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Research report

Responses in the right posterior superior temporal sulcus show a feature-based response to facial expression

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ABSTRACT

The face-selective region of the right posterior superior temporal sulcus (pSTS) plays an important role in analysing facial expressions. However, it is less clear how facial expressions are represented in this region. In this study, we used the face composite effect to explore whether the pSTS contains a holistic or feature-based representation of facial expression. Aligned and misaligned composite images were created from the top and bottom halves of faces posing different expressions. In Experiment 1, participants performed a behavioural matching task in which they judged whether the top half of two images was the same or different. The ability to discriminate the top half of the face was affected by changes in the bottom half of the face when the images were aligned, but not when they were misaligned. This shows a holistic behavioural response to expression. In Experiment 2, we used fMR-adaptation to ask whether the pSTS has a corresponding holistic neural representation of expression. Aligned or misaligned images were presented in blocks that involved repeating the same image or in which the top or bottom half of the images changed. Increased neural responses were found in the right pSTS regardless of whether the change occurred in the top or bottom of the image, showing that changes in expression were detected across all parts of the face. However, in contrast to the behavioural data, the pattern did not differ between aligned and misaligned stimuli. This suggests that the pSTS does not encode facial expressions holistically. In contrast to the pSTS, a holistic pattern of response to facial expression was found in the right inferior frontal gyrus (IFG). Together, these results suggest that pSTS reflects an early stage in the processing of facial expression in which facial features are represented independently.

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1. Introduction

Interpreting the facial expressions of others is important to effective social interaction (Bruce & Young, 2012). Facial expressions result from characteristic patterns of movement of the facial muscles that can easily be seen in static photographs (usually showing the apex of the movement itself) or in videos (Johnston, Mayes, Hughes, & Young, 2013). However, little is known about how expressions are encoded at the neural level. The most widely-used neural model of face perception (Haxby, Hoffman, & Gobbini, 2000) proposes that the superior temporal sulcus (STS) is a key neural structure in the perceptual analysis of facial expressions, and this is borne out by a number of studies that have implicated STS in neural responses to expression (Calder & Young, 2005; Psalta, Young, Thompson, & Andrews, 2014) and social perception from visual cues (Allison, Puce, & McCarthy, 2000).

Relatively few studies address the question of *how* STS encodes expression. Said, Moore, Engell, Todorov, and Haxby (2010) were able to demonstrate that patterns of activation to different facial expressions across voxels in posterior STS (pSTS) were correlated with the rated perceptual similarities of the expressions themselves, suggesting that the functional organisation of pSTS reflects this underlying perceptual structure. Similarly, Harris, Young, and Andrews (2012) found that right pSTS responded to changes in facial expression regardless of whether or not these changes crossed or remained within emotional category boundaries, which again suggests a form of encoding that is largely driven by the perceptual input. Importantly, Harris, Young, and Andrews (2014) showed that right pSTS is relatively insensitive to contrast reversal, which implies that the critical perceptual input for pSTS involves feature shapes. Contrast reversal is known to have a dramatic effect on face identity recognition, but it has relatively little effect on the recognition of expression because information about feature shapes that is critical to interpreting facial expressions is conveyed through the position of edges that remain largely invariant to contrast reversal (Bruce & Young, 1998).

Here, we take the study of the perceptual representation used by pSTS a step further by asking whether it represents features such as the eyes and mouth independently from each other, or as part of a perceptual whole (the face). The critical test of holistic processing that we use for this purpose is the expression composite effect. Composite effects have been demonstrated in many studies of facial identity perception (Rossion, 2013; Young, Hellawell, & Hay, 1987), but their extension to understanding facial expression perception is less well-known. The paradigm involves combining the top half of one facial expression with the bottom half of another expression and determining whether this combination of different parts results in the perception of a new whole expression (Calder & Jansen, 2005; Calder, Young, Keane, & Dean, 2000; Palermo et al., 2011; Prazak & Burgund, 2014). The critical test of holistic perception involves contrasting performance between images in which the top and bottom halves are aligned into a highly face-like overall configuration, or misaligned so that they are less face-like. Contrasting aligned and misaligned versions of composite images created from the top and bottom parts of different facial expressions makes it possible to differentiate responses based on face features, which will be equivalent across aligned and misaligned image variants, from holistic responses that will only be evident for aligned and not for misaligned images.

In this study, we used the facial expression composite effect to investigate whether neural responses to facial expression in right pSTS reflect feature changes or are dependent on the face as a perceptual whole. To do this, we first established in a behavioural study that the stimuli and presentation parameters we intended to use in fMRI elicited a robust expression composite effect. We then compared neural responses in right pSTS to composite expressions in which the top (eye region) and bottom (mouth region) parts were aligned into an overall face-like configuration with neural responses to misaligned stimuli created by shifting one part horizontally with respect to the other (see Fig. 1). Misalignment still allows the separated parts of the face to be encoded as features, but it interferes with the integration of expressive information from the eye and mouth region into a perceptual whole (Calder et al., 2000).

Our fMRI experiment used a block design adaptation paradigm in which participants viewed blocks comprising a series of facial expressions that were all the same (no change condition) or that varied across the top half of each image (top change condition) or across the bottom half of each image (bottom change condition). During these blocks, participants were asked to fixate between the eyes (i.e., in the top half of each face) and further to encourage fixation they had to detect the presentation of an occasional small red spot at the fixation point. The no change condition, with identical stimuli throughout the block, served as a baseline that will lead to maximal adaptation of neural responses, and the top change or bottom change conditions measured any release from adaptation in neural regions that can encode these changes. The stimuli were aligned into overall face-like composites, or horizontally misaligned so that they were not face-like (see Fig. 1), allowing us to establish whether the pattern of neural responses across conditions involving no change, top change, or bottom change was dependent on the presence of a face-like (aligned) configuration.

2. Material and methods

2.1. Participants

Sixteen participants took part in experiment 1 (8 male, 8 female, mean age 27.6 ± 4.4). Twenty-seven participants took part in experiment 2 (17 male, 10 female, mean age 24.7 ± 5.0). All participants had normal or corrected-to-normal vision, with no known history of neurological disorder and no abnormalities that were immediately evident from structural MRI in experiment 2. Written consent was obtained from all participants and the studies were approved by the York Neuroimaging Centre Research Ethics Committee and the Department of Psychology Ethics Committee at the University of York. One participant was removed from the fMRI analysis due to excessive head movement.