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Evidence that identity-dependent and identity-independent neural populations are recruited in the perception of five basic emotional facial expressions

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ABSTRACT

Major cognitive and neural models of face perception view that the mechanisms underlying the extraction of facial expression and facial identity information involve separable visual systems. Using the visual adaptation paradigm, we explored the sensitivity of happy, sad, angry, disgusted and fearful facial expressions to changes in identity. Contrary to what would be predicted by traditional face perception models, larger expression aftereffects were produced when the identity of the adapting and test stimuli was the same compared to when the identity differed, suggesting the involvement of identity-dependent neurons in processing these expressions. Furthermore, for all five expressions, the aftereffects remained significant when the adapting and test stimuli differed in identity, suggesting the involvement of identity-independent neural populations. The extent to which the aftereffect transferred across changes in identity was the same for all emotional expressions. Consequently, there is no evidence that the processing of individual facial expressions depend on facial identity differentially. Implications of these findings are discussed.

1. Introduction

Major cognitive and neural theories of face perception suggest that the processes underlying the extraction of facial expression and facial identity information involve separable visual systems (Bruce & Young, 1986; Haxby, Hoffman, & Gobbini, 2000, 2002). According to the neural framework by Haxby and Colleagues, after an early stage of perceptual analysis occurring in the inferior occipital gyrus, two distinct codes are generated in different regions of the brain. Visuoperceptual representations of changeable facial aspects, including facial expressions, are thought to be mediated by the superior temporal sulcus, while visuoperceptual representations of invariant characteristics of a face, like facial identity, are thought to be coded by the lateral fusiform gyrus (Haxby et al., 2000).

The notion that these two facial dimensions are processed by parallel neural systems has been widely accepted and evidence purported to support this independence has accumulated largely from the domains of human patient studies (Humphreys, Donnelly, & Riddoch, 1993), single-cell studies (Hasselmo, Rolls, & Baylis, 1989; Perrett et al., 1984) and human behavioural studies (Campbell, Brooks, de Haan, & Roberts, 1996; Young, McWeeny, Hay, & Ellis, 1986). In line with the Haxby and Colleagues framework, some early single-cell studies (Hasselmo et al., 1989; Perrett et al., 1984), for example, have observed that neurons in the superior temporal sulcus were more likely to be preferentially responsive to facial expressions whereas neurons in the inferotemporal areas were more likely to be preferentially responsive to facial identity information.

On the other hand, the notion that facial expression information is coded completely free from identity-based visual information has been met with some criticism (Calder & Young, 2005; Ganel & Goshen-Gottstein, 2004). Even early single-cell studies observed that a small sample of neurons responded to both facial expression and identity information, indicating that the segregation is relative rather than absolute (see Hasselmo et al., 1989; Perrett et al., 1984). Calder and Young (2005) point out that many dissociation studies implicating distinct facial expression and identity coding systems have failed to rule out alternative neuropsychological causes that are not visuoperceptual in nature. For example, an impairment in accessing person-specific semantic knowledge or an impairment in learning (and, consequently, recognising) new faces will give rise to the inability to name faces, but not facial expressions, without implicating separable visual representational systems (Calder & Young, 2005).

Recent neuroimaging (Gobbini & Haxby, 2007; Vuilleumier & Pourtois, 2007) and single-cell studies (Gothard, Battaglia, Erickson, Spitler, & Amaral, 2007; Perrett, Hietanen, Oram, & Benson, 1992; Sugase, Yamane, Ueno, & Kawano, 1999) suggest that a number of interactions between the mechanisms underlying the coding of facial expression and identity information may occur in the brain. In a recent single-cell study, Gothard et al. (2007) found that a high

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proportion of cells (64%) in the monkey amygdala, a structure believed to receive input from both the inferotemporal cortex and superior temporal sulcus, were responsive to both facial expression and facial identity information. Consequently, the amygdala may play a role in integrating these two facial aspects, a notion further supported by recent research that have demonstrated amygdalae involvement in facial expression perception (see Adolphs, 2006, for a review) and also in (neutral) facial identity matching (Wright & Liu, 2006).

1.1. Breaking down the category of facial expressions

Presumably as a result of major face perception models, which view that the coding of all facial expressions are mediated by a single module (Bruce & Young, 1986) or discrete region of the brain (Haxby et al., 2000), the literature has generally failed to break down the category of facial expressions and explore the relationship between facial expression and identity processing at the level of individual expressions. In contrary to major face perception frameworks, neuropsychological (e.g., Calder et al., 1996; Gray, Young, Barker, Curtis, & Gibson, 1997) neuroimaging (e.g., Blair, Morris, Frith, Perrett, & Dolan, 1999; Calder, Keane, Manes, Antouin, & Young, 2000) and psychophysical (e.g., Hsu & Young, 2004) evidence has suggested that the perception of some classes of emotional facial expressions involve the recruitment of at least partially distinct neural substrates (also see Posamentier & Abdi, 2003). Thus, rather than facial expressions being mediated by a single system, evidence points to dissociable but interlocking systems involved in the perception of disgust (Calder et al., 2000; Gray et al., 1997), fearful (Calder et al., 1996), sad and angry facial expressions (Blair et al., 1999), though it is unclear if the available data implicates differential overlap at the visuoperceptual level.

If different neural populations are indeed optimally tuned to the representation of certain expressions (or classes of expressions), then the trend seen in the literature of generalising across all emotional expressions may overlook what may be important differences between different types of facial expressions in regard to their relationship to facial identity visual processing. Although there is a general lack of research that has explored the possibility of a differential relationship between the processing of facial identity and certain facial expressions, there exists some indirect evidence in the context of neuroimaging studies. fMRI studies suggest that the amygdala modulates the activation of visual areas implicated in facial identity processing, namely the fusiform gyrus, via a hypothesised neural connection between the amygdala and the visual cortex (see Vuilleumier & Pourtois, 2007). The driving force for the activation of the amygdala, and subsequent modulation of the fusiform region, appears to be largely due to low spatial frequency information, which particularly favours fearful faces (e.g., wide open eyes and mouth), and, to a lesser extent, other threatening facial expressions. Consistent with this notion, Surguladze et al. (2003) demonstrated that the fusiform region of the human brain was significantly more activated by the presentation of threatening than non-threatening facial expressions.

Thus, the processing of individual facial expressions appears to be mediated by at least partially distinct neural substrates. Furthermore, the processing of some facial expressions appears to interact more heavily than other facial expressions in brain regions traditionally thought to be mediated by facial identity. Consequently, it is important to examine if the practice of generalising across all facial expressions makes sense when exploring the relationship between the visual processes underlying facial expression and facial identity.

1.2. Visual aftereffects and its use in face perception research

Visual aftereffects refer to illusory phenomena in which the prolonged viewing of a visual stimulus (the adapting stimulus) results in some form of distortion in the perception of a subsequently viewed visual stimulus (the test stimulus) (Suzuki & Cavanagh, 1998). Adaptation is believed to desensitise the contribution of visual neural populations that optimally fire at a particular range of values along a visual dimension encompassed in an adapting stimulus. A subsequently presented stimulus that contains similar values along the same dimension of the adapting stimulus, having usually been processed by the now 'adapted' neuron population, is generally perceived to be skewed away along the dimension and appear less similar to the adapting stimulus (Robbins, McKone, & Edwards, 2007; Suzuki & Cavanagh, 1998).

Recent evidence has indicated that the adaptation paradigm can be used to tap into the visual coding mechanisms that underlie the representation of a number of facial dimensions. Some studies (e.g., Anderson & Wilson, 2005; Leopold, O' Toole, Vetter, & Blanz, 2001) have demonstrated 'identity aftereffects', where adapting to the face of a certain identity makes an average face appear distorted along the opposite side of an 'identity trajectory'. That is, an average face would appear to have facial features that are 'opposite' to the original adapting face and thus would be perceived as more dissimilar. Visual aftereffects have also been demonstrated to influence judgements along the facial dimensions of sex (male–female dimension) and race (Caucasian–Asian dimension) (Webster, Kaping, Mizokami, & Duhamel, 2004). 'Expression aftereffects' have been reported in studies that used test stimuli along a number of theoretical emotional expression continua, such as happy–sad, anger–fear and disgust–surprise (e.g., Fox & Barton, 2007; Webster et al., 2004). Thus, for example, adapting to a happy face makes a subsequent face along a happy–sad continuum appear sadder. Hsu and Young (2004) reported expression-specific aftereffects, in which adapting to an image of a person exhibiting a fearful face had resulted in stimuli along a neutral–fear continuum of the same person to look more neutral. This change in perceived expression was also seen when adapting to a happy and sad face and judging test stimuli along a neutral–happy and neutral–sad continuum, respectively. On the other hand, adapting to an expression that was incongruent to the test stimuli did not result in these aftereffects in most cases, indicating that distinct neural populations underlying the representations of specific emotional expressions had been temporarily adapted.

Some studies have used the adaptation paradigm to explore the nature of the relationship between facial expressions and facial identity (e.g., Burke, De Sousa, & Palermo, 2006; Fox & Barton, 2007), though none have used a methodology that allows a clear systematic exploration of this in relation to individual emotional expressions.

Fox and Barton (2007) not only found expression aftereffects in conditions when the adapting and test stimuli were congruent in identity, but also a smaller but significant expression aftereffect in conditions when the adapting and test stimuli were incongruent in identity. This was argued to reflect evidence of neurons that code expression independently of identity information. That is, populations of neurons that code happy facial expressions (for example) that are insensitive to the invariant configuration of a person (their facial identity). On the other hand, as transference was greater for the congruent identity condition, it was argued that there exists a population of neurons that were adapted in the congruent identity condition but not in the incongruent identity condition, and therefore indicates that there are also neurons that code expression in a way that is dependent on facial identity information. Fox and Barton (2007) found this pattern for all three expression pairs (happy–sad, anger–afraid, disgust–surprised) and also found no interaction between the expression pairs in terms of the extent of transference across the congruent and incongruent identity conditions.

On the other hand, the use of a continuum that is composed of two (contrasting) facial expressions results in it not being possible to disentangle the contribution of each expression within the pair. This is a potential limitation if the two facial expressions in the same continuum (e.g., anger and fearful) are mediated by at least partially distinct neural networks. In other words, an expression aftereffect obtained from using an expression–expression continuum may potentially reflect the neural adaptation of two representational systems. Consequently, in order to systematically explore the relationship between facial identity and individual facial expressions, the use of neutral–expression continua, similar to that employed by Hsu and Young (2004), may be more appropriate.

The primary objective of the current study is to individually explore if happy, sad, angry, disgusted and fearful facial expressions are coded independent or dependent of identity-based information. Past studies have suggested that these five emotional expressions are 'basic' and universal in nature and each has an important and distinct signal value (Ekman, 1984; Izard, 1971). If specialised perceptual systems have evolved to process certain emotional expressions, then it is likely that the current study will tap into each system by the use of these fundamental emotional expressions. The current study employs the visual aftereffect paradigm due to its ability to tap into visual coding mechanisms with a degree of precision that is not available with most other behavioural paradigms.

2. Method

2.1. Participants

Fifteen participants (nine males),[1] consisting of undergraduate students enrolled at Macquarie University, each completed five 2-hour sessions. All participants, except one, were naive to the aims and purpose of the experiment. Participants were aged between 20 and 47 years (*M* = 24.33 years, SD = 7.05 years) and had normal or corrected-to-normal vision. Participants were paid 14 Australian dollars per session for their participation. The study was approved by the Macquarie University Ethics Review Committee, and all participants gave informed signed consent before commencing the study.

2.2. Stimulus preparation and apparatus

The stimuli consisted of 12 grayscale digitised photographs that individually displayed the faces of two different Caucasian females in their early twenties, each posing closed-mouth versions of six different facial expressions (happy, sad, anger, disgust, fear and neutral) (see Fig. 1). The images were created for the purpose of this study and had been selected from a larger pool of colour photographs that were taken using a Kodak EasyShare SX6490 4.0 mega pixel digital camera.

The decision to create new face stimuli for the purpose of this study, rather than use pre-existing face databases, was based on two key considerations that rendered current databases to be limited. Firstly, it was important to control for a number of facial dimensions across the two individuals such that facial identity was the only invariant facial aspect that would be manipulated in the incongruent identity adapting-test condition. This made it essential for gender, age and race to be controlled, particularly given that previous evidence suggests that faces differing in gender or race may be processed by different perceptual mechanisms (e.g., Cunningham et al., 2004; Michel, Rossion, Han, Chung, & Caldara, 2006; Williams & Mattingley, 2006; although see Fox & Barton, 2007). Secondly, it was considered important that no gross topological changes in features between images within a neutral–expression continuum would be seen, namely changes from a closed to open mouth. This would otherwise result in discrete differences at a point along the generated morph continuum (i.e. the presence/absence of teeth), which may introduce a certain response strategy that would override the presence of an effect due to the expression per se (Calder, Young, Perrett, Etcoff, & Rowland, 1996). The decision to use female faces in the current study was based on past evidence indicating that facial expressions are more accurately recognised when conveyed by females (see Palermo & Coltheart, 2004).

The original colour images were converted to grayscale, resized to have a standardised interpupillary distance and then cropped to 470×600 pixels (16.5×21.2 cm). All image manipulations were

Fig. 1. Neutral, happy, sad, disgusted, angry and fearful facial expression prototypes: posed by identity A (top) and identity B (below).

[1] A total of 18 participants had completed at least one session of the experiment, though three individuals had withdrawn from the experiment before completing all five sessions. These participants' data were not included in the final analysis.

made using the GNU Image Manipulation Program, Version 2.2.14.[2] Furthermore, any visible blemishes and jewellery were removed and the contrast and brightness levels were adjusted manually in order that each image appeared similar to each other in terms of overall brightness. The background of each image was filled with black, and a black oval frame, with a dark grey edge, was applied over each image, such that most of the individual's outer hairline was covered. A 'blank face' stimulus was also created. This was an image of a grey oval that replaced the face area and was the same size and resolution as the face stimuli.

Two versions of these 12 face images were used in the experiment. One version remained at a resolution of 470 × 600 pixels and would be used, along with the blank face image, as adapting stimuli. A second version was reduced to 80% of this size (376 × 480 pixels; 13.3 × 16.9 cm) and would be used as 'prototypes' to create the ten morph continua.

The stimuli were presented on a 19-in. RGB Sony Tritron monitor using a PowerMac G4 computer, with a screen resolution of 1600 × 1200 pixels. The presentation of stimuli was controlled using SuperLab (Version 4 OSX) software.

2.2.1. Recognition of facial expression for facial stimuli

A short study was undertaken in order to assess the recognisability of the facial expressions in the facial stimuli. This was considered important given the new nature of the stimuli. Twenty-four participants (11 females), ranged between 20 and 59 years ($M = 26.13$, $SD = 10.17$), made facial expression judgements on the 12 prototype images that were used in the current study. Participants were told that these were closed-mouth versions of facial expressions and were able to choose from a list of seven emotional facial expressions (neutral, happy, sad, anger, disgust, fear and surprise). Images were randomly presented to the participant. Although surprise was not used in this study, it was included as an option because it is commonly confused with fearful expressions (see Etcoff & Magee, 1992). It was considered important to determine how well the fearful stimuli could be recognised given a reasonable alternative and whether the closed-mouth nature of the stimuli would unacceptably make it indistinguishable from surprise. The recognisability was found to be above 75% for all prototype images except in the case of the identity B anger (64%) and the identity A fear (42%) and identity B fear (42%) images. The percentage of responses for each facial expression type is shown in Fig. 2 and indicates the types of errors made by the participants. The high fear–surprise confusion is similar to the findings of past studies that have included a surprise option (e.g., Palermo & Coltheart, 2004).

2.2.2. Preparation of test images (morphing the prototypes)

Using WinMorph Version 3.0.1,[3] the five basic emotional facial expressions (happy, sad, anger, disgust and fear), from each of the two identities, were morphed with their respective neutral image to create ten neutral–expression continua, holding the identity constant within each morph sets (see Fig. 3). Morphing is a technique that enables a series of intermediate images to be generated from the gradual blending of two images. The shift in shape and pigmentation from the neutral prototype to a basic emotional expression prototype always occurred in a linear fashion, with each successive image reflecting a 5% increment towards the basic emotional expression image and, conversely, a 5% decrement away from the neutral image. The 19 images generated in each of the 10 neutral–expression continua (each

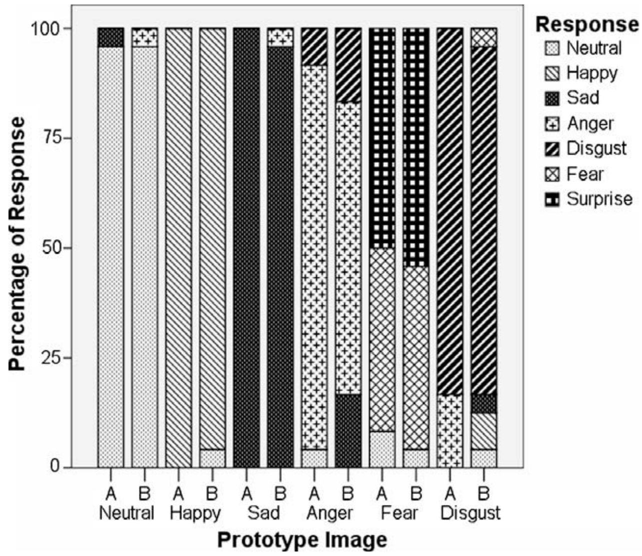


Fig. 2. Recognisability of the 12 prototype images. The percentage of responses for each image is shown along with the type of errors made by participants.

with a dimension of 376 × 480 pixels), reflecting the 5–95% morph level range, were used as test stimuli in the experiment.

2.3. Design and procedure

The psychophysical method of constant stimuli was used in order to measure the shift in the perceived expression of the face stimuli. In each of the five sessions, 38 test stimuli (two neutral–expression continua × 19 images making up each continuum) were presented 10 times in each block, resulting in a total of 380 trials in the baseline block and 380 trials in the test blocks. Each block was further subdivided into two halves, with each test stimuli being randomly presented five times in each half-block.[4]

Each session was designed as a two-choice expression classification task, which was based on the perceived facial expression conveyed by the test stimuli (e.g., 'happy' or 'neutral'). Each session measured the aftereffects of one of the five basic emotional expressions that were of interest in this study, with each participant completing a session featuring happy, sad, angry, disgusted and fearful emotional facial expressions. Each session was identical in structure, though there was specificity in the stimuli and response choice used in each of the five sessions. Namely, a session intended on assessing the various aftereffects of a particular expression – the *feature expression* of that session – (i.e. disgust) would present the two continua that conveyed the feature expression (i.e. the identity A neutral–disgust continuum and the identity B neutral–disgust continuum) as test stimuli, and a prototype of the feature expression (i.e. the identity A disgust prototype) as an adapting stimulus. The participant would decide if the test stimuli conveyed the feature expression (i.e. press the key labelled 'disgust') or a neutral face (press the key labelled 'neutral'). A maximum of two participants were tested at a given time and the order in which participants completed the five sessions was randomised.

In order to gain data for the recognisability of the prototype images, as well allowing the participants to gain a sense of familiarity with the two identities, participants were shown each of the 12 images at the beginning of their first session and were asked to judge the conveyed facial expression (choosing from neutral, happy, sad, anger, disgust, fear and surprise). Their responses were included in the data seen in Fig. 2.

[2] The GNU Image Manipulation Program, version 2.2.14 is a free program that runs on Windows 98 or higher. It is available at http://www.gimp.org/. The development team can be contacted at webmasters@gimp.org.

[3] WinMorph Version 3.0.1. is a free program that runs on Windows 98 or higher and can be downloaded at http://www.debugmode.com/winmorph/. The author can be contacted at satish@debugmode.com.

[4] This allowed the participant to take a short 5 min break in the middle of a block.

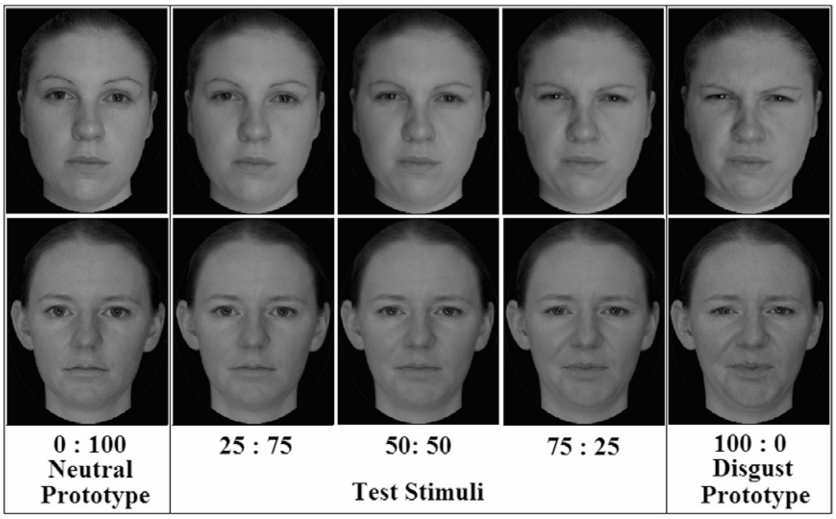


Fig. 3. Examples of the test stimuli used in the session with disgust as the feature expression. Each continuum was composed of 19 images that were generated using two endpoint prototype images (far left and far right). Values correspond to the morph level of each image (in 5% increments/decrements) relative to the neutral and expression prototype images (assigned 0:100 and 100:0, respectively).

The procedure for a session will now be described. For simplification, the session with happy as the feature expression (the 'happy' session) will be used as an example, bearing in mind that each participant completed four other sessions (i.e. sad, anger, disgust and fear).

Before commencing the session, the four prototypes that were used to create the test stimuli of that particular session were displayed all at once on the computer screen for the participant to view. For example, participants would view the identity A and identity B neutral prototypes, and the identity A and identity B happy prototypes for the session with happy as the feature expression. The experimenter pointed out the images and asked the participant to look at the faces for about a minute before proceeding. During the session, participants sat at a distance of approximately 60 cm from the computer monitor and the lights were turned off.

A session comprised of a baseline block followed by a test block. These were designed in order to obtain an estimate of the 'balance point' along each of the two continua in each block, which is the point in which a participant perceives an image to be conveying the feature expression in 50% of its trials, after adapting to the blank face (in the baseline block) or after adapting to the prototype image of the feature expression (in the test block). Thus, in the baseline block of the 'happy' session, it was of interest to find the balance point along the neutral–happy identity A continuum and the balance point along the neutral–happy identity B continuum, after adapting to the blank face stimulus. In the test block of the 'happy' session, it was of interest to find the balance point along the neutral–happy identity A continuum and the balance point along the neutral–happy identity B continuum, after adapting to the identity A happy prototype image.

From these measures, the magnitude of the expression aftereffect in two conditions of interest could be obtained. The *congruent identity* condition refers to the instances where the adapting and test stimuli remained of the same identity (e.g., adapting to identity A and testing to an image along an identity A continuum). The *incongruent identity* condition refers to the instances where the adapting and test stimuli changed in identity (e.g., adapting to identity A and testing to an image along an identity B continuum).

In the baseline block, the participant first adapted to the blank face stimulus for 60 s. The participant then completed the trials. A trial consisted of the presentation of the same blank face stimulus for 5 s, followed by the presentation of an 'orienting stimulus' for 150 ms, a test stimulus for 750 ms and, finally, a black screen (see Fig. 4). Each stimulus in the sequence was presented in the centre of the screen and disappeared before the appearance of the following stimulus. The orienting stimulus served to orientate the viewer to the spatial location of the proceeding (smaller) test stimulus in order to allow the participant to visually focus on the smaller area before the test stimuli appeared. The test stimulus was an image randomly taken from the two neutral–expression continua (one of identity A the other of identity B) needed to assess the aftereffects of the feature expression. For example, in the session with happy as the feature expression, the test stimuli were images randomly taken from the neutral–happy identity A and neutral–happy identity B continua. On the black screen display, the participant's task was to judge the facial expression conveyed in the test stimuli, by pressing either a button marked 'neutral' or a button marked with the feature expression (i.e. 'happy'), with a response initiating the next trial. The 5 s adapting stimulus at the beginning of every trial served to ensure that neural adaptation remained in effect across the entire block.

Once each of the test stimuli from the two continua had been randomly presented five times each, the participant was allowed a 3-min break, and the blank face stimulus was shown once again for 60 s before proceeding with the second half of the baseline block (where each test image would be randomly presented another five times). Thus there was a total of 380 trials in the baseline block. The test stimuli were 80% the size of the adapting stimulus in order that the aftereffects in this study could not be accounted for by low-level adaptation (see Yamashita, Hardy, De Valois, & Webster, 2005; although see Butler, Oruc, Fox, & Barton, 2008). The baseline block lasted for approximately 50 min.

The structure of the test block was identical to that of the baseline block, except that all instances of the blank face were replaced with the prototype image of the feature expression. The experiment was counterbalanced such that, during the test block, half ($n = 7$) of the participants always adapted to the feature expression conveyed by identity A throughout their five sessions, and half ($n = 8$) always adapted to the feature expression conveyed by identity B throughout their five sessions. The test block also lasted for 50 min.

2.4. Analysis

The data obtained in a session was represented along a plot, showing the shift in the percentage of times that a participant judged the test stimuli to be conveying the feature expression from

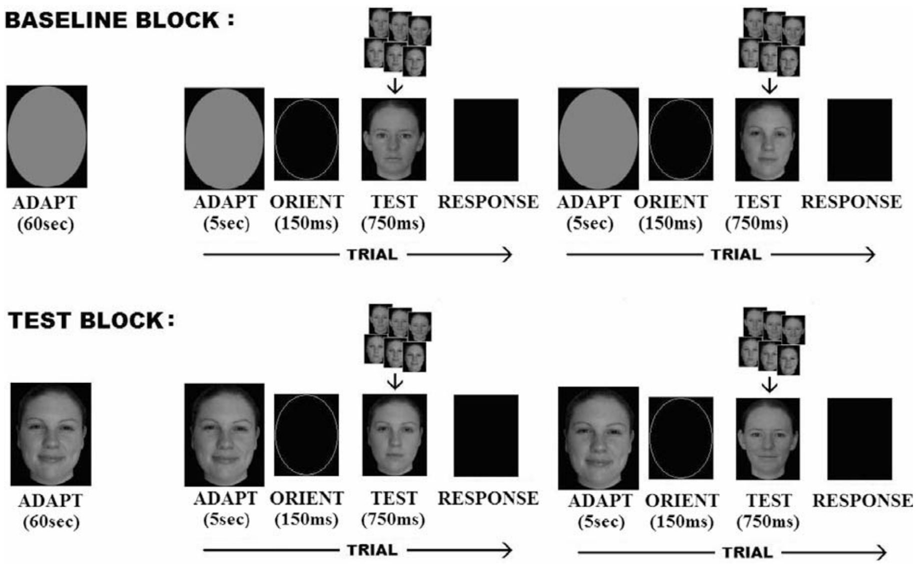


Fig. 4. Design of an experimental session with happy as the feature emotional facial expression. Firstly, in the baseline block, participants judged if randomly selected test stimuli from the identity A and identity B neutral–happy continua had conveyed a 'neutral' or 'happy' facial expression, following adaptation to a blank face stimulus. Secondly, in the test block, participants judged if test stimuli, randomly drawn from the same continua, had conveyed a 'neutral' or 'happy' expression, following adaptation to a happy facial expression prototype. The baseline block always proceeded the test block. The experiment counterbalanced the identity of the adapting stimulus between participants. Each participant completed four other sessions that were identical in structure, though each session centred on a different feature expression resulting in the presentation of different adapting and test stimuli (sad, anger, disgust or fear).

baseline to test, for both congruent and incongruent identity conditions. Weibull functions were fit to the data of each participant and from this the estimated points along the continua – the balance points – at which the participant perceived the feature expression 50% of the time (and conversely perceived neutral 50% of the time) were obtained. The Weibull functions were fit using Kaleidagraph© Version 4.0 by Synergy Software, using two free parameters including the slope. The independent variable of interest was the change in the balance point expressed in terms of percent morph change, and this was averaged across the group. (see Fig. 5 for an example of psychometric data obtained in the session with disgust as the feature expression). The magnitude of the expression aftereffect for a condition was obtained by subtracting the balance point obtained in the baseline block from that obtained in the test block.

3. Results

An initial analysis was undertaken to assess any differences between the counterbalance groups. The data were submitted to a three-way mixed measures ANOVA, with the five-level 'expression type' (happy, sad, anger, disgust and fear) and the two-level 'congruency condition' (the magnitude of the expression aftereffect in the congruent identity condition and the magnitude of the aftereffect in the incongruent identity condition) within factors, and the two-level 'counterbalance' (adapted to identity A or adapted to identity B) as a between subjects factor. There were no significant two or three-way interactions involving the counterbalance variable. Consequently, the counterbalance groups were collapsed in further analyses.

The data were submitted to a two-way repeated measures ANOVA, consisting of the five-level 'expression type' and two-level 'congruency condition' within factors as defined above. There was a significant main effect of 'congruency condition' ($F(1, 14) = 24.53$, $p < .001$). This indicates that larger expression aftereffects were seen when the adapting and test stimuli were congruent in identity ($M = 18.3$, $SE = 1.8$) compared to when the adapting and test stimuli were incongruent in identity ($M = 8.75$, $SE = 1.15$), averaged across the five expression groups. This was further explored at the level of individual expressions using paired sample T-tests. The difference between the expression aftereffect obtained in the congruent identity condition and the expression aftereffect obtained in the incongruent identity condition was significant for happy ($M = 7.78$ $p = .027$), sad ($M = 10.03$, $p = .015$), anger ($M = 9.77$, $p = .004$), disgust ($M = 8.45$, $p = .006$) and fear ($M = 11.82$, $p = .037$) using Bonferroni correction. This sensitivity of the aftereffect to changes in identity suggests the existence of a neural population that is adapted in the congruent identity condition but not in the incongruent identity condition, reflecting the contribution of a neural representation of facial expressions that is dependent on facial identity.

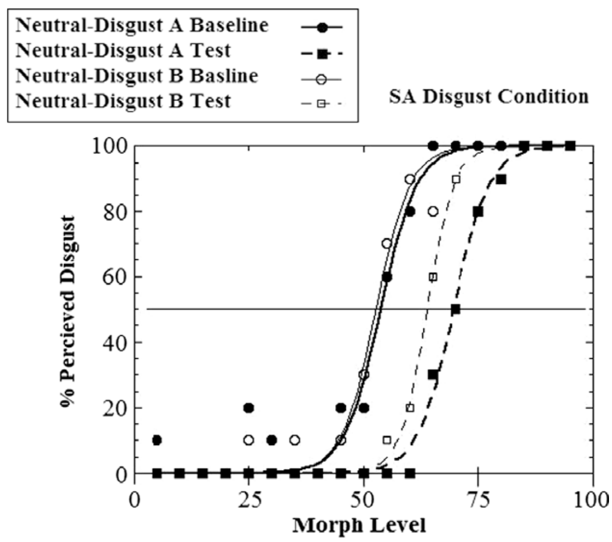


Fig. 5. Psychometric data of participant SA showing the shift in the percentage of disgust judgements from baseline to test, for both congruent and incongruent identity conditions. Adapting and testing to images that are congruent in identity (thick black lines) produces aftereffects that are larger in magnitude compared to adapting and testing to images that are incongruent in identity (thin black lines).

The 'expression type' × 'congruency condition' interaction was found to be non-significant ($F(4,56) < 1$, NS). Thus, there was no significant difference between the extent to which the magnitude of the expression aftereffect differed between the congruent and incongruent identity conditions for all of the five expression groups. Consequently, there is no evidence that the processing of individual facial expressions depend on facial identity differentially (see Table 1).

The 'expression type' main effect reached statistical significance ($F(4,56) = 2.706$, $p = 0.04$). A post hoc complex comparison was undertaken to explore the source of this tendency. Uncorrected *p*-values are reported for these comparisons, however neither were significant after Bonferroni correction. It suggested that the expression aftereffects (averaged across congruency condition) tended to be smaller for the happy expression condition relative to the other four expression groups ($F(1,14) = 6.368$, $p = 0.024$, NS [after correction]). The differences in the magnitude of the expression aftereffects, averaged across congruency condition were found to be largest between happy and sad ($F(1,14) = 9.571$, $p = 0.008$, NS [after correction]).

In order to assess the magnitude of the aftereffect obtained in the incongruent identity condition, a two-factor repeated measures ANOVA was undertaken, consisting of the five-level 'expression type' (happy, sad, anger, disgust and fear) and the two-level 'test' (balance point obtained in the baseline and test block from the incongruent identity condition) within factors. The main effect of test was found to be significant ($F(1, 14) = 55.49$, $p < 0.001$) and there was no expression × test interaction ($F(4, 56) = 1.15$, NS). This was further explored at the level of individual expressions using paired sample *T*-tests using. The expression aftereffect obtained in the incongruent identity condition was significant for sad ($M = 10.97$, $p < 0.001$), angry ($M = 9.13$, $p < 0.001$), disgust ($M = 7.42$, $p = 0.045$), fear ($M = 10.3$, $p = 0.011$), and of borderline significance for happy ($M = 5.8$, $p = 0.090$) using Bonferonni correction. Thus, within each expression condition, there was evidence that the aftereffect transferred across changes of identity to some extent and therefore suggests the existence of a neural population underlying the representation of each expression that is identity-independent.

4. Discussion

According to influential neural and cognitive accounts of face perception, the mechanisms underlying the perception of facial expressions and facial identity are separate and distinct, and this partition occurs immediately during early visual analysis, such that each divergent route incorporates distinct representations of the relevant facial dimensions. In systematically exploring the visual coding of five basic emotional facial expressions, the current study found evidence that is inconsistent with these frameworks. The results of this study suggest that there are two types of neural populations that are involved in the visual coding of happy, sad, angry, disgusted and fearful emotional facial expressions: a population of neurons that are identity-independent and a population of neurons that are identity-dependent. The first population can be inferred by the observation that the expression aftereffects transferred, to some extent, across changes in identity. The second population of neurons can be inferred by the observation that the magnitude of the expression aftereffect was greater when both adapting and test images were of the same identity. The current study used test stimuli that differed in size to the adapting stimuli. Consequently, this study can rule out the possibility that the larger aftereffect magnitude seen in the congruent identity conditions may have been due to the contribution of low-level retinotopic adapted neurons (see Yamashita et al., 2005 although see Butler et al., 2008). It is important to note that the balanced design of the experiment ensured that the pattern of aftereffects seen in an expression condition could not be attributed to any differences between the images themselves, namely differences between the images in terms of the intensity of the facial expressions that were conveyed in the images.

Evidence for the involvement of both identity-independent and identity-dependent neural populations in the visual coding of emotional expressions is consistent with recent psychophysical studies (e.g., Burke et al., 2006; Fox & Barton, 2007). The current study extends from these previous studies by using an alternative methodology to demonstrate evidence that all five basic emotional expressions are processed by both identity-dependent and identity-independent neurons. As previously mentioned, given that facial expressions may be processed by separable systems, exploring the relationship between the visual coding of facial expression and facial identity may need to be undertaken at the level of individual facial expressions.

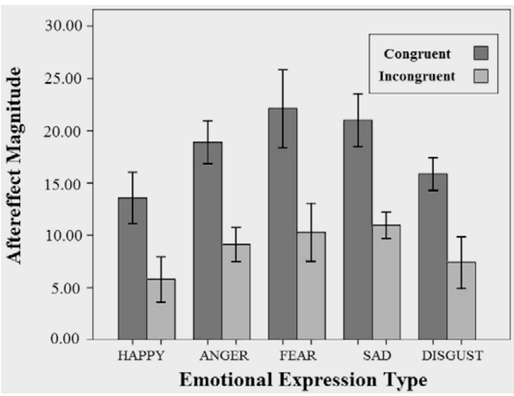
The findings suggest the existence of neural representations of facial expressions that are identity-dependent. This is consistent with recent single-cell (e.g., Perrett et al., 1992; Sugase et al., 1999) and imaging (e.g., Gobbini & Haxby, 2007; Surguladze et al., 2003; Vuilleumier & Pourtois, 2007) studies that have demonstrated interactions between identity and expression processing in the brain. Nevertheless, the present study also suggests the existence of neural representations of happy, sad, angry, disgusted and fearful faces that are insensitive to changes in identity (e.g., neurons that are identity-independent). These neurons are more in line with the expression analysis system posited by the Bruce and Young (1986) and Haxby and Colleagues model. Taken together, neither the view of a strict segregation nor of complete unity between the processes underlying the coding of facial expressions and facial identity can fully account for the present findings.

No significant differences were found between the five basic emotional expressions in the extent to which the expression aftereffect failed to transfer across changes in identity. The current study therefore found no evidence to demonstrate the view that specialised neural mechanisms underlying the visual coding of specific classes of emotional expressions overlap with a system that codes facial identity to differing degrees.

4.1. Possibility of a criterion shift

It could also be argued that the expression aftereffects seen in this experiment are not based on the adaptation of neurons that

Table 1
Clustered bar chart showing the magnitude of the expression aftereffects obtained in the congruent and incongruent identity conditions as a function of the expression type. Error bars indicate ±1 SEM.



code the visual representations of facial expressions but rather that they reflect a temporary change in the participant's criterion for what they regard as a good example of an expression. For example, after viewing a high-strength image, such as the happy prototype, and then being tested with a weaker (morphed) example of that emotional expression, participants may have been less likely to categorise the test stimuli as 'happy' (and therefore more 'neutral') because there reference point is based on the previously viewed happy stimulus (Hsu & Young, 2004). Indeed, past researchers (e.g., Steward, Brown, & Chater, 2002) have demonstrated that the classification of stimulus is related to the contrast produced when paired with another stimulus (see Hsu & Young, 2004). On the other hand, it has been previously demonstrated that expression aftereffects are sensitive to the length of time that the adapting stimulus is present (Hsu & Young, 2004). In other words, if a criterion change due to the adapting stimulus is the sole reason for an image to be deemed less happy relative to a baseline measure (rather than being perceived as less happy), then the duration of the time adapting to the face stimuli should be irrelevant to induce the effects seen in this study. In contrast, Hsu and Young (2004) have demonstrated that expression aftereffects are entirely abolished when the adapting stimulus is presented for a duration that is not long enough for neural adaptation but is sufficient for any new criterion to be formed. As Hsu and Young (2004) also used neutral–expression continua, their results are directly compatible with the present study. Thus, the expression aftereffects seen in this experiment are most likely to be due to the adaptation of neurons tuned to facial expressions rather than a form of criterion change.

4.2. Conclusion

The results suggest that the representations of happy, sad, angry, disgusted and fearful facial expressions involve the recruitment of identity-dependent and identity-independent neurons. Given that small proportions of cells that code both identity and expression information have been found in the superior temporal sulcus (Hasselmo et al., 1989; Perrett et al., 1992; Sugase et al., 1999) and the inferior temporal gyrus (Hasselmo et al., 1989), these regions are possible candidates for the former.

Of note, while there is evidence indicating that the representation of facial expressions involve both identity-dependent and identity-independent neural components, a recent study by Fox, Oruc, and Barton (2008) indicates that the representation of facial identity is, in contrast, independent of variations in facial expression. Using a similar methodology to their previous study (i.e. Fox & Barton, 2007), Fox et al. (2008) found that, in the case of both novel and familiar faces, the size of the identity aftereffect was not modulated when the adapting and test stimuli were congruent or incongruent in facial expression. Therefore, there appears to be an asymmetrical relationship between the processing of facial expression and facial identity.

Altogether, the current findings allow some insight into the architecture of the visual mechanisms underlying the visual coding of five basic emotional facial expressions and have implications to current models of face perception.

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