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Brain regions involved in processing facial identity and expression are differentially selective for surface and edge information

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ABSTRACT

Although different brain regions are widely considered to be involved in the recognition of facial identity and expression, it remains unclear how these regions process different properties of the visual image. Here, we ask how surface-based reflectance information and edge-based shape cues contribute to the perception and neural representation of facial identity and expression. Contrast-reversal was used to generate images in which normal contrast relationships across the surface of the image were disrupted, but edge information was preserved. In a behavioural experiment, contrast-reversal significantly attenuated judgements of facial identity, but only had a marginal effect on judgements of expression. An fMR-adaptation paradigm was then used to ask how brain regions involved in the processing of identity and expression responded to blocks comprising all normal, all contrast-reversed, or a mixture of normal and contrast-reversed faces. Adaptation in the posterior superior temporal sulcus – a region directly linked with processing facial expression – was relatively unaffected by mixing normal with contrast-reversed faces. In contrast, the response of the fusiform face area – a region linked with processing facial identity – was significantly affected by contrast-reversal. These results offer a new perspective on the reasons underlying the neural segregation of facial identity and expression in which brain regions involved in processing invariant aspects of faces, such as identity, are very sensitive to surface-based cues, whereas regions involved in processing changes in faces, such as expression, are relatively dependent on edge-based cues.

Introduction

Models of human face perception suggest that facial identity and expression are processed along two different neural pathways (Bruce and Young, 1986, 2012; Haxby et al., 2000). Support for the idea of separable pathways in face perception comes from neuroimaging studies that have investigated the selectivity of face regions in the human brain (Andrews and Ewbank, 2004; Hoffman and Haxby, 2000; Winston et al., 2004). A posterior part of the superior temporal sulcus (pSTS) is thought to be important in processing movements of the face, such as changes in gaze and expression, which are important for social interactions (Baseler et al., 2013; Engell and Haxby, 2007; Harris et al., 2012; Psalta et al., 2013). In contrast, a region in the fusiform gyrus, the fusiform face area (FFA), is considered to be important for the representation of facial characteristics that are important for recognition (Davies-Thompson et al., 2013; Grill-Spector et al., 2004; Rotshtein et al., 2005).

Central to understanding this neural segregation of analyses of identity and expression is the question of the extent to which it may be driven by visual properties of faces themselves (Calder and Young, 2005). Bruce and Young (1998) drew attention to the fact that any facial image consists of a set of edges created by abrupt changes in reflectance that define the shapes and positions of facial features and a broader pattern of surface pigmentation resulting from local changes in the reflectance properties of the skin. These properties of shape and pigmentation may contribute differentially to the perception of identity and expression. Bruce and Young (1998) suggested that feature shapes (i.e. edge-based information) may be critical for perceiving facial expressions, with surface pigmentation being relatively important to identity.

A useful way of testing the importance of edge- and surface-based cues in face perception is with contrast reversal (as in a photo negative). In a contrast-reversed image the edges that define feature shapes remain in the same positions, despite the huge change in overall surface properties. A variety of evidence shows that facial expressions can still be recognised in contrast-reversed images (Bruce and Young, 1998; Magnussen et al., 1994; White, 2001). Recognition of facial identity, however, is severely disrupted by contrast-reversal, showing the importance of surface patterns to the recognition of facial identity (Bruce and Langton, 1994; Burton et al., 2005; Russell et al., 2006). Although high spatial frequency, edge-based information also makes an important contribution to the perception of identity (Burton et al., 2005; Fiorentini et al., 1983; Goffaux et al., 2005), it does not support recognition on its own. For example, line drawings of faces are not usually

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sufficient for the accurate recognition or discrimination of identity (Davies et al., 1978; Leder, 1999) unless they are caricatured (Rhodes and Tremewan, 1994) or given some limited textural information by 'thresholding' the original image (Bruce et al., 1992).

A broad distinction, then, can be made between the visual information that is important for different aspects of face perception. For the perception of facial identity, contrast patterns and edge-based shape cues can both convey useful information. However, the perception of facial expression is relatively dependent on edge-based, shape cues that correlate with movements of the facial muscles, and less dependent on textural contrast patterns. Here, we introduce a striking demonstration of this reliance of facial expression perception on shape information rather than contrast patterns by showing that, behaviourally, facial expression perception is insensitive to contrast-reversal to the point where it is not difficult to match expressions across normal and contrast-reversed images, despite the large differences between the images. As expected, however, identity perception is markedly impaired under the same conditions. We then used this critical behavioural demonstration to investigate whether face-selective regions forming the components of Haxby et al.'s (2000) core neural system for face perception are also sensitive to different aspects of the face image. To address this issue, we used contrast-reversal in combination with an fMR-adaptation paradigm (Andrews et al., 2010; Davies-Thompson et al., 2013; Harris et al., 2012) to determine the relative contribution of surface- and edge-based visual information to the neural representations underlying facial expression and identity. Importantly, for the fMR-adaptation paradigm we did not ask participants explicitly to attend to either expression or identity. Because previous studies have found that task can influence responses in regions of the ventral stream (Avidan et al., 2003; Ishai et al., 2004), our aim was to probe those aspects of the visual image coded by neural regions of interest irrespective of task. This was important because we did not want to bias the response in different regions with a task that could involve explicit or implicit judgements of either expression or identity. Instead, we used a neutral task of detecting a red spot positioned on some of the face images to ensure that participants looked at each face but did not need to respond to its identity or expression.

The fMR adaptation experiment investigated neural responses to stimulus blocks showing repeated images of the same face or a sequence that alternated between two different face images varying in identity and expression. The difference in overall response between blocks with repeated images and blocks with alternating different images gives a measure of neural adaptation. This measure of neural adaptation was applied to independently-localised face-selective regions thought to be involved in the perception of identity (FFA) and expression (pSTS) across three different image manipulation conditions. These conditions involved blocks in which stimuli were all contrast-positive (normal greyscale images), all contrast negative, or a mix of contrast-positive and contrast-negative images. Our hypothesis was that mixing normal and contrast-reversed images within a stimulus block should affect neural responses in face regions that are sensitive to surface-based cues, but it should not have a significant effect on responses in face regions that primarily represent edge-based information. Hence a region that shows adaptation to the blocks of mixed normal and contrast-reversed images must favour edge-based (shape) over surface-based (texture) information. This is a strong criterion because it involves adaptation to consistent shape cues present in normal and contrast-reversed images despite the substantial change in image properties.

Materials and methods

Participants

32 participants (21 females; mean age, 21) took part in the behavioural study (Experiment 1) and 25 different participants (16 females; mean age, 25 years) took part in the fMR-adaptation study (Experiment 2). All participants were right-handed and had normal or corrected-to-normal vision. All participants gave written informed consent. The study was approved by the YNIC Ethics Committee at the University of York.

Stimuli

Face stimuli were Ekman faces selected from the Facial Expressions of Emotion Stimuli and Tests (FEEST) set (Young et al., 2002). The identities of these faces were unfamiliar to the participants. Four individuals posing five expressions (anger, disgust, fear, happiness and sadness) were selected based on the following three main criteria: (i) A high recognition rate for all expressions (mean recognition rate in a six-alternative forced-choice experiment: 94%; Young et al., 2002), (ii) consistency of the action units (muscle groups) across different individuals posing a particular expression, and (iii) visual similarity of the posed expression across individuals. Using these criteria to select the individuals from the FEEST set helped to minimise variations in how the expressions were posed. To avoid the use of the external features of the face which make little contribution to perception of expression, images were cropped so that only the internal features were visible. To generate the contrast-reversed faces, the value of each pixel in the image was subtracted from the mid-grey value and then added to the original grey value.

Experiment 1

First, we determined the effect of contrast-reversal on perceptual judgements of facial identity and expression. Participants had to match the identity or expression of positive and negative faces. There were four stimulus conditions: (1) *same-expression*, *same-identity* (2) *same-expression*, *different-identity* (3) *different-expression*, *same-identity* and (4) *different-expression*, *different-identity*. Each trial consisted of 2 faces that were presented sequentially. Pairs of images were either both male or both female. Each face was presented for 900 ms and separated by an inter-stimulus interval of 300 ms. Trials were separated by 2.5 s during which participants had to report via a key press whether the identity or expression was the same/different (2AFC). Each phase of the experiment had two runs. In one run, participants matched expression, in the other identity. Both runs were identical in terms of the presented stimuli. The order of runs was counterbalanced across participants.

In the first phase of the experiment, images in each trial could be both positive or both negative. Each combination of contrast and condition was presented 20 times in a counterbalanced order, giving a total of 160 trials. 16 participants took part in the first phase of the experiment. In the second phase of the experiment, one image in each trial was positive and the other image was negative. The order of positive and negative images within trials was counterbalanced across conditions. Each condition was presented 32 times in a counterbalanced order, giving a total of 128 trials. 16 participants took part in the second phase of the experiment.

Experiment 2

Next, we determined how face-selective regions in the brain (OFA, FFA, and pSTS) responded to blocks of positive, negative and mixed (positive and negative) contrast faces. To achieve this, the images used in Experiment 1 were incorporated into a block design fMR-adaptation paradigm in which stimuli were presented in blocks, with 6 images in each block. There were six conditions (types of block) in the experiment:

(1) *same-face*, *positive* — all 6 images in the block showed contrast-positive versions of the same face identity with the same expression

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