recognize identity and expression, we used factor analysis to derive a factor reflecting adaptation of common identity/expression dimensions and used multiple regression to test whether this common adaptation predicts identity and expression recognition ability. If it does, then we would have evidence consistent with a functional role for adaptive coding of these common dimensions in our ability to recognize faces and their expressions. Of course, we do not expect the coding of identity and expression to be based solely on common dimensions. Dimensions that are selective for each attribute would also contribute to our ability to recognize identity and expression. To test this hypothesis, we used regression to determine whether identity and expression aftereffects contribute independently to identity and expression recognition ability, respectively.

2. Method

2.1 Participants

The sample consisted of 355 adults, comprising 292 Caucasian (207 females; *M* = 20.3 years, *SD* = 2.3 years, range = 18-29; 85 males; *M* = 20.9 years, *SD* = 2.4 years, range = 17-29) and 63 Asian (47 females; *M* = 20.4 years, *SD* = 2.4 years, range = 17-30; 16 males; *M* = 20.1 years, *SD* = 1.7 years, range = 18-24) participants. All were undergraduate psychology students from the University of Western Australia who participated for course credit. A large sample (over 300) is recommended for the factor analyses planned (Field, 2013). The specific sample size was determined by the size of the class.

2.2 Procedure

Participants were tested in groups of up to 10 students as part of a psychology laboratory class for a Perception unit taken by both second and third year students. All participants completed the aftereffect tasks (identity, expression, gaze, tilt, in that order) in a session lasting just under two hours. The third-year students also returned for a second session (N = 165), during which they completed the recognition tasks (expression recognition, CFMT, CCMT, in that order). The second session took approximately 45 minutes. The mean time between sessions was 7 days (SD = 0.6, range = 2-10 days). Participants followed written instructions to complete the tasks and save data. Experimenters were available to provide technical support. Silence was encouraged and generally maintained. All tasks were run on PCs and presented on 20 inch LED monitors with a refresh rate of 60 Hz and a resolution of 1600 x 900. The viewing distance was approximately 60 cm. The gaze and tilt aftereffect tasks were programmed in E-Prime 2.0 Professional and all the other tasks were programmed in Cedrus Superlab 4.07. Informed consent and demographic information were obtained at the beginning of the first session.

2.3 Aftereffect Tasks

The four aftereffect tasks were all similar in structure, with participants first receiving training on the discriminations that would be required, and then completing adaptation trials. All stimuli were grey scale. On adaptation trials an adapting stimulus (a face or a grating) was shown for 8000 ms (four 2000 ms exposures separated by 150 ms blank interstimulus intervals), followed by a test stimulus (face or grating) for 400 ms. On half the adaptation trials a small asterisk appeared (in the centre of the screen for 150 ms in one of the interstimulus intervals), which had to be reported (when present) at the end of the trial, to help ensure good attention to the adapting stimuli. The three face aftereffect tasks all included a small size change between adapting and test stimuli, with free viewing allowed, to minimize the contribution of low-level adaptation. Examples of the stimuli are shown in Figure 1. The tilt aftereffect naturally reflects low-level adaptation and so no size change was used.

2.3.1. Face Identity Aftereffect Task

This task has been widely used to measure adaptive, norm-based coding of identity. It measures how adaptation to a particular identity biases perception towards the opposite identity in face space. We used a version adapted from a previous study (Rhodes et al., 2014). Participants were first trained to identity four male targets. Then, on adaptation trials they viewed an adapting antiface, followed by a target face presented at low identity strength (15%), which they had to identify (see above for exposure durations). On one third of the trials target faces were presented at high identity strengths (90%). These much easier trials were included to maintain participants' motivation, but were not used to calculate aftereffects. As described above, an attentional control task was also included. Adapting faces measured approximately 7.0° x 7.2° and test faces were 80% (linear dimensions) smaller. The adapting faces were antifaces that lay opposite each target identity in face space on match trials (e.g., adapt antiDan, test Dan) but not on mismatch trials (e.g., adapt antiJim, test Dan). The identity aftereffect is measured as identification accuracy on match trials (N = 16) minus identification accuracy on mismatch trials (N = 16). It has acceptable reliability (Rhodes et al., 2014) (and Table 1).

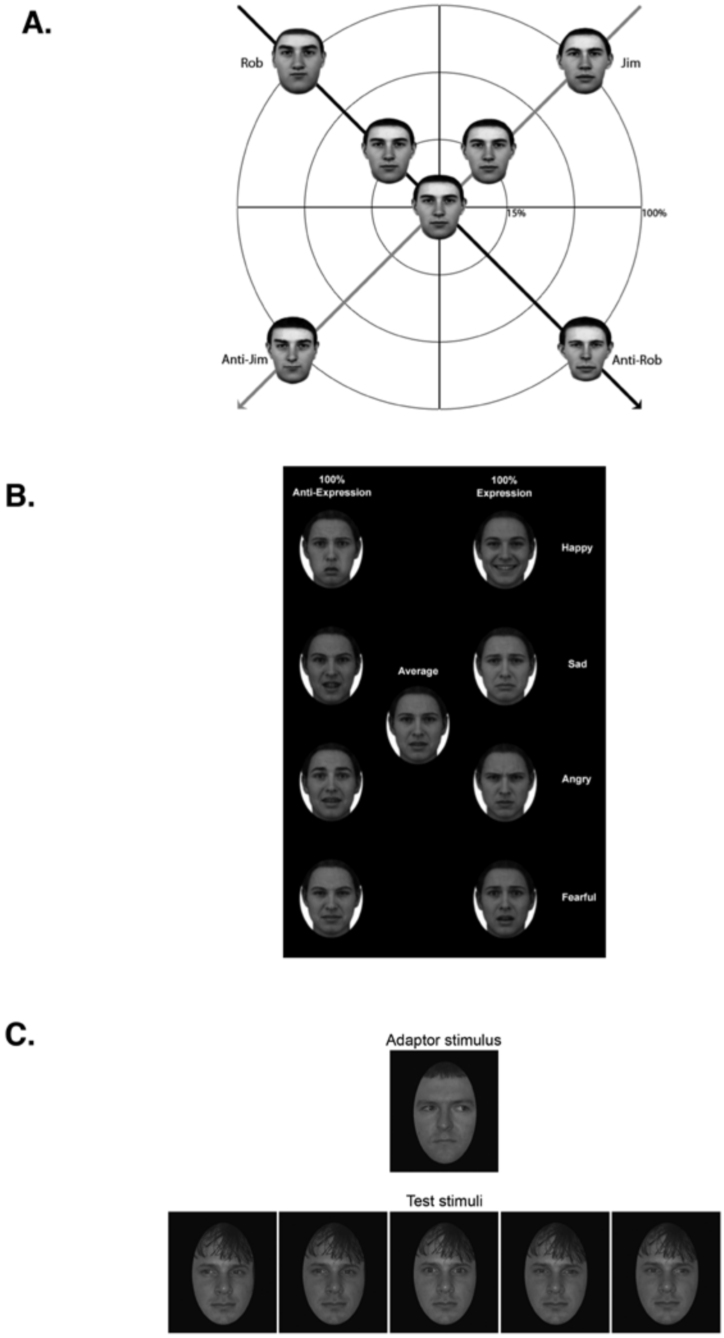

Figure 1. Examples of adapt and test faces. A. Face identity aftereffect task, B. Expression aftereffect task, C. Gaze aftereffect task.

2.3.2 Expression Aftereffect Task

This task has been used previously to measure adaptive, norm-based coding of expression (Burton, Jeffery, Skinner, Benton, & Rhodes, 2013; Skinner & Benton, 2010). We used Burton et al.'s version, which includes four target expressions (happy, sad, angry and fearful) with 100% antiexpressions as adaptors. The test stimulus was Skinner and Benton's (2010) average expression face (except on a small minority of trials, where 50% strength expressions were shown to help maintain motivation). The adaptation trial sequence and attentional control task were the same as for the identity aftereffect task. Adapting faces measured approximately 6.4° x 8.1° and test faces were 80% smaller. The expression aftereffect is calculated as the proportion of responses opposite the adapting antiexpression (e.g. "sad" after an anti-sad adaptor) (out of a total of 32 trials). It has acceptable reliability (Table 1).

2.3.3 Gaze Aftereffect Task

The stimulus faces (6 male, 6 female) were taken from a previous study (Jenkins, Beaver, & Calder, 2006). The task began with a baseline phase, in which test faces were presented for 400 ms each. Faces were presented at five different gaze deviations (10° left, 5° left, direct 0°, 5° right, 10° right) and participants had to indicate whether gaze was directed to the left or right (of the observer). Participants then completed adaptation trials, showing adapting faces with 25° right gaze and test faces at five different gaze deviations (10° left, 5° left, direct 0°, 5° right, 10° right). The adaptation trials had the same structure, timings and attentional control task as the identity and expression tasks. Adapting faces measured 6.6° x 10.8° and test faces were 80% smaller. All faces were used as both adapt and test faces, but the adapt and test faces on a given trial were always different identities. The gaze aftereffect was calculated as the total proportion of "right" responses on baseline trials (N = 60) minus the total proportion of “right” responses on adaptation trials (N = 60). Reliability was acceptable (Table 1).

2.3.4 Tilt Aftereffect Task

This task was identical to the gaze aftereffect task, except that the stimuli were oriented sinewave gratings (1.44 cycles per degree) displayed in a circular aperture (6.5° diameter). Participants adapted to gratings tilted to 20° (clockwise). Test gratings were presented at five different orientations (-6°, -2°, 0° vertical, 2°, 6°). Participants completed both baseline and adaptation trials. The trial structure (exposure durations, attention control task, etc) was identical to that of the face aftereffect tasks (see above). The only difference was that there was no size change between adapt and test stimuli. The tilt aftereffect was calculated as the total proportion of “right” responses on baseline (N = 60) trials minus the total proportion of “right” responses on adaptation trials (N = 60). Reliability was good (Table 1).

2.4 Recognition Measures

2.4.1 Cambridge Face Memory Test (CFMT)

The CFMT is a widely used, well-validated and reliable test of face recognition ability (Bowles et al., 2009; Duchaine & Nakayama, 2006). Briefly, it tests memory for six male Caucasian faces, under three conditions: test faces (3AFC) that match the images studied, test faces that are different images from the study faces and test faces that are different images with visual noise added. We used the total score (maximum of 72) as the dependent measure. Reliability for the current sample was acceptable (Table 1).

2.4.2 Cambridge Car Memory Test (CCMT)

The CCMT is a reliable test of non-face recognition that is structured identically to the CFMT, but uses cars instead of faces (for details see Dennett et al., 2011). Reliability for the current sample was acceptable (Table 1).

2.4.3 Face-selective Recognition Measure

We used residuals from a regression that predicted CFMT scores from CCMT scores (CFMT Residuals) as an explicit measure of face-selective identity recognition ability (DeGutis, Wilmer, Mercado, & Cohan, 2013).

2.4.4 Expression Recognition Test

This task measures labelling of the six basic facial expressions (happy, sad, angry, surprised, disgusted and fearful). It was slightly modified (briefer exposures used, 48/144 faces were replaced to improve reliability and validity) from a reliable test developed by Palermo and colleagues (Palermo, O'Connor, et al., 2013). Participants had to label the expressions of 144 Caucasian faces (24 for each emotion), displayed for 400 ms each (cf. 1000 ms in Palermo, O'Connor, et al., 2013), using the mouse to select the correct label from a list shown on screen. We used the total score (maximum of 144, chance = 24) as the dependent measure. Reliability was acceptable (Table 1).

3. Results

3.1 Descriptive statistics and reliability

Table 1 shows reliabilities and descriptive statistics. Reliability was acceptable for all measures, although generally lower than those reported previously. This difference may be due to the use of group testing in the present study. Only CFMT Residuals and CCMT scores were normally distributed, but skew and kurtosis were within acceptable limits for parametric analyses for all variables (Table 1) (Stuart &

Kendall, 1958).[1] Asterisk detection in the attention control task during adaptation was excellent for all four aftereffect tasks (Ms > .90, SDs < .09).

Table 1

Reliability and descriptive statistics for outcome measures

	Reliability	*N*	Min	Max	Mean	*SD*	Skew	Kurtosis
Face Identity AE	.52	345	-0.31	0.75	0.27	0.22	-0.17	-0.34
Expression AE	.67	348	0.09	0.91	0.56	0.14	-0.15	-0.24
Gaze AE	.62	352	-0.18	0.50	0.23	0.09	-0.02	1.20
Tilt AE	.67	338	-0.27	0.60	0.24	0.10	-0.12	1.87
CFMT	.77	163	33.00	72.00	56.54	8.78	-0.50	-0.23
CFMT Residuals	.74	162	-2.67	2.06	0.0	1.00	-0.39	-0.25
CCMT	.72	165	33.00	72.00	50.26	8.13	-0.05	-0.33
Expression Recognition	.68	164	77.00	131.00	113.71	9.15	-1.18	1.81

Notes. Reliabilities are Spearman-Brown corrected split-half reliabilities (means from 50 random splits). AE – aftereffect. CFMT – Cambridge Face Memory Test. CCMT – Cambridge Car Memory Test. CFMT Residuals are residuals from a regression using CCMT scores to predict CFMT scores.

3.2 Initial examination of ethnicity, sex and age effects

3.2.1 Ethnicity

Table 2 shows scores for Asian and Caucasian participants on all measures. Although an own-race advantage for face identity recognition was expected, this was not the case here, perhaps because many of the Asian participants would have been born in Australia (unfortunately, we did not collect information on place of birth). A very similar result has been reported in another study using an Australian Asian population (see Table 1 in McKone, Stokes, et al., 2012). Independent *t*-tests

[1] Gaze and tilt aftereffect scores were dropped for participants (gaze N = 1, tilt N = 17) who scored below chance (0.5) on baseline recognition tasks (with a clear gap from the rest of the distribution) indicating left-right response confusion.

(assuming equal variances) showed no significant differences between Asian and Caucasian scores on any measure, *t*s < 1.50, *p*s > .13 (dfs range from 160 to 350). We retained both ethnicities for all subsequent analyses and will not distinguish between them in our subsequent analyses.

Table 2

Performance of Caucasian and Asian participants on all outcome measures. There was no significant effect of ethnicity on any measure.

Measure	Ethnicity	*N*	Mean	*SD*
Face Identity AE	Caucasian	285	.28	.21
	Asian	60	.27	.24
Expression AE	Caucasian	285	.56	.14
	Asian	63	.56	.15
Gaze AE	Caucasian	289	.23	.09
	Asian	63	.22	.10
Tilt AE	Caucasian	281	.24	.10
	Asian	57	.25	.10
CFMT	Caucasian	135	56.94	8.98
	Asian	28	54.61	7.58
CFMT Residuals	Caucasian	134	.02	1.03
	Asian	28	-.20	.89
CCMT	Caucasian	137	50.59	8.01
	Asian	28	48.64	8.64
Expression Recognition	Caucasian	136	114.20	9.13
	Asian	28	111.36	9.04

3.2.2 Sex

Table 3 shows scores for female and male participants on all outcome measures. The only significant sex difference was for car recognition. Males performed significantly better than females, as found previously (Dennett et al., 2011), $t(163) = 2.94$, p = .004. All other *t*s < 1.86, *p*s > .07. Therefore, subsequent analyses will not include sex as a factor.

Table 3

Performance of female and male participants on all outcome measures. The only significant sex difference was for car recognition (CCMT).

Measure	Sex	*N*	Mean	*SD*
Face Identity AE	female	246	.26	.22
	male	99	.31	.21
Expression AE	female	249	.55	.14
	male	99	.57	.14
Gaze AE	female	251	.22	.10
	male	101	.23	.08
Tilt AE	female	240	.25	.11
	male	98	.23	.10
CFMT	female	116	56.75	8.48
	male	47	56.02	9.54
CFMT Residuals	female	115	.04	.99
	male	47	-.17	1.04
CCMT	female	116	49.08	7.30
	male	49	53.06	9.31
Expression Recognition	female	116	113.92	8.77
	male	48	113.21	10.08

3.2.3 Age

Age correlated positively with face identity recognition scores (CFMT), $r = .183$, $p = .020$, $N = 163$, as found previously (Germine, Duchaine, & Nakayama, 2011). Age also correlated significantly with car recognition scores (CCMT), $r = .155$, $p = .047$, $N = 165$, indicating improvement in non-face recognition performance. However, there was evidence for improvement in face-selective recognition, because age remained significantly correlated with face identity recognition, $r = .155$, $p = .05$, df = 158, when non-face (car) recognition and gender were controlled. In addition, the correlation between age and face-selective recognition (CFMT Residuals) was marginally significant, $r = .140$, $p = .075$, $N = 162$. Age also correlated significantly with expression recognition, $r = .176$, $p = .024$, $N = 164$, and this correlation remained significant, $r = .168$, $p = .033$, df = 160, when non-face (car) recognition and gender were controlled. These results provide evidence for face-selective improvement in identity and expression recognition over the age range tested here. The parallel improvement in identity and expression recognition is consistent with a role for common perceptual dimensions in the coding of identity and expression.

Age did not correlate significantly with any aftereffects, *r*s from -.064 to .046, *p*s > .242, *N*s from 338 to 352. This result is interesting given that adaptive coding of identity and expression is linked to the ability to recognize these attributes in adults (Palermo et al., 2015; Palermo, Jeffery, et al., 2013; Rhodes et al., 2014). Intriguingly, the present results suggest that age-related changes in face recognition performance during early adulthood are not driven by changes in adaptive coding of those attributes, and may be unrelated to individual differences in performance in this age range.

3.3 Relationships between identity and expression aftereffects

Correlations between aftereffects are shown in Table 4. There was a small-to-moderate positive correlation (.153, with an upper bound set by reliability of .59) between identity and expression aftereffects. We suggest that this association may reflect adaptation of common dimensions that code both identity and expression. Importantly, neither identity nor expression aftereffects correlated significantly with either gaze or tilt aftereffects, so the link cannot be attributed to individual differences in attention to faces per se or in adaptability more generally. Moreover the correlation between identity and expression aftereffects remained when we controlled for gaze aftereffects, r = .151, p = .003, df = 336, or tilt aftereffects, r = .153, p = .003, df = 326. Identity aftereffects also correlated significantly more strongly with expression than tilt aftereffects, z = 1.88, p = .030, N = 323 (1-tailed) and marginally more strongly with expression than gaze aftereffects, z = 1.61, p = .053, N = 337 (1-tailed).

The link between identity and expression aftereffects was confirmed by a principal axis factor analysis, with oblimin rotation (allowing for correlated factors), on all four aftereffects. Two factors emerged with eigenvalues greater than one. Gaze and tilt aftereffects loaded (.39, .37, respectively) on the first factor (eigenvalue = 1.23), which explained 30.7% of the variance. Loadings of identity and expression aftereffects on this factor were very low (-.04, .07, respectively). Face identity and expression aftereffects loaded (.36, 39, respectively) on the second factor (eigenvalue = 1.07), which explained 26.9% of the variance. Loadings of gaze and tilt aftereffects on this factor were very low (.08, -.05, respectively). The Kaiser-Meyer-Olkin (KMO) measure was 0.52, indicating acceptable sampling adequacy (Field, 2013, p.685).

Table 4

Pearson correlations between performance measures. Significance levels and Ns are shown below the correlations.

	Expression AE	GazeAE	TiltAE	CFMT	CCMT	CFMT Resids	ExpRecog
Face Identity AE	.153**	.030	-.010	.192*	.112	.161*	.070
	.005	.586	.853	.016	.162	.046	.386
	339	342	329	156	158	155	157
Expression AE	1	.056	.034	.123	.035	.111	.149
		.300	.540	.121	.660	.162	.059
	348	346	331	161	163	160	162
GazeAE		1	.152**	-.054	-.030	-.040	-.166*
			.005	.496	.703	.619	.034
		352	335	161	163	160	162
TiltAE			1	.031	-.137	.077	-.080
				.701	.086	.343	.322
			338	156	158	155	157
CFMT				1	.215**	.959**	.377**
					.006	.000	.000
				163	162	162	161
CCMT					1	-.071	.075
						.368	.337
					165	162	164
CFMT Residuals						1	.362**
							.000
						162	161

Notes. *p < .05; **p < .01. AE – Aftereffect, CFMT – Cambridge Face Memory Test, CCMT – Cambridge Car Memory Test. CFMT Residuals – residuals from regression predicting CFMT scores from CCMT scores. ExpRecog – Expression Recognition.

3.4 Relationships between identity and expression recognition performance

Face identity recognition (CFMT) and expression recognition were moderately strongly and significantly correlated (*r* = .377, Table 4). Therefore, some participants were better at processing both aspects of faces than others (see also Palermo, O’Connor, et al., 2013). This correlation remained substantial when we controlled for non-face recognition, $r = .370$, $p < .0001$, $df = 158$, and was marginally larger than the correlation between face (CFMT) and non-face (CCMT) recognition, $z = 1.62$, $p = .052$, $N = 161$ (1-tailed). Moreover, face-selective identity recognition ability (CFMT Residuals) also correlated moderately strongly with expression recognition (Table 4), so the link cannot be attributed to shared individual differences in more general recognition abilities. Importantly, this link is consistent with a common representation underlying the perception of face identity and expression.

3.5 Relationships between aftereffects and performance

We used multiple regression to test whether adaptation of common identity/expression dimensions, identified by our factor analysis above, predicts performance on those attributes. For each performance measure (CFMT, CFMT Residuals, Expression Recognition), we conducted a regression with the common identity/expression adaptation factor, the common gaze/tilt adaptation factor and age as predictors. The gaze/tilt factor was included to ensure that any link was specific for identity/expression adaptation. The final results appear as Model 1 in Tables 5-7. Cook's leverage values for all models were well below the recommended cut-off of 1.0 (Field, 2013).

We also used multiple regression to test for independent effects of identity and expression adaptation on performance. For each performance measure, we conducted an initial regression with all four aftereffect scores (identity, expression, gaze, tilt) and age as predictors. The final results appear as Model 2 in Tables 5-7. We predicted that identity, but not expression, aftereffects would predict face identity recognition (CFMT and/or CFMT_Residuals), and that expression, but not identity, aftereffects should predict expression recognition. Gaze and tilt adaptation were not expected to predict either identity or expression recognition.

3.5.1 Predicting face identity recognition ability

The common identity/expression adaptation factor, but not the common gaze/tilt adaptation factor, was a significant predictor of face identity recognition ability (Model 1 Table 5, Figure 2). This important result links adaptation of dimensions that code both identity and expression to our ability to recognize these attributes. Age was also a significant predictor, as found previously (Germine et al., 2011). Additional regressions confirmed that the identity/expression adaptation factor was not a predictor of general visual recognition memory. It did not predict either car recognition (CCMT) (β = .14, p = .104) or car-selective recognition (CCMT residuals from a regression predicting CCMT from CFMT scores) (β = .12, p = .187).

Table 5. Significant predictors of face identity recognition ability (CFMT scores).

Outcome Variable	Predictors	B	SE B	95% CI	β	p
CFMT scores						
Model 1	Identity/Exp factor	3.86	1.61	.68, 7.03	.21	.018
	Gaze/Tilt factor	-1.41	1.56	-4.53,1.71	-.08	.372
	Age	.83	.32	.20, 1.46	.21	.010
Model 2	Face Identity AE	8.35	3.23	1.97, 14.73	.21	.011
	Expression AE	5.77	5.35	-4.82, 16.35	.09	.283
	Gaze AE	-11.64	8.88	-29.20, 5.91	-.11	.192
	Tilt AE	5.40	6.97	-8.39, 19.18	.06	.440
	Age	.94	.32	.30, 1.58	.24	.004

Notes. CFMT – Cambridge Face Memory Test. AE – Aftereffect. Exp – Expression. Model 1 uses factor scores and Model 2 uses aftereffects as predictors.

Identity, but not expression, adaptation was a significant predictor of face identity recognition (CFMT scores) (Model 2 Table 5, Figure 2). This result demonstrates that the link between face adaptation and face recognition ability reported previously (Rhodes et al., 2014) is specific to the adaptive coding of identity, and cannot be attributed to individual differences in attention to faces more generally. As expected, neither gaze nor tilt adaptation predicted performance (Model 2 Table 5). Again, age was a significant predictor (Model 2 Table 5). Additional regressions showed that identity aftereffects were not a general predictor of visual recognition memory. They did not predict either car recognition (CCMT) (β = .12, p = .151) or car-selective recognition (CCMT_residuals) (β = .09, p = .309).

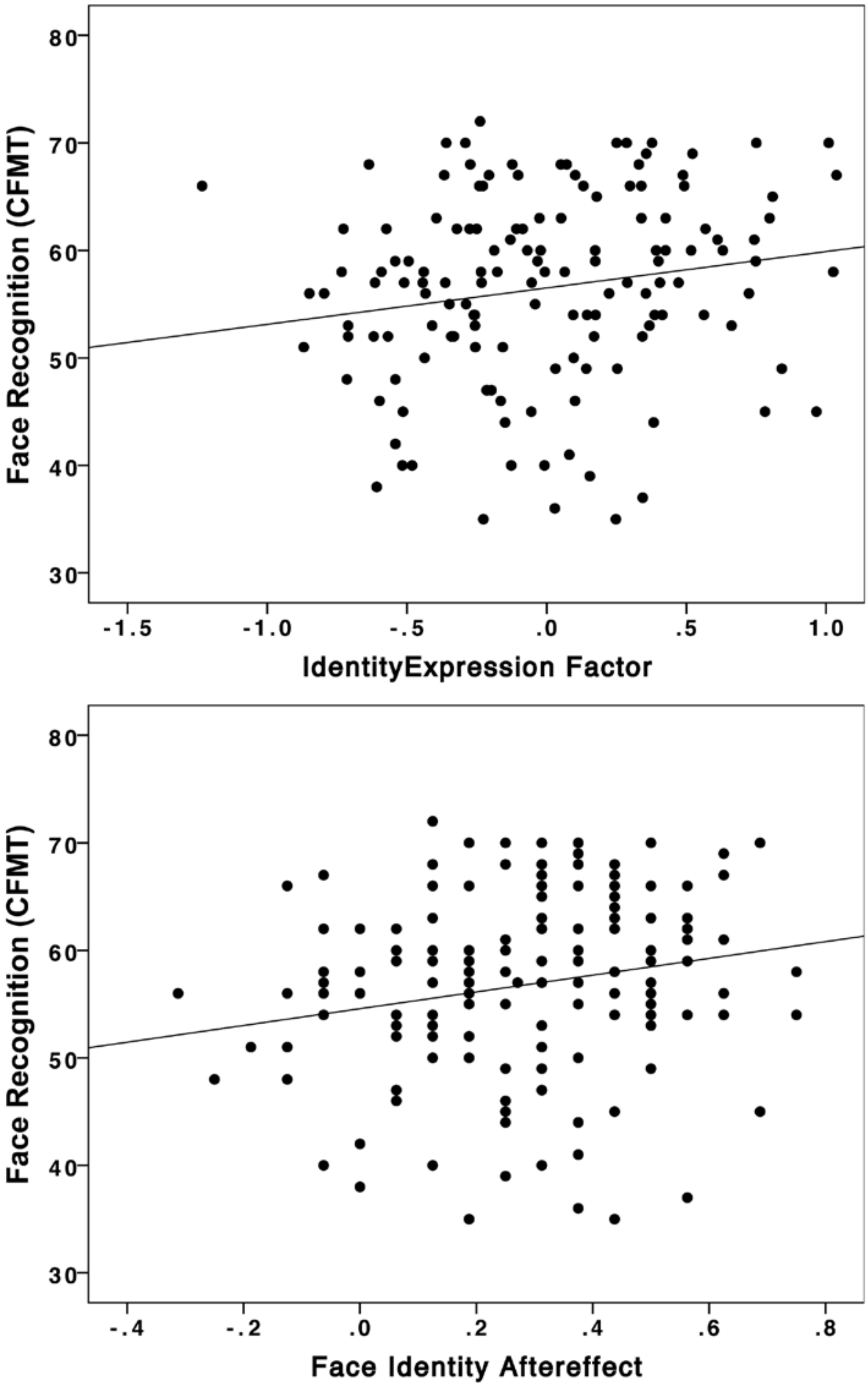

Figure 2. Scatterplots with best-fitting regression lines illustrating the relationship of face recognition ability (CFMT) with the identity/expression adaptation factor (top) and identity aftereffects (bottom).

3.5.2 Predicting face-selective recognition ability

The identity/expression adaptation factor (but not the gaze/tilt adaptation factor) was a marginally significant predictor of face-selective recognition ability (CFMT Residuals) (Model 1 Table 6, Figure 3). This result links adaptation of common dimensions that code both identity and expression (but not gaze and tilt) specifically to face identity recognition ability rather than to visual memory more generally. Age was also a significant predictor (Model 2 Table 6). Thus age-related improvements in face recognition ability cannot be attributed to more general improvements in visual memory.

Identity adaptation was also a significant predictor of face-selective recognition ability (Model 2 Table 6, Figure 3). Age was the only other significant predictor (Model 2 Table 6).

Table 6

Significant predictors of face-selective identity recognition ability (CFMT Residuals).

Outcome Variable	Predictors	B	SE B	95% CI	β	p
CFMT Residuals						
Model 1	Identity/Exp factor	.35	.19	-.03, .72	.16	.069
	Gaze/Tilt factor	-.05	.19	-.42, .32	-.02	.795
	Age	.08	.04	.00, .15	.17	.038
Model 2	Face Identity AE	.80	.38	.05, 1.56	.17	.037
	Expression AE	.57	.63	-.68, 1.82	.07	.368
	Gaze AE	-1.17	1.05	-3.24, .91	-.09	.268
	Tilt AE	1.05	.82	-.58, 2.68	.11	.203
	Age	.09	.04	.02, .17	.20	.017

Notes. CFMT Residuals – Residuals from regression predicting CFMT scores from CCMT scores. CFMT – Cambridge Face Recognition Test. CCMT – Cambridge Car Recognition Test. AE – Aftereffect. Exp – Expression. Model 1 uses adaptation factor scores and Model 2 uses aftereffects as predictors.

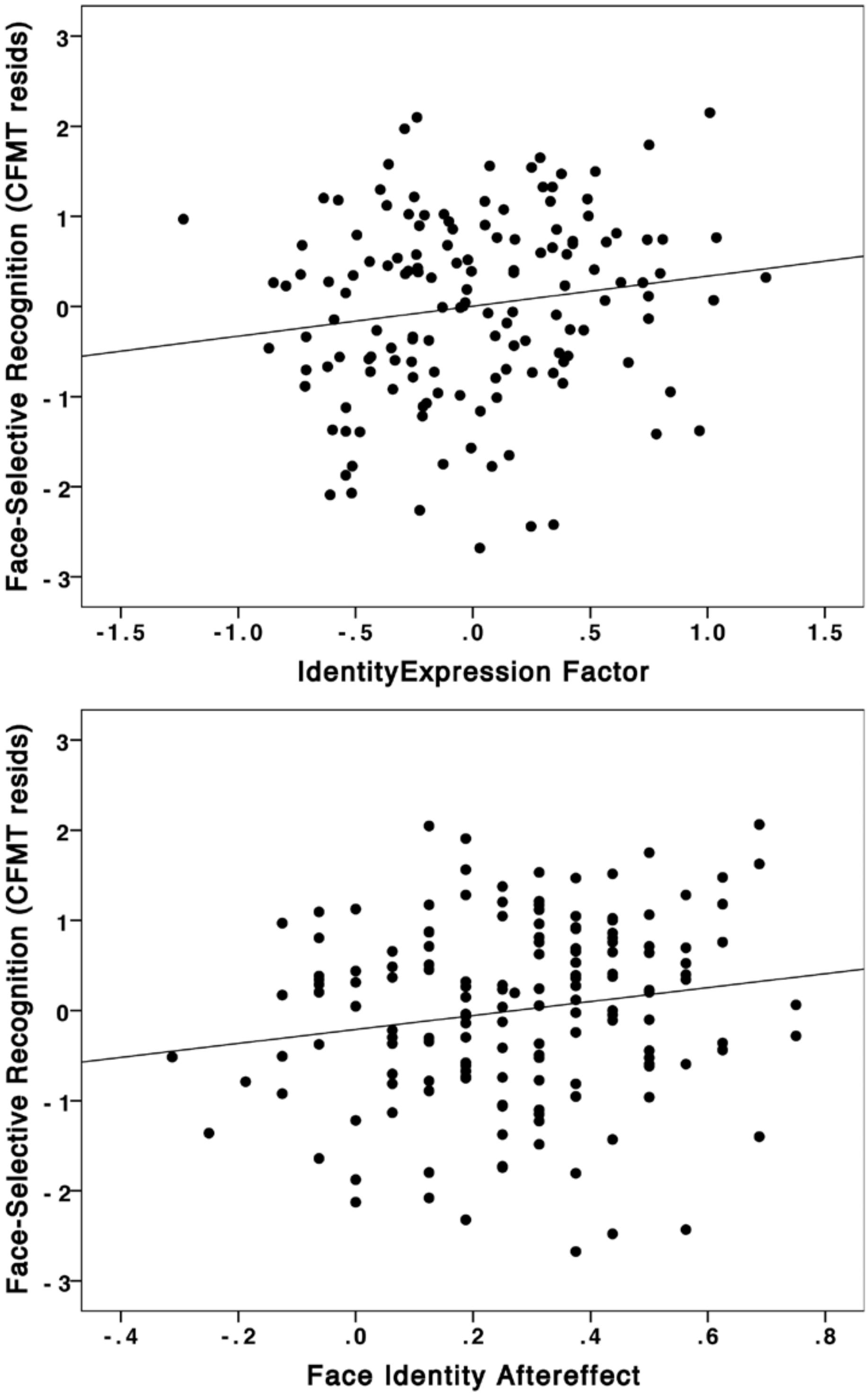

Figure 3. Scatterplots with best-fitting regression lines illustrating the relationship of face-selective identity recognition ability (CFMT Residuals) with the identity/expression adaptation factor (top) and identity aftereffects (bottom).

3.5.3 Predicting expression recognition ability

The identity/expression adaptation factor was a significant predictor of expression recognition ability (Model 1 Table 7, Figure 4). This result suggests a functional role for adaptation of dimensions that code both identity and expression in expression recognition ability. Curiously, however, gaze/tilt adaptation also predicted expression recognition ability, although in this case less adaptation predicted better recognition (Model 1 Table 7, Figure 5). Age was also a significant predictor (Model 1 Table 7). This developmental improvement in expression recognition during early adulthood is a new finding.

Expression, but not identity, adaptation was a significant predictor of expression recognition ability (Model 2 Table 7, Figure 4). This result shows that the link between expression adaptation and expression recognition ability reported previously (Palermo et al., 2015) is specific to the adaptive coding of expression, and cannot be attributed to individual differences in attention to faces more generally. Gaze adaptation also predicted expression recognition ability, again with less adaptation predicting better recognition (Model 2 Table 7, Figure 5). Again age was a significant predictor (Model 2 Table 7).

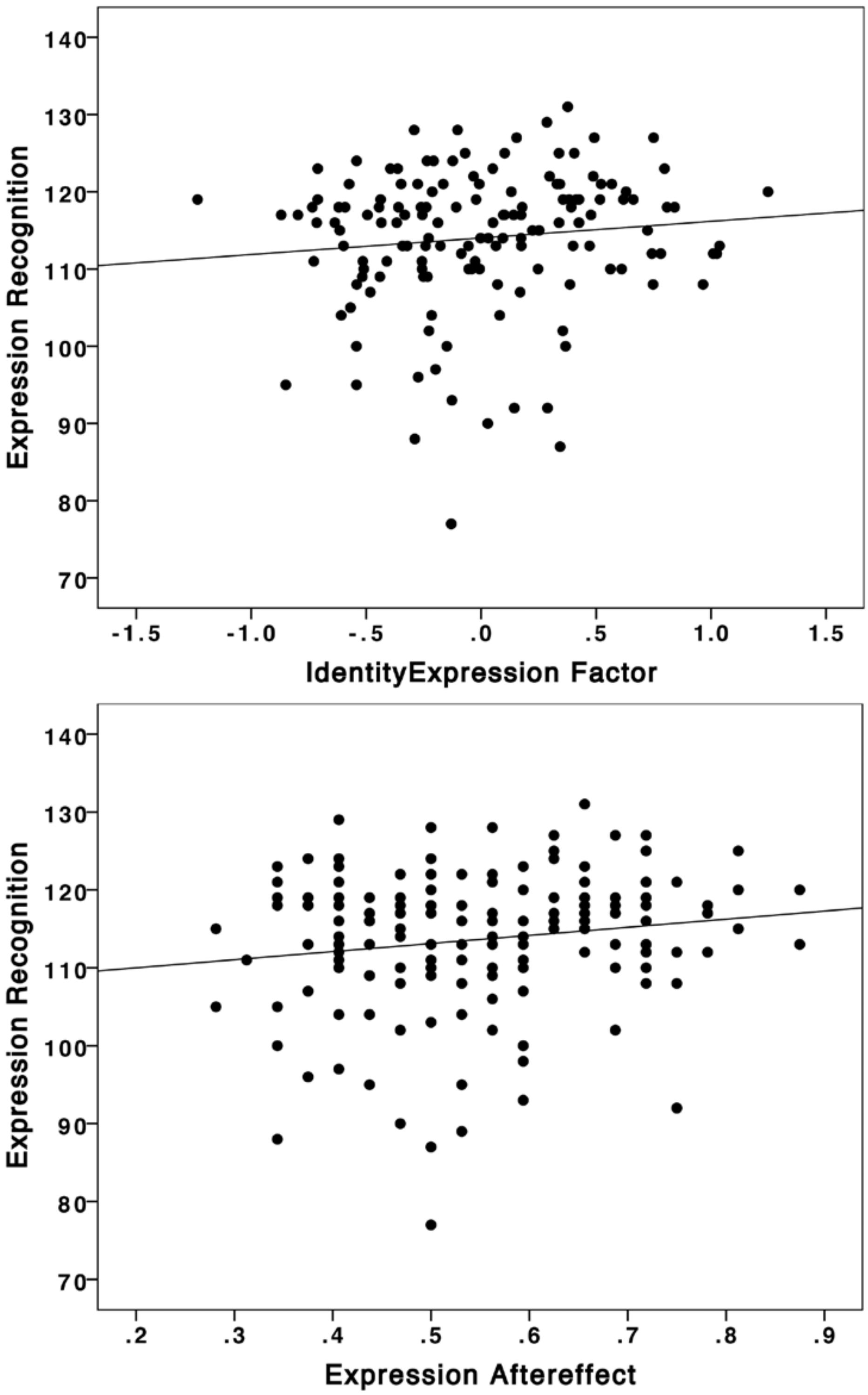

Figure 4. Scatterplots with best-fitting regression lines illustrating the relationship of expression recognition ability with the identity/expression adaptation factor (top) and expression aftereffects (bottom).

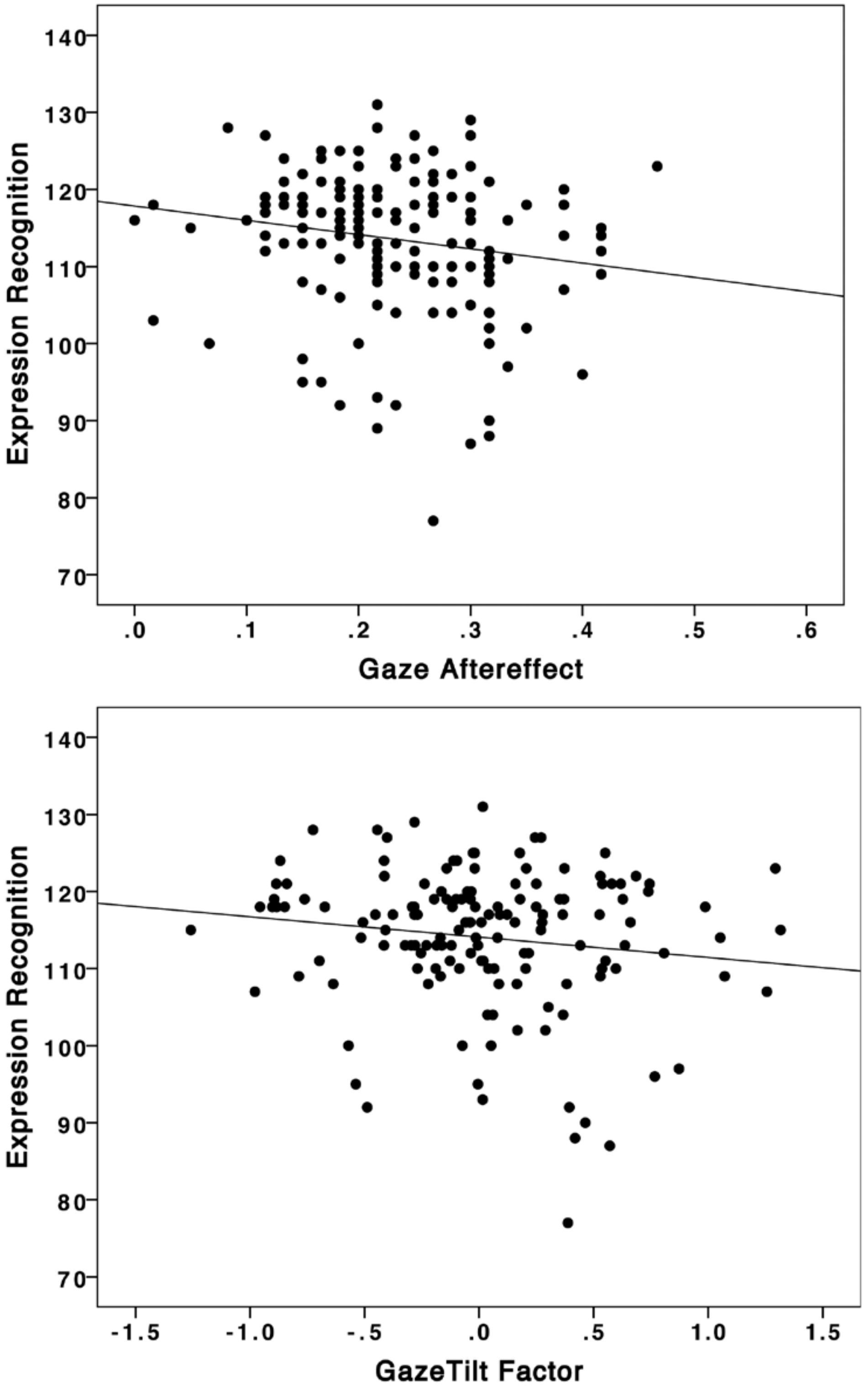

Figure 5. Scatterplots with best-fitting regression lines illustrating the relationships of expression recognition ability with gaze aftereffects (top) and the gaze/tilt adaptation factor (bottom).

Table 7

Significant predictors of expression recognition ability.

Outcome Variable	Predictors	B	SE B	95% CI	β	p
Expression Recognition						
Model 1	IdentityExp factor	3.50	1.65	.23, 6.76	.18	.036
	GazeTilt factor	-3.60	1.58	-6.73, -.47	-.20	.024
	Age	.75	.33	.10, 1.40	.18	.023
Model 2	Identity AE	2.90	3.31	-3.65, -.44	.07	.383
	Expression AE	11.46	5.52	.56, 22.37	.17	.040
	Gaze AE	-22.54	9.00	-40.33, -4.76	-.20	.013
	Tilt AE	-2.10	7.11	-16.16, 11.96	-.02	.768
	Age	.82	.33	.16, 1.47	.20	.015

Notes. AE – Aftereffect. Model 1 uses adaptation factor scores and Model 2 uses aftereffects as predictors.

4. General Discussion

We used individual differences in perceptual aftereffects to test whether there is a common visual representation underlying the coding of identity and expression (Calder & Young, 2005). Specifically, we asked whether face space contains dimensions that code both attributes. Our results suggest that it does. Identity and expression aftereffects were significantly positively correlated, and loaded on a single factor in a factor analysis. Moreover, adaptation of these common dimensions significantly predicted recognition of both attributes. These results suggest that there are common dimensions that code both identity and expression and that the adaptive updating of these dimensions by experience plays an important functional role in recognizing both identity and expression. More generally, they show why the visual coding of identity and expression cannot be completely distinct, as assumed in the traditional models.

We can rule out several alternative accounts of the association between identity and expression aftereffects. Their association cannot be attributed to individual differences in attention to faces generally, because in that case identity and expression aftereffects would also have correlated with gaze aftereffects. Nor can it be attributed to individual differences in attention during adaptation or in general visual adaptability, because in those cases all four aftereffects would have correlated. The dissociations from gaze and tilt aftereffects cannot be attributed to poor reliability of those aftereffects (see Table 1). Instead, we propose that the association between identity and expression aftereffects reflects adaptation of dimensions in face space that code both attributes.

We note that the correlation between identity and expression aftereffects was small to moderate (r = .15) and well below the upper limit of .59 set by reliability. Thus there is substantial additional variance that could reflect adaptation of other dimensions that more selectively code identity and expression. We found some evidence for such dimensions. Identity aftereffects significantly predicted face identity recognition ability, independent of expression aftereffect, and expression aftereffects significantly predicted face expression recognition ability independent of identity aftereffects. These results are consistent with a role for attribute-selective dimensions in recognizing identity and expression.

Principal Components Analysis of face images has demonstrated that common, as well as attribute-selective, image components can support the mathematical discrimination of identities and expressions (Calder et al., 2001). The present results suggest that some common dimensions also contribute to our human ability to recognize face identity and expression. Thus they support conjectures that the PCs (eigenfaces) identified in PCA are analogous to dimensions in a perceptual face space (Calder, 2011; Calder et al., 2001).

Some of the common dimensions used to code identity and expression might be holistic dimensions, like the eigenfaces identified by PC analyses. In this case, the association of identity and expression aftereffects, and their dissociation from gaze aftereffects, might at least partly reflect individual differences in the ability to code such holistic dimensions, which may be less important for gaze processing. However, one can easily think of other kinds of dimensions that would be common to identity and expression, but unrelated to gaze, perception. These would include spatial relations that vary with both identity and expression (e.g., eyebrow height - low for anger, high for surprise) and feature attributes that vary with identity and expression (e.g., lip thickness - decreases for anger).

There is considerable evidence that both identity and expression are adaptively coded relative to norms that are updated by experience (Rhodes & Leopold, 2011; Skinner & Benton, 2010; Webster & MacLeod, 2011). To the extent that there are common dimensions for coding identity and expression, there would be common norm values. Given our present results, we propose that the adaptive coding of both identity and expression occurs in a single high-level face space with a norm that represents average values for both the common and selective dimensions. Recent evidence that both identity-independent and identity-dependent representations of expression are coded relative to perceptual norms further supports this account (Skinner & Benton, 2012).

This account assumes that we have measured adaptation of high-level face-coding mechanisms. Several lines of evidence support this interpretation. First, face identity aftereffects were linked to face-selective recognition ability, rather than visual memory more generally. Second, adaptation of the common identity/expression adaptation factor was also (marginally) linked to face-selective identity recognition ability. Third, face identity aftereffects like those measured here are diminished for inverted faces, which do not tap high-level face coding mechanisms very effectively (Rhodes, Evangelista, & Jeffery, 2009). Finally, we minimized the contribution of low-level retinotopic adaptation by using a size change between adapt and test faces and allowed free scanning of the adapting stimuli. Overall, therefore, our findings suggest that a high-level perceptual face space contains dimensions that are common to the coding of identity and expression, as well as dimensions that are selective for each attribute.

It is interesting to consider what face-selective areas might code the common dimensions observed here. The Occipital Face Area (OFA) computes an early visual representation of face parts that may be common to both identity and expression (Fairhall & Ishai, 2007; Haxby et al., 2000; Pitcher, Walsh, & Duchaine, 2011; Pitcher, Walsh, Yovel, & Duchaine, 2007). However, it seems unlikely that the common dimensions are coded by the OFA because identity aftereffects are larger for upright than inverted faces (Rhodes et al., 2009) whereas the OFA is insensitive to orientation (Yovel & Kanwisher, 2005). Instead the FFA is sensitive to orientation (Yovel & Kanwisher, 2005) and could potentially code the common dimensions. In this case our results would add to the growing evidence that the FFA codes expression as well as identity (Fox et al., 2009).

If a common visual representation underlies the perception of identity and expression, then identity and expression recognition ability should also be linked. We found that this was indeed the case, replicating Palermo and colleagues' (2013) recent report that face recognition ability (CFMT scores) correlates with expression recognition. Importantly, we also found that this link was face selective, i.e., face-selective identity recognition (CFMT residuals) correlated significantly with expression recognition and neither correlated significantly with non-face (car) recognition (CCMT). Therefore, the association between identity and expression recognition ability cannot be attributed to general visual recognition ability or to other general perceptual or cognitive abilities, because these would also affect performance on non-face recognition. This link between identity and expression recognition ability may stem, at least partly, from the existence of common dimensions in face space that code both attributes.

Our results add to the growing evidence that adaptive coding of faces plays a functional role in face recognition ability. We replicated previous evidence linking identity adaptation to face recognition ability (Dennett et al., 2012; Rhodes et al., 2014) and linking adaptive coding of expression to expression recognition ability (Palermo et al., 2015). Importantly, we also demonstrated some selectivity of those links for the adapting attribute, in that identity aftereffects did not predict expression recognition and expression aftereffects did not predict identity recognition. Therefore, any links between adaptation and recognition ability cannot be attributed to some unspecified third factor, like interest in faces or attention during adaptation. An important new finding was that adaptation of dimensions that code both identity and expression predicted recognition of those attributes.

We found an unexpected link between gaze and tilt adaptation. Gaze aftereffects correlated significantly with tilt aftereffects, but not with identity or expression aftereffects. This link between gaze and tilt aftereffects might reflect the need for spatial left-right judgments in both tasks, judgments that could be made using a co-ordinate system that is common to both gaze and tilt direction. Thus, just as common dimensions for coding identity and expression may generate the observed link between identity and expression aftereffects, this common spatial co-ordinate system may generate the observed link between gaze and tilt aftereffects.

The dissociation of gaze aftereffects from expression aftereffects is interesting, given that gaze and expression have long been considered to be processed in the same visual pathway (Haxby et al., 2000) and the well-known interactions between the perception of gaze and expression (Adams & Kleck, 2003, 2005; Ewbank, Jennings, & Calder, 2009). We note, however, that some of these interactions have proved difficult to replicate (Bindemann, Burton, & Langton, 2008). We speculate that the dissociation between expression and gaze adaptation obtained here might be related to the fact that gaze direction is signalled by a simple feature (or features, if the two eyes are considered separately), whereas expression is often signalled across multiple features and coded holistically (Calder & Jansen, 2005; Calder et al., 2000). This difference might also explain why the gaze/tilt recognition factor and gaze adaptation were negatively associated with expression recognition. Perhaps individuals who can better direct attention to a single feature, such as the eyes, (which should increase gaze adaptation, cf. Rhodes et al., 2011), would code faces less holistically and thus be poorer at recognizing a range of expressions, especially when shown relatively briefly as in our expression recognition task.

An alternative possibility is that our gaze task reflects adaptation of low-level mechanisms that are unrelated to face processing. However, this seems very unlikely. Our gaze aftereffects were obtained despite changes in identity and head size (between adapting and test faces), thus minimizing contributions of low-level adaptation. Gaze aftereffects also survive changes in head orientation (Jenkins et al., 2006) and are sensitive to higher-level properties, such as relative gaze direction in the two eyes (Stiel, Clifford, & Mareschal, 2014) and expressions in the rest of the face (despite identical eyes) (Seyama & Nagayama, 2006). Moreover, gaze perception itself is affected by information in the rest of the face (e.g., head direction, Langton, Honeyman, & Tessler, 2004; Wollaston, 1824) and is better for upright than inverted faces (Schwaninger, Lobmaier, & Fischer, 2005), both indicating higher-level face processing. Finally, although the gaze aftereffects obtained here did not correlate with the other face aftereffects (for expression or identity) they did correlate (negatively) with expression recognition, which again suggests that they did tap aspects of face processing.

Identity recognition improved with age over the range tested here (17-30 years), indicating late maturation of face recognition ability. Non-face (car) recognition also improved with age. However, age remained significantly correlated with both face identity and expression recognition, when non-face recognition was controlled. Germine and colleagues (2011) have reported similar improvement that was selective for faces, with no improvement in memory for inverted faces or names. Our results demonstrate more directly that face–selective memory matures late (see also Susilo, Germine, & Duchaine, 2013; Weigelt et al., 2014). Therefore, they challenge claims that face recognition is quantitatively mature in early childhood (McKone, Crookes, Jeffery, & Dilks, 2012). We found no age-related increase in any face aftereffects, consistent with other evidence for early maturity of adaptive face-coding mechanisms (Jeffery et al., 2010; Jeffery, Read, & Rhodes, 2013; Jeffery et al., 2011) and face perception generally (e.g., Weigelt et al., 2014).

We also found new evidence that expression recognition improves with age from 17-30 years. Thus late maturation extends beyond identity recognition to expression recognition. Importantly, this parallel improvement in identity and expression recognition with age is also consistent with a common perceptual representation underlying the recognition of identity and expression.

4.1 Conclusions

We conclude that the visual coding of face identity and expression is not as distinct as claimed by influential models of face processing. Instead, we found that higher-level perceptual face space contains some dimensions that code both identity and expression, as well as dimensions that are selective for each attribute. Moreover, individual differences in the adaptive coding of these common dimensions are linked to individual differences in the ability to recognize both attributes. These results highlight a role for common dimensions in our ability to recognize faces and their expressions, and show why higher-level visual processing of these attributes cannot be entirely distinct.

Acknowledgements

This research was supported by the Australian Research Council Centre of Excellence in Cognition and its Disorders (CE110001021), an ARC Professorial Fellowship to Rhodes (DP0877379), an ARC Discovery Outstanding Researcher Award to Rhodes (DP130102300), an ARC Discovery grant to Palermo (DP110100850) and an ARC Australian Postdoctoral Fellowship to Jason Bell (DP110101511). It was also supported by the UK Medical Research Council under project code MC-A060-5PQ50 (Andrew J. Calder). Ethical approval was granted by the Human Research Ethics Committee of the University of Western Australia. We thank the following individuals for assistance with testing: Azhani Noor Amiruddin, Karen Clunies-Ross, Serena Cribb, Robert Green, Julie Ji, Thomas McDougall, Helen Shield and Ken Tan. We dedicate this paper to the memory of our collaborator and friend, Andy Calder (1965-2013), whose work inspired this research.

References

Adams, R. B., & Kleck, R. E. (2003). Perceived gaze direction and the processing of facial displays of emotion. *Psychological Science, 14*(6), 644-647.

Adams, R. B., & Kleck, R. E. (2005). Effects of direct and averted gaze on the perception of facially communicated emotion. *Emotion, 5*(1), 3-11.

Bindemann, M., Burton, A. M., & Langton, S. R. H. (2008). How do eye gaze and facial expression interact? *Visual Cognition, 16*(6), 708-733.

Bowles, D. C., McKone, E., Dawel, A., Duchaine, B., Palermo, R., Schmalzl, L., . . . Yovel, G. (2009). Diagnosing prosopagnosia: Effects of ageing, sex, and participant–stimulus ethnic match on the Cambridge Face Memory Test and Cambridge Face Perception Test. *Cognitive Neuropsychology, 26*(5), 423-455.

Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology, 77*, 305-327.

Burton, N., Jeffery, L., Skinner, A. L., Benton, C. P., & Rhodes, G. (2013). Nine-year-old children use norm-based coding to visually represent facial expression. *Journal of Experimental Psychology: Human Perception and Performance, 39*(5), 1261.

Calder, A. J. (2011). Does facial identity and facial expression recognition involve separate visual routes? In A. J. Calder, G. Rhodes, M. H. Johnson & J. V. Haxby (Eds.), The Oxford Handbook of Face Perception (pp. 427-448). Oxford: Oxford University Press.

Calder, A. J., Burton, A. M., Miller, P., Young, A. W., & Akamatsu, S. (2001). A principal component analysis of facial expressions. *Vision research, 41*(495-518).

Calder, A. J., & Jansen, J. (2005). Configural coding of facial expressions: The impact of inversion and photographic negative. *Visual Cognition, 12*(3), 495-518.

Calder, A. J., & Young, A. W. (2005). Understanding the recognition of facial identity and facial expression. *Nature Reviews Neuroscience, 6*, 641-651.

Calder, A. J., Young, A. W., Keane, J., & Dean, M. (2000). Configural information in facial expression perception. *Journal of Experimental Psychology: Human Perception and Performance, 26*(2), 527-551.

Clifford, C. W. G., & Rhodes, G. (Eds.). (2005). *Fitting the Mind to the World: Adaptation and After-Effects in High-Level Vision*. Oxford: Oxford University Press.

DeGutis, J., Wilmer, J. B., Mercado, R. J., & Cohan, S. (2013). Using regression to measure holistic face processing reveals a strong link with face recognition ability. *Cognition, 126*, 87-100.

Dennett, H. W., McKone, E., Edwards, M., & Susilo, T. (2012). Face aftereffects predict individual differences in face recognition ability. *Psychological Science, 23*(11), 1279-1287.

Dennett, H. W., McKone, E., Tavashmi, R., Hall, A., Pidcock, M., Edwards, M., & Duchaine, B. (2011). The Cambridge Car Memory Test: A task matched in format to the Cambridge Face Memory Test, with norms, reliability, sex differences, dissociations from face memory, and expertise effects. *Behavior research methods, 44*, 587-605.

Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants. *Neuropsychologia, 44*(4), 576-585.
Ellamil, M., Susskind, J. M., & Anderson, A. K. (2008). Examinations of identity invariance in facial expression adaptation. *Cognitive, Affective and Behavioural Neuroscience, 8*(3), 273-281.
Ewbank, M. P., Jennings, C., & Calder, A. J. (2009). Why are you angry with me? Facial expressions of threat influence perception of gaze direction. *Journal of Vision, 9*(12), 1-7.
Fairhall, S. L., & Ishai, A. (2007). Effective connectivity within the distributed cortical network for face perception. *Cerebral Cortex, 17*(10), 2400-2406.
Field, A. P. (2013). *Discovering statistics using IBM SPSS Statistics 4th Edition*. London: SAGE publications Ltd.
Fitousi, Daniel, & Wenger, Michael J. (2013). Variants of independence in the perception of facial identity and expression. *Journal of Experimental Psychology: Human Perception and Performance, 39*(1), 133.
Fox, C. J., & Barton, J. J. S. (2007). What is adapted in face adaptation? The neural representations of expression in the human visual system. *Brain Research, 1127*, 80-89.
Fox, C. J., Moon, S. Y., Iaria, G., & Barton, J. J. (2009). The correlates of subjective perception of identity and expression in the face network: an fMRI adaptation study. *Neuroimage, 44*(2), 569-580.
Fox, C. J., Oruc, I., & Barton, J. J. S. (2008). It doesn't matter how you feel. The facial identity aftereffect is invariant to changes in facial expression. *Journal of Vision, 8*(11), 1–13.
Frisby, J. P. (1980). *Seeing: Illusion, brain and mind*. Oxford: Oxford University Press.
Ganel, T., & Goshen-Gottstein, Y. (2004). Effects of familiarity on the perceptual integrality of the identity and expression of faces: the parallel-route hypothesis revisited. *Journal of Experimental Psychology: Human Perception and Performance, 30*(3), 583.
Germine, L. T., Duchaine, B., & Nakayama, K. (2011). Where cognitive development and aging meet: Face learning ability peaks after age 30. *Cognition, 118*(2), 201-210.
Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*, 223-233.
Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2002). Human neural systems for face recognition and social communication. *Biological Psychiatry, 51*, 59-67.
Jeffery, L., McKone, E., Haynes, R., Firth, E., Pellicano, E., & Rhodes, G. (2010). Four-to-six-year-old children use norm-based coding in face-space. *Journal of Vision, 10*(5), 1-19.
Jeffery, L., Read, A., & Rhodes, G. (2013). Four year-olds use norm-based coding for face identity. *Cognition, 127*(2), 258-263.
Jeffery, L., Rhodes, G., McKone, E., Pellicano, E., Crookes, K., & Taylor, E. (2011). Distinguishing norm-based from exemplar-based coding of identity in children: Evidence from face identity aftereffects. *Journal of Experimental*

Psychology: Human Perception and Performance, 37(6), 1824-1840. doi: 10.1037/a0025643
Jenkins, R., Beaver, J. D., & Calder, A. J. (2006). I thought you were looking at me: Direction-specific aftereffects in gaze perception. *Psychological Science, 17*(6), 506-513.
Kawasaki, H., Tsuchiya, N., Kovach, C. K., Nourski, K. V., Oya, H., Howard, M. A., & Adolphs, R. (2012). Processing of facial emotion in the human fusiform gyrus. *Journal of Cognitive Neuroscience, 24*(6), 1358-1370.
Langton, S. R. H., Honeyman, H., & Tessler, E. (2004). The influence of head contour and nose angle on the perception of eye-gaze direction. *Perception & Psychophysics, 66*(5), 752-771.
Mather, G., Verstraten, F., & Anstis, S. M. (1998). *The Motion Aftereffect: A Modern Perspective*. Cambridge, MA: MIT Press
McKone, E., Crookes, K., Jeffery, L., & Dilks, D. D. (2012). A critical review of the development of face recognition: Experience is less important than previously believed. *Cognitive Neuropsychology, 29*(1-2), 174-212.
McKone, E., Stokes, S., Liu, J., Cohan, S., Fiorentini, C., Pidcock, M., . . . Pelleg, M. (2012). A robust method of measuring other-race and other-ethnicity effects: The Cambridge Face Memory Test format. *PloS one, 7*(10), e47956.
Palermo, R., Jeffery, L., Lewandowsky, J., Fiorentini, C., Irons, J., & Rhodes, G. (2015). Individual differences in facial expression recognition ability are linked to adaptive coding of facial expression and self-reported levels of anxiety. *in preparation*.
Palermo, R., Jeffery, L., Lewandowsky, J., Fiorentini, C., McKone, E., Irons, J. L., . . . Burton, N. (2013). Individual differences in the ability to recognize facial expressions are associated with the strength of adaptive expression coding but not the strength of holistic expression coding. *Journal of Vision, 13*(9), 1272-1272.
Palermo, R., O'Connor, K. B., Davis, J. M., Irons, J., & McKone, E. (2013). New tests to measure individual differences in matching and labelling facial expressions of emotion, and their association with ability to recognise vocal emotions and facial identity. *PloS one, 8*(6), e68126.
Palermo, R., Willis, M. L., Rivolta, D., McKone, E. C., Wilson, E., & Calder, A. J. (2011). Impaired holistic coding of facial expression and facial identity in congenital prosopagnosia Original Research Article. *Neuropsychologia, 49*(5), 1226-1235.
Pitcher, D., Walsh, V., & Duchaine, B. (2011). The role of the occipital face area in the cortical face perception network. *Experimental Brain Research, 209*(4), 481-493.
Pitcher, D., Walsh, V., Yovel, G., & Duchaine, B. (2007). TMS evidence for the involvement of the right occipital face area in early face processing. *Current Biology, 17*, 1568-1573.
Rhodes, G., Evangelista, E., & Jeffery, L. (2009). Orientation-sensitivity of face identity aftereffects. *Vision research, 49*, 2379-2385.
Rhodes, G., Jeffery, L., Evangelista, E., Ewing, L., Peters, M, & Taylor, L. (2011). Enhanced attention amplifies face adaptation. *Vision research, 51*, 1811-1819.

Rhodes, G., Jeffery, L., Taylor, L., Hayward, W. G., & Ewing, L. (2014). Individual differences in adaptive coding of face identity are linked to face recognition ability. *Journal of Experimental Psychology: Human Perception & Performance, 40*(3), 897-903.

Rhodes, G., & Leopold, D. A. (2011). Adaptive norm-based coding of face identity. In A. J. Calder, G. Rhodes, M. H. Johnson & J. V. Haxby (Eds.), *The Oxford Handbook of Face Perception* (pp. 263-286). Oxford: Oxford University Press.

Schwaninger, A., Lobmaier, J. S., & Fischer, M. H. (2005). The inversion effect on gaze perception reflects processing of component information. *Experimental Brain Research, 167*(1), 49-55.

Schweinberger, S. R., Burton, A. M., & Kelly, S. W. (1999). Asymmetric dependencies in perceiving identity and emotion: Experiments with morphed faces. *Perception and Psychophysics, 6*, 1102-1115.

Schweinberger, S. R., & Soukup, G. R. (1998). Asymmetric relationships among perceptions of facial identity, emotion, and facial speech. *Journal of Experimental Psychology: Human Perception and Performance, 24*(6), 1748-1765.

Seyama, J., & Nagayama, R. S. (2006). Eye direction aftereffect. *Psychological research, 70*(1), 59-67.

Skinner, A. L., & Benton, C. P. (2010). Anti-expression aftereffects reveal prototype-referenced coding of facial expressions. *Psychological Science, 21*(9), 1248-1253.

Skinner, A. L., & Benton, C. P. (2012). The expressions of strangers: Our identity-independent representation of facial expression. *Journal of Vision, 12*(2), 1-13.

Stiel, B., Clifford, C. W. G., & Mareschal, I. (2014). Adaptation to vergent and averted eye gaze. *Journal of Vision, 14*(1), 15.

Stuart, Alan, & Kendall, Maurice George. (1958). *Advanced theory of statistics (Vol 1)*. London: Charles Griffin & Co.

Susilo, T., Germine, L., & Duchaine, B. (2013). Face recognition ability matures late: Evidence from individual differences in young adults. *Journal of Experimental Psychology: Human Perception and Performance, 39*(5), 1212.

Wang, Y., Fu, X., Johnston, R. A., & Yan, Z. (2013). Discriminability effect on Garner interference: evidence from recognition of facial identity and expression. *Frontiers in Psychology, 4*.

Webster, M. A. (2011). Adaptation and visual coding. *Journal of Vision, 11*(5), 1-23. doi: 10.1167/11.5.3

Webster, M. A., & MacLeod, D. I. A. (2011). Visual adaptation and face perception. *Philosophical Transactions of the Royal Society: Biological Sciences, 366*, 1702-1725.

Weigelt, S., Koldewyn, K., Dilks, D. D., Balas, B., McKone, E., & Kanwisher, N. (2014). Domain‐specific development of face memory but not face perception. *Developmental Science, 17*(1), 47-58.

Wollaston, W. H. (1824). On the apparent direction of eyes in a portrait. *Philosophical Transactions of the Royal Society of London*, 247-256.

Yankouskaya, A., Booth, D. A., & Humphreys, G. W. (2012). Interactions between facial emotion and identity in face processing: Evidence based on

redundancy gains. *Attention, Perception, & Psychophysics, 74*(8), 1692-1711.
Yovel, G., & Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology, 15*(24), 2256-2262.