Neuropsychologia 102 (2017) 217–228

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Impaired processing of facial happiness, with or without awareness, in developmental prosopagnosia

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ARTICLE INFO

Keywords:
Emotion
Happy
Expression
Adaptation
Face
Spatial frequencies

ABSTRACT

Developmental prosopagnosia (DP) is associated with severe, lifelong deficits in face recognition, with such cases often cited as support for a dissociation between the processing of facial identity and emotion. Here we examine the evidence against this dissociation and propose that the processing of facial happiness, either with or without awareness, is actually integrated within the same neural network involved in facial identity recognition. We also test this hypothesis on a group of DP cases and neurotypical controls (NT) by adapting them to expressionless neutral faces, intact happy faces and hybrid faces. Despite these hybrid faces being explicitly identified as expressionless due to their higher spatial frequencies taken from a neutral face, their low spatial frequencies convey happy facial expressions that participants are unaware of. After adaptation, participants were asked to judge the facial expressions of face stimuli that were morphed incrementally in varying degrees of sad through to happy. Both groups exhibited emotion adaptation aftereffects to the intact happy faces, although this effect was smaller in DP. Whereas NT produced emotion adaptation aftereffects without awareness of the happy emotion in the hybrid faces; as a group, those with DP did not. Furthermore, our DP cases also exhibited deficits in judging the emotion of the happiest morphed test faces. Our results indicate that the processing of happy facial expressions, with or without awareness, is likely integrated within the face recognition network. We hypothesise that the previously identified abnormalities in the fusiform gyrus in those with DP is the most likely structure responsible for these deficits.

1. Introduction

Prominent models of face perception posit that facial identity processing occurs through brain regions that are distinct from those that process facial emotion (Bruce and Young, 1986; Haxby and Gobbini, 2011; Haxby et al., 2000). According to these models, facial identity perception is accomplished primarily through the occipital face area (OFA; Gauthier et al., 2000) and parts of the fusiform gyrus (otherwise known as the 'fusiform face area' due to its specialisation in processing faces, FFA; Kanwisher et al., 1997). By contrast, the superior temporal sulcus (STS; Puce et al., 1998) is thought to separately process facial expressions (Haxby and Gobbini, 2011; Haxby et al., 2000). This distinction between identity and emotion processing has also been interpreted as reflecting relatively static and unchangeable information, such as a face's identity, in the OFA and FFA, versus more dynamic or changeable aspects of face perception, such as speech and facial expressions, in the STS (Bate and Bennetts, 2015; Haxby and Gobbini, 2011; Pitcher et al., 2014).

More recently, converging behavioural, neuroimaging and neuropsychological evidence has challenged these dissociation models. For example, TMS to the right OFA has been shown to disrupt emotion discrimination (Pitcher, 2014; Pitcher et al., 2008), thus implicating its functional contribution to emotion perception. Similarly, a number of neuroimaging studies have highlighted the FFA's role in processing facial expressions (Fox et al., 2009; Tsuchiya et al., 2008; Van den Stock et al., 2008). Conversely, the STS has exhibited neural sensitivity to facial identity, both in humans (Fox et al., 2009) and in monkeys (Perrett et al., 1983). These converging findings suggest that contrary to traditional face perception models, emotion and identity perception are integrated across the 'core' cortical face perception regions.

In contrast to the 'core' regions that encompass the OFA, FFA and STS, the amygdala is a subcortical structure that is considered to be an 'extended' part of the face perception network (Haxby and Gobbini, 2011). This region is also thought to be highly important in the perception of emotion, regardless of whether the viewer is aware of the emotional information they are viewing or not (De Cesarei and

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http://dx.doi.org/10.1016/j.neuropsychologia.2017.06.020
Received 20 October 2016; Received in revised form 5 June 2017; Accepted 18 June 2017
Available online 23 June 2017
0028-3932/

Codispoti, 2013; Johnson, 2005; Pessoa and Adolphs, 2010, Tamietto and De Gelder, 2010). However, amygdala damage has been shown to produce greater levels of impairment in the processing of negative emotions, such as fear and sadness (Adolphs and Tranel, 2004; Adolphs et al., 1994, 1999; Anderson and Phelps, 2000; Calder, 1996; Laeng et al., 2010; Vuilleumier et al., 2004), while entirely sparing explicit judgements of facial happiness (Adolphs and Tranel, 2004). This point is bolstered by another study which found an amygdala lesion patient was able to process the low spatial frequencies (LSF; the coarse, holistic visual information conveyed by a face) of happy, but not sad or fearful, facial expressions without conscious awareness (Laeng et al., 2010). These latter two findings are particularly relevant, as they seem to suggest that the amygdala can be redundant in processing happy facial information either with, or without, conscious awareness. Instead, these pieces of indirect evidence hint that facial happiness might be processed through a cortical route that includes the FFA.

Direct evidence that facial happiness is processed through the FFA comes from neuroimaging and neuropsychological research. Tsuchiya et al. (2008) found that activity in the ventral temporal cortex (which includes the FFA) was associated with the discrimination of facial happiness over fear. Differential neural responses have also been apparent in the FFA of neurotypical individuals viewing happy versus neutral facial expressions (Van den Stock et al., 2008). In the same study, developmental prosopagnosia (DP) cases, individuals who suffer from lifelong impairments in face recognition, had a reduction in their FFA's differential neural activity when viewing these two different facial expressions. These findings not only indicate that the FFA is partly specialised for the processing of facial happiness, but that its ability in DP to distinguish neutral from happy facial expressions might be compromised.

DP cases exhibit abnormalities throughout their cortical face perception areas' grey matter volume, connectivity and neural responses to faces (Avidan et al., 2014; Behrmann et al., 2007; Garrido et al., 2009; Gomez et al., 2015; Lohse et al., 2016; Lueschow et al., 2015; Rivolta et al., 2014; Song et al., 2015; Thomas et al., 2008; Zhang et al., 2015). Early studies seemed to indicate that those with DP were spared in their emotion recognition abilities (Behrmann et al., 2007; Dinkelacker et al., 2010; Duchaine et al., 2003a, 2003b; Van den Stock et al., 2008), thus supporting the proposed dissociation between emotion and identity perception. However, recent work employing paradigms designed to be more sensitive in detecting emotion perception deficits have shown that those with DP are indeed impaired when processing facial expressions (Biotti and Cook, 2016; Palermo et al., 2011b). However, both of these recent studies collapsed their results across different emotions, making the reader unable to tell which specific emotions the DP cases were impaired in perceiving. If facial happiness is heavily reliant upon the FFA, then those with DP may exhibit a specific impairment in their processing of facial happiness due to their FFA abnormalities.

Remarkably, no study to date has shown that DP cases are impaired in their perception of facial happiness or abnormal in their processing of emotion without conscious awareness. The processing of facial emotion without awareness is thought to occur in a qualitatively different way, that is through the amygdala, in contrast to when it is processed with awareness through the cortex (Tamietto and De Gelder, 2010). DP cases have been shown to exhibit amygdala that are typically intact both structurally and in their functioning (Behrmann et al., 2007; Dinkelacker et al., 2010; Van den Stock et al., 2008). If the processing of facial emotion without awareness occurs through this subcortical route as is commonly argued (Tamietto and De Gelder, 2010), then we should expect those with DP to be unimpaired when attempting to process such information. By contrast, if facial happiness were to traverse a cortical route which includes the FFA, then those with DP will likely exhibit impairments in perceiving happy facial expressions.

One way that facial happiness processing can be tested in DP is through the use of an emotion adaptation paradigm. After viewing a happy face for a few seconds, subsequently presented faces appear sadder: the so called "adaptation aftereffect" (Wang et al., 2016; Webster et al., 2004). These aftereffects are thought to arise due to neuronal populations specialised in detecting the adaptor's characteristics (i.e., facial happiness) becoming habituated to this information (Frisby, 1981). Adaptation aftereffects therefore index how well a participant's brain can process facial happiness. It has recently been shown that adaptation aftereffects can be more sensitive in detecting subtle emotion perception differences than explicit emotion discrimination judgments (Liu et al., 2014; Luo et al., 2017). In this respect, adaptation paradigms are actually a better way of examining emotion perception in DP cases who might otherwise falsely evince neurotypical processing of emotion through explicit recognition tasks (e.g., Duchaine et al., 2003a, b; Palermo et al., 2011b).

Numerous studies have previously examined conscious awareness and face adaptation (Adams et al., 2010; Amihai et al., 2011; Moradi et al., 2005; Shin et al., 2009; Stein and Sterzer, 2011; Yang et al., 2010). It has recently been shown that a hybrid face, where a happy facial expression in the hybrid's LSF was masked from participants' awareness by the higher spatial frequencies (HSF) of a neutral face, might be able to produce similar emotion adaptation aftereffects as those induced by intact happy faces in neurotypical participants (Prete et al., 2016). If we were to observe diminished or non-existent emotion adaptation aftereffects in DP to either an intact happy or neutral-happy hybrid face, then it would imply that their neuronal populations involved in detecting facial happiness are not performing as they should be.

The first aim of the present study was to test whether individuals with DP can process happy facial emotion, with or without conscious awareness, in a neurotypical manner. Remarkably, no prior study has examined emotion processing without awareness in DP, despite awareness typically being argued as modulating how facial emotions are processed in qualitatively different ways (Tamietto and De Gelder, 2010). To test this, we employed an emotion adaptation paradigm whereby a group of DP cases and controls were adapted to intact neutral faces, intact happy faces, and hybrid faces (Laeng et al., 2010; Schyns and Oliva, 1999). Fig. 1 gives examples of the stimuli used and the experimental procedure. While our participants will be aware of the emotion conveyed by the happy faces, they will not be aware of the happy emotion conveyed by the hybrids' LSF due to the remaining spatial frequencies conveying a neutral expression (Laeng et al., 2010). As DP cases have abnormalities in their grey matter volume throughout their cortical face perception network including the FFA, we anticipate that they should exhibit non-existent or diminished emotion adaptation aftereffects to the hybrid, and possibly intact happy, faces. Such a result would imply that the processing of the LSF of happy facial emotion is reliant upon the face recognition network due to associative face recognition deficits in DP. By contrast, if our DP cases were to exhibit neurotypical adaptation aftereffects to the happy and hybrid faces, then it would suggest that emotion processing is dissociable from that of identity. A second aim of our study was to test whether DP cases' also experience impairment in explicitly judging facial happiness. To assess this, we examined our DP cases' consistency, sensitivity and response times when making judgments of emotion to our test faces.

2. Methods

2.1. Participants

Ten controls and 10 DP cases (both groups had 3 males) participated in this experiment. The controls were matched to the DP cases for gender, ethnicity and roughly their age: control range 20–40 years (mean age 28.5 years) with the DP range 19–46 years (mean age 29 years). All participants had normal or corrected to normal vision and were compensated financially for their time. The study was approved by the Institutional Review Board at Nanyang Technological University, Singapore. While the controls did not complete our neuropsychological tests for face processing impairment, none