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# Adaptive norm-based coding of facial identity

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## Abstract

Identification of a face is facilitated by adapting to its computationally opposite identity, suggesting that the average face functions as a norm for coding identity [Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience*, 4, 89–94; Leopold, D. A., Rhodes, G., Müller, K. -M., & Jeffery, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society of London, Series B*, 272, 897–904]. Crucially, this interpretation requires that the aftereffect is selective for the opposite identity, but this has not been convincingly demonstrated. We demonstrate such selectivity, observing a larger aftereffect for opposite than non-opposite adapt-test pairs that are matched on perceptual contrast (dissimilarity). Component identities were also harder to detect in morphs of opposite than non-opposite face pairs. We propose an adaptive norm-based coding model of face identity.

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**Keywords:** Face perception; Adaptation and aftereffects; Psychophysics

## 1. Introduction

Adaptive coding mechanisms are widespread in low-level vision, with sensory neurons dynamically adapting to prevailing (average) stimulus values (Barlow, 1990; Blake-More & Sutton, 1969; Helson, 1964; Hosoya, Baccus, & Meister, 2005; Webster, 2003; Werblin, 1973). Adaptive coding is neurally and computationally efficient, because it focuses energetically costly neural signals on uncommon (non-average) inputs and alerts the system to potentially important changes in the environment (Barlow, 1990). The operation of such adaptive mechanisms can be seen in perceptual aftereffects of brightness, hue, direction of motion, and other simple sensory attributes (Clifford & Rhodes, 2005; Frisby, 1980).

Recent reports of aftereffects for complex stimuli such as faces and bodies suggest that similar adaptive mechanisms are also used in higher-level vision (for a review, see Clifford & Rhodes, 2005). What looks normal in faces and bodies is

dynamically updated by experience, so that exposure to consistently distorted stimuli makes undistorted stimuli appear distorted in the opposite way (MacLin & Webster, 2001; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Rhodes et al., 2004; Webster & MacLin, 1999; Winkler & Rhodes, 2005). These aftereffects generalize across changes in image size implicating adaptation of higher-level neural mechanisms (e.g., Rhodes et al., 2004; Zhao & Chubb, 2001).

How might such adaptive coding mechanisms underlie our ability to discriminate thousands of faces despite their similarity as visual patterns? Many theorists have proposed that the average face, which lies at the center of a computational face-space (whose dimensions correspond to whatever we use to discriminate faces) could function as a norm or prototype against which individuating (identity) information is coded (Diamond & Carey, 1986; Goldstein & Chance, 1980; Hebb, 1949; Hochberg, 1978; Leopold, O'Toole, Vetter, & Blanz, 2001; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Rhodes, Brennan, & Carey, 1987; Rhodes, 1996; Valentine, 1991). This proposal is controversial, with other theorists rejecting prototype models in

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favor of exemplar models (Hintzman, 1986; Nosofsky, 1988, 1991; Valentine, 2001).

Leopold et al. (2001) found that identification of a face (Jim) was facilitated by adapting to the opposite identity (AntiJim), but not to some other face (AntiFred). Similar results have been reported using synthetic faces (Anderson & Wilson, 2005). Adaptation to a face shifts the norm or average towards that face, so that the opposite face now deviates more from the norm than it did before, becoming easier to identify (Anderson & Wilson, 2005; Leopold, Rhodes, Müller, & Jeffery, 2005; Rhodes et al., 2005). This identity aftereffect has therefore been taken as evidence that identity is coded relative to the average face.

Crucially, this interpretation requires that the aftereffect is *selective* for computationally opposite identities and is not a generalized contrast effect in which perception is biased non-selectively away from an adapting identity, in *all* directions in face-space. Leopold et al. (2001) sought evidence for the required selectivity, by comparing the aftereffects for opposite and non-opposite adapting faces. However, the non-opposite adapting faces were more similar to the test faces than were the opposite adapting faces (see Leopold et al., 2001, Fig. 1). The same was true in Anderson and Wilson (2005). Failure to equate perceptual contrast is a serious problem because aftereffects often decrease as the adapting and test stimuli become more similar (Clifford, 2002). Therefore, the apparent selectivity of the aftereffect for opposite adapt-test pairs could be an artifact of their greater perceptual contrast. A second problem is that identity thresholds have been measured using trajectories that are ideal for detecting a perceptual bias towards the opposite identity, but not for detecting perceptual biases towards other identities. This is because identification has only been tested using identities that span opposite adapt-test pairs.

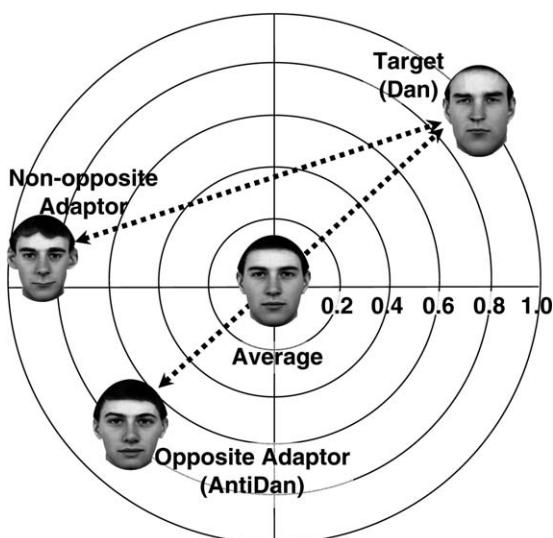


Fig. 1. An opposite (anti-face, face) and non-opposite adapt-test pair.

## 2. Experiment 1

We measured the face identity aftereffect for computationally opposite and non-opposite adapt-test pairs that were matched on perceptual contrast (perceived dissimilarity). Opposite pairs consisted of target faces and their anti-faces. Non-opposite adapt-test pairs were generated by replacing the anti-face in each pair with another face that was judged to be equally perceptually dissimilar to the target, but which was not opposite it in face-space. Aftereffects were calculated by comparing identification thresholds after adaptation with those obtained in an unadapted baseline. Identification thresholds were measured using opposite trajectories for opposite adapt-test pairs and using non-opposite trajectories for non-opposite adapt-test pairs. Each test trajectory consisted of a series of images that morphed the relevant adapt and test identities in varying proportions, from 100% adapt identity to 100% test identity. All images had the texture of an average male face, so that only shape was varied. Identification thresholds were obtained using the method of constant stimuli. If the aftereffect is selective for computationally opposite faces, then it should be restricted to, or larger for, opposite than non-opposite adapt-test pairs. By matching the perceptual dissimilarity of opposite and non-opposite adapt-test pairs we can be confident that any selectivity of the aftereffect for opposite pairs is not due to greater perceptual contrast between those pairs. Previous studies have shown that the identity aftereffect generalizes across changes in image size (Anderson & Wilson, 2005) and retinal position (Leopold et al., 2001) implicating adaptation of high-level coding mechanisms. Here we used adapt and test stimuli of the same size.

### 2.1. Method

#### 2.1.1. Participants

Six naïve participants (4 female, 2 male) and 1 non-naïve female took part.

#### 2.1.2. Stimuli

Four easily discriminable target faces were selected from a pool of greyscale photographs of twenty young male faces (Fig. 2). An anti-face (Fig. 2) was constructed for each face by caricaturing the structure of the average face (constructed from the original pool of twenty male faces) away from the target face by 80%, using Gryphon Morph (after Leopold et al., 2001). All faces had the texture of the average face. The resulting images were sharpened and placed in an oval mask which hid the outer hairline, but not the inner hairline or face outline. Images subtended a viewing angle of  $15.3^\circ \times 20.2^\circ$ , when viewed from 45 cm.

For each target, we chose a non-opposite, “same-distance” matched face (Fig. 2), that was equally perceptually dissimilar to the target as was its anti-face. These were selected from an additional 30 male faces (the 16 remaining faces from the original set of 20 plus 14 additional faces, all

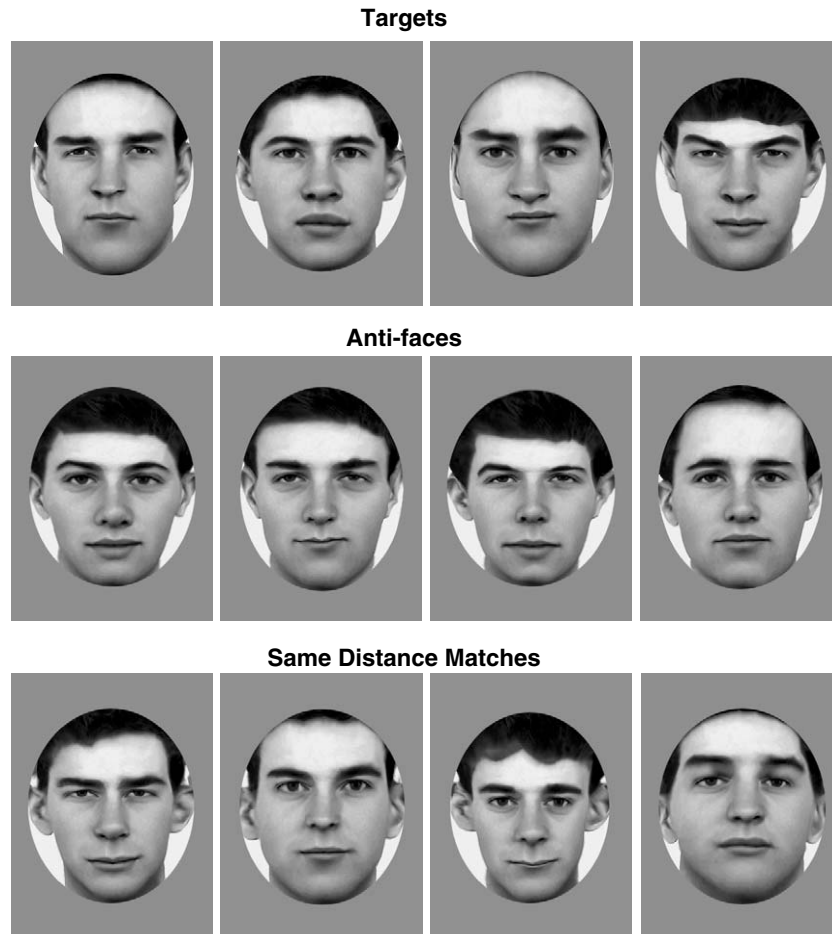


Fig. 2. The four target faces (top), their corresponding anti-faces (middle) and corresponding same-distance matches (bottom) used in Experiment 1.

with the average colors) to be equally similar to the target face as its corresponding anti-face (Table 1). Similarity was assessed on a 7-point scale by 17 judges (11 female). They first viewed all the faces (4 targets, 4 anti-faces, and 30 test faces) for 1500 ms each to familiarize them with the range of faces they would see. They then rated all 256 pairs (4 targets  $\times$  30 test faces; 4 anti-faces  $\times$  30 test faces, the 4 targets paired with the 4 anti-faces, the 4 targets paired with each other, and the 4 anti-faces paired with each other). Mean similarity ratings ranged from 1.7 to 5.9 ( $M=3.6$ ,  $SD=0.9$ ). Reliability was excellent (Cronbach  $\alpha=0.88$ ). To select “same-distance” matches for each target the target-test pairs with the closest mean similarity rating to the target-anti-face pair were chosen. Table 1

Table 1  
Mean similarity ratings for target, anti-face; target, same-distance and anti-face, same-distance pairs

Target	Target, anti-face	Target, same-distance	Anti-face, same-distance
1	2.2 (1.4)	2.4 (1.6)	4.1 (1.6)
2	3.3 (3.3)	3.4 (1.5)	3.9 (1.5)
3	1.7 (1.1)	1.8 (1.2)	4.1 (1.6)
4	2.1 (1.0)	2.1 (1.1)	3.9 (1.4)
Mean	2.3 (0.7)	2.4 (0.7)	4.0 (0.1)

Standard deviations are shown in brackets.

shows mean similarity ratings for targets, anti-faces, and non-opposite, “same-distance” faces.

We created an opposite and a non-opposite test trajectory for each target using Gryphon’s morph to make a series of morphs between the target and its 80% anti-face (Opposite trajectory) and the target and its non-opposite match (Non-opposite trajectory). Each trajectory consisted of 17 morphs, in which the contribution of the target face was varied in 5% increments, from 0% (no target face) to 80% (see Fig. 3).<sup>1</sup>

### 2.1.3. Procedure

**2.1.3.1. Training.** Participants were shown each of the four male targets and their corresponding names (Dan, Jim, Rob, and Ted) and told they would need to identify each individual by pressing labeled keyboard keys. They were then shown each face six times, in random order, and asked who it was. Each face remained on the screen until the participant responded. Feedback was provided if the answer was incorrect and participants were told the correct name. They were then told that they would do some practice trials

<sup>1</sup> For the opposite continua these levels correspond to “identity strengths” ranging from  $-0.8$  to  $+0.6$ .

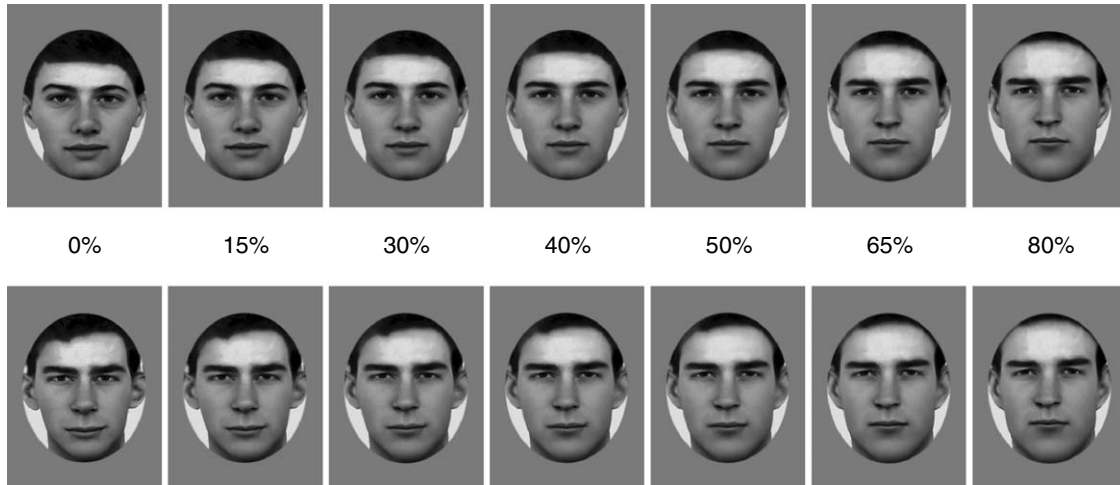


Fig. 3. Seven morphs from an opposite (top row) and a non-opposite trajectory (bottom row) used in Experiment 1. The percent of the target face in each morph is shown in the middle row.

in which the faces would now be shown briefly and feedback would come in the form of a beep if incorrect. Each trial consisted of a black fixation cross for 150 ms, a 500 ms blank ISI, the stimulus for 500 ms, then a blank screen which remained until a response was provided. Participants completed 20 trials (5 presentations of each face in random order) after which the stimulus duration was reduced to 200 ms for a further 20 trials.

**2.1.3.2. Baseline.** Participants completed two baselines for each trajectory, one before adaptation (Pre-Baseline) and one after (Post-Baseline). In this phase, identification thresholds were established for the test stimuli in the absence of any adapting stimuli. Participants were told they would be asked to identify some “weaker” versions of the four learned identities. They were also told that they would see some faces that were clearly none of the four targets and to respond randomly or with the name of the identity who

was closest. Each baseline comprised 16 blocks of 136 trials. Each block consisted of all 136 stimuli (4 targets × 17 target × 2 axes) presented in random order. No feedback was provided. Each baseline session took approximately one hour and 15 min.

**2.1.3.3. Adaptation.** There were two kinds of adapting trials: opposite adaptation trials, in which participants adapted to an anti-face and were tested on a morph of that anti-face and the corresponding target face, and non-opposite adaptation trials, in which participants adapted to a same-distance matched face and were tested on a morph of that face and the corresponding target. Each trial began with a 500 ms blank isi followed by a black fixation cross displayed for 150 ms, followed by the adapting face for 5000 ms, a blank isi of 150 ms and then the target for 200 ms followed by a blank screen, which remained until a response was made (Fig. 4). Participants were told that

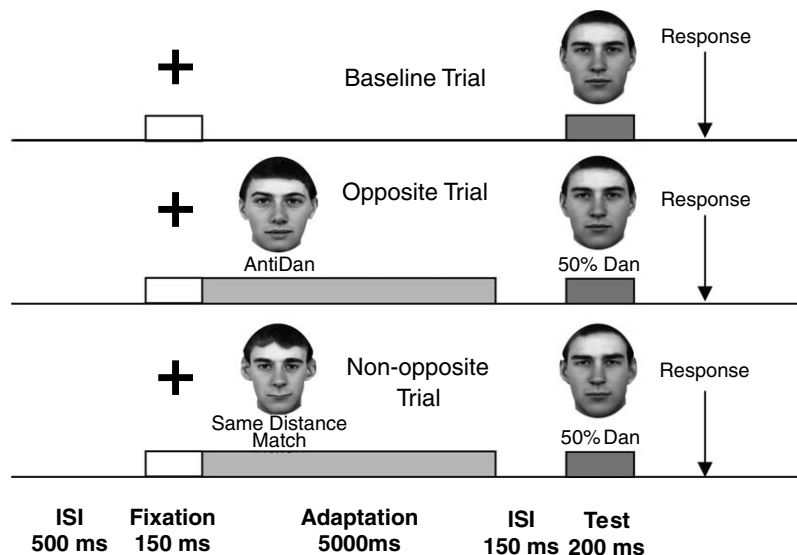


Fig. 4. Trial structure and conditions used in Experiment 1. The Baseline Trail shown is for an opposite trajectory.

their task was the same as for the Baseline phase but that this time each face they must identify would be preceded by another face, which they should attend to. They then completed four practice trials before starting the task proper.

A complete set of 136 adaptation trials was split into two blocks of 68 trials. These two blocks were alternated with participants completing 9 blocks in the first session and another 9 blocks in the second. Each session took approximately one hour and 15 min. Five participants completed the sessions over 3 to 4 days and the remaining two completed them over several weeks. Each session began with the same training trials as preceded Baseline, to ensure good familiarity with the target faces.

## 2.2. Results and discussion

Responses were scored as correct if they corresponded to the target from which the morph was made. Following Leopold et al. (2001) a four parameter logistic function was fitted to the data for each condition, for each participant. Individual identification thresholds were calculated as the mean of each function. A clear aftereffect was seen for the opposite test trajectories (Fig. 5, top). On average, adaptation reduced identification thresholds by 11.9%, from pre-adaptation baseline thresholds of 55.4 (SD = 4.6) to post-adaptation thresholds of 43.5 (SD = 4.9). Pre-adaptation baselines were similar to post-adaptation baseline thresholds (53.2, SD = 3.64). The aftereffect was significant when compared to either baseline (Pre:  $t(6) = 4.63$ ,  $p = 0.004$ ,  $d = 2.51$ ; Post:  $t(6) = 4.45$ ,  $p = 0.004$ ,  $d = 2.26$ ). The aftereffect can also be seen for individual participants (Fig. 5, top right).

The results for non-opposite test trajectories were more complex (Fig. 5, bottom). On average, identification thresholds were reduced by 10.6%, from pre-adaptation thresholds of 41.2 (SD = 5.9) to post-adaptation thresholds of 30.6 (SD = 5.8),  $t(6) = 10.61$ ,  $p = 0.002$  ( $d = 1.81$ ). However, baseline performance also showed substantial improvement for some participants (Fig. 5, bottom right). On average, thresholds dropped by 5% from pre-adaptation ( $M = 41.2$ ) to post-adaptation baseline sessions ( $M = 36.2$ , SD = 5.4). Clearly experience with non-opposite trajectories resulted in substantial learning, unlike experience with opposite trajectories. This learning effect was confirmed using additional participants (2 male, 2 female, all naive) who completed three baseline sessions without any adaptation over 3 to 4 days (Fig. 6). Average thresholds decreased from 49.5 to 41.5 to 40.1 for non-opposite trajectories. The decrease was considerably smaller for opposite trajectories (60.1, 56.9, 55.1 for sessions 1–3, respectively).

Given the strong learning effect for non-opposite trajectories the identity aftereffect cannot be measured by comparing adaptation thresholds with pre-adaptation baseline thresholds. When we compared them instead with post-adaptation baselines, the aftereffect (5.6%, SD = 3.3) was significant,  $t(6) = 4.56$ ,  $p = 0.004$  ( $d = 1.01$ ). However, it was about half the size of the aftereffect on the opposite trajec-

tory (9.7%, SD = 5.8) and significantly smaller than it,  $t(6) = 2.92$ ,  $p = 0.026$  ( $d = 0.81$ ). The selectivity of the aftereffect for opposite identities was confirmed by testing two additional participants (1 non-naïve female, who had previously participated and 1 naïve male) for whom baseline blocks were interleaved with adapting blocks (2 sessions per day, over 2 days) (Fig. 7). Compared with the aftereffect for opposite trajectories (11.2%, LJ; 6.8%, RB) (Fig. 7, top) the aftereffect for non-opposite trajectories was smaller (3.7%, LJ; 4.3%, RB) (Fig. 7, bottom). These results indicate that an identity aftereffect occurs for non-opposite as well as opposite identities but that it is significantly larger for opposite identities. The small aftereffect observed after adapting to non-opposite identities may be a consequence of their similarity to the opposite (anti) faces (see Table 1). Thus the aftereffect they produce biases perception toward a face somewhat resembling the corresponding target, facilitating recognition of the target relative to the other identities. This facilitation would be expected to reduce and eventually be eradicated as the adapting face moves further away (orthogonally) from the opposite (anti) face in face-space.

In addition to the difference in aftereffects, there are striking differences in baseline performance in the two conditions. First, for opposite baselines (Figs. 6 and 7) performance on the 0% targets, i.e., the anti-faces, was below chance (25%), indicating a reluctance to choose the computationally opposite identity when faced with an unlearned identity. No such reluctance was seen for non-opposite identities. This result provides further evidence that computationally opposite, but not other equally dissimilar, but non-opposite, faces are perceived as opposites and that identity is coded relative to the average.

A second striking difference was that the identification thresholds were considerably lower for non-opposite (41.2) than opposite trajectories (55.4),  $t(6) = 10.41$ ,  $p < 0.001$  ( $d = 2.68$ ), with the whole function lying well to the left of that for opposite morphs. These baseline differences demonstrate that target identities were much more difficult to detect when morphed with opposite than with non-opposite identities. For example, targets were identified less than 40% of the time in 50/50 morphs of opposite identities, but over 80% of the time in 50/50 morphs of non-opposite (but equally perceptually dissimilar) identities,  $t(6) = 9.54$ ,  $p < 0.001$  ( $d = 3.57$ ).

This greater “visibility” of the target identities in non-opposite morphs may explain the substantial learning observed for non-opposite morphs (see above). Participants could reliably detect the target in 50/50 non-opposite morphs and may have noticed the similarity of those morphs to weaker morphs (e.g., 20/80) thereby associating the weaker morphs with the target identities (via transitivity of similarity), resulting in improved identification. Such learning was not observed for opposite morphs, where similarity of 50/50 morphs to the targets was weaker and dropped more sharply with decreasing contributions of the target to the morph.

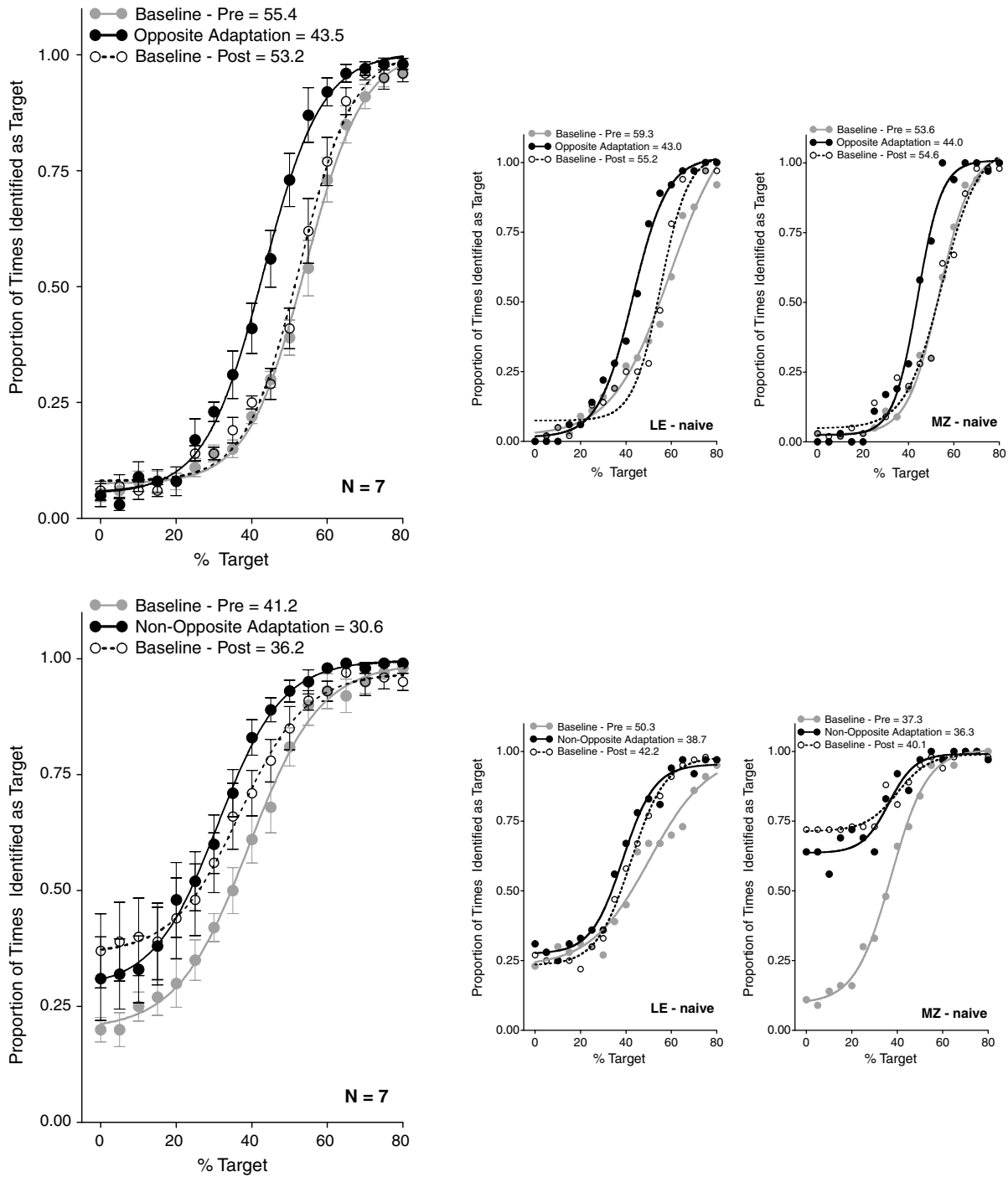


Fig. 5. Identification curves for opposite (top) and non-opposite (bottom) adapt-test pairs in Experiment 1. The left graphs show data averaged across seven participants (mean thresholds in legends) and the right graphs show data from two individual participants (individual thresholds in legends).

### 3. Experiment 2

The results of Experiment 1 provided preliminary evidence that component identities are more difficult to perceive in morphs of computationally opposite than non-opposite identities. We tested this difference more directly in Experiment 2, by asking participants to rate the similarity of 50/50 morphs to their component faces for both types of morph. Greater difficulty detecting the com-

ponent identities in opposite-morphs than non-opposite morphs would demonstrate the importance of vector direction in the representation of identity and provide further evidence for the perceptual opponency of computationally opposite faces.

Because the identity vectors of opposite identities lie in opposite directions they will cancel in opposite-morphs resulting in an identity that is close to the average in face-space. Difficulty detecting the component identities in

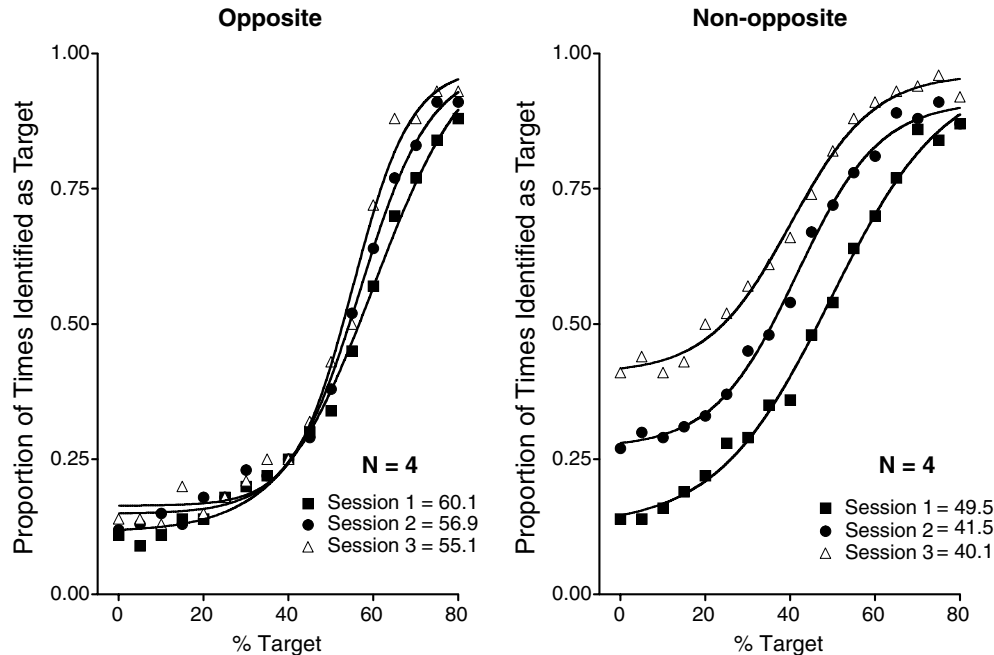


Fig. 6. Average identification curves from four participants who completed three baseline sessions in Experiment 1 (mean thresholds in legends).

opposite-morphs would, therefore, be consistent with another prediction of norm-based coding, namely that the average face has a “neutral” identity. In contrast, non-opposite morphs will have a vector direction midway between the component vector directions, supporting some resemblance to those identities.

### 3.1. Method

#### 3.1.1. Participants

Sixteen first year psychology students (6 male) participated for course credit (Mean age = 19.4 years, SD = 4.0).

#### 3.1.2. Stimuli

The four male faces, their anti-faces, and same-distance-matched faces from the previous experiment were used. Opposite morphs were created by combining each face with its anti-face in Gryphon Morph to create a 50% morph. The non-opposite morphs were similarly made by combining each face and its same-distance partner to create a 50% morph. Thus 8 morphs were created. An additional 50/50 morph between a new face and its anti-face was made for use in practice trials.

#### 3.1.3. Procedure

Participants were told they would be shown face pairs on the screen and asked to rate their similarity on a seven point scale from 1-“Not similar at all” to 7-“Very similar.” They were encouraged to use the full range of the scale. Each pair contained a morph and one of its component faces. Participants were required to make 16 similarity judgements (4 identities  $\times$  2 morph types  $\times$  2 component faces). The face pairs remained on the screen until a

response was made. The position of each component face and morph (left or right) was balanced across participants. The 16 pairs were presented in random order. Before rating the pairs, participants were shown all the stimuli (16 faces), one at a time for 1 s each, to provide them with an idea of the range of faces they would see. After completing two practice trials they commenced the test trials. The session lasted approximately 5 min.

### 3.2. Results and discussion

A two-way ANOVA was conducted on mean similarity ratings, with morph type (opposite, non-opposite) and component (face, anti-face/same-distance-match) as repeated measures factors. There was a significant main effect of morph type,  $F(1, 15) = 55.13$ ,  $p < 0.0001$ ,  $\eta^2 = 0.3$  with opposite morphs rated as less similar to their component faces ( $M = 3.5$ ,  $SE = 0.2$ ) than were non-opposite morphs ( $M = 4.5$ ,  $SE = 0.2$ ). No other effects were significant. Therefore, computationally opposite identities cancel more strongly in morphs than do non-opposite identities, providing further evidence for their perceptual opponency and that identity is coded relative to the average face.

## 4. General discussion

Our results show that computationally opposite identities in face-space are perceived as opposites. Brief exposure to a face selectively biases perception towards the opposite identity and opposite identities tend to “cancel” in face morphs. These perceptual opponent properties are not shared by other equally dissimilar, but non-opposite, pairs of identities, suggesting a special role for the average face in

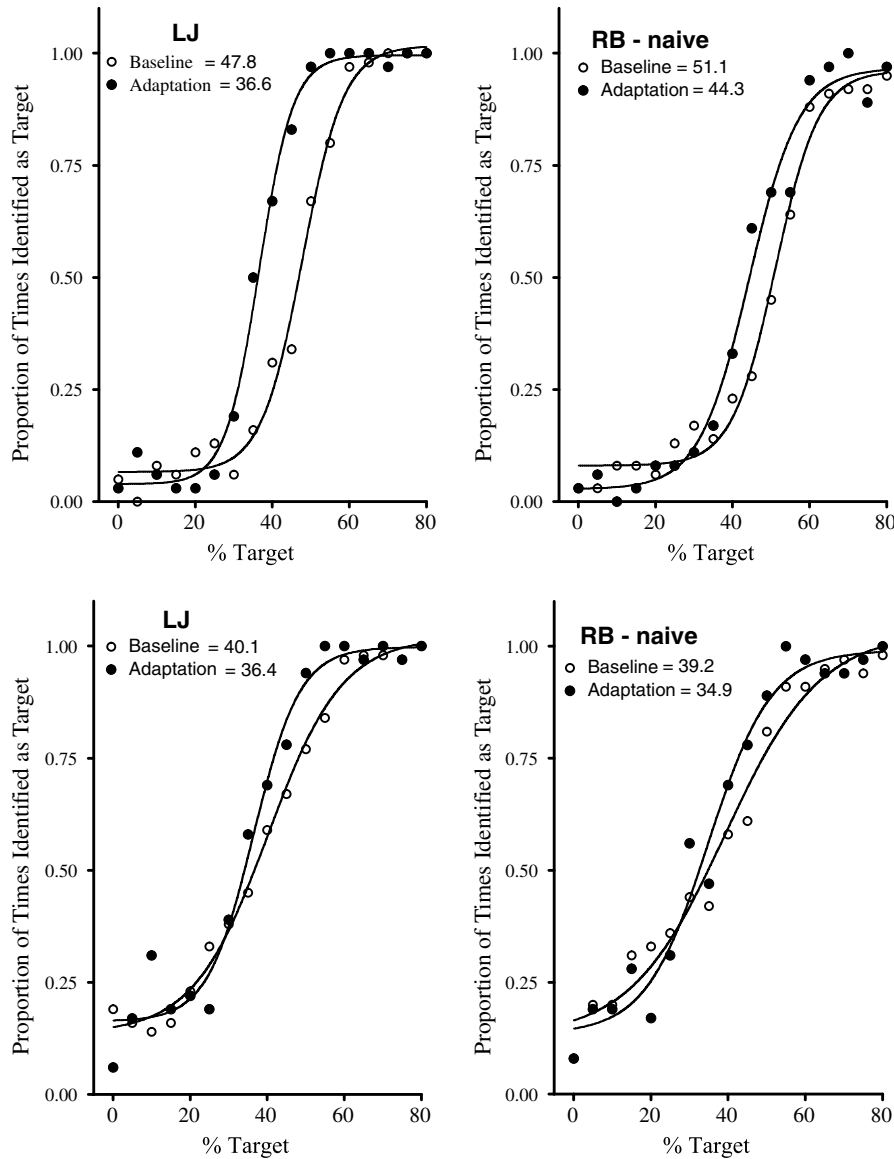


Fig. 7. Individual identification curves for opposite (top) and non-opposite (bottom) trajectories for two participants who completed interleaved adaptation and baseline blocks in Experiment 1 (individual thresholds in legends).

coding identity. These results indicate that facial identity is coded relative to an average face, which is dynamically tuned by experience.

Specifically, we propose that facial identity is coded by pairs of neural populations that are adaptively tuned to above-average and below-average values, respectively, of each dimension in face-space (Fig. 8). The values of each face on each dimension of face-space are signaled by the relative activation of the paired populations, with equal activation signaling average values. The identity aftereffect occurs because viewing a face temporarily suppresses activity in the member of each pair that responds more strongly to that face. For example, a face with large eyes will more strongly activate, and so more strongly suppress, neurons that respond to above-average eye size. As a result, a face with average sized eyes, which previously activated the paired populations equally, now selectively activates the

below-average population. Similarly for all the other dimensions of the face, so that viewing a face biases perception towards the opposite identity. As a result, the previously average face takes on the identity opposite to the adapting face (Fig. 8).

Emerging evidence suggests that neural face coding mechanisms have just the response properties predicted by this model. Faces which lie further from the average generate stronger neural responses in human face-selective brain areas (Loffler et al., 2005) and face-selective neurons in monkeys (Leopold, Bondar, Giese, & Logothetis, 2006). These response properties are exactly what would be expected if face-selective neurons adapt to average values of the dimensions on which faces are coded and support the proposed model.

As noted earlier, exemplar theorists have challenged prototype models, arguing that explicit norms or prototypes



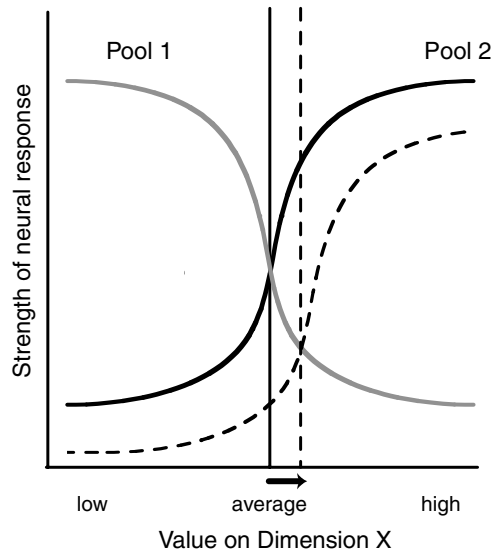


Fig. 8. Adaptive coding model for facial identity (adapted from Rhodes et al., 2005). For each dimension of face-space, there are two populations of neurons. The two populations are shown for one dimension. Pool 1 codes below-average and Pool 2 codes above-average values on dimension X. Average values are coded implicitly, by equal activation of the two populations. Exposure to an adapting face with a high value on dimension X will shift the perceived average towards the adapting face (dotted vertical line) and make a previously neutral, average face take on the opposite identity. The aftereffect results from a temporary reduction in responsiveness of Pool 2 neurons, which respond strongly to the adapting face.

are not needed to explain “prototype-like” effects (e.g., Hintzman, 1986; Nosofsky, 1988, 1991; Valentine, 2001; but see Smith, 2002). However, the model proposed here shows that individuating information can be coded as deviations from average or prototype without an explicitly represented average. Knowledge of average population values is coded implicitly in the tuning of face coding neurons. Adaptive coding models, which are widely used to code simple sensory properties and are proposed here for the coding of facial identity, take us beyond the traditional exemplar/prototype dichotomy (see also Ashby & Maddox, 2005).

Stronger neural signals for faces that lie further from the average in face-space may explain why distinctive faces, which lie further from the average, are easier to recognize than more typical faces (Going & Read, 1974; Johnston & Ellis, 1995; Light, Kayra-Stuart, & Hollander, 1979; Valentine, 1991; Valentine & Bruce, 1986) and why exaggerating a face’s deviation from the average, by caricaturing, can enhance recognition (Byatt & Rhodes, 1998; Lee, Byatt, & Rhodes, 2000; Rhodes, Carey, Byatt, & Proffitt, 1998; Rhodes et al., 1987). Distinct patterns of neural activity would be expected to be more discriminable when represented by stronger than weaker neural signals. The model is also consistent with well-known behavioral sensitivity to the central tendency of the population of faces encountered (Bruce, Doyle, Dench, & Burton, 1991; Inn, Walden, & Solso, 1993; Reed, 1972; Solso & McCarthy, 1981a, 1981b; Strauss, 1979; Walton & Bower, 1993). This sensitivity

appears to be present early in infancy and perhaps even at birth (De Haan, Johnson, Maurer, & Perrett, 2001; Rubenstein, Kalakanis, & Langlois, 1999; Walton & Bower, 1993) and may be fundamental to the development of face recognition expertise.

For ease of expression we have talked as if there is a single face-space with a single norm. However, distinct norms may be used for visually distinct face categories. For example, opposite figural aftereffects can be induced simultaneously in upright and inverted faces (Rhodes et al., 2004), which is not possible unless there are distinct norms for upright and inverted faces. Similar results have been obtained for faces of different races (Jaquet & Rhodes, 2006b) and sexes (Jaquet & Rhodes, 2006a; Little, DeBruine, & Jones, 2005). Distinct norms for structurally distinct face categories may enable selective coding of the dimensions that best discriminate the faces within each category. Interestingly, the boundaries between these categories also appear to be dynamically altered by experience, so that unexpected stimuli are more readily perceived (Webster, Kaping, Mizokami, & Duhamel, 2004).

Adaptive coding mechanisms are widely used in low-level vision to code sensory information. The present results suggest that they are also used in higher-level vision (see also Clifford & Rhodes, 2005). The adaptive face coding mechanisms proposed here may operate in a similar way as low-level mechanisms given the similar time courses of face identity aftereffects and aftereffects for simpler stimulus attributes (Leopold et al., 2005).

Adaptive coding mechanisms are neurally and computationally efficient. But do they facilitate discrimination of frequently or recently experienced faces? Initial attempts to address this question have produced mixed results. There is evidence of facilitation of synthetic faces lying close to the average (Wilson, Loffler, & Wilkinson, 2002) and a trend for enhanced discrimination of synthetic faces lying close to the average following adaptation to a matching compared with a non-matching anti-face (Anderson & Wilson, 2005). Other studies have failed to find enhanced discrimination of real faces lying close to the average (Rhodes et al., 2005; Rhodes & Maloney, 2006). However, brief exposure to the average face for a particular race improves identification of faces from that race compared to those from another race, suggesting that adaptive mechanisms can function to enhance performance with real faces (Watson, Rhodes, & Clifford, 2006).

Aftereffects have been called the psychologist’s micro-electrode because of their power to reveal the neural coding mechanisms underlying visual experience (Frisby, 1980). Although initially used to study coding of low-level sensory properties, they are increasingly being used to study the coding of complex stimuli such as faces (for recent reviews, see Clifford & Rhodes, 2005). Here, we have argued that the selectivity of the face identity aftereffect for computationally opposite faces provides strong evidence that facial identity is coded relative to an average face, thus resolving a long-standing debate about how faces are coded.

## Acknowledgments

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