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Dynamic stimuli demonstrate a categorical representation of facial expression in the amygdala

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Face-selective regions in the amygdala and posterior superior temporal sulcus (pSTS) are strongly implicated in the processing of transient facial signals, such as expression. Here, we measured neural responses in participants while they viewed dynamic changes in facial expression. Our aim was to explore how facial expression is represented in different face-selective regions. Short movies were generated by morphing between faces posing a neutral expression and a prototypical expression of a basic emotion (either anger, disgust, fear, happiness or sadness). These dynamic stimuli were presented in block design in the following four stimulus conditions: (1) *same-expression change, same-identity*, (2) *same-expression change, different-identity*, (3) *different-expression change, same-identity, and* (4) *different-expression change, different-identity*. So, within a *same-expression change* condition the movies would show the same change in expression whereas in the *different-expression change* conditions each movie would have a different change in expression. Facial identity remained constant during each movie but in the different identity conditions the facial identity varied between each movie in a block. The amygdala, but not the posterior STS, demonstrated a greater response to blocks in which each movie morphed from neutral to a different emotion category compared to blocks in which each movie morphed to the same emotion category. Neural adaptation in the amygdala was not affected by changes in facial identity. These results are consistent with a role of the amygdala in category-based representation of facial expressions of emotion.

1. Introduction

Transient changes in facial musculature that signal current emotional state are critical for effective social interactions. A prominent model of face perception has proposed that a neural pathway from the occipital face area (OFA) to the posterior superior temporal sulcus (pSTS) is involved in processing transient facial signals such as facial expression and eye gaze. In this model the STS is thought to have reciprocal connections with the amygdala which is recruited for further analysis of facial expression (Haxby, Hoffman, & Gobbini, 2000). The sensitivity of the STS and amygdala to a range of facial expressions has been demonstrated across a variety of experiments (Adolphs, Tranel, Damasio, & Damasio, 1994; Adolphs et al., 1999; Andrews & Ewbank, 2004; Baseler, Harris, Young, & Andrews, 2013; Engell & Haxby, 2007; Harris, Young, & Andrews, 2012; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001).

>However, relatively little is known regarding how facial expression is encoded in these regions. Models of facial expression perception have debated whether facial expressions are represented as belonging to discrete categories of emotion or as gradations along continuous dimensions (see Bruce & Young, 2012). Although usually treated as incompatible opposites there is evidence for both accounts. Evidence for categorical perception of expression is shown by the consistency with which basic emotions are recognized (Ekman, 1972) and by the increased sensitivity to changes in facial expression that alter the perceived emotion (Calder, Young, Perrett, Etcoff, & Rowland, 1996; Etcoff & Magee, 1992). In contrast, continuous or dimensional models are better able to explain the systematic confusions that occur when labeling facial expressions (Woodworth & Schlosberg, 1954). Continuous models can also account for the fact that we are readily able to perceive differences in intensity of a given emotional expression (Calder, Young, Rowland, & Perrett, 1997; Young et al., 1997) and for variation in the way that basic emotions are expressed (Rozin, Lowery, & Ebert, 1994).

Previously, we offered evidence supporting a synthesis of the above accounts at the neural level by demonstrating that expression is represented in the brain in both a categorical and a continuous manner (Harris et al., 2012). Specifically, by morphing static images of faces to create equal physical changes between images that either fell within the same emotion category or

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crossed the boundary between different emotion categories, we showed that the amygdala is more sensitive to between than within-category changes (showing a more categorical representation of facial expression) whereas the pSTS is equally sensitive to within and between-category change (indicating a more continuous representation).

In this current study, we aimed to further explore the categorical representation of expression in the amygdala using dynamic stimuli. Dynamic changes in facial expression can provide a stringent test of categorical representations, as dynamic movies necessarily incorporate continuous transient changes in expression, and many of these changes need to be disregarded in order to assign dynamic expressions into discrete categories. We used short movies that always showed a change from a neutral resting expression to an intense emotional expression. These movies were created by animating morphed images of facial expressions of basic emotions from the Ekman and Friesen (1976) series. We then used a block fMR-adaptation design to compare neural responses to blocks involving a series of these short movies in which the final expressions were either the same (e.g. all fear) or different (mixed emotions). So within a block participants we saw a series of movies which displayed a dynamic change from a neutral expression to the apex of an emotion. In the same-expression change conditions the same change in expression was displayed across all movies (e.g. all neutral to fear). In the different expression conditions each movie had a different facial expression change (neutral to fear, neutral to disgust, neutral to happy etc). These same and different expression blocks could be presented with either the same or different facial identity. In the same identity conditions each movie would show the same person across the block, whilst in the different identity conditions each movie would show a different person.

This design incorporates contrasts that provide substantial criteria for a category-based response to moving expressions. A neural region using a predominately categorical representation of expression should show a greater response to the different compared to the same change in expression conditions, as these conditions involve a change in the emotion category. Moreover, a region showing a response based primarily on emotional categories should also be relatively insensitive to changes in facial identity. However, if a region does not represent expression into emotion categories it should respond equally to the same and different expression blocks, because all of the movies are based on morphed sequences of images that undergo continuous changes. From Harris et al.'s (2012) results with static expressions, we predicted that the amygdala, but not the pSTS, would demonstrate a categorical representation of expression.

2. Method

2.1. Subjects

Nineteen participants took part in this experiment (14 females; mean age, 23). All participants were right-handed and had normal or corrected-to-normal vision. Visual stimuli ($8^{\circ} \times 8^{\circ}$) were back-projected onto a screen located inside the magnetic bore, 57 cm from subjects′ eyes. All subjects provided written informed consent and the study was given ethical approval by the York Neuroimaging Centre Ethics Committee.

2.2. Localiser scan

A functional localiser was used to independently identify regions of interest. This localiser involved a block design with five different conditions: (1) *faces*, (2) *bodies*, (3) *inanimate objects*, (4) *places*, and (5) *scrambled images* of the former categories. Face images were taken from the Psychological Image Collection at Stirling (PICS; http://pics.psych.stir.ac.uk/). These images varied in viewpoint (frontal, $\frac{3}{4}$ view, profile) and expression (neutral, happy, speaking) within a block. Both male and female faces were used. Body images were taken from a collection at the University of Bangor (http://www.bangor.ac.uk/~pss811/), and contained clothed male and female headless bodies in a variety of postures. Images of places consisted of a variety of unfamiliar indoor scenes, houses and buildings, city scenes and natural landscapes. Stimuli in the object condition consisted of different inanimate objects including tools, ornaments, and furniture. Fourier-scrambled images were created by randomizing the phase of each two-dimensional frequency component in the original image, while keeping the power of the components constant. Scrambled images were generated from the images used in the other stimulus categories.

Each stimulus block consisted of 10 images from a single stimulus condition. Each image within a block was presented for 700 ms and followed by a 200 ms blank screen, resulting in a total block length of 9 s. Stimulus blocks were separated by a 9 s gray screen with a central fixation cross. Each condition was repeated four times in a counterbalanced design resulting in a total scan length of 7.2 min. All participants viewed the same sequence of blocks and images. To ensure participants maintained attention throughout the experiment, participants had to detect the presence of a red dot superimposed onto 20% of the images. No significant differences in red dot detection were evident across experimental conditions (Accuracy: 96.5%, $F_{(1,18)}=0.71$; RT: 673.4 ms, $F_{(1,18)}=1.95$, $p=0.18$).

2.3. Experimental scan

2.3.1. Stimuli

The initial face stimuli were Ekman faces selected from the Young et al. Facial Expressions of Emotion Stimuli and Tests (FEEST) set (Young, Perrett, Calder, Sprengelmeyer, & Ekman, 2002). Five 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: 93% 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 minimize variations in how the expressions were posed.

The frames for the movies were generated by morphing between each individual′s neutral expression and each of their prototype expressions in 5% steps using Psycho-Morph (Tiddeman, Burt, & Perrett, 2001). Movies were generated by playing the morphed images in sequence using Adobe Premiere Pro. The first (neutral) frame was played for 160 ms and the final frame (prototype expression) was played for 280 ms. The 18 intermediate frames were each played for 40 ms. Validation of the movie stimuli was demonstrated in an expression-classification experiment, in which recognition rates of the dynamic expressions were compared to the recognition rate for the equivalent original prototype expression. Participants either classified the static or dynamic expressions in a 5AFC task. 20 participants (11 females; mean age 29) rated the static expressions and 20 participants (12 females; mean age 27) rated the dynamic expressions. The static stimuli were shown for an equivalent amount of time as the dynamic stimuli and both were followed by a 2 s gray screen, during which participants could make their response. This experiment found that recognition accuracy for the static expression was 83.6% and for the dynamic expressions 84.3%.

2.3.2. Procedure

The aim of this experiment was to investigate the nature of the representation of expression in the amygdala and pSTS. There were four conditions in this experiment which all involved blocks showing a sequence of movies each of which involved a dynamic change in expression from a neutral pose to a basic emotion: (1) *same-expression change, same-identity*, (2) *same-expression change, different-identity*, (3) *different-expression change, same-identity*, and (4) *different-expression change, different-identity*. The *same-expression change* conditions involved 5 movies all displaying the same change in expression (i.e. all neutral to the same emotion). In the *different-expression change* conditions each of the 5 movies displayed a change from neutral to a different basic emotion. Each movie was created using the face of a single model (identity). In the *same-identity* conditions the same identity was shown in each of the 5 movies, and in the *different-identity* conditions each of the 5 movies had a different facial identity. The movie stimuli were presented in blocks, with 5 movies per block. Each movie was presented for 1160 ms and separated by a gray screen presented for 200 ms. Successive stimulus blocks were separated by a 9 s fixation gray screen. Each condition was presented 10 times in a counterbalanced order, giving a total of 40 blocks. This resulted in total scan duration of 10.5 min. To ensure participants maintained attention throughout the experiment, participants had to push a button when they detected the presence of a red dot, which was superimposed onto 20% of the movies. No significant differences in red dot detection were evident across experimental conditions (Accuracy: 96.0%, $F_{(1,18)}=0.14$; RT: 646.7 ms, $F_{(1,18)}=0.35$).

2.4. Imaging parameters and fMRI analysis

Data was collected using a GE 3T HD Excite MRI scanner at York Neuroimaging Centre at the University of York. A Magnex head-dedicated gradient insert coil was