THE EFFECT OF IMAGE INVERSION ON THE PERCEPTION OF FACIAL EXPRESSION

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Abstract

The Thatcher illusion provides a compelling example of the cost of face inversion. When the eyes and the mouth are turned upside-down relative to the rest of the face - a transform now known in the research literature as 'thatcherization' - the facial expression appears grotesque. This distortion of the face is immediately perceived when the face is upright. However, when the image is inverted the grotesque appearance is no longer visible. The aim of this thesis was to explore the behavioural and neural basis of this compelling illusion. This thesis provides a significant contribution to our understanding of the Thatcher Illusion using a combination of neuroimaging and behavioural results. The key findings of this thesis are that the neural basis of the Thatcher illusion is founded on the orientation-sensitivity of face-selective regions which are involved in the processing of facial expression. Behavioural findings suggest that the perception of the Thatcher illusion is still evident in the absence of configural information. Our findings demonstrated that a key component of the Thatcher illusion is to be found in orientation-specific encoding of the expressive features (eyes and mouth) of the face. This challenges previous interpretations of the Thatcher illusion that are based on a disruption of configural processing. Further results suggest that the effect of inversion found in the Thatcher illusion is not specific to grotesque expressions, but reflects a more general orientation-specific encoding of expressive features. Finally, the selectivity of the Thatcher illusion to the processing of expression is shown by the lack of effect of thatcherization on the processing of facial identity. These results provide further support for the idea that different processes underlie the perception of identity and expression.

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Acknowledgement

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I declare that this work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

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Chapter 1

1.1 Face Perception

1.1.1 Models of face processing

The cognitive model of face perception of Bruce and Young (1986) (Figure 1) proposes that face perception occurs along parallel and hierarchical processing streams. The first stage involves the structural encoding of the visual information in the face. The representation of structural information of the face depends on the viewing conditions such as illumination, angle of face and further on facial features and configurations such as eye gaze, expression, mouth position. The structural representation is then analysed by two separate routes. One route is involved in the extraction of identity from the faces, followed by name retrieval and recalling semantic information. A second route is assumed to be involved in the analysis of changeable aspects of faces such as expression, speech and eye gaze.

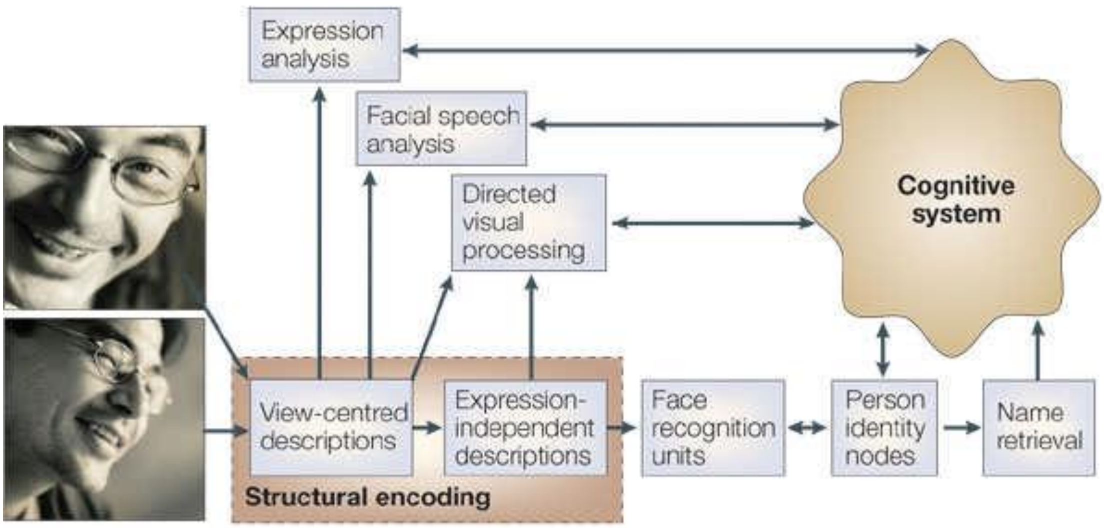

Figure 1.1: *The cognitive model of face perception (Bruce and Young, 1986). The model contains separate parallel processing routes for identity recognition and changeable aspects such as expression. (adapted from Calder and Young, 2005).*

Since the development of Bruce and Young's (1986) model of face processing, a lot of behavioural evidence emerged to support the notion that face recognition posited different routes for the recognition of facial identity and facial expression (Calder and Young, 2005; Bruce, 1986; Campbell, Brooks, de Haan and Roberts, 1996; Young, McWeeny, Hay and Ellis, 1986). For example, judgements of facial familiarity do not affect an individual's ability to identify facial expression; nor do judgments of facial expression affect the ability to judge a face's familiarity (Calder and Young, 2005; Bruce, 1986). Similarly, Bruce (1986) demonstrated that no effect of familiarity was apparent when college students were asked to make precise judgments of expressions of familiar academic staff and unfamiliar faces. In a similar vein, Young, McWeeny, Hay and Ellis (1986) asked participants to decide whether or not simultaneously presented pairs of faces were of the same or different identity (varying in expression) or of the same or different expression (varying in familiarity). They revealed no difference in reaction time between the time taken to process familiar and unfamiliar faces for expression discrimination, but there was faster reaction time for processing familiar than unfamiliar facial stimuli for identity discrimination. These results highlight the fact that facial expression is processed independently from processes involved in facial identity.

The Bruce and Young model was not explicit about neural topography of the separate components. However, a neural model of face processing introduced by Haxby and colleagues (Haxby, Hoffman and Gobbini , 2000; Figure 2) also emphasizes a distinction between the representation of invariant (relatively non-changeable) aspects of faces, which underline the recognition of a unique identity and the perception of information that facilitate social communication found in the representation of changeable (dynamic) characteristics of faces, such as expression, gaze and lip speech.

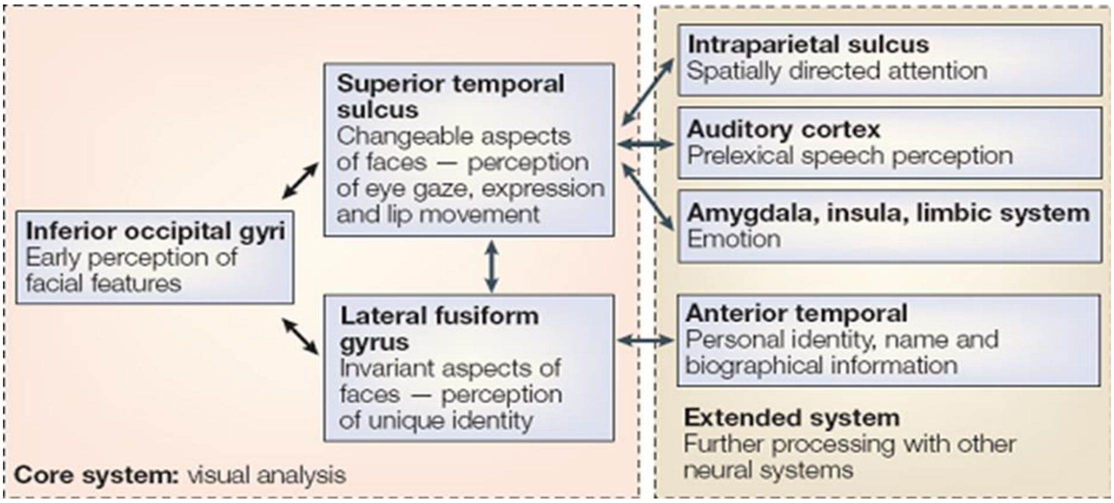

Figure 1.2: *The functional model of face recognition (Haxby, Hoffman, and Gobbini, 2000). The model is divided into two systems: The core system consists of three regions of occipitotemporal visual extrastriate cortex, and the extended system, consists of regions responsible for other cognitive functions of the neural systems. (adapted from Calder and Young, 2005).*

The model includes two sub-systems: the core system and the extended system. The core system comprises three regions in a hierarchical organization in which the inferior occipital gyri or occipital face area (OFA) sends inputs to the lateral fusiform gyrus or fusiform face area (FFA) for the retrieval of invariant aspects of faces such as facial identity and to the superior temporal sulcus (STS) for the perception of expression and eye-gaze. Haxby et al. (2000) also proposed that an extended neural system is involved in the further processing of faces. For example, regions in the intraparietal sulcus use facial cues such as gaze direction and head position to direct attention. Regions such as amygdala and insula, process the emotional content of expression found in faces. The superior temporal gyrus participates in retrieving phonemic content of speech-related lip movement. Finally, systems for representing biographic semantic knowledge in the anterior temporal lobe are responsible in retrieving information such as name and other information associated with a face. The core system for the visual analysis of faces is distinguished from the extended system that extracts the meaning of information gathered from the face. This implies that the coordinate activity of multiple regions is essential for the visual analysis of information found in faces.

The concept of separate routes for the recognition of identity and expression is also supported by a variety of evidence from cognitive neuropsychology, functional imaging and single-cell recordings in non-human primates. Neural support for the functional independence of the two processes is found in patients with impairment in the visual recognition of facial identity and facial expression. For example, Tranel, Damasio and Damasio (1988) conducted a series of experiments to assess the ability to recognize the meaning of facial expressions, gender, and age in patients with severe impairments of the recognition of facial identity. They found that some patients with severe impairments of facial identity recognition showed relatively intact ability to recognize facial expressions and argued that different forms of cognitive recognition depend on different neural substrates. Similarly, Parry, Young, Saul and Moss (1991) found that brain-injured patients who have problems in recognizing facial expression were better at recognizing facial identity in three "forced-choice" face processing tasks designed to test facial expression recognition and identity (familiar face recognition, and unfamiliar face matching).

They argued that specific face properties are processed through independent cognitive processes.

Recent examples of patients that showed a marked discrepancy between the processing of identity and expression come from studies of developmental prosopagnosia (Duchaine, Paerker and Nakayama, 2003; Nuun, Postma and Pearson, 2001). For example, NM showed severely weak performance on five out of six tests of facial identity recognition, yet she performed very similar to normal controls on four different tests of emotion recognition (Duchaine, Paerker and Nakayama, 2003). In another study of development prosopagnosia, EP's ability to judge age, sex and expression from faces, to identify facial parts and to make correct face/non-face decisions were intact, but he was impaired at recognizing famous and very familiar faces and he performed poorly on a test of unfamiliar face matching (Nuun, Postma and Pearson, 2001).

Functional imaging studies also provide support for dissociation in the processing of facial identity and expression (Winston, Henson, Fine-Goulden and Dolan, 2004; George et al., 1999; Parry, Young, Saul and Moss, 1991). Several experiments suggested that one region – the fusiform facial area (FFA) – is important for processing facial identity (Grill-Spector, Knouf and Kanwisher, 2004). For example in fMR-adaptation experiments, the response in the FFA was modulated by successful face recognition and showed a reduced response (adaptation) to repeated images with the same identity (Rotshtein, Henson, Treves, Driver and Dolan, 2005; Andrews and Ewbank, 2004; Yovel and Kanwisher, 2005; Davies-Thompson and Andrews, 2009). In contrast, changeable aspects of faces, such as facial expression, are processed in the STS (Hoffman and Haxby 2000; Winston, O'Doherty and Dolan, 2003). Neuroimaging evidence repeatedly proposed that the perception of facial expression is dependent on STS (Hoffman and Haxby 2000; Winston, O'Doherty and Dolan, 2003; Narumoto, Okata, Sadato, Fukui and Yomekura, 2001; Harris, Young and Andrews, 2012). For example, Narumoto, Okata, Sadato, Fukui and Yomekura (2001) reported attention to emotion modulated activity in the right STS using an emotion-matching task. Subjects were presented with a single face stimulus and they were required to match the visually presented image with regard to the contour of an emotional expression face varying in valence (happy and fearful) and in arousal (sad and fearful). The results indicated that selective attention to facial emotion enhanced activity in the STS and concluded that this region plays a unique role in the processing of facial emotion recognition within the distributed face neural system. In a recent study, Harris, Young and Andrews (2012) used morphed emotional faces to study how facial expressions of emotions are represented in the human brain. Participants were presented with faces that varied in facial expression and identity. Their results show that STS indicated selectivity to changes in facial expression and this sensitivity was independent of chances in facial identity. Another interesting outcome of the study was that the sensitivity in the STS was largely based on a continuous rather a categorical representation of facial expression. In this case, participants viewed an array of images generated by morphing between expression that could be the same, could present the same emotion but involve a physical change (within-expression change), or could differ in physical properties by similar amount but perceived as two different emotions (between-expression change). They concluded that STS was similarly sensitive to all changes in facial expression, indicating activity in both within and between emotional expression changes.

Further studies showing support for the distinction between facial identity and expression comes from single unit recording in monkeys (Hasselmo, Rolls and Baylis, 1989). In a non-human primate study testing 45 neurons on a stimulus set depicting conspecifics with different expressions, Hasselmo, Rolls and Baylis, (1989) found 15 neurons in inferotemporal regions responding to different identities and 9 neurons in STS responsive to expression. Neurons responsive to expression were found primarily in the superior temporal sulcus, while neurons responsive to identity were mostly found in the inferior temporal gyrus. Moreover, a single-cell recording study in humans while performing a recognition and face matching task showed that there are independent cell populations in the STS that respond specifically to expression (Fried, Mateer, Ojemann, Wohns and Fedio, 1982).

It could seem that there is sufficient evidence to conclude that the processing of identity and expression occur independently however, there are other compelling evidence that provide limited support for the assumed independence between the two facial dimensions (Calder and Young, 2005; Bruce and Young, 2012; Calder, 2011). Recent evidence reinforces the view that there is a common visual framework that supports the representation of at least some aspects of facial identity and facial expression. For example, according to Calder (2011) a modified system of face recognition (Figure 3) cast into doubt the assumed independence between face recognition and expression processing. In this model facial identity and expression are coded in a single multidimensional framework with some dimensions coding facial expression, some facial identity, and other coding both dimensions.

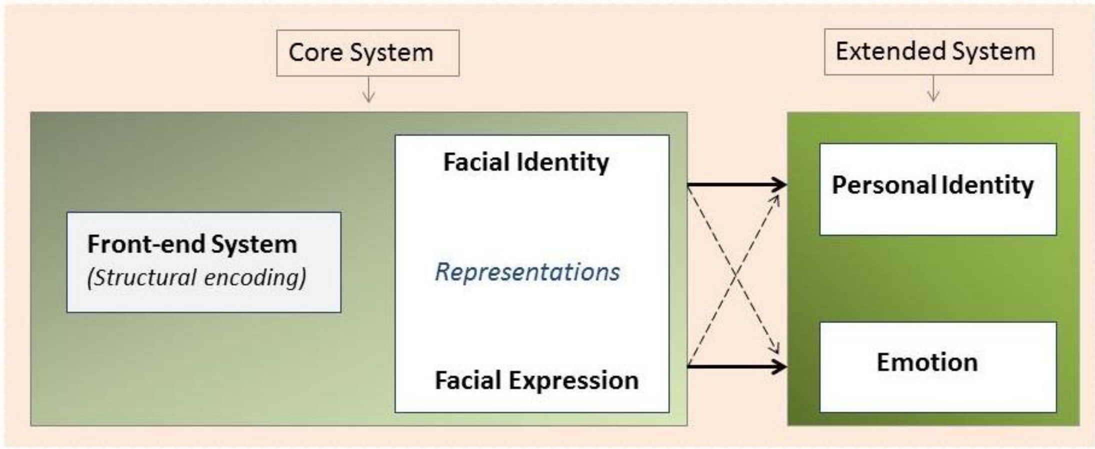

Figure 1.3: *A modified model of face recognition (Calder, 2011) suggesting that the visual form of facial identity and facial expression are coded in a single multidimensional framework with some dimensions coding facial expression, some facial identity, and other coding both dimensions.(adapted from Calder, 2011).*

Evidence of a common representational framework between facial identity and expression recognition comes from multiple sources, including behavioural studies (Ganel and Goshen-Gottstein, 2004; Schweinberger and Soukup, 1998; Campbell and Burke, 2009; Fox and Barton, 2007), neurophysiological case studies of brain-injured patients (Young, Hellawell, Van De Wal and Johnson, 1996; Etcoff, 1984), neuroimaging studies (Fox, Moon, Iaria and Barton, 2009; Ganel, Valyear, Goshen-Gottstein and Goodale, 2005; Cohen-Kadosh, Henson, Cohen Kadosh, Johnson and Dick, 2010; Fairhall and Ishai, 2007) and finally single neuron recordings (Perrett et al., 1984; Gothard, Battaglia, Erickson, Spitler and Amaral, 2007; Tsuchiya, Kawasaki, Oya, Howard and Adolphs, 2008).

The concept of associate routes for the recognition of identity and expression is supported by a variety of evidence from cognitive behavioural studies using Garner's selective attention paradigm (Garner, 1974). Studies have demonstrated that the ability to judge expression can be influenced by changes in identity (Ganel and Goshen-Gottstein, 2004; Schweinberger and Soukup, 1998; Campbell and Burke, 2009). Schweinberger and Soukup (1998) investigated the effect of variation of identity and expression in healthy participants. They observed that classification of faces for expressions could not be performed irrespective of identity, whereas variation in facial expression did not influence response time when faces were classified for identity. They concluded that there is an asymmetric dependence in the processing of facial identity and facial expression. This study fits with other behavioural results that have shown that, the adaptation effect observed when continued exposure to a specific facial expression causes the perception of a subsequent test expression to be more pronounced if the adapting and test expressions are from the same person relative to different (Campbell and Burke, 2009; Fox and Barton, 2007). These results suggest that these two facial properties interact as changes in facial identity affect perception of facial expression but not visa versa. Similar to Schweinberger and Soukup (1998), Ganel and Goshen-Gottstein (2004) used Garner's task to observe the effect of familiarity on the perception of faces varying in familiarity and expression. Their results showed that the perceptual pathways processing identity and expression are interconnected in that identity serves as a reference from which expressions can be more easily understood and derive.

Further support for the idea that the pathways involved in the perception of identity and expression may not be completely independent can be found in the way the image statistics of the face vary with changes in expression and identity. Principal components analysis demonstrated that primary components related with changes to the face are linked with changes in identity or expression, but others reflect changes in both identity and expression (Calder et al. 2001). Calder's results suggested that accurate recognition of facial identity and expression can be performed by a unique system coding the visual representation of both facial identity and expression.

There is also some neurophysiological case studies of brain-injured patients that support evidence against complete independence. Etcoff (1984) used a categorization task to see if brain injured patients could differentially pay attention to both facial dimensions and showed that right brain injured patients had difficulty perceptually unraveling both identity and expression stimuli. Etcoff used the same paradigm with normal and left brain injured patients with opposite results. Another interesting case that supports the depended coding of the two dimensions comes from a patient that indicated facial expression impairment after a partial bilateral amygdalotomy (Young, Hellawell, Van De Wal and Johnson, 1996). The patient was poor at recognizing emotional facial expression while being tested in expression and identity matching tasks. Even though she was able to perform relatively well on identity tasks and was able to match faces that were wearing different disguises, she was unable to perform on identity matching task when the expression was changing even though the identity of the person was constant. Young et al. (1996) concluded that the inability to understand facial expression could have led patient to confuse facial expression differences with different identity. This findings support the conclusion of dependent visual pathway of facial expression and identity.

Functional imaging studies also provide support for this association posing a problem for the dual route account. For example, neuroimaging studies addressing both facial identity and facial expression processing show that the fusiform gyrus contributed to the recognition of both facial properties (Fox, Moon, Iaria and Barton, 2009; Calder, 2001). For example, Fox et al. (2009) used morphed stimuli in an fMRI adaptation paradigm and presented subjects with successive pairs of faces from a continuum that ranged from that do or do not cross categorical boundaries of facial identity and facial expression. The study has shown a complete overlap in the FFA and pSTS, for identity and expression where FFA indicated activation for facial expression which were morphed. This findings suggest that FFA codes both identity and expression facial properties. Similarly, pSTS showed sensitivity to facial identity and expression. The empirical findings of this study provide evidence against the complete independence of identity and expression in these regions of the core face processing network. Similarly, other neuroimaging research provided further support to the view that the FFA is involved in the processing of both facial properties (Ganel, Valyear, Goshen-Gottstein and Goodale, 2005; Cohen-Kadosh, Henson, Cohen Kadosh, Johnson and Dick, 2010; Fairhall and Ishai, 2007).

Finally, there are also single neuron recording studies that acknowledge the existence of an integration mechanism involved in the perception of expression and identity. For example single neuron recordings in non-human primates, shown that monkeys STS contain cells which are active to both expression and identity (Perrett et al., 1984). Likewise, recording in monkey’s amygdala found a similar pattern of selectivity in coding facial expression and identity with 64% of the activated cells indicating a particular sensitivity in both categories (Gothard, Battaglia, Erickson, Spitler and Amaral, 2007). Additionally, Intracranial recordings in human implicated the ventral temporal cortex in the common coding of expression and identity facial properties (Tsuchiya, Kawasaki, Oya, Howard and Adolphs, 2008).

In summary, the prevailing view in face perception research over the past years claimed that facial identity and expression are processed through entirely distinct and parallel visual pathways. Several behavioural, neuroimaging, neurophysiological findings are consistent with this hypothesis, but other findings suggest that face recognition and emotional expression processing are not always so clearly dissociable and can sometimes interact. Hence, our understanding of the functional and neural basis of face perception is still insufficient to draw any final conclusions and the perceptual and neural representation of facial identity and expression recognition requires further throughout exploration.

1.2 Face Inversion Effect (FIE)

The phenomenon called the Face Inversion Effect (FIE) occurs when participants have to recognize faces that are displayed inverted (i.e. rotated 180^{o}) compared to upright face images (Dekowska, Kuniecki and Jaskowski, 2008). Many people are very good at recognizing faces in their normal orientation, however once the face is viewed in an upside-down orientation our ability to recognize it drops significantly. The results of many experiments on inversion show that participants make on average 30% more errors in recognition of inverted faces compared to upright faces (Yin, 1969; Valentine, 1988; Yarmey, 1971). In contrast, recognition of other objects like houses, planes and dogs, shows a much smaller effect of inversion (Yin, 1969; Valentine, 1988; Yarmey, 1971). These findings are often used to support the idea that face perception is mediated by a specialized system which operates according to rules that differ from those for any other objects (Rhodes, Brake and Atkinson, 1993).

1.2.1 Neural basis of the FIE

1.2.1.1 Neurological studies of the FIE

Neuropsychological studies of patients with impairment in visual processing provide evidence that upright and inverted faces are represented using distinct cognitive mechanisms (Farah, 2004). Evidence from prosopagnosia suggests that different processes are involved in the perception of upright and inverted faces. For example, people with prosopagnosia are impaired in their ability to discriminate upright faces, but often perform at a similar level to normal controls with inverted faces (Farah, Wilson, Drain and Tanaka, 1995; Duchaine, Yovel and Nakayama, 2007).

1.2.1.2 Functional Magnetic Resonance Imaging (fMRI) – FIE

fMRI studies of neurologically healthy individuals have examined how upright and inverted faces are represented in the brain. These studies report that the face-selective fusiform area (FFA) showed greater response to upright faces than to inverted faces (Epstein, Higgins, Parker, Anguirre and Cooperman, 2006; Yovel and Kanwisher, 2005). Similarly, the STS also showed a significant decrease in activation for face inversion (Gauthier, Tarr, Anderson, Skudlarski and Core, 1999; Haxby et al., 1999). In contrast to the FFA and STS, the OFA has similar neural responses to upright and inverted faces (Yovel and Kanwisher, 2005). Yovel and Kanwisher (2005) employed an event-related fMR-adaptation design in which the response to different stimuli is compared to the response to identical stimuli. FFA showed a larger adaptation effect to upright than inverted faces, which was consistent with the behavioural experiment, measured by a face identity discrimination task of upright and inverted faces. In addition to FFA, two other regions the STS and the OFA were examined with the STS showing a lower response to inverted than upright faces like the FFA, however only the FFA response was correlated across subjects with the behavioural inversion effect. The role of OFA showed dissociation from FFA and showed similar response to both upright and inverted faces and no correlation with the behavioural inversion effect. These findings suggested that OFA is sensitive to physical information of the face rather than to the invariant aspects like identity.

In another study Haxby et al. (1999), compared the effects of inversion on upright and inverted faces and non-face objects (houses) in regions responsive to upright faces and non-face objects. The results showed a small effect of inversion in face selective regions and an increased response in regions that respond mostly to houses than faces. These results suggest that even though faces do invoke activity in face responsive regions, however the perceptual processes reflected by an inverted face are insufficient to uniquely identify the face. This leads to the recruitment of areas which are more specific to non-face objects.

1.2.1.3 Neurophysiological studies – FIE

Studies using Magnetoencephalography (MEG) and Event-related potentials (ERP) methods have shown that a face stimulus is processed in the extrastriate cortex as soon as 100ms after its presentation indicated by evoked potential peak in the P1 (Halit, deHaan and Johnson, 2000; Herrmann, Ellgring and Fallgatter, 2004). Furthermore, presentation of a face usually evokes a negative wave with an average latency of 170 ms (N170) which is distributed bilaterally over the occipito-temporal cortex (Bentin and Deouell, 2000; Liu, Harris and Kanwisher, 2002). Recent ERP studies tried to determine the neural basis of faces and objects (Bentin, Allison, Puce, Perez and McCathy, 1996; Gauthier, Skudlarski, Gore and Anderson, 2000). It is found that the N170 it is smaller when participants are presented with different categories of objects like houses, shoes, cars (Rossion and Jacques, 2008). Furthermore, the N170 is sensitive to face orientation. The amplitude of this component was delayed and higher when inverted images of faces were presented (Bentin, Allison, Puce, Perez and McCathy, 1996). Further studies of patients with implanted electrodes have led to the discovery of another face specific potential the N200. This amplitude is generated by a region of the fusiform gyrus and the posterior inferior temporal cortex and similar to the N170 seems to be a correlate of the early stages of structural face encoding. This potential is also sensitive to face inversion (Puce, Allison and McCarthy, 1999; Allison et al., 1994).

1.2.1.4 Transcranial Magnetic Stimulation (TMS) – FIE

In an investigation of the causal role of the face selective region right OFA and object-selective region right LO in the discrimination of upright and inverted faces Pitcher, Walsh and Duchaine, (2011) used TMS. They were particularly interested to explain which mechanisms contribute to the perception of inverted faces and whether mechanisms that are not face specific contribute to upright face recognition. Participants performed a match-to-sample discrimination task were they had to judge whether a probe stimulus was the same or different from the sample stimulus. Face images were presented in the upright and inverted orientation while TMS was delivered over right OFA and right LO. They found that TMS delivered over right OFA disrupted both upright and inverted face discrimination, while TMS delivered over right LO disrupted inverted face discrimination only. Their results provided evidence that upright faces are processed through face-specific mechanism whereas inverted faces are represented by both face-specific and object-specific mechanisms.

1.3 The Thatcher Illusion

The Thatcher Illusion is a classic example of the FIE. The Thatcher Illusion or Thatcher effect is a phenomenon where it becomes more difficult to detect local feature changes in an inverted face, despite identical changes being obvious in an upright face. It is named after the British former Prime Minister Margaret Thatcher on whose photograph the effect was most famously demonstrated.

This illusion involves inverting the eyes and mouth by 180^0 relative to the rest of the face (Thompson, 1980; Figure 3). This manipulation referred to as thatcherization and when the image orientation is changed it produces two different types of facial stimuli: (i) *Upright thatcherized face* - an unaltered face (upright normal) is modified by rotating the features by 180^0, leaving the remaining face intact (ii) *Inverted thatcherized face* - the entire image of the modified thatcherized face is turned upside down.

This manipulation is an impressive example of how the perception of a face can be changed by changing its orientation. When the face it is presented upright, the face appears grotesque. However, when it is presented upside-down it appears normal. Indeed, when comparing normal and thatcherized faces in the upside-down orientation, it is difficult to distinguish between a normal (undistorted) face and a (distorted) thatcherized face. Consequently, inverted thatcherized faces and normal faces are perceptually similar and the grotesqueness of inverted thatcherized faces is lost.

Figure 1.4: *Demonstration of the original Thatcher Illusion (Thompson, 1980). The left panel shows the original image (undistorted) and right panel the thatcherized (distorted) image. Flip page for upright images.*

1.3.1 Theoretical accounts of the Thatcher Illusion

The Thatcher illusion demonstrates an advantage for processing upright faces. Studies of the Thatcher illusion suggest that information encoded from the upright Thatcher stimuli must be different from that encoded for inverted Thatcher stimuli (Bartlett and Searcy, 1993). Even though upright and inverted thatcherized faces are identical in every way except their orientation, it appears that upright faces engage the processes by which we normally recognize faces and inverted faces do not. However, the specific processes underlying the Thatcher Illusion are still under debate.

The Thatcher Illusion has been explained by at least three competing hypotheses:

1. Expression disruption theory (Valentine, 1988; Yin, 1969),
2. The frame of reference theory (Parks, 1983),

3. The dual processing model (Bartlett and Searcy, 1993; Leder and Bruce, 2000).

1.3.1.1 Expression disruption theory

The expression disruption theory proposed by Valentine (1988) suggests that inversion of a face has a negative effect on the perception of expression. Yin (1969) also claims that the type of facial processing most affected by inversion might be the perception of facial expression. In an upright face, thatcherization generates a grotesque facial expression that is easily observed as we focus on the image holistically. During inversion, holistic processing is impaired, so the inversion of a thatcherized face reduces the perception of a grotesque expression.

However, a number of studies have explored the extent to which normal facial expressions are affected by the orientation of the face (Birgit, Seidel, Kainz and Carbon, 2009; McKelvie, 1995; Fallshore and Bartholow, 2003; Prkachin, 2003; Calvo and Nummenmaa, 2008). In contrast to the Thatcher illusion, there appears to be a much smaller effect of inversion on the recognition of normal facial expressions (Calvo and Nummenmaa, 2008; Birgit, Seidel, Kainz and Carbon, 2009). For example, Birgit, Seidel, Kainz and Carbon (2009) used five different emotional faces in two different presentation times (200ms and unlimited). They observed that when presentation time was limited, an effect of inversion was observed in some of the emotional faces (angry and neutral) however in the unlimited time presentation disgust and sadness were affected. Neutral faces did not indicate any inversion sensitivity in the unlimited time presentation and this was due to the required presentation time for correct extraction of the missing emotional content. The inconsistent cost of inversion on the perception of facial expression contrasts with the substantial effect of inversion found in the Thatcher illusion.

1.3.1.2 The frame of reference theory

A second explanation of the Thatcher Illusion was proposed by Rock (1973). It was suggested that the effect of inverting mono-oriented stimuli reflects the interaction of two frames of reference. The suggested frames of reference are:

1. Object-centered frame: incorporates information about the spatial relationship of internal parts of an object. It is conveyed by the structure of the stimulus itself as well as by prior learning (Parks, 1983).
2. Non-object centered frame: Is based on the external environment, or alternatively on the viewer's egocentric sense of up versus down based on retinal coordinates. Rock (1988) proposes a retinal factor which assigns direction to an object relative to the environment, based on a person's own perception of "up" and "down".

The object-centered frame of reference proposes that the internal parts of an object are assigned a specific orientation or direction relative to the whole object (Parks, 1983). However, when internal parts are locally inverted (i.e. eyes and mouth in thatcherized images) the orientation of those parts conflicts with the orientation of the rest of the object. This orientation effect is perceived when the object is viewed in its canonical (or upright) orientation.

In addition to the object-centered frame, Rock (1988) proposes a non-object centered frame in which a retinal factor assigns direction to an object relative to the environment, based on a person's own perception of "up" and "down". In an effort to explain the frame of reference hypothesis Kohler (1940) bent down until his head was inverted and looked backwards between his legs at pictures of a face. When the picture remained upright he had difficulty in perceiving the face, but when it was held upside-down he had no such a difficulty. According to Park, Coss and Coss (1985) any account of a face inversion considers the interaction between reference frames. When thatcherized faces are presented upright the location of tops and bottoms of features are reinforced by both frames of reference and therefore the grotesqueness of both eyes and mouth is more obvious. However, when the image is inverted, frame of reference created by the orientation of the whole image becomes less powerful, and local directional differences between the internal parts and the whole object are less apparent.

1.3.1.3 The dual processing model

The most dominant account of the Thatcher Illusion originates from the dual processing model (Collishaw and Hole, 2002; Leder and Bruce, 2000) - *featural* and *configurational* information. According to the featural hypothesis we use facial parts to perceive a face by involving information such as the shape of the nose, and the size of the eyes and mouth. On the other hand, the configurational hypothesis relates mostly to spatial relationships (i.e. distance and/or position of features). According to this perspective, upright faces are processed by both featural and configural processes.

According to Maurer, LeGrand and Mondlock (2002), there is no consensus about the terminology of configural processing and there are different senses in which configural processing has been used in the literature. Particularly, this phenomenon can be divided in three different types: 1) first-order relational information, that is the basic arrangement of face features with two eyes above the nose, above the mouth; (2) holistic information, that integrates facial features into a whole; (3) second-order relational information, that encodes the spatial information among facial features. Across the literature specific importance is places on holistic configuration as the collective cooperation of both featural and configurational information are perceived as a single entity to help us recognise and identify the whole face (Tanaka and Farah, 1993).

The disturbed perception of the face when it is upside-down is thought to result mainly in the manipulation of configural information (Diamond and Carey, 1986; Yin, 1969). According to Hole and Bourne (2010) the Face inversion effect and the Thatcher Illusion probably affect second-order configural processing, as they make it hard to extract the fine details of the special interrelationships within the faces. Furthermore, upside-down orientation does not influence featural information processing as it is thought to be processed regardless of orientation (Farah, Wilson, Drain, and Tanaka, 1995; Tanaka and Sengco, 1997; Carbon, Schweinberger, Kaufmann and Leder, 2005). In experiments done to check how inversion affects the configurational and featural information within the face Searcy and Bartley (1996) demonstrated that the alteration of a featural part (i.e. blackening parts of the teeth) still persists with the face inversion but when these alterations are affecting the configurational parts of the face as in thatcherized faces changes are perceptually lost by the face rotation (Leder and Bruce, 2000).

Bartlett and Searcy (1993) conducted three different experimental manipulations to test possible explanations of the Thatcher Illusion. These manipulations included faces in which the eyes and mouths had been inverted ("thatcherized" faces), the eyes and mouths had been moved (spatially distorted faces), and finally faces posing grotesque expressions. Judgements of face pairs revealed orientation sensitivity for both thatcherized and distorted faces, but not grotesque-expression faces. Bartlett and Searcy's experiments were interpreted as strongly supporting the configural hypothesis and suggested that configural and featural information were used in rating and categorizing upright face pairs, but in inversion the configural information was disrupted and only featural information was used. These theories suggest that facial configuration and features are essential components for facial recognition but their active use depends on the actual orientation of the face.

Based on the aforementioned experiments the perceived normality of inverted thatcherized faces is explained by the dissociable disruption of featural and configural information (Bartley and Searcy, 1993). In inverted thatcherized faces, the configural information processes are disrupted but the featural information processes are still effective (Carbon, Schweinberger, Kaufmann and Leder, 2005). However, the inconsistency in research investigations associated with the different type of definitions of configural processing make it difficult to define specific hypotheses to test the mechanisms underlying the Thatcher Illusion.

1.3.2 Neural correlates of the Thatcher Illusion

In the latest decade behavioural evidence deriving from models of face processing were complemented by neuroimaging and electrophysiological studies in an effort to understand the neuronal correlates of Thatcher Illusion. A great effort was placed by Event-related potential studies (ERPs) of the P100 or P1, N170 and P250 over the occipito-temporal cortex. These components can be modulated in latency and/or amplitude by configural changes (i.e thatcherized faces) and face inversion (Boutsen, Humphreys, Praamstra and Warbrick, 2006; Rossion et al., 1999). In particular, the N170 component (defined by Boutsen, Humphreys, Praamstra and Warbrick, (2006) as negative deflection reaching maximum amplitude 150-200 ms post-stimulus at occipito-temporal electrode sites) has been interpreted as a face-sensitive neural correlate because it indicated larger amplitude to faces than to objects, and is increased in latency and/or amplitude by face inversion (Bentin, Allison, Puce, Perez and McCathy, 1996; Rossion et al., 1999). Also, early positive components P1 and late component P250 showed a unique sensitivity to face inversion (Rossion et al., 1999).

There are currently three ERP studies that investigated the effect of Thatcher Illusion on different ERP components (Milivojevic, Clapp, Johnson and Corballis, 2003; Carbon, Schweinberger, Kaufmann and Leder, 2005; Boutsen, Humphreys, Praamstra and Warbrick, 2006). Milivojevic, Clapp, Johnson and Corballis (2003), investigated neural mechanisms in the occipito-temporal cortex using ERP. Participants were presented with thatcherized and normal faces in 6 different orientations (0˚ to 300˚) and had to decide whether the faces were male or female. The mean amplitude of the 4 different time segments of P1, N170, P250 and late components (300-500 ms) were calculated. Results indicated that there was an increase in amplitude when thatcherized faces were presented upright in the early positive component of P1 and negative component N170 as well as over P250 and later components. In particular when the thatcherized faces were presented upright there was a significant increase in amplitude in all of the four components. Interestingly, when the faces were inverted, thatcherization had no significant effect in any of the time windows. Milivojevic, Clapp, Johnson and Corballis (2003) concluded that their findings supported the perceptual illusion; that is, the difference between normal and thatcherized faces could not be perceived in an inverted orientation.

In a later study, Carbon, Schweinberger, Kaufmann and Leder (2005), measured ERPs to normal and thatcherized faces presented in three different orientations (0^o, 90^o and 180^o). Participants performed an identity classification task on thatcherized and normal familiar faces presented in two different time windows (34 ms or 200 ms). Carbon, Schweinberger, Kaufmann and Leder (2005), found an effect of thatcherization for the N170 component with increased amplitude by thatcherized upright faces but reduced amplitude when thatcherized faces were presented in the inverted orientation. In contrast to Milivojevic, Clapp, Johnson and Corballis (2003), Carbon, Schweinberger, Kaufmann and Leder (2005) have found that only the N170 had a significant increase when thatcherized faces were presented but not any of the other ERP components. The influence of the thatcherization on the N170 was independent of the two different presentation times used in the experiment. Interestingly, there was a strong effect of orientation on the N170 and later components for thatcherization and normal faces. This finding demonstrated different amplitudes for inverted normal and thatcherized faces, where thatcherization resulted in smaller amplitude in the N170 and larger N170 in normal faces. The study supports that there is a clear difference of N170 amplitudes between inverted thatcherized and normal faces, demonstrating that inverted faces do not escape subjective perception (processed in the same was as normal faces) as suggested by the Thatcher Illusion.

More recently, Boutsen, Humphreys, Praamstra and Warbrick (2006), used faces and houses (normal and thatcherized) in upright and inverted orientation, to investigate the effects of featural and configurational changes on the perception of faces and objects. The experiment consisted of a chair detection task: the detection of chairs among houses and faces (chair task). Boutsen and colleagues found evidence for a decrease in the amplitude of the N170 component for thatcherized faces when compared to normal faces. This modulation was evident for both upright and inverted stimulus presentations. They also found a delayed response for upright but not inverted thatcherized faces. These findings contrast with previous studies (Milivojevic, Clapp, Johnson and Corballis, 2003; Carbon, Schweinberger, Kaufmann and Leder, 2005) requiring identity or gender classification that reported an increased N170 amplitude for the upright thatcherized compared to normal thatcherized faces. There results proposed that inverted normal faces are distinguishable from inverted thatcherized faces, though the effect is not as distinguishable as when faces are presented in the upright orientation.

Although these ERP studies revealed the timing of neural responses to thatcherized images, they were not able to relate this to specific face-processing pathways. To address this issue other studies have used fMRI to probe the neural correlates of the Thatcher illusion (Rotshtein, Malach, Hadar, Graif and Hendler, 2001; Donnelly et al., 2011). Donnelly et al. (2011) used fMRI to explore brain regions associated with the discrimination of thatcherized from normal faces. Using a two alternative forced choice (2AFC) task, participants were required to discriminate which of the two faces is grotesque when a thatcherized and a normal face were presented simultaneously in the upright or inverted orientation. The thatcherized faces were manipulated either in the eyes, mouth or both. They report a distributed pattern of response in which face-selective regions such as the FFA are more responsive to inverted face images. Also, discrimination of inverted faces was associated with increased activation of brain areas that are typically involved in object perception (Lateral Occipital cortex). However, upright thatcherized faces are primarily discriminated via activation of emotional/social evaluation areas (medial frontal and subcallosal cortex, the middle temporal and the parahippocampal gyri).

Rotshtein, Malach, Hadar, Graif and Hendler (2001), used fMR-adaptation paradigm to investigate whether emotional attributes interact with sensory and perceptual properties of face stimuli using normal and thatcherized faces. A behavioural study performed before the FMR-adaptation paradigm, showed that upright thatcherized faces were judged bizarre and unpleasant, and upright normal faces were judged as the least bizarre. However, inverted thatcherized faces showed intermediate levels of deviation from upright normal faces. The fMR experiment was a block design with 4 experimental conditions of same and different identity of normal and thatcherized face images. All conditions were presented in the upright and inverted orientation throughout the experiment. Subjects were asked to perform a covert one-back-matching task through the whole run in which they were instructed to indicate whether or not two successive faces were identical. In the same identity repetition block the difference was related to the stimuli (i.e contrast), in the different block the difference was related to the identity of the face. Their fMRI results suggested that thatcherized images elicited a significantly greater response compared to normal faces in face-selective regions of the fusiform gyrus and lateral occipital lobe. In the inverted orientation the same patterns of response were observed for normal and thatcherized faces. Hence, these results might suggest that neural effects of Thatcherization for inverted faces might not parallel the perceptual illusion.

1.4 Thesis Aims

The overall objectives of this thesis are to use the Thatcher illusion to explore the behavioural and neural responses to upright and inverted facial expression. The main aims of the thesis are:

- **Aim 1** – In chapter 2, I investigated the neural basis of the Thatcher illusion. Specifically, I asked whether brain regions involved in processing facial expression are sensitive to orientation using fMRI.
- **Aim 2** – In chapter 3, I asked whether the Thatcher illusion can be explained by configural processing. Participants judged whether two simultaneously presented whole face images were identical or different. Next, the same task was repeated, but with only the mouth or eye region visible (i.e. in the absence of configural information).
- **Aim 3** – In chapter 4, I compared the effect of inversion on the recognition of facial expressions of emotion. The aim was to determine whether inversion affects the recognition of normal facial expressions in a similar way to thatcherized expressions.
- **Aim 4** – In chapter 5, I investigated whether the Thatcher illusion is evident for non-grotesque expressions.
- **Aim 5 –** In chapter 6, I asked whether thatcherization can affect judgements of facial identity.

Chapter 2

2.1 THE THATCHER ILLUSION REVEALS ORIENTATION-DEPENDENCE IN BRAIN REGIONS INVOLVED IN PROCESSING FACIAL EXPRESSION

2.1.1 Abstract

Although the processing of facial identity is known to be sensitive to the orientation of the face, it is less clear whether orientation-sensitivity extends to the processing of facial expression. To address this issue, fMRI was used to measure the neural response to the Thatcher illusion. Using an fMR-adaptation paradigm, we found a release from adaptation to upright images that changed from a normal to a thatcherized configuration in the superior temporal sulcus - a region directly linked to the processing of facial expression. However, this release from adaptation was not evident when the faces were inverted. These results show that regions involved in processing facial expression display a pronounced orientation-sensitivity.

2.1.2 Introduction

The impairment in the processing of facial identity following inversion is well established (Yin, 1969; Diamond and Carey, 1986; Valentine, 1988). However, studies often report a much smaller effect of inversion on the perception of facial expressions (Calvo and Nummenmaa, 2008; Prkachin, 2003; Birgit, Seidel, Kainz and Carbon, 2009; McKelvie, 1995; Fallshore and Bartholow, 2003), with the recognition of some expressions, such as happiness, not being affected by inversion (McKelvie, 1995; Calvo and Nummenmaa, 2008).

These studies reporting relatively small costs of inversion on the perception of facial expression form a noticeable contrast to the Thatcher illusion, which involves turning the eyes and the mouth upside-down relative to the rest of the face (a transform we will call 'thatcherization'). Following thatcherization, the facial expression appears grotesque when the face is upright (Thompson, 1980; Bartlett and Searcy, 1993; Parks, Coss and Coss, 1985). Strikingly, however, when the image is inverted the grotesque appearance is no longer visible. Although it does not offer a completely satisfactory account (see Thompson, Anstis, Rhodes, Jeffery and Valentine, 2009), the Thatcher illusion is often thought to result from a disruption of configural or holistic processing that in an upright face allows the perception of the grotesque expression (Bartlett and Searcy, 1993; Rhodes, Brake and Atkinson, 1993; Leder, Candrian, Huber and Bruce, 2001; Boutsen and Humphreys, 2003).

The Thatcher illusion demonstrates a degree of independence between the processing of facial identity and expression. The identity of a thatcherized face can be recognized when the face is upside down, albeit with some difficulty, whereas the ability to perceive the grotesque facial expression is completely lost. Inversion appears to be having a differential effect on the processing of facial expression and identity. This dissociation is consistent with a variety of evidence that facial identity and expression are processed along parallel processing streams (Haxby, Hoffman and Gobbini, 2000; Young and Bruce, 2011).

Despite the importance of the Thatcher illusion for showing the selectivity of face processing, the precise neural processes underlying this phenomenon remain unclear. ERP and fMRI studies have shown both increased (Milivojevic, Clapp, Johnson and Corballis, 2003; Carbon, Schweinberger, Kaufmann and Leder, 2005; Rotshtein, Malach, Hadar, Graif and Hendler, 2001) and decreased (Boutsen, Humphreys, Praamstra and Warbrick, 2006) responses when comparing thatcherized to normal face images. However, these studies have not directly measured the sensitivity to a change in the image from a normal to a thatcherized image that arises for upright faces only – the perceptual hallmark of the Thatcher illusion. It is this strong dissociation between the perception of expression in upright and inverted stimuli that makes the Thatcher illusion such a striking perceptual phenomenon, and understanding how the dissociation arises is essential to understanding the illusion.

Here, we have used the powerful fMR-adaptation technique (Grill-Spector, Henson and Martin, 2006) with a robust block design to probe the neural correlates of this key perceptual property of the Thatcher illusion - the loss of sensitivity to the change in expression between inverted normal and thatcherized faces. A functional localiser scan was used to identify core face-selective regions in visual cortex (Haxby, Hoffman and Gobbini, 2000). We then tested the sensitivity of each region to the thatcherization of upright and inverted facial expressions. The principle behind fMR-adaptation is that repetition of a stimulus causes a reduction or habituation in the neural response, leading to a lower fMR signal. The sensitivity of the neural representation can then be determined for different changes to the stimulus. If the underlying neural representation is insensitive to a particular type of change in the stimulus, the reduction in fMR signal for this type of change will be similar to the overall reduction produced by repetitions of identical stimuli. However, if the underlying neural representation is sensitive to this change, the fMR signal will remain at its original (non-adapted) level. Here, we compared the response to stimuli that alternated between normal and thatcherized images with the response to blocks of stimuli in which the images were all normal or all thatcherized. Our reasoning was that any region that contributes to the perception of the Thatcher illusion should show an increased response to a series of images that keeps changing from a normal to a thatcherized expression across a block of trials compared to blocks of images that were all normal or all thatcherized. Moreover, this difference in response should be evident for upright, but not inverted faces.

2.1.3 Materials and Methods

2.1.3.1 Participants and Stimuli

10 participants took part in the behavioural experiment (6 Female; mean age: 23 ± 2.1) and 27 participants took part in the imaging experiment (18 Females; mean age: 22.5 ± 3.0). Written consent was obtained for all participants and the study was approved by the York Neuroimaging Centre Ethics Committee. Photographs of 6

familiar female faces (Britney Spears, Natalie Portman, Angelina Jolie, Claudia Schiffer, Jessica Simpson, Cheryl Cole) were used. Each face was thatcherized by inverting the mouth and eyes areas by 180^0, creating a new set of 6 thatcherized images (Figure 1). Finally, the normal and thatcherized images were themselves rotated by 180^0 to produce two additional sets of inverted images. Visual stimuli (~6^o x 8^o) were presented ~57 cm from the subjects' eyes. In the scanner, images were back-projected onto the screen located inside the magnetic bore.

Figure 2.1: *Images from the six identities used in this study shown in their thatcherized (top row) and normal configuration (bottom row). Flip page for upright view.*

2.1.3.2 Behavioural Experiment

A behavioural Experiment was used to validate the stimuli and demonstrate the difficulty of perceiving physical changes between thatcherized and non-thatcherized images when these are inverted. Participants viewed two upright or two inverted images presented consecutively on each trial and had to indicate by a button press whether the two images were physically the same (i.e. identical images) or different in any way. Each image was presented for 800 ms and images were separated by an interval of 200 ms. These timings were identical to those used in the fMRI study.

There were 6 different image pairs (Figure 2 A, B):

(i) normal-normal, same Identity; two identical images of a normal face.

(*ii) thatcherized-thatcherized, same identity;* two identical images of a thatcherized face.

(iii) normal-thatcherized, same identity; the normal face and the thatcherized face of the same person.

(iv) normal-normal, different Identity; normal face images of two different people.

(v) thatcherized-thatcherized, different identity; thatcherized face images of two different people.

(vi) normal-thatcherized, different identity; a normal face and a thatcherized face of two different people.

In each run, there were 18 trials for each condition, giving a total of 108 trials. The experiment involved two separate runs in which the images were all inverted or all upright.

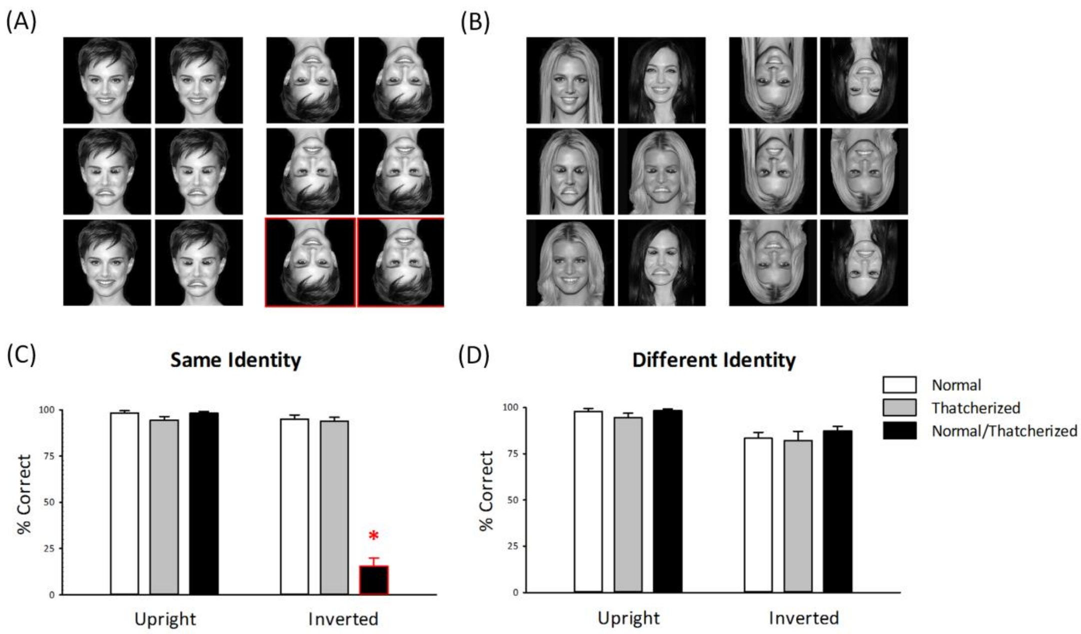

Figure 2.2: *Behavioural Experiment: Pairs of faces with (A) the same identity image or (B) different identities were presented in the upright or inverted orientation. Faces could both be normal (top), both be thatcherized (middle) or one normal and one thatcherized (bottom). Participants were asked to report whether the images were completely identical or different in any way. % correct performance was determined for (C) same identity and (D) different identity faces. Performance was above chance (50%) for all conditions except for the same-identity normal/thatcherized inverted condition (red), where below-chance performance reflects failure to see any difference between the stimuli Chance = 50% correct. Error bars represent ± S.E.M, *P < 0.001.*

2.1.3.3 fMRI Experiment

To determine the neural correlates of the Thatcher illusion, we measured responses to normal and thatcherized faces using fMR-adaptation paradigm with the same stimulus conditions as in the behavioural experiment. Our prediction was that, if a face-selective region is sensitive to the perceptual change created by thatcherization of face images, it should show a significantly higher response to alternations between the normal and thatcherized images (*normal-thatcherized*) compared to images that were all normal (*normal-normal*) or all thatcherized (*thatcherized-thatcherized*). In contrast, if a region is not sensitive to thatcherized images, it should show a similar response to all conditions. We measured this sensitivity to thatcherization for upright and for inverted images.

In contrast to the behavioural experiment, images in the fMR study were presented in a blocked design. There were 6 images in each block. In a same identity block, the same face identity was repeated 6 times. In the different identity condition, 6 different facial identities were presented. In the *normal-normal* and *thatcherized-thatcherized* blocks, the 6 face images were either all normal or all thatcherized. In the *normal-thatcherized* blocks, alternate images were normal or thatcherized. Images in the block were shown for 800 ms followed by 200 ms interval. The presentation timings for images and ISIs were therefore the same as those for the behavioural experiment, but the use of 6 images per block gave an overall duration of 6 s per block. Blocks were separated by a 9 s fixation grey screen. Each of the 6 conditions was repeated 6 times in a pseudo-randomized, counterbalanced design, giving a total of 36 blocks. There were two experimental runs. In the first run, images were shown in an inverted orientation. In the second run, images were shown in an upright orientation.

To maintain a consistent attentional load across stimulus blocks, a red dot was superimposed on 16% of the images. Participants were told to respond with a button press as soon as they saw the image with the red dot. Other than this red dot task, the experiment involved passive viewing of the face images. Participants correctly reported the occurrence of the red dot on over 95% (upright: 98.6 ± 0.75, inverted: 98.3 ± 0.67) of trials. Importantly, there was no significant difference in the rate of detection (inverted: $F_{2,52} = 0.19$, $p = .82$; upright: $F_{2,52} = 0.53$, $p = .59$) or reaction time (inverted: $F_{2,52} = 0.62$, $p = .54$; upright: $F_{2,52} = 1.25$, $p = .29$) across the different conditions.

To identify face-selective regions of interest a separate localizer scan was performed for each participant. There were four conditions: faces, objects, places, and scrambled faces. Images from each condition were presented in a blocked design with five images in each block. Each image was presented for 1 s followed by a 200 ms fixation cross. Blocks were separated by a 9 s grey screen. Each condition was repeated five times in a counterbalanced design.

All experimental scans were acquired using a GE 3T HD (General Electric, Signal HD Excite) magnetic resonance imaging (MRI) scanner at the York Neuroimaging Centre (YNiC) at the University of York. An eight channel phased array head-dedicated gradient insert coil (GE Milwaukee) tuned to 127.4 MHz was used to acquire MRI data. A gradient-echo EPI sequence was used to collect data from 38 contiguous axial slices (TR 3 s, TE min/full approx. 32.7-45 ms, flip-angle = 90^{o}, FOV 288 mm x 288 mm, in- plane resolution 2.25 mm x 2.25 mm, slice thickness 3 mm).

Statistical analysis of the fMRI data was carried out using FEAT (http://www.fmrib.ox.ac.uk/fsl). The initial 9 s of data from each scan were removed to minimize the effects of magnetic saturation. Motion correction was followed by spatial smoothing (Gaussian, full-width at half-maximum 6mm) and temporal high-pass filtering (cut off, 0.01 Hz). Face selective regions were determined from the localiser scan using a standard localiser approach (Andrews et al., 2010). The averaged contrasts of face>place, face>object, faces>scrambled were thresholded at $p < 0.001$ (uncorrected). Regions were defined independently for each individual. The time series of each voxel within a region was converted from units of image intensity to percentage signal change. All voxels in a given region were then averaged to give a single time series in each region for each participant. The peak response was then calculated 9 seconds after the onset of the block.

2.1.4 Results

2.1.4.1 Behavioural Experiment

To determine the degree to which Thatcher illusion was evident in our images, we used a behavioural paradigm in which participants observed two consecutively presented images. These pairs of images could be both normal (*normal-normal*), both thatcherized (*thatcherized-thatcherized*) or one normal and one thatcherized (*normal-thatcherized*). The images could also be of the same or a different identity, and the image pairs could be presented upright or inverted. Participants were simply asked to indicate by a button press whether the two images were completely identical or different in any way.

Accuracy judgements (Figure 2 C, D) show that participants were able to perform this task at well above chance level (50%) in all conditions except when an inverted normal image was paired with an inverted thatcherized image with the same identity. The high error rate found for inverted stimuli in the normal-thatcherized condition reflects a failure to notice differences between normal and thatcherized versions of the same person's face when these images are inverted.

A 3 x 2 ANOVA determined the effect of Condition (*normal-normal, thatcherized-thatcherized, normal-thatcherized*) and Orientation (*upright, inverted*). For the same identity images, there was a significant effect of Condition ($F_{2,18}$ = 168.7, $P < 0.001$) and Orientation ($F_{1,9}$ = 209.7, $p < 0.001$). There was also a significant interaction between Condition x Orientation ($F_{2,18}$ = 172.6 $p < 0.001$). This reflects the fact that participants were unable to judge the difference between a normal and a thatcherized image when they were inverted. Accuracy on *normal-thatcherized* trials (15.6 ± 4.4 %) was significantly lower compared to the *normal-normal* trials (95.0 ± 2.3 %, t_9 = -13.42, $p < .001$) or *thatcherized-thacherized* trials (93.9 ± 2.1 %, t_9 = 15.66, $p < .001$) when the faces were *inverted*. However, there was no difference between the *normal-thatcherized* and the *normal-normal* (t_9 = 0.01, p = .99) or *thatcherized-thatcherized* (t_9 = 2.69, p = .08) conditions when the faces were *upright*. For the different identity images there was a significant effect of Orientation ($F_{1,9}$ = 18.33, $p < 0.01$), but no significant effect of Condition ($F_{2,18}$ = 1.82, p = 0.19) or any interaction between Condition x Orientation ($F_{2,18}$ = 0.46, p = .64). The effect of orientation was due to a lower accuracy for *inverted* compared to *upright* images.

2.1.4.2 fMRI experiment

Figure 3A shows the location of the three face-selective regions in the occipital and temporal lobes identified by the functional localiser scan (Haxby et al, 2000): fusiform face area (FFA), occipital face area (OFA) and superior temporal sulcus (STS). The coordinates of each region are shown in Table 1. Each region was defined separately for each individual, and all further analyses were performed on the mean time courses of voxels in the ROIs. There was no significant difference between the patterns of response between the right and left hemispheres ($F < 0.7$, $p > .08$) or any significant interactions between Condition and Hemisphere ($F < 2.0$, $p > .16$). So, all further analyses were based on a pooled analysis in which the right and left hemisphere voxels are combined in each ROI.

Table 2.1: *Mean MNI coordinates of face-selective regions of interest*

Region	Hemisphere	n	x	y	z
FFA	L	26	- 40	- 54	- 22
	R	26	42	- 56	- 22
OFA	L	22	- 38	- 86	- 12
	R	25	42	- 82	- 12
STS	L	12	- 46	- 60	6
	R	22	48	- 60	6

Figure 3B shows the response to upright and inverted faces across all image conditions of the same or different identity. The peak responses of face selective regions were analysed using a 2-way ANOVA (Condition x Orientation) for same identity or different identity faces. In the STS, there was a main effect of Condition ($F_{2,46} = 3.76$, $p < 0.05$) and Orientation ($F_{1,23} = 4.14$, $p < 0.05$) for the same identity faces. There was also an interaction between Condition and Orientation ($F_{2,46} = 3.03$, $p < 0.05$). This interaction was due to an increased response to *normal-thatcherized* condition compared to both the *normal-normal* ($t_{21} = 2.80$, $p < 0.05$) and *thatcherized-thatcherized* ($t_{21} = 2.26$, $p < 0.05$) conditions in the *upright* orientation. Consistent with the behavioural and perceptual properties of the Thatcher illusion, there was no difference between the *normal-thatcherized* condition and either the *normal-normal* ($t_{21} = 0.72$, $p = .48$) or *thatcherized-thatcherized* ($t_{21} = 0.56$, $p = .58$) conditions when the images were *inverted*. For the different identity faces, there was a no main effect of Condition ($F_{2,46}$ = 2.05, p = .14) and Orientation ($F_{1,23}$ = 3.41, p = .08) and no significant interaction between Condition and Orientation ($F_{2,46}$ = 0.71, p = .50).

This orientation-sensitive response to thatcherized faces was not evident in other face-selective regions. In the FFA, there was a main effect of Condition ($F_{2,52}$ = 4.83, p < 0.05), but no effect of Orientation ($F_{1,26}$ = 0.70, p = .41) and no significant interaction between Condition and Orientation ($F_{2,52}$ = 1.81, p = .17) for same identity faces. The main effect of condition was due to a smaller response to *normal-normal* or *thatcherized-thatcherized* conditions compared to the *normal-thatcherized* condition for both the *upright* (t_{26} = 2.99, p < 0.01) and *inverted* (t_{26} = 2.41, p < 0.05) orientation. In the different identity images there were no main effect of Condition ($F_{2,52}$ = 2.46, p = .10), Orientation ($F_{1,26}$ = 0.065, p = .80) or any significant interaction between Condition x Orientation ($F_{2,52}$ = 1.58, p = .22), suggesting that patterns of response did not differ across conditions.

In the OFA, we found no main effect of Condition ($F_{2,50}$ = 0.444, p = .64) or Orientation ($F_{1,25}$ = 0.11, p = .74) and no significant interaction between Condition x Orientation ($F_{2,50}$ = 1.77, p = .18) for same identity faces. Similarly, for the different identity conditions, there was no significant effect of Condition ($F_{2,50}$ = 1.99, p = .15) or Orientation ($F_{1,25}$ = 0.023, p = .88) and there was no significant interaction between Condition x Orientation ($F_{2,50}$ = 2.19, p = .12). This suggests that OFA shows a similar pattern of responses across all conditions and orientations.

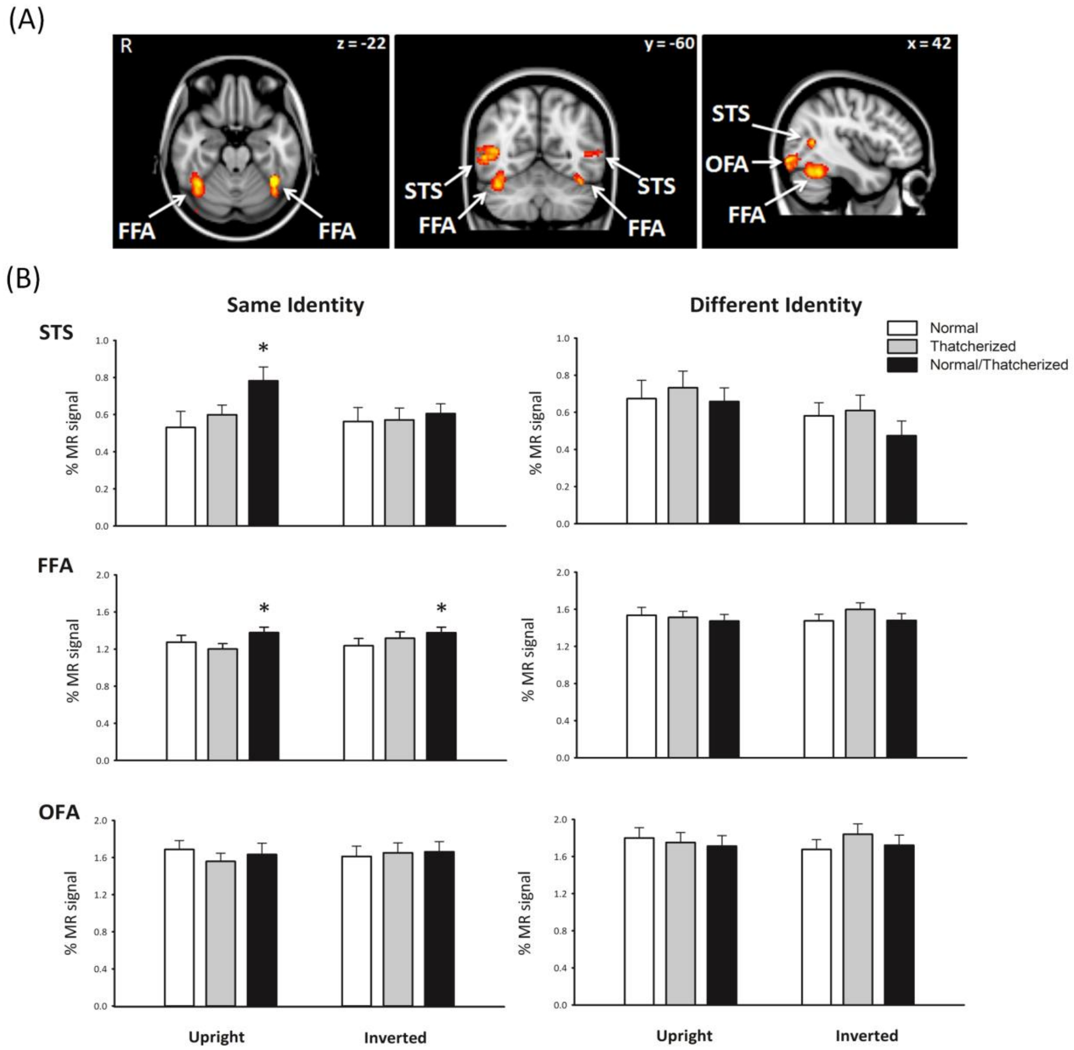

Figure 2.3: *(A) Location of face-selective regions (FFA, OFA, STS) defined from an independent localiser scan. Images follow radiological convention, with the left hemisphere shown on the right. (B) Responses in face selective regions to Normal, Thatcherized or Normal/Thatcherized images presented in an upright or inverted orientation. The peak average responses across subjects are shown in the STS, FFA and OFA for the same and different identity faces. Crucially, the STS showed an increased response to the alternating Normal/Thatcherized face condition for upright but not for inverted images with the same identity. Error bars represent ± S.E.M *P < 0.05.*

2.1.5 Discussion

This study used the Thatcher illusion to ask whether the neural processes involved in judgements of facial expression are sensitive to the orientation of the image. We found that the ability to discriminate behaviourally between a normal and a thatcherized image of the same person's face was substantially impaired when the images were inverted. In contrast, participants could easily make this discrimination when the faces were upright. A neural correlate of this behavioural effect was evident in the STS – a face-selective region that is thought to be involved in the processing of facial expression (Allison, Puce, and McCarthy, 2000; Engell and Haxby, 2007; Harris, Young and Andrews, 2012; Baseler, Harris, Young and Andrews, 2013). We found an increased response in the STS when there was a change in the image from a normal to a thatcherized face during a block of trials. Consistent with the behavioural findings, this sensitivity to a change in image from a normal to a thatcherized face was no longer apparent when the faces were inverted.

The selectivity of the response in the STS can be seen by contrasting it with the responses of other face-selective regions. The FFA – a region involved in processing facial identity (Grill-Spector, Knouf and Kanwisher, 2004; Rotshtein, Henson, Treves, Driver and Dolan, 2005) - was sensitive to a change in the configuration between normal and thatcherized faces, but this response was evident for both upright and inverted faces. In contrast, activity in the OFA was not sensitive to the thatcherization of face images and revealed no difference in response between upright and inverted images.

Previous studies have failed to find a consensus on the critical neural processes that underpin the orientation-sensitivity to thatcherized expressions that is the hallmark of the illusion. Event-related potential (ERP) studies in humans have shown that thatcherization increases the ERP response to faces and that this increase is attenuated when the face is inverted (Milivojevic, Clapp, Johnson and Corballis, 2003; Carbon, Schweinberger, Kaufmann and Leder, 2005). However, other studies have reported that thatcherized faces reduce the evoked response to faces, but that this effect was reduced by inversion (Boutsen, Humphreys, Praamstra and Warbrick, 2006). Although these ERP studies were able to reveal the timing of neural responses to thatcherized images, they were not able to relate this to specific face-processing pathways. To address this issue, Rotshtein, Malach, Hadar, Graif and Hendler (2001), used fMRI to compare the response of upright and inverted images in different regions of visual cortex. They found that upright thatcherized images elicited a significantly greater response compared to normal faces in the fusiform gyrus, lateral occipital lobe and amygdala. However, contrary to the perception of the Thatcher illusion, a similar pattern of response was also evident with inverted faces. Donnelly et al. (2011) compared neural activity to simultaneously presented normal and thatcherized faces. They reported a distributed pattern of response in which face-selective regions such as the FFA were more responsive when discriminating inverted images, whereas an increased response to upright faces was evident in regions associated with social and emotional cognition.

The inability of previous reports to show an orientation-sensitive neural response that can explain the Thatcher illusion may reflect a key difference between the present design and that of previous studies. Rather than determining the neural sensitivity to a change from a normal to a thatcherized image, these earlier reports simply compared the overall response to normal face images with the overall response to thatcherized images. In this study, we instead used fMR-adaptation to directly measure the sensitivity to a change in the image from a normal to a thatcherized image. We found that the face-selective region in the STS was more responsive to a change between normal and thatcherized images compared to when the images were either all normal or all thatcherized. Critically, we show that the sensitivity of the STS to thatcherization was not evident when the faces are inverted. Our finding that the STS is sensitive to the orientation of thatcherized images confirms the critical role of this region for the processing facial expression (Allison, Puce, and McCarthy, 2000; Engell and Haxby, 2007; Harris, Young and Andrews, 2012; Baseler, Harris, Young and Andrews, 2013).

To be socially meaningful, changes in expression and gaze direction must often be tracked across an individual whose invariant features (identity) remain constant. The increased response in the STS to sequences of faces, which change from a normal to a thatcherized configuration, but not in identity, is therefore consistent with the role of this region in social communication (Allison, Puce, and McCarthy, 2000; Engell and Haxby, 2007; Harris, Young and Andrews, 2012). Indeed, this result integrates well with recent studies that have shown that the STS is most sensitive to changes in expression of faces with the same identity (Andrews and Ewbank, 2004; Baseler, Harris, Young and Andrews, 2013). Presumably, this reflects the critical social importance of monitoring changes in a particular individual's expression.

The majority of studies on face inversion effects have focussed on the perception of facial identity. A variety of evidence has shown that judgements of facial identity are impaired when faces are turned upside down (Yin, 1969; Valentine, 1988). These findings have been complemented by neuroimaging studies that have investigated the effect of face inversion in face-selective regions of the fusiform gyrus (Kanwisher, Tong and Nakayama, 1998; Aguirre, Singh and D'Esposito, 1999; Haxby et al., 1999; Yovel and Kanwisher, 2004; 2005; Mazard, Schiltz and Rossion, 2006; Schiltz and Rossion, 2006). Although they differ in the magnitude of the inversion effect, the majority of studies report a decreased response in the fusiform gyrus to inverted faces. These studies also report reduced fMR-adaptation to facial identity in the FFA with inverted compared to upright faces (Yovel and Kanwisher, 2004; Mazard, Schiltz and Rossion, 2006; Schiltz and Rossion, 2006). Rather than explore a release from adaptation to changes in identity, we measured the sensitivity to changes in expression. We found a release from adaptation in the FFA when there was a change in expression from a normal to a thatcherized image. However, in contrast to the STS and the perception of the Thatcher illusion, this increased FFA response was still evident when the faces were presented upside down. Interestingly, the release from adaptation to a thatcherized expression was only apparent when the identity of the faces was unchanged within a block. When the identity of the images was varied, there was no additional increase in response to thatcherized images. This is likely to reflect the sensitivity of the FFA to image changes that are associated with changes in facial identity (Davies-Thompson, Newling and Andrews, 2013).

In conclusion, our results demonstrate clear evidence for orientation-dependent sensitivity to changes in facial expression in a key component of the neural network underlying face perception. We found activity in the STS was sensitive to changes between normal and thatcherized images when the faces were upright, but that there was no difference in response when the faces were inverted. In contrast, the FFA was sensitive to thatcherization of face images in both an upright and inverted configuration. This functional dissociation provides a neural explanation for the Thatcher illusion and confirms that the STS plays a key role in the perception of facial expression. The implication of these results is that the neural processing of facial expression is sensitive to the orientation of the image.

Chapter 3

3.1 ORIENTATION-SENSITIVITY TO FACIAL FEATURES EXPLAINS THE THATCHER ILLUSION

3.1.1 Abstract

The dramatic perceptual effect of inversion in the Thatcher illusion is commonly thought to result from a disruption of configural processing. Here, we show the limitations of this account and instead demonstrate that the effect of inversion in the Thatcher illusion is better explained by a disruption to the processing of purely local facial features. Using a matching task, participants were asked to decide whether two simultaneously presented whole face images were identical or different. We found that participants were easily able to discriminate normal and thatcherized versions of the same face when they were presented in an upright orientation. However, when the images were inverted, the ability to discriminate between the normal and thatcherized images was substantially attenuated. Next, we asked whether this pattern would be evident when only the eye region or only the mouth region of each face was shown. We again found a significant reduction in the ability to discriminate normal and thatcherized versions of facial features (the eye or the mouth regions) when the image was inverted. These results demonstrate that a key component of the Thatcher illusion is to be found in orientation-specific encoding of the expressive features (eyes and mouth) of the face.

3.1.2 Introduction

The impairment in face perception following inversion is often taken as evidence for the specialised processing of faces (Yin, 1969; Diamond and Carey, 1986; Valentine, 1988). The Thatcher illusion provides a compelling example of the cost of face inversion. When the eyes and the mouth are turned upside-down relative to the rest of the face - a transform now known in the research literature as 'thatcherization' - the facial expression appears grotesque (Thompson, 1980). This distortion of the face is immediately perceived when the face is upright. However, when the image is inverted the grotesque appearance is no longer visible.

The effect of inversion on the perception of facial expression seen in the Thatcher illusion is widely attributed to disruption of configural processing. The distinction between piecemeal processing of local features (such as eyes and mouths) and configural properties based on spatial inter-relationships between the features of the face (the configuration) was introduced by Carey and Diamond (1977), who maintained that configural processing is impaired by inversion whereas feature processing is largely equivalent across upright and inverted faces. For upright faces, then, Carey and Diamond (1977) argued that both configural and featural processing are possible, whereas for inverted faces only feature processing can be used. From this perspective, it follows that the cause of the disruptive effect of inversion in the Thatcher illusion reflects the disruption of configural processing, and many researchers have adopted this intuitively appealing line of reasoning.

The idea of the importance of configural information in upright face perception has been popularised and elaborated to such an extent that Maurer, LeGrand and Mondloch (2002), found it necessary to distinguish three different types of configural information involved in face processing that were often elided: (1) first-order relational information, that is the basic arrangement of face features with two eyes above the nose, above the mouth; (2) holistic information, that integrates facial features into a whole and (3) second-order relational information, that encodes the spatial relationships between facial features. In these terms, the inability to detect the grotesque expression in inverted thatcherized images is generally thought to be due to reduced sensitivity to the second-order configuration of the face (Bartlett and Searcy, 1993; Rhodes, 1988; Murray, Yong and Rhodes, 2000; Maurer, LeGrand and Mondloch, 2002; Hoehl and Peykarjou, 2012; Carbon and Leder, 2005).

Although many studies have shown that the ability to perceive second-order configural properties of the face may indeed be affected by inversion, these effects are not as strong as the Thatcher illusion (Rhodes, Brake and Atkinson, 1993; Bartlett and Searcy, 1993; Leder, Candrian, Huber and Bruce, 2001; Maurer, LeGrand and Mondloch, 2002; Boutsen and Humphreys, 2003). This suggests that existing explanations of the illusion may not be sufficient (Talati, Rhodes and Jeffery, 2010). Similarly, whilst demonstrations of holistic face perception such as the composite effect show strong effects of inversion (Young, Hellawell and Hay, 1987; Rossion, 2013), holistic processing is not usually considered to be the cause of the Thatcher illusion.

In the present study, we therefore revisited configural accounts of the Thatcher illusion by investigating whether the effect of inversion on the illusion might still be evident when configural information concerning the whole face and the inter-relationships between face parts is entirely absent. Thus was achieved by presenting local regions of the face (eyes or mouth) in isolation. First, though, we measured the perceptual impact of the Thatcher illusion by asking participants to judge whether two whole face images presented upright or inverted were identical or different (in any way). Our prediction was that participants should be more able to discriminate normal from thatcherized versions of a face image when presented upright, but that performance should be reduced when presented upside down. Next, we asked participants to perform the same task, but with only the mouth or the eye region of each image. Based on configural accounts of the illusion, we would predict there should be no difference in discrimination for upright and inverted presentations of these local features, since no information concerning the overall configuration is present. However, if the illusion is based on a disruption to feature-based processing, we would expect a similar disruption in perception when the images are inverted.

3.1.3 Materials and Methods

3.1.3.1 Participants

Twelve participants took part in Experiment 1 (mean age 25.1, ± 3.7; 7 Female) and 12 participants took part in Experiment 2 (mean age 20.8, ± 2.6; 9 Female). The study was approved by the Psychology Department Ethics Committee at the University of York. Participants were students from the University of York.

3.1.3.2 Stimuli

Face stimuli were Ekman faces selected from the Facial Expressions of Emotion Stimuli and Tests (FEEST) set (Young, Perrett, Calder, Sprengelmeyer and Ekman, 2002). Seven individuals posing five expressions (happiness, anger, disgust, fear 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. Each face image was thatcherized by inverting the mouth and eyes by 180^{o}. Figure 1 shows examples of images from Experiment 1 and 2.

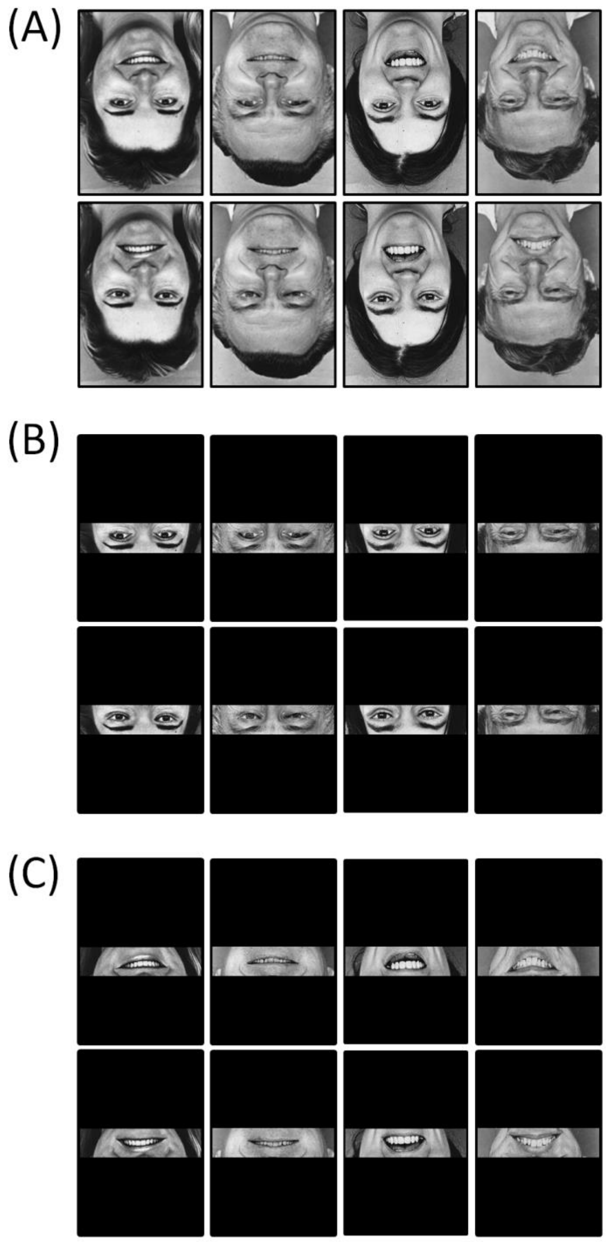

Figure 3.1: *Examples of normal and thatcherized images. (A) Whole face images show normal (top) and thatcherized (bottom) expressions from different individuals used in Experiment 1. (B) and (C) show the corresponding images from the eye region and mouth region, respectively that were used in Experiment 2. Invert page for the upright view of images.*

3.1.3.3 Experiment 1

The aim of Experiment 1 was to determine ability to discriminate normal from thatcherized face images in upright and inverted orientations. Visual stimuli (7 x 11^{o}) were viewed at a distance of approximately 57 cm. Participants were presented simultaneously with two whole face images to the left and right of a fixation cross. The centre of each image was 5^{o} from the fixation cross. Images were presented for 800 ms and participants were asked to indicate whether the images were completely identical or different in any way. There were 6 conditions (Figure 2 A,B):

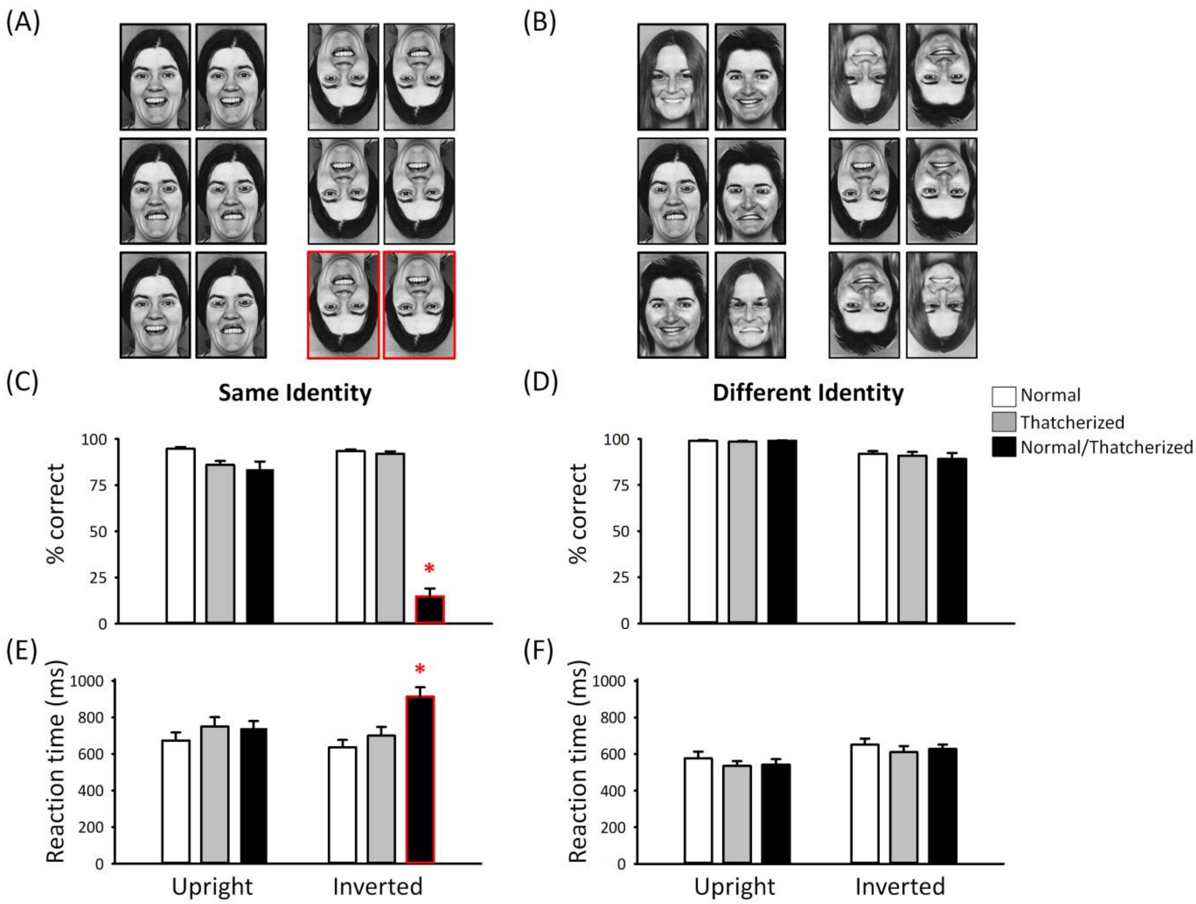

Figure 3.2: *Experiment 1: Pairs of faces with (A) the same identity image or (B) different identity were presented in the upright or inverted orientation. Pairs of faces could both be normal (top), both be thatcherized (middle) or be normal and thatcherized (bottom). Participants were asked to report whether the images were identical or different. % correct performance was determined for (C) same identity and (D) different identity faces.*

*Performance was well above chance (50%) for all conditions except for the same-identity normal/thatcherized inverted condition (red, *p<0.001). This demonstrates that participants were unable to discriminate the grotesque expression from a normal expression when the faces were inverted, leading to below-chance performance (chance = 50% correct). Reaction Time (ms) was also measured for (E) same identity and (F) different identity faces. Reaction time was similar for all conditions except for the same-identity normal/thatcherized inverted condition (red, *p<0.001). Error bars represent ± standard error across participants.*

(i) normal-normal, same Identity; two identical images of a normal face.

(*ii) thatcherized-thatcherized, same identity;* two identical images of a thatcherized face.

(iii) normal-thatcherized, same identity; the normal face and the thatcherized face of the same person.

(iv) normal-normal, different Identity; normal face images of two different people.

(v) thatcherized-thatcherized, different identity; thatcherized face images of two different people.

(vi) normal-thatcherized, different identity; a normal face and a thatcherized face of two different people.

There were 72 trials for each condition. % correct responses and reaction time to each condition was determined for each participant. The experiment involved two separate runs in which the images were all inverted or all upright. The faces also varied in identity. This ensured that participants were focussed on all aspects of the face when making similarity judgements.

3.1.3.4 Experiment 2

The aim of Experiment 2 was to determine the ability to discriminate normal and thatcherized faces in upright and inverted orientations when only the mouth region or only the eye region of each image was shown (see Figure 3A, 3B and Figure 4A, 4B). Stimuli were created by horizontally cropping the faces from Experiment 1, so that only a strip containing the eye region or the mouth region remained. Examples are shown in Figure 2 (eye region) and Figure 3 (mouth region). Note that cues to the upright or inverted orientation of each horizontal strip are implied by the eyebrows and the shape of the corresponding part of the face outline (Figure 1). Visual stimuli (7 x 2^{o}) were viewed at a distance of approximately 57 cm. The procedure and image conditions were identical to Experiment 1. Trials with eye regions or with mouth regions were presented in separate blocks.

3.1.4 Results

3.1.4.1 Experiment 1

To determine the degree to which Thatcher illusion was evident in our images, we used a behavioural paradigm in which participants observed two simultaneously presented whole face images. These pairs of images could be both normal (*normal-normal*), both thatcherized (*thatcherized-thatcherized*) or one normal and one thatcherized (*normal-thatcherized*). The images could also be of the same or a different identity, and the image pairs could be presented upright or inverted. Participants were simply asked to indicate by a button press whether the two images were identical or different in any way.

Accuracy judgements (Figure 2C, 2D) show that participants were able to perform this task at well above chance level (50%) in all conditions except when an inverted normal image was paired with an inverted thatcherized image (*normal-*

thatcherized) with the same identity. The high error rate found for inverted stimuli in the *normal-thatcherized same identity* condition reflects a failure to notice any differences between normal and thatcherized versions of the same person's face when these images are inverted. A 3 x 2 ANOVA was carried out to determine the effect of Condition (*normal-normal, thatcherized-thatcherized, normal-thatcherized*) and Orientation (*upright, inverted*) on accuracy. This was run separately for the same identity and different identity conditions.

Accuracy for the same identity images is shown in Figure 2C. There was a significant effect of Condition ($F_{2,22}$= 147.8, $p < 0.001$) and Orientation ($F_{1,11}$ = 83.5, $p < 0.001$). There was also a significant interaction between Condition * Orientation ($F_{2,22}$ = 228.1, $p < 0.001$). The significant interaction was due to the lower accuracy in *normal-thatcherized* condition (14.8 ± 4.3 %) compared to *normal-normal* (93.4 ± 0.1 %; $t(11)$ = 18.5, $p < 0.001$) or *thatcherized-thatcherized* (92.0 ± 1.3 %; $t(11)$ = 17.3, $p < 0.001$) conditions when the images were *inverted*. In contrast, there was no difference between the *normal-thatcherized* (83.7 ± 4.0 %) and the *thatcherized* (85.9 ± 2.2 %), ($t(11)$ = 0.6, p = .59) conditions and only a small difference when comparing *normal-thatcherized* (83.7 ± 4.0 %) to *normal (*94.6 ± 1.0 %*),* ($t(11)$ = 2.9, $p < 0.01$) when the images were upright. A similar pattern was evident for reaction time. Accuracy for the different identity images is shown in Figure 2D. There was no significant effect of Condition ($F_{2,22}$ = 1.2, p = .33) or any interaction between Condition * Orientation ($F_{2,22}$ = 1.2, p = .33). However, there was a significant effect of Orientation ($F_{1,11}$ = 13.8, $p < 0.001$). The effect of Orientation was due to a lower accuracy for *inverted* compared to *upright* images for *normal* (99.0 ± 0.4 % upright;

91 ± 1.6 % inverted; *t(11)* = 4.2, *p* = 0.001), *thatcherized* (98.5 ± 0.5 % upright; 90.9 ± 2.1 % inverted; *t(11)* = 3.7, $p < 0.01$) and *normal-thatcherized* (99.0 ± 0.3 % upright; 89.2 ± 3.2 % inverted; *t(11)* = 3.0, $p < 0.05$) conditions.

RT measurements to the different conditions are shown in Figure 1. A 3 x 2 ANOVA was carried out to determine the effect of Condition (*normal-normal, thatcherized-thatcherized, normal-thatcherized*) and Orientation (*upright, inverted*) on the same identity and different identity conditions. Response time for the same identity conditions is shown in Figure 2E. There was a significant effect of Condition ($F_{2,20}$ = 8.4, $p < 0.01$) and a significant interaction between Condition * Orientation ($F_{2,20}$ = 15.9, $p < 0.001$). However, there was no significant effect of Orientation ($F_{1,10}$ = 0.9, *p* = .37). The significant effect of Condition was due to slower RT to the *normal-thatcherized* condition (914.5 ± 50.3 ms) compared to *normal-normal* (637.4 ± 40.3; *t(10)* = 4.2, $p < 0.01$) or *thatcherized-thatcherized* (700 ± 48; *t(10)* = 3.1, $p < 0.01$) conditions when the images were inverted. In contrast, there was no difference between the *normal-thatcherized* and the *normal-normal* (*t(11)* = 1.9, *p* = .09) or *thatcherized-thatcherized* (*t(11)* = 0.2, *p* = .847) conditions when the faces were *upright*. Response time for the different identity images is shown in Figure 2F. There was a significant effect of Condition ($F_{2,22}$= 4.5, $p < 0.05$) and a significant effect of Orientation ($F_{1,11}$ = 5.3, $p < 0.05$). However, there was no interaction between Condition * Orientation ($F_{2,22}$ = 0.1, *p* = .94). The significant effect of Orientation was due to a slower response to *inverted* (629.4 ± 31 ms) compared to *upright* (551.6 ± 30 ms) faces.

3.1.4.2 Experiment 2

The aim of Experiment 2 was to determine the effect of inversion on ability to discriminate normal from thatcherized images when only the mouth or only the eye region was shown.

Eye region

The ability to discriminate differences based on the eye region is shown in Figure 3. Accuracy judgements show that participants were able to perform this task above chance (50%) in all conditions except when an inverted normal image was followed by an inverted thatcherized image with the same identity. A 3 x 2 ANOVA was carried out to determine the effect of Orientation on judgements of *normal*, *thatcherized* and *normal-thatcherized* images.

For the same identity images (Figure 3C), there was a significant effect of Condition ($F_{2,22}$= 35.0, p < 0.001) and Orientation ($F_{1,11}$ = 20.5, p = 0.001) on accuracy. There was also significant interaction between Condition * Orientation ($F_{2,22}$ = 28.2, p < 0.001). The interaction was due to lower accuracy for the *normal-thatcherized* condition (40.1 ± 7.1%) compared to both the *normal-normal* (87.7 ± 2.7 %; *t(11)* = 5.9, p < 0.001) and *thatcherized-thatcherized* (91.7 ± 1.9%) conditions when the images were *inverted*. In contrast, there was no significant difference between the *normal-thatcherized* (87.2 ± 3.4 %) and the *thatcherized-thatcherized* (84.3 ± 4.3; *t(11)* = 0.8, p = .45) conditions and only a slight difference between the *normal-thatcherized* and *normal-normal* upright conditions 95.4 ± 1.8 %*; t(11)* = 3.2, p < 0.01) when the images were presented upright. For the different identity images (Figure 3D), there was a significant effect of Condition ($F_{2,22}$ = 24.9, p < 0.001), but there was no significant effect of Orientation ($F_{1,11}$ = 2.1, p = .17) and no interaction between Condition * Orientation ($F_{2,22}$ = 0.5, p = .64). The effect of Condition was due to higher accuracy for the *normal-thatcherized* (98 ± 0.8 %) condition compared to the *normal-normal* (91 ± 2.0 %) and *thatcherized-thatcherized* (93 ± 1.1 %) conditions.

Next, we measured RT to each condition. For the same identity conditions (Figure 3E), there was a significant effect of Condition ($F_{2,22}$ = 4.9, p < 0.05), but no significant effect of Orientation ($F_{1,11}$ = 0.5, p = .84) or any significant interaction between Condition * Orientation ($F_{2,22}$ = 2.3, p = .12). The significant effect of Condition was due to a faster RT for *normal-normal* condition (962 ± 81 ms) compared to *thatcherized/thatcherized* (997 ± 86 ms) *and normal-thatcherized* (1098 ± 113 ms) conditions. For the different identity images (Figure 3F), there was no significant effect of Condition ($F_{2,22}$ = 0.6, p = .55), Orientation ($F_{1,11}$ = .08, p = 0.78) and no significant interaction between Condition * Orientation ($F_{2,22}$ = 1.7, p = .21).

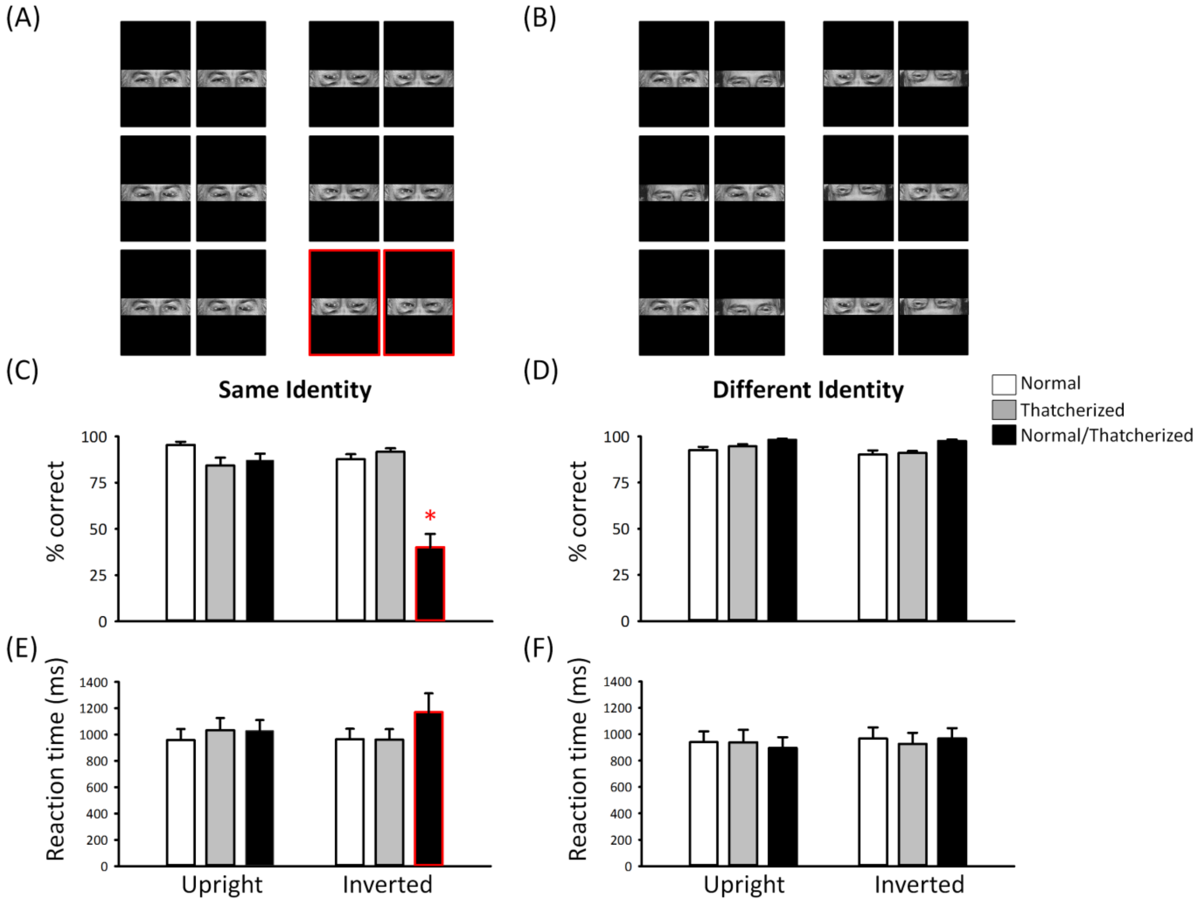

Figure 3.3: *Experiment 2: Pairs of eye regions with (A) the same identity image or (B) different identities were presented in the upright or inverted orientation. Pairs of eye regions could both be normal (top), both be thatcherized (middle) or be normal and thatcherized (bottom). Participants were asked to report whether the images were identical or different. % correct performance was determined for (C) same identity and (D) different identity faces. Performance was above chance (50%) for all conditions except for the same-identity normal/thatcherized inverted condition (red, *p<0.001). Reaction time was similar for all conditions except for the same-identity normal/thatcherized inverted condition (red). Error bars represent ± standard error across participants.*

Mouth region

The ability to discriminate differences in the mouth region is shown in Figure 3. Accuracy judgements show that participants were able to perform this task above chance (50%) in all conditions except when an inverted normal image was followed by an inverted thatcherized image with the same identity. A 3 x 2 ANOVA was carried out to determine the effect of Orientation on judgements of *normal*, *thatcherized* and *normal-thatcherized* images.

Accuracy for the same identity images is shown in Figure 4C. There was a significant effect of Condition ($F_{2,22}$= 29.5, $p < 0.001$) and Orientation ($F_{1,11} = 12.2$, $p < 0.01$). There was also significant interaction between Condition * Orientation ($F_{2,22} = 15.0$, $p < 0.001$). The significant interaction was due to the lower proportion of correct responses to *normal-thatcherized* (47.9 ± 8.8) images compared to *normal-normal* (94.5 ± 1.5%; *t(11)* = 5.1, $p < 0.001$) or *thatcherized-thatcherized* (90.0 ± 2.5 %; *t(11)* = 4.6, $p = 0.001$) when the images were *inverted*. In contrast, there was no significant difference between the *normal-thatcherized* (87.2 ± 2.9 %) and the *thatcherized-thatcherized* (91.1 ± 1.4 %; *t(11)* = 0.8, $p = .45$) conditions, and only a small difference when comparing the *normal-thatcherized* condition to the *normal-normal* (93.5 ± 1.4 %*; t(11)* = 2.4, $p < 0.05$) condition. Accuracy for the different identity images is shown in Figure 4D. There was a significant effect of Condition ($F_{2,22} = 5.2$, $p < 0.05$) and a significant effect of Orientation ($F_{1,11} = 11.8$, $p < 0.01$). However there was no significant interaction between Condition * Orientation ($F_{2,22} = 0.6$, $p = .56$). The effect of Condition was due to a higher number of correct responses in the *normal-thatcherized* (98.4 ± 0.7 %) condition compared to the *normal-normal* (96 ± 1.2 %) or *thatcherized-thatcherized* (95 ± 1.6 %) conditions. The effect of Orientation was due to a higher number of correct responses to upright (98 ± 1.0 %) compared to inverted (94.9 ± 1.3%) images.

Next, we determined the effect of Condition and Orientation on RT values. Reaction Time for the same Identity conditions is shown in Figure 4E. There was a significant effect of Condition ($F_{2,22}$ = 6.6, p < 0.01), but no significant effect of Orientation ($F_{1,11}$ = 2.3, p = .16) and no significant interaction between Condition * Orientation ($F_{2,22}$ = 1.9, p = .17). The significant effect of Condition was due to a slower reaction time of *normal-thatcherized* (982 ± 69.4 ms) compared to *normal-normal* (837 ± 60 ms) or *thatcherized-thatcherized* (921 ± 61 ms) upright images. Reaction time for the different identity images is shown in Figure 4F. There was a significant effect of Condition ($F_{2,22}$ = 10.1, p < 0.01), but no significant effect of Orientation ($F_{1,11}$ = .83, p = .38) or any significant interaction between Condition * Orientation ($F_{2,22}$ = .23, p = .80). The significant effect of Condition was due to a faster reaction time to the *normal-thatcherized* condition (838 ± 58 ms) compared to the *normal-normal* (880 ± 59ms) or *thatcherized-thatcherized* (870 ± 60 ms) conditions.

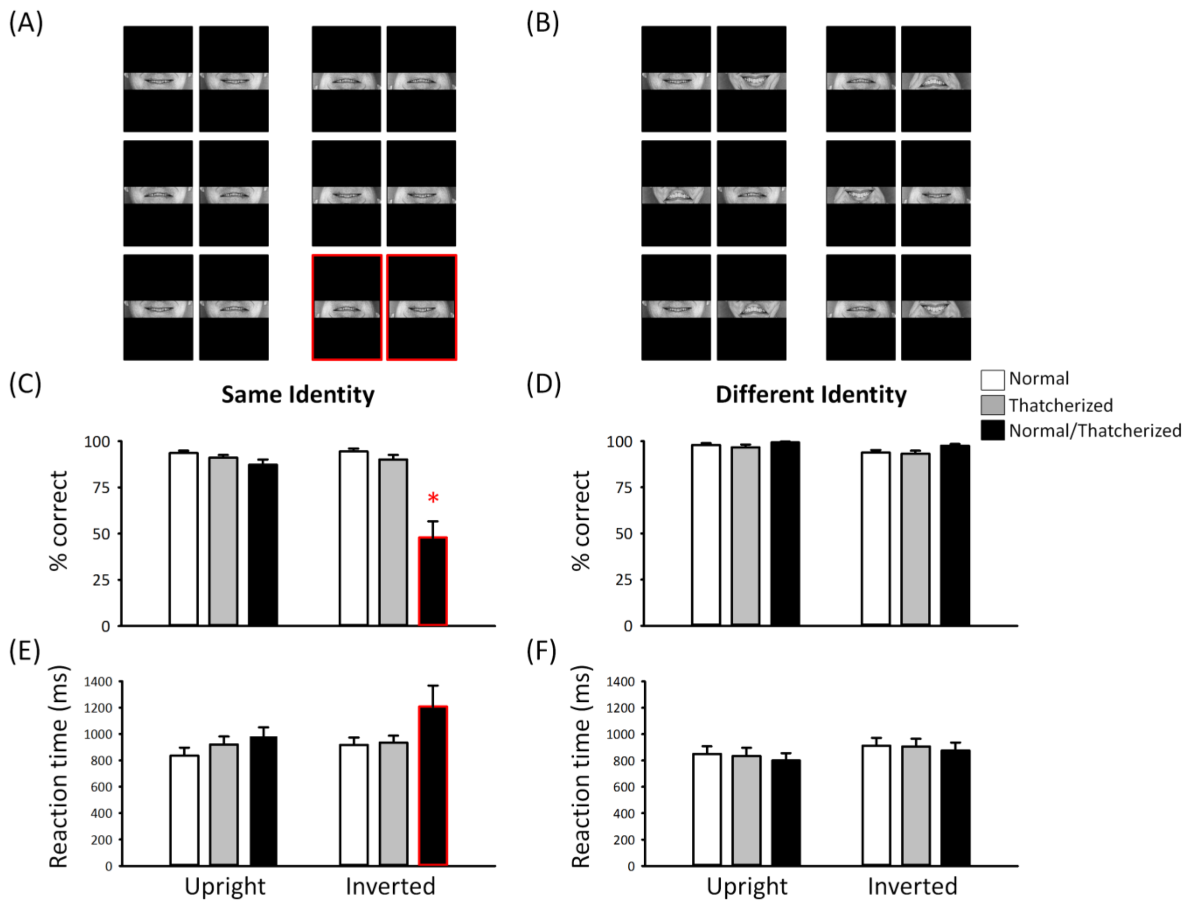

Figure 3.4: *Experiment 3: Pairs of mouth regions with (A) the same identity image or (B) different identities were presented in the upright or inverted orientation. Pairs of mouth regions could both be normal (top), both be thatcherized (middle) or be normal and thatcherized (bottom). Participants were asked to report whether the mouth images were identical or different. % correct performance was determined for (C) same identity and (D) different identity faces. Performance was above chance (50%) for all conditions except for the same-identity normal/thatcherized inverted condition (red, *p<0.001). Reaction time was similar for all conditions except for the same-identity normal/thatcherized inverted condition (red). Error bars represent ± standard error across participants.*

Image differences

The key finding across each experiment was that inversion severely disrupted the ability to discriminate normal from thatcherized images of the same face or of the eye or mouth regions from the same face. So, we determined the low-level differences between the image properties of normal and thatcherized images created from the same face. First, we calculated the mean absolute difference in grey value across corresponding pixels in pairs of images from the same identity (Figure 5A). Next, we measured the correlation of grey values from corresponding pixels in the same image pairs (Figure 5A). These analyses were performed on the whole face (as used in Expt. 1) and on the eye and mouth regions (Expt. 2). An ANOVA revealed a significant effect of pixel differences across the different image conditions ($F_{2,10}$ = 28.4, p < 0.001). This was due to a progressive increase in difference between images from the whole face (5.6 ± 1.2) to the mouth (15.3 ± 1.8) and the eye (21.4 ± 3.3) regions. An ANOVA on the correlation values also revealed a significant effect ($F_{2,10}$ = 28.0, p < 0.001). Again this was due to a progressive decline in the similarity of the images from the whole face (0.95 ± 0.01) to the mouth (0.78 ± 0.03) and eye (0.71 ± 0.03) regions. These results highlight that the reduced ability to discriminate normal from thatcherized images when they were inverted was evident despite substantial low-level differences in the images.

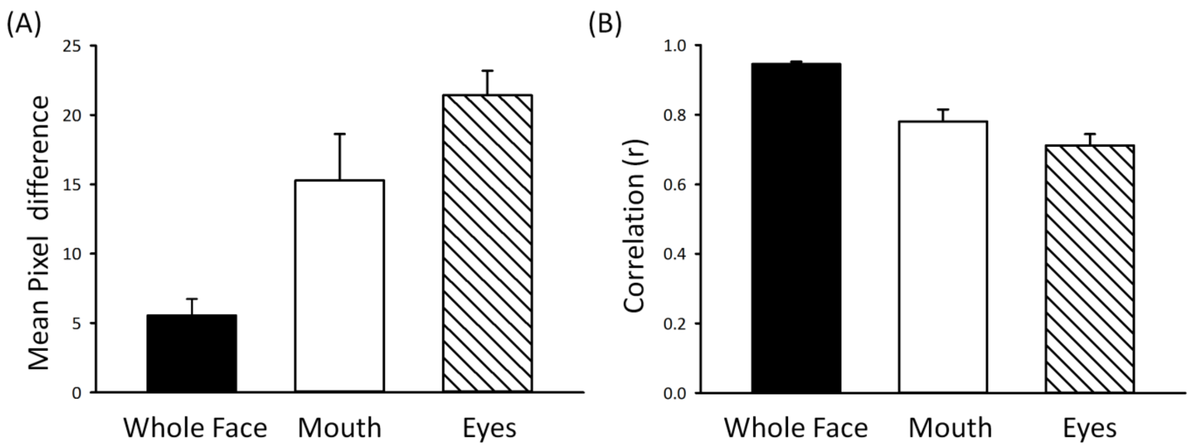

Figure 3.5: *Mean differences and correlations across normal and thatcherized versions of images of the same identity. (A) low-level differences between the image properties of normal/thatcherized conditions of the same identity across the different features (whole*

face, mouth and eyes) and (B) correlation between corresponding pixel values in images of normal/thatcherized conditions of the same identity, across the different features (whole face, mouth and eyes) used in the study. Errors represent SEM.

3.1.5 Discussion

Previous attempts to explain the dramatic effect of orientation in the Thatcher illusion have held that its cause lies in the disruption of configural processing (Bartlett and Searcy, 1993; Bertin and Bhatt, 2004; Edmonds and Lewis, 2007). Configural processing is thought to be essential to perceiving the grotesque expression, and its disruption leads to the expression not being seen correctly when the image is upside down. The aim of this study was to explore the role of spatial configuration in the Thatcher illusion. Participants judged whether simultaneously presented images were identical, or different in any way.

We found that participants were easily able to discriminate a normal face from a thatcherized version of the same face when the images were presented upright. However, when the images were inverted, performance fell below chance level because participants simply failed to notice the difference between the images. This simple perceptual test offers strong evidence of how poorly the inverted thatcherized expression is perceived.

To determine whether the illusion could be explained by a disruption to the face configuration, we measured performance when only the eye region or only the mouth region of each image was visible. Again, participants were easily able to discriminate a normal from a thatcherized version of the same image when upright. However, when the images were inverted, participants were at chance levels.

Our results suggest that previous attempts to explain the Thatcher illusion have been mistaken in ignoring the possibility that inversion disrupts feature processing. Instead, locally-inverted facial features (mouth or eyes) are themselves perceived as being abnormal, if they are interpreted as being in an upright orientation. However, when the image is interpreted as inverted, the precision with which the features are encoded is diminished and the features do not look grotesque. As we show that these effects can be found for the face as a whole and for the isolated mouth and eye regions, this effect cannot be explained by a disruption to configural processing. Rather, our analysis of the Thatcher illusion shows that it depends primarily on sophisticated perceptual encoding of local face regions that are taken to be upright by the perceptual system. When the perceptual system interprets the features as being inverted, it is less able to encode them accurately.

A further remarkable aspect of the Thatcher illusion is that the low-level differences between a normal and thatcherized image are identical in the upright and inverted orientations. So, it seems odd that, when participants were only asked to make a simple visual discrimination between images based on any differences whatsoever, they failed to get above chance with the inverted images. In Experiment 2, the only cue to the orientation of the face is the jaw line for the mouth region and the eye brows / bridge of the nose for the eye region. Nevertheless, it appears that these cues are sufficient to provide the critical orientation cues that influence our perception of the facial features. The findings suggest that low-level image discrimination of faces can be influenced by the context in which the face is perceived. This fits with a recent study that demonstrated how the global properties of natural images (including faces) can influence low-level feature detectors (Neri, 2011; 2014). It is possible that the inability to detect image differences may reflect feedback from higher to lower visual regions.

The Thatcher illusion also demonstrates a degree of independence between the processing of facial identity and expression. The identity of a thatcherized face can still be recognized when the face is upside down, albeit with some difficulty, whereas the ability to perceive the grotesque facial expression is completely lost. Inversion appears to be having a differential effect on the processing of facial expression and identity. This dissociation is consistent with a variety of evidence that facial identity and expression are processed along parallel processing streams (Haxby, Hoffman and Gobbini, 2000; Young and Bruce, 2011; Bruce and Young, 2012). In a recent study, we found a neural correlate of the Thatcher illusion in the STS – a face-selective region that is thought to be involved in the processing of facial expression (Allison, Puce and McCarthy, 2000; Engell and Haxby, 2007; Harris, Young and Andrews, 2012; Baseler, Harris, Young and Andrews, 2013). This was reflected by an increased response in the STS when there was a change in the image from a normal to a thatcherized face. However, there was no increase in response from a normal to a thatcherized face when the faces were inverted.

In conclusion, our results show that the inability to detect the grotesque expression in the inverted Thatcher illusion can be explained by a reduced sensitivity to inverted facial features. This interpretation contrasts with previous work that has suggested that the Thatcher illusion reflects configural processing. We do not of course deny other clear evidence that configural processing plays a role in face perception and that it is disrupted by inversion. However, we suggest that the explanation of the Thatcher illusion lies with the orientation-specific encoding of local expressive features (eyes and mouth).

Chapter 4

4.1 INVERSION IMPROVES RECOGNITION OF FACIAL EXPRESSION IN THATCHERIZED IMAGES

4.1.1 Abstract

The marked effect of inversion in the Thatcher illusion contrasts with other studies that only report a small effect of inversion on the recognition of facial expressions. To address this discrepancy, we compared the effect of inversion and thatcherization on the recognition of facial expressions. We found that inversion of normal faces only caused a small reduction in the recognition of facial expressions. In contrast, thatcherization of upright images resulted in a much larger reduction in the recognition of facial expressions. Paradoxically, inversion of thatcherized faces caused a relative increase in the recognition of facial expressions. Together, these results suggest that different processes explain the effects of inversion on the recognition of facial expressions and on the perception of the Thatcher illusion. The grotesque perception of thatcherized images is based on a more orientation-sensitive representation of the face. In contrast, the recognition of facial expression is dependent on a more orientation-insensitive representation. A similar pattern of results was evident when only the mouth or eye region was visible. These findings demonstrate that a key component of the Thatcher illusion is to be found in orientation-specific encoding of the features of the face.

4.1.2 Introduction

The impairment in the perception and recognition of facial identity following inversion is a well-established phenomenon in face perception (Yin, 1969; Diamond and Carey, 1986; Valentine, 1988). Although the face inversion effect (FIE) is a robust finding across many aspects of face processing, the effect of inversion on the perception of facial expression is less clear. Inversion has been shown to have a small effect on the recognition of negative emotions, but little effect on the recognition of positive emotions, such as happiness (PrKachin, 2003; McKelvie, 1995; Fallshore and Bartholow, 2003; Calvo and Nummenmaa, 2008; Goren and Wilson, 2006).

The relatively small and inconsistent cost of inversion on the perception of facial expression contrasts with the substantial effect of inversion found in the Thatcher illusion. Turning the eyes and the mouth upside-down relative to the rest of the face (a transform we will call 'thatcherization') results in the perception of a grotesque facial expression when the face is upright, but when the image is inverted the grotesque appearance is no longer visible (Thompson, 1980).

The effect of inversion on the perception of facial expression seen in the Thatcher illusion is widely attributed to disruption of configural processing. The distinction between piecemeal processing of local features (such as eyes and mouths) and configural properties based on spatial inter-relationships between the features of the face (the configuration) was introduced by Carey and Diamond (1977), who maintained that configural processing is impaired by inversion whereas feature processing is largely equivalent across upright and inverted faces. For upright faces, they argued that both configural and featural processing are possible, whereas for inverted faces only feature processing can be used. From this perspective, it follows that the cause of the disruptive effect of inversion in the Thatcher illusion reflects a disruption of configural processing, and many researchers have adopted this intuitively appealing line of reasoning.

The aim of this study was to address the discrepancy between the effect of inversion on the recognition of facial expressions and the perception of the Thatcher illusion. First, we compared the relative effect of inversion and thatcherization on the recognition of expression from a validated set of face stimuli (Young, Perrett, Calder, Sprengelmeyer and Ekman, 2002). Our prediction was that the disruption to the canonical presentation of facial features in the thatcherized images should have a large effect on the recognition of expression. In contrast, inversion of face images should have a much smaller effect on the recognition of expression. Next, we asked how inversion affects the recognition of facial expression in thatcherized faces. Based on previous studies, our prediction was that the inversion of thatcherized images should lead to a further modest reduction in the recognition of facial expression. However, in a thatcherized face, the features have an orientation typically found in upright faces. So, it is also possible that recognition performance will be improved. Previous studies have suggested that the Thatcher illusion can be explained by the disruption of configural processing (Carey and Diamond, 1977; Bartlett and Searcy, 1993). To address the importance of configural processing, we asked whether a similar pattern of results is evident when the key expressive features (mouth region or eye region) are shown in isolation. If the same pattern of results can be found when only featural information is present, this would challenge configural explanations of the Thatcher illusion. On the other hand, if the effects seen in the whole face are dependent on configural processing, we would not expect to see a similar pattern of results when only the eye or mouth region are visible.

4.1.3 Materials and Methods

4.1.3.1 Participants

Twelve participants took part in the experiment 1 (6 Female; mean age 20.5, ± 1.8) and 20 participants took part in Experiment 2 (16 Female; mean age 19.1, ± 1.6). The study was approved by the Psychology Department Ethics Committee at the University of York. Participants were students from the University of York.

4.1.3.2 Stimuli

Face stimuli were Ekman faces selected from the Facial Expressions of Emotion Stimuli and Tests (FEEST) set (Young, Perrett, Calder, Sprengelmeyer and Ekman, 2002). Six individuals posing different expressions 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. Each face image was Thatcherized by inverting the mouth and eyes by $180^{o.}$ Visual stimuli (7×11^{o}: whole face, 7×2^{o}: mouth or eye region) were presented on a computer monitor at a distance of approximately 57 cm from the participants. NBS Presentation (http://www.neurobs.com) stimulus delivery software was used to present images.

4.1.3.3 Design

Figure 1A shows examples of images from Experiment 1. We compared the effect of inversion and thatcherization on the recognition of facial expressions of emotion using whole face images. There were 6 facial expressions: neutral, happiness, anger, disgust, fear and sadness. Images were presented in an upright or inverted orientation. They could also be normal or thatcherized. In total, there were 24 conditions that included 6 expressions x 4 conditions (upright normal, inverted normal, upright thatcherized, inverted thatcherized). Individual images from each condition were presented for 800 ms followed by a 2 s interstimulus fixation screen. Participants were instructed to press a button to indicate which expression they had seen (6-AFC). There were 24 trials for each condition and a total of 576 trials for the whole experiment. Trials were presented in a counterbalanced, pseudo-randomized order.

Figure 1B and 1C shows examples of images from Experiment 2. The design and procedure for Experiment 2 was identical to Experiment 1. The only difference was that participants judged facial expressions of emotion from face images in which either only the mouth region or only the eye region was visible.

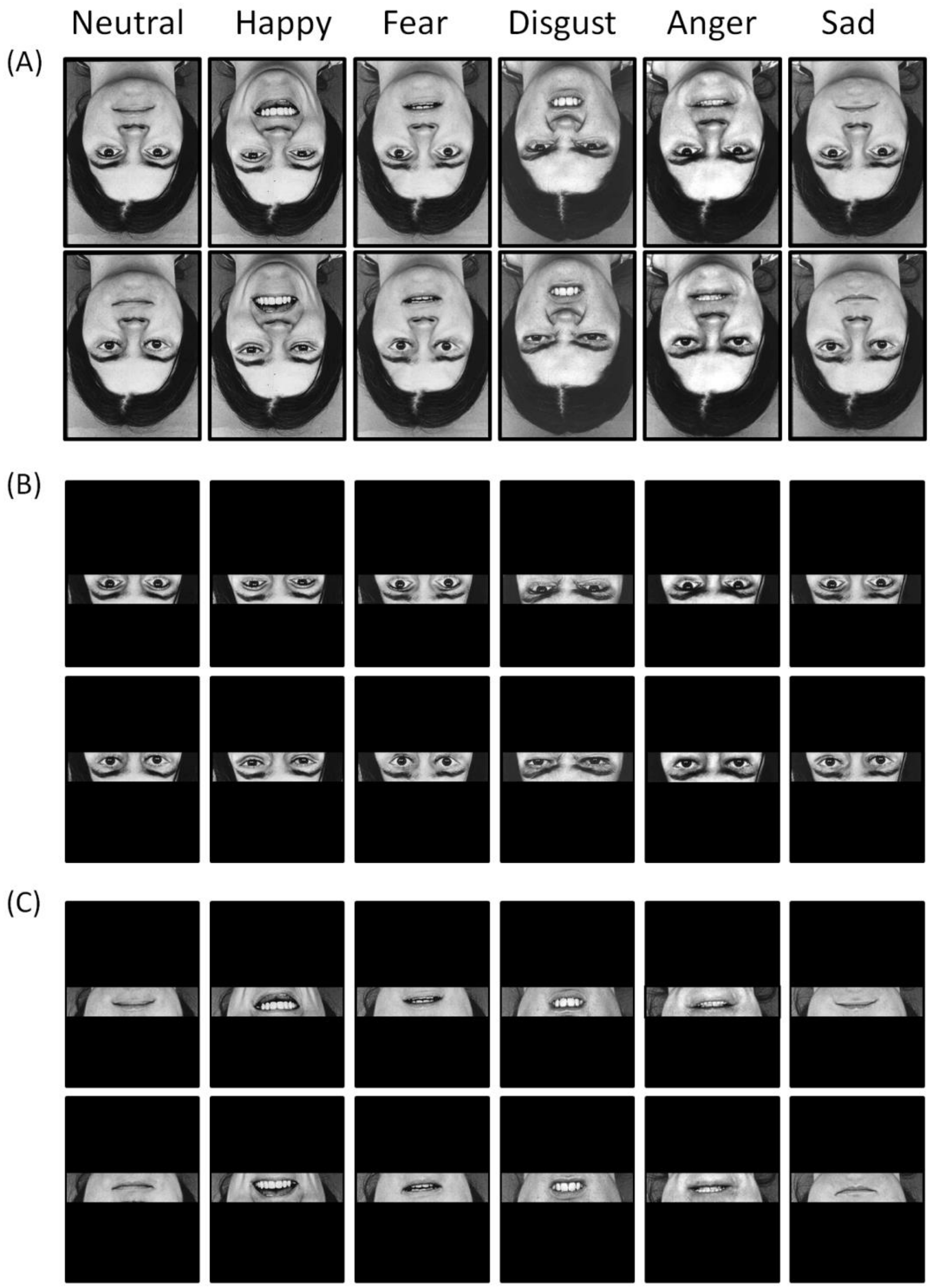

Figure 4.1: *Example images from Experiment 1 and Experiment 2. (A) Whole face images showing the 6 facial expressions of emotion: neutral, happy, fear, disgust, anger, sad (left to right). (B) and (C) show the corresponding images from the eye region and mouth region, respectively. Images were shown in a normal (top row) or thatcherized configuration (bottom row). Invert page for the upright view of images.*

4.1.4 Results

4.1.4.1 Experiment 1

Recognition Accuracy (whole face)

The aim of Experiment 1 was to determine the effect of inversion on the recognition of expression in normal and thatcherized whole faces. Figure 2 shows the recognition accuracy for each facial expression. A 3-way ANOVA with Expression (neutral, happy, fear, disgust, anger, sad), Condition (normal, thatcherized) and Orientation (upright, inverted) was performed on the data. This revealed a significant effect of Expression ($F_{5,55} = 16.8$, $p < 0.001$) and Condition ($F_{1,11} = 53.0$, $p < 0.001$). There was a non-significant trend for an effect of Orientation ($F_{1,11} = 4.5$, $p = .06$), but there was a significant interaction between Expression * Orientation ($F_{5,55} = 9.9$, $p < 0.001$). This suggests that inversion had a different effect on different emotional expressions. Finally, there was a significant interaction between Condition * Orientation ($F_{1,11} = 44.3$, $p < 0.001$). This suggests that inversion had a different effect on the recognition of expression in normal compared to thatcherized images. To determine how the perception of different facial expressions is affected by Orientation and Thatcherization, a 2 (Condition) x 2 (Orientation) ANOVA was performed independently for each expression.

For Neutral, there was a significant effect of Condition ($F_{1,11} = 30.3$, $p < 0.001$). The effect of Condition was due to lower recognition of *thatcherized* (72.7 ± 4.4) compared to *normal* (90.5 ± 2.5) faces. There was also an effect of Orientation ($F_{1,11} = 6.9$, $p < 0.05$) and a significant interaction between Condition * Orientation ($F_{1,11} = 7.3$, $p < 0.05$). This interaction is explained by no difference in recognition between *inverted* (88.5 ± 3.4) and *upright* (92.4 ± 1.5) *normal* faces ($t(11) = 0.15$, $p = .89$), but a higher recognition of *inverted* (84.4 ± 2.8) compared to *upright* (61.1 ± 5.9) *thatcherized* faces ($t(11) = 3.7$, $p < 0.01$). Finally, the recognition of *upright normal* faces was significantly higher than the recognition of *inverted thatcherized* faces ($t(11) = 2.7$, $p < 0.05$).

For Happy, there was a significant effect of Condition ($F_{1,11} = 25.8$, $p < 0.001$). The effect of Condition was due to lower recognition of *thatcherized* (63.3 ± 8.1) compared to *normal* (94.0 ± 4.3) faces. There was no significant effect Orientation ($F_{1,11} = 2.7$, $p = .13$), but there was a significant interaction between Condition * Orientation ($F_{1,11} = 6.5$, $p < 0.05$). This interaction is explained by no difference in recognition between *inverted* (91.7 ± 2.9) and *upright* (96.2 ± 1.4) *normal* faces ($t(11) = 1.6$, $p = .14$), but a higher recognition of *inverted* (76.9 ± 3.5) compared to *upright* (49.7 ± 12.7) *thatcherized* faces ($t(11) = 2.6$, $p < 0.05$). Finally, the recognition of *upright normal* faces was significantly higher than the recognition of *inverted thatcherized* faces ($t(11) = 6.3$, $p < 0.001$).

For Fear, there was a significant effect of Condition ($F_{1,11} = 10.8$, $p < 0.01$). The effect of Condition was due to lower recognition of *thatcherized* (67.0 ± 4.0) compared to *normal* (81.8 ± 4.5) faces. There was also an effect of Orientation ($F_{1,11} = 6.5$, $p < 0.05$) and a significant interaction between Condition * Orientation ($F_{1,11} = 23.2$, $p < 0.01$). This interaction is explained by no difference in recognition between *inverted* (80.6 ± 4.3) and *upright* (83.0 ± 4.7) *normal* faces ($t(11) = 1.1$, $p = .30$), but a higher recognition for *inverted* (81.9 ± 3.9) compared to *upright* (58.0 ± 4.4) *thatcherized* faces ($t(11) = 4.5$, $p < 0.001$). Finally, the recognition of *upright normal* faces was not significantly different from the recognition of *inverted thatcherized* faces ($t(11) = 0.9$, $p = .37$).

For Disgust, there was no significant effect of Condition ($F_{1,11} = 0.0$, $p = .96$) and Orientation ($F_{1,11} = 2.8$, $p = .12$). However, there was a significant interaction between Condition * Orientation ($F_{1,11} = 5.2$, $p < 0.05$). This interaction is explained by no difference in recognition between *inverted* (74.7 ± 3.5) and *upright* (73.6 ± 3.0) *thatcherized* faces ($t(11) = 0.4$, $p = .70$), but a higher recognition for *upright* (78.1 ± 3.6) compared to *inverted* (67.7 ± 4.7) *normal* faces ($t(11) = 2.6$, $p < 0.05$). Finally, the recognition of *upright normal* faces was not significantly different from the recognition of *inverted thatcherized* faces ($t(11) = 1.1$, $p = .29$).

For Anger, there was a significant effect of Condition ($F_{1,11} = 46.7$, $p < 0.001$). The effect of Condition was due to lower recognition of *thatcherized* (47.6 ± 4.6) compared to *normal* (65.6 ± 3.6) faces. There was also an effect of Orientation ($F_{1,11} = 15.8$, $p < 0.01$) and a significant interaction between Condition * Orientation ($F_{1,11} = 6.9$, $p < 0.05$). This interaction is explained by a lower recognition of *inverted* (53.1 ± 4.2) compared to *upright* (78.1 ± 2.8) *normal* faces ($t(11) = 5.9$, $p < 0.001$), but no difference in recognition for *inverted* (43.4 ± 3.1) compared to *upright* (51.7 ± 6.0) *thatcherized* faces ($t(11) = 1.4$, $p = .18$). Finally, the recognition of *upright normal* faces was significantly higher than the recognition of *inverted thatcherized* faces ($t(11) = 10.4$, $p < 0.001$).

For Sad, there was a significant effect of Condition ($F_{1,11} = 9.4$, $p < 0.01$). The effect of Condition was due to lower recognition of *thatcherized* (42.1 ± 6.3) compared to *normal* (52.3 ± 6.5) faces. There was also an effect of Orientation ($F_{1,11}$

= 45.0, $p < 0.001$). The effect of Orientation was due to higher recognition of *upright* (63.4 ± 7.4) compared to *inverted* faces (30.9 ± 5.4). There was no significant interaction between Condition * Orientation ($F_{1,11} = 2.1$, $p = .18$).

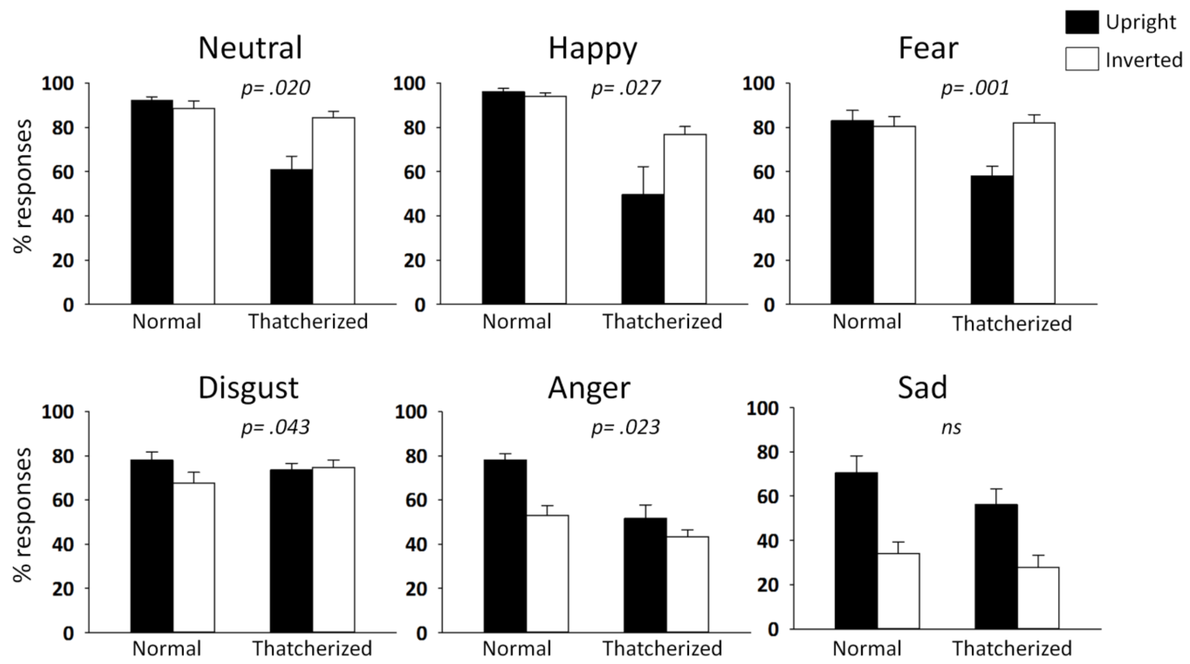

Figure 4.2: *Recognition of facial expression in the whole face. Normal and thatcherized images were presented in an upright or inverted orientation. There was a significant interaction between the orientation of the image and whether the image was normal or thatcherized. This effect was due to lower recognition of inverted compared to upright normal faces, but higher recognition of inverted compared to upright thatcherized faces. The p-values for the interaction are shown for each emotional expression. Error bars represent ± standard error across participants.*

To investigate the patterns of errors, a confusion matrix was generated (Figure 3). This shows how participants responded to different emotional expressions. The majority of responses were evident along the diagonal (correct). It is also interesting to note that the pattern of incorrect responses was not obviously different for normal or thatcherized images. For example, the correlation in correct performance between upright normal and inverted normal was $r = .94$ ($p < 0.001$). Similarly, the correlation in correct performance between upright normal and upright thatcherized was $r = .95$ ($p < 0.001$). Finally, the correlation between upright thatcherized and inverted thatcherized was $r = .91$ ($p < 0.001$). Together, this suggests that the effects of inversion and thatcherization reflect a lower number of correct responses rather than a different pattern of response.

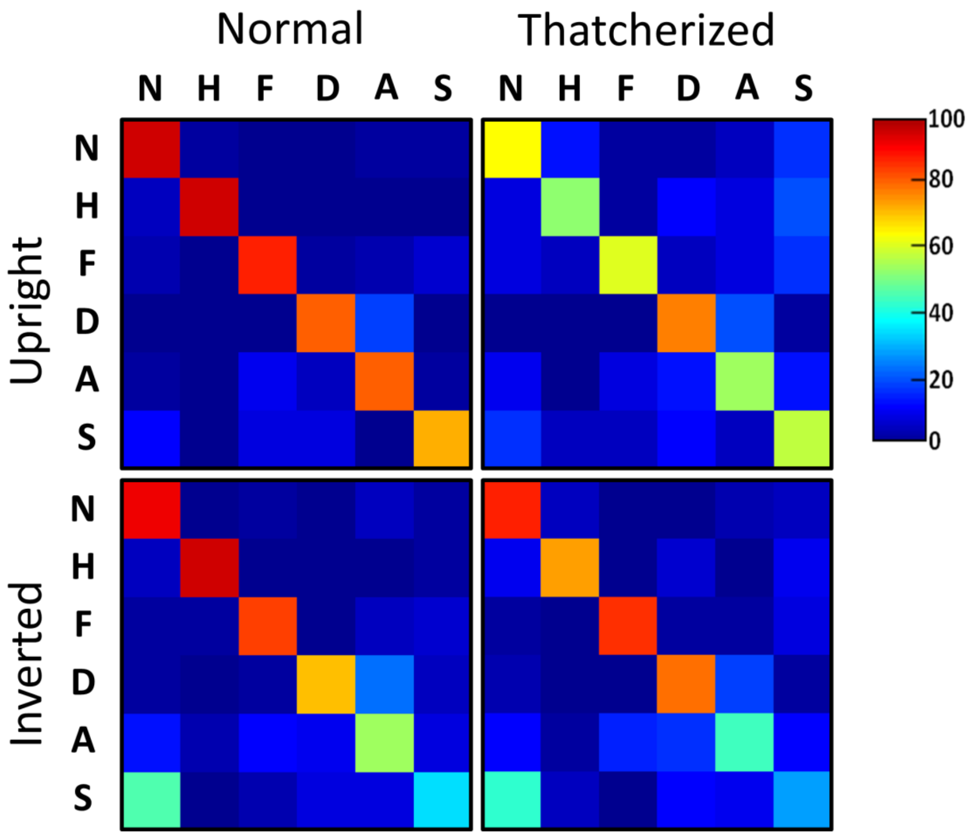

Figure 4.3: *Confusion matrices for the presented and perceived emotional expressions in whole faces. The y-axis represents the expression that was presented and the x-axis represents the expression that was reported. Correct performance is shown along the diagonal elements, whereas errors or confusion are shown on the off-diagonal elements. Colour bar represents accuracy in %.*

Reaction Time (whole face)

A 3-way ANOVA with Expression * Condition * Orientation was performed on the reaction time data in Experiment 1 (Table 1). There was an effect of Orientation ($F_{1,7}$ = 6.6, $p < 0.05$). This was due to lower RT to upright (1409 ± 85 ms) compared to inverted (1598 ± 99 ms) faces. There was a significant effect of Condition ($F_{1,7}$ = 16.1 $p < 0.01$). This was due to lower RT to normal (1456 ± 88 ms) compared to thatcherized (1551 ± 96 ms) faces. Finally, there was also an effect of Expression ($F_{5,35}$ = 7.5, $p < 0.001$). This was due to differences in RT across the different expressions (neutral: 1401 ± 157 ms, happy: 1401 ± 160, Fear: 1586 ± 151 ms, Disgust: 1443 ± 154 ms, Anger: 1624 ± 159 ms, Sad: 1568 ± 175 ms). There was a significant interaction between Condition * Expression ($F_{5,35}$ = 2.6, $p < 0.05$), but no significant interaction of Expression * Orientation ($F_{5,35}$ = 0.7, p = .61) and no significant interaction between Expression * Condition * Orientation ($F_{5,35}$ = 0.8, p = .44).

Table 4.2: *Average reaction time values for correct responses to emotional expression to the whole face in Experiment 1.*

	Normal		Thatcherized	
	Upright	Inverted	Upright	Inverted
Neutral	1257.2 ± 269.3	1470.6 ± 374.4	1401.7 ± 263.2	1475.0 ± 346.5
Happy	1219.0 ± 283.4	1427.2 ± 299.3	1430.4 ± 227.4	1527.3 ± 468.0
Fear	1477.8 ± 305.8	1662.61 ±	1544.9 ± 302.4	1659.7 ± 278.9
Disgust	1344.6 ± 333.6	1572.4 ± 289.2	1308.8 ± 299.6	1545.3 ± 309.0
Anger	1430.4 ± 298.6	1658.0 ± 315.2	1642.8 ± 357.9	1764.5 ± 299.0
Sad	1388.4 ± 281.7	1568.8 ± 282.1	1473.4 ± 298.9	1842.4 ± 533.8

4.1.4.2 Experiment 2

The aim of Experiment 2 was to determine the effect of inversion on the recognition of facial expressions in normal and thatcherized faces when only the eye or mouth region was shown.

Recognition Accuracy (eye region)

Figure 4 shows the % correct recognition for each facial expression in the eye region. To determine the effect of inversion and thatcherization, we performed a 3 way ANOVA with Expression (neutral, happy, fear, disgust, anger, sad), Condition (normal, thatcherized) and Orientation (upright, inverted). There was a significant effect of Expression ($F_{5,95}$ = 55.3, p < 0.001), a significant effect of Condition ($F_{1,19}$ = 74.8, p < 0.001) and a significant effect of Orientation ($F_{1,19}$ = 135.6, p < 0.001). There was also a significant Condition * Orientation interaction ($F_{1,19}$ = 91.9, p < 0.001). This suggests that inversion has a different effect on the recognition of facial expression in normal and thatcherized faces. There was also a significant interaction of Expression * Condition interaction ($F_{5,95}$ = 7.6, p < 0.001) and Expression * Orientation ($F_{5,95}$ = 26.8, p < 0.001). The interaction between Expression * Condition * Orientation was also significant ($F_{5,95}$ = 28.9, p < 0.001). To determine how the perception of different facial expressions is affected by Orientation and Thatcherization, a 2 (Condition) * 2 (Orientation) ANOVA was performed independently for each expression.

For Neutral, there was a significant effect of Condition ($F_{1,19}$ = 36.9, p < 0.001). The effect of Condition was due to lower recognition of *thatcherized* (34.7 ± 4.7) compared to *normal* (54.6 ± 44) faces. There was also an effect of Orientation

($F_{1,19}$ = 14.9, $p < 0.001$) and a significant interaction between Condition * Orientation ($F_{1,19}$ = 111.9, $p < 0.001$). This interaction is explained by lower recognition of *inverted* (32.8 ± 4.1) compared to *upright* (76.4 ± 4.7) *normal* images ($t(19) = 9.5$, $p < 0.001$), but higher recognition of *inverted* (47.5 ± 4.6) compared to *upright* (21.9 ± 4.8) *thatcherized* images ($t(19) = 5.1$, $p < 0.001$). Finally, the recognition of *upright normal* faces was significantly higher than the recognition of *inverted thatcherized* faces ($t(19) = 6.0$, $p < 0.001$).

For Happy, there was a significant effect of Condition ($F_{1,19}$ = 40.7, $p < 0.001$) and Orientation ($F_{1,19}$ = 61.6, $p < 0.001$). The effect of Condition was due to lower recognition of *thatcherized* (31.3 ± 6.4) compared to *normal* (47.4 ± 4.9) images. The effect of Orientation was due to an increased recognition of *upright* (52.9 ± 5.4) compared to *inverted* (25.7 ± 5.9) images. There was no significant interaction between Condition * Orientation ($F_{1,19}$ = 1.3, p = .26).

For Fear, there was a significant effect of Condition ($F_{1,19}$ = 27.1, $p < 0.001$). The effect of Condition was due to lower recognition of *thatcherized* (66.0 ± 4.1) compared to *normal* (82.4 ± 3.5) faces. There was also an effect of Orientation ($F_{1,19}$ = 9.5, $p < 0.01$) and a significant interaction between Condition * Orientation ($F_{1,19}$ = 95.8, $p < 0.001$). This interaction is explained by the lower recognition of *inverted* (76.1 ± 4.4) compared to *upright* (88.6 ± 2.6) *normal* images ($t(19) = 3.0$, $p < 0.01$), but higher recognition for *inverted* (82.5 ± 3.7) compared to *upright* (48.6 ± 4.5) *thatcherized* images ($t(19) = 5.9$, $p < 0.001$). Finally, the recognition of *upright normal* faces was not significantly different from the recognition of *inverted thatcherized* faces ($t(19) = 1.7$, p = .11).

For Disgust, there was no significant effect of Condition ($F_{1,19} = 0.3$, $p = .60$) or Orientation ($F_{1,19} = 0.6$, $p = .45$). There was also no significant interaction between Condition * Orientation ($F_{1,19} = 0.71$, $p = .41$).

For Anger, there was a significant effect of Orientation ($F_{1,19} = 60.2$, $p < 0.001$). The effect of Orientation was due to an increased recognition of *upright* (79.1 ± 3.8) compared to *inverted* (46.8 ± 4.0) images. There was no effect of Condition ($F_{1,19} = 2.6$, $p = .13$) and no significant interaction between Condition * Orientation ($F_{1,19} = 3.7$, $p = .07$).

For Sad, there was a significant effect of Condition ($F_{1,19} = 5.3$, $p < 0.05$) and Orientation ($F_{1,19} = 153.3$, $p < 0.001$). The effect of Condition was due to higher recognition of *normal* (40.4 ± 3.8) compared to *thatcherized* images (34.2 ± 3.6). The effect of Orientation was due to higher recognition in *upright* (58.8 ± 4.2) compared to *inverted* (15.8 ± 3.2) images. However, there was no significant interaction between Condition * Orientation ($F_{1,19} = 0.9$, $p = .35$).

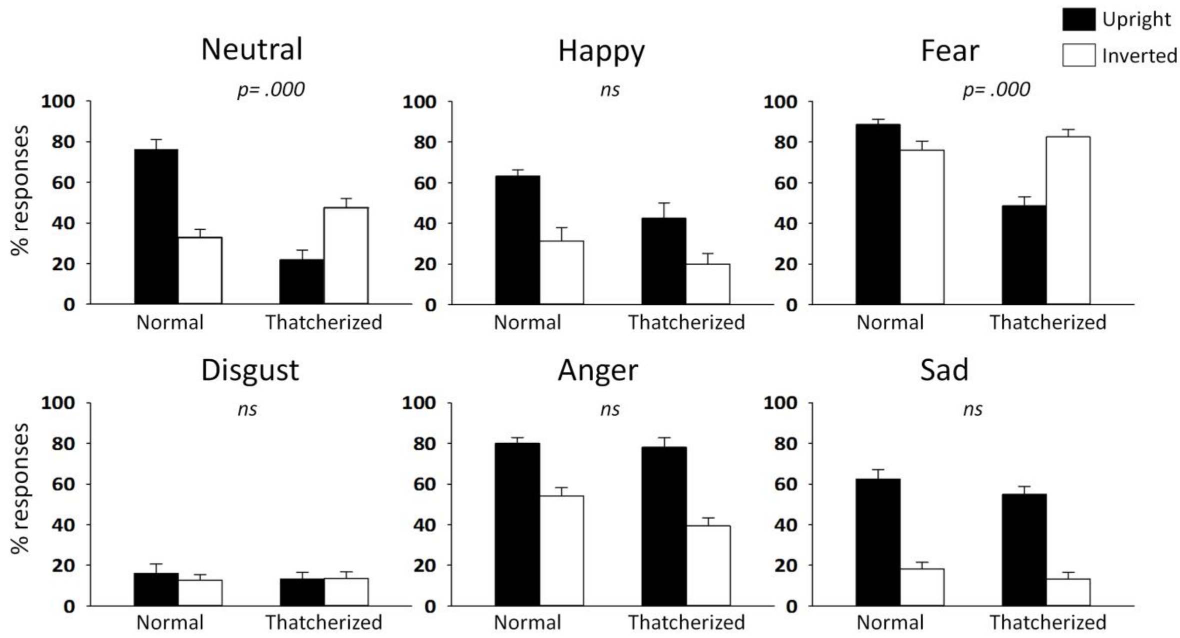

Figure 4.4: *Recognition of facial expression in the eye region. Normal and thatcherized images were presented in an upright or inverted orientation. There was a significant interaction between the orientation of the image and whether the image was normal or thatcherized. This effect was due to lower recognition of inverted compared to upright normal faces, but higher recognition of inverted compared to upright thatcherized faces. The p-values for the interactions are shown for each emotional expression. Error bars represent ± standard error across participants.*

To investigate the patterns of errors, a confusion matrix was generated (Figure 5). This shows how participants responded to different emotional expressions. The pattern of incorrect responses was not obviously different for normal or thatcherized images. Rather, it appears that thatcherized and inverted images had a lower number of correct responses. For example, the correlation in correct performance between upright normal and inverted normal was $r = .80$ ($p < 0.001$). Similarly, the correlation in correct performance between upright normal and upright thatcherized was $r = .80$ ($p < 0.001$). Finally, the correlation between upright thatcherized and inverted thatcherized was r = .64 ($p < 0.001$). Together, this suggests that the effects of inversion and thatcherization reflect a lower number of correct responses rather than a different pattern of response.

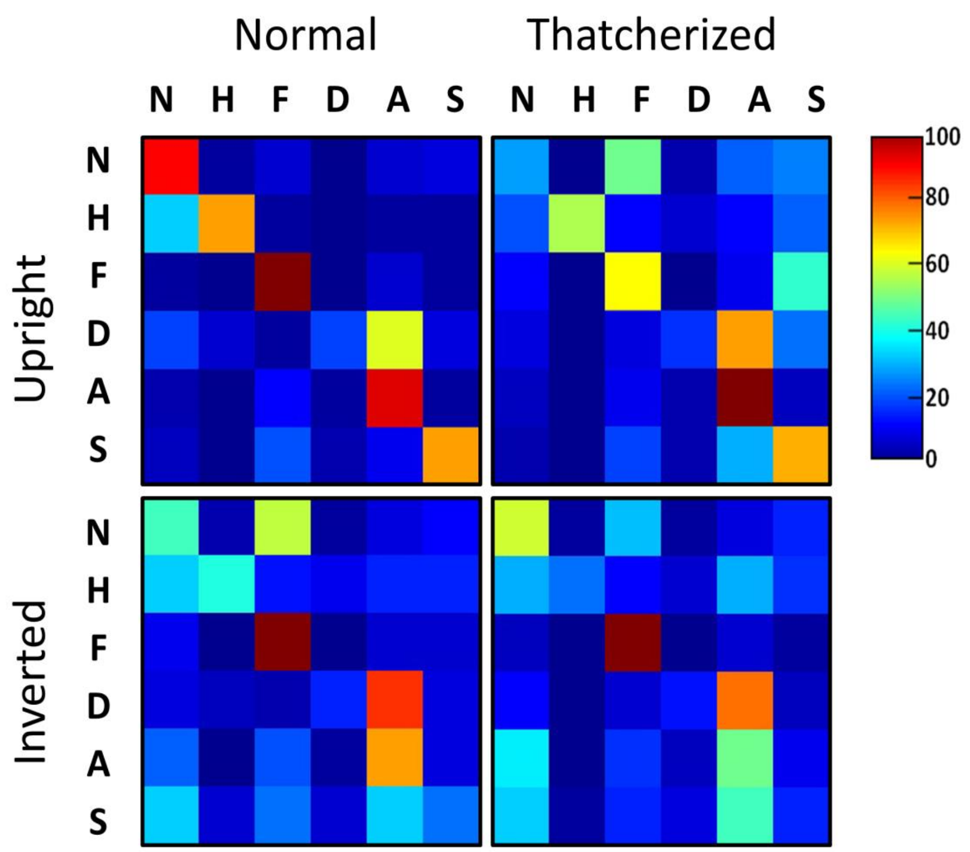

Figure 4.5: *Confusion matrices for the presented and perceived emotional expressions in the eye region. The y-axis represents the expression that was presented and the x-axis represents the expression that was reported. Correct performance is shown along the diagonal elements, whereas errors or confusion are shown on the off-diagonal elements. Colour bar represents accuracy in %.*

Reaction Time (eye region)

A 3 way ANOVA with Expression (neutral, happy, fear, disgust, anger, sad), Condition (normal, thatcherized) and Orientation (upright, inverted) was performed on the reaction times to the eye region in Experiment 2 (Table 2). There was a significant effect of Condition ($F_{1,2}$ = 31.7, $p < 0.05$). This was due to lower RT for normal (1403 ± 25 ms) compared to thatcherized (1510 ± 28 ms) faces. There was no significant effect of Expression ($F_{5,10}$ = 1.4, p = .30) or Orientation ($F_{1,2}$ = 1.8, p = .31). There was also no significant interaction of Condition * Orientation ($F_{1,2}$ = 0.7, p = .50), Expression * Condition ($F_{5,10}$ = 1.3, p = .32) or Expression * Orientation ($F_{5,10}$ = 1.4, p = .31). The interaction between Expression * Condition * Orientation was also not significant ($F_{5,10}$ = 2.5, p = .11).

Table 4.3: *Average reaction time values for correct responses to emotional expression when only the eye region of the face was visible in Experiment 2.*

	Normal		Thatcherized	
	Upright	Inverted	Upright	Inverted
Neutral	1166.1 ± 64.6	1462.8 ± 100.8	1666.4 ± 159.6	1526.2 ± 80.3
Happy	1247.9 ± 78.6	1463.1 ± 115.5	1335.9 ± 66.5	1488.5 ± 106.1
Fear	1281.7 ± 82.4	1336.2 ± 97.6	1600.7 ± 120.0	1373.9 ± 95.7
Disgust	1769.9 ± 89.8	1807.8 ± 139.9	1500.0 ± 52.2	1820.7 ± 119.5
Anger	1110.7 ± 47.0	1316.7 ± 59.5	1227.2 ± 61.6	1626.1 ± 99.1
Sad	1331.8 ± 52.0	1546.0 ±	1284.7 ± 58.8	1672.5 ± 157.4

Recognition Accuracy (mouth region)

Figure 6 shows the % correct recognition for each facial expression in the mouth region. To determine the effect of inversion and thatcherization on recognition of facial expressions, we performed a 3 way ANOVA with Expression (neutral, happy, fear, disgust, anger, sad), Condition (normal, thatcherized) and Orientation (upright, inverted). There were significant effects of Expression ($F_{5,95}$ = 86.4, $p < 0.001$), Condition ($F_{1,19}$ = 98.1, $p < 0.001$) and Orientation ($F_{1,19}$ = 11.1, $p < 0.01$). There was a significant interaction of Condition * Orientation ($F_{1,19}$ = 68.4, $p < 0.001$). This suggests that inversion has a different effect on the recognition of facial expression in normal and thatcherized faces. There was also a significant interaction between Expression * Condition ($F_{5,95} = 29.0$, $p < 0.001$), Expression * Orientation ($F_{5,95} = 5.1$, $p < 0.01$). To determine how the perception of different facial expressions is affected by Orientation and Condition, a 2 * 2 ANOVA was performed independently for each expression.

For neutral, there was no effect of Condition ($F_{1,19} = 0.1$, $p = .33$) or Orientation ($F_{1,19} = 0.6$, $p = .45$). However, there was a significant interaction between Condition * Orientation ($F_{1,19} = 9.1$, $p < 0.01$). The significant interaction is explained by no difference in recognition between *inverted* (84.7 ± 3.3) and *upright* (86.1 ± 3.6) *normal* faces ($t(19) = 0.9$, $p = .38$), but a higher recognition of *inverted* (88.3 ± 2.8) compared to *upright* (79.4 ± 4.9) *thatcherized* faces ($t(19) = 2.3$, $p < 0.05$). Finally, the recognition of *upright normal* faces was not significantly different from the recognition of *inverted thatcherized* faces ($t(19) = -1.6$, $p = .88$).

For happy, there was a significant effect of Condition ($F_{1,19} = 63.1$, $p < 0.001$). The effect of Condition was due to lower recognition of *thatcherized* (54.4 ± 7.0) compared to *normal* (84.2 ± 3.0) faces. There was also an effect of Orientation ($F_{1,19} = 0.4$, $p = .56$) and a significant interaction between Condition * Orientation ($F_{1,19} = 19.9$, $p < 0.001$). This interaction was due to lower recognition of *inverted* (77.5 ± 3.8) compared to *upright* (90.8 ± 2.2) *normal* faces ($t(19) = 3.6$, $p < 0.01$), but higher recognition of *inverted* (71.3 ± 2.7) compared to *upright* (37.5 ± 11.2) *thatcherized* images ($t(19) = 2.3$, $p < 0.05$). Finally, the recognition of *upright normal* faces was significantly higher than the recognition of *inverted thatcherized* faces ($t(19) = 6.3$, $p < 0.001$).

For fear, there was no significant effect of Condition ($F_{1,19} = 2.5$, $p = .13$) or Orientation ($F_{1,19} = 1.5$, $p = .24$). There was also no significant interaction between Condition * Orientation ($F_{1,19} = 3.7$, $p = .07$).

For disgust, there was no significant effect of Condition ($F_{1,19} = 3.6$, $p = .07$). However, there was a significant effect of Orientation ($F_{1,19} = 20.5$, $p < 0.001$) and a significant interaction between Condition * Orientation ($F_{1,19} = 52.8$, $p < 0.001$). This interaction was due to lower recognition of *inverted* (43.3 ± 4.2) compared to *upright* (71.1 ± 3.7) *normal* images ($t(19) = 7.7$, $p < 0.001$), but no significant difference in recognition between *inverted* (54.7 ± 4.8) and *upright* (53.9 ± 4.8) *thatcherized* images ($t(19) = 1.8$, $p = .08$). Finally, the recognition of *upright normal* faces was significantly higher than the recognition of *inverted thatcherized* faces ($t(19) = 4.2$, $p < 0.001$).

For anger, there was a significant effect of Condition ($F_{1,19} = 8.7$, $p < 0.01$). The effect of Condition was due to lower recognition of *thatcherized* (18.4 ± 4.2) compared to *normal* (23.6 ± 4.7) faces. There was also an effect of Orientation ($F_{1,19} = 7.7$, $p < 0.05$) and a significant interaction between Condition * Orientation ($F_{1,19} = 10.4$, p < 0.01). This interaction was due to lower recognition of *inverted* (16.1 ± 3.9) compared to *upright* (31.1 ± 5.5) *normal* images ($t(19) = 3.5$, $p < 0.01$), but no difference in recognition of inverted (21.1 ± 3.9) compared to *upright* (15.6 ± 4.4) *thatcherized* images ($t(19) = 1.9$, $p = .07$). Finally, the recognition of *upright normal* faces was significantly higher than the recognition of *inverted thatcherized* faces ($t(19) = 3.4$, $p < 0.05$).

For sad, there was no significant effect of Condition ($F_{1,19}$ = 0.9, p = .35), but there was a significant effect of Orientation ($F_{1,19}$ = 20.8, p < 0.001). The effect of Orientation was due to lower recognition of *inverted* (8.4 ± 3.0) compared to *upright* (21.4 ± 4.7) images. There was no significant interaction between Condition * Orientation ($F_{1,19}$ = 1.0, p = .32).

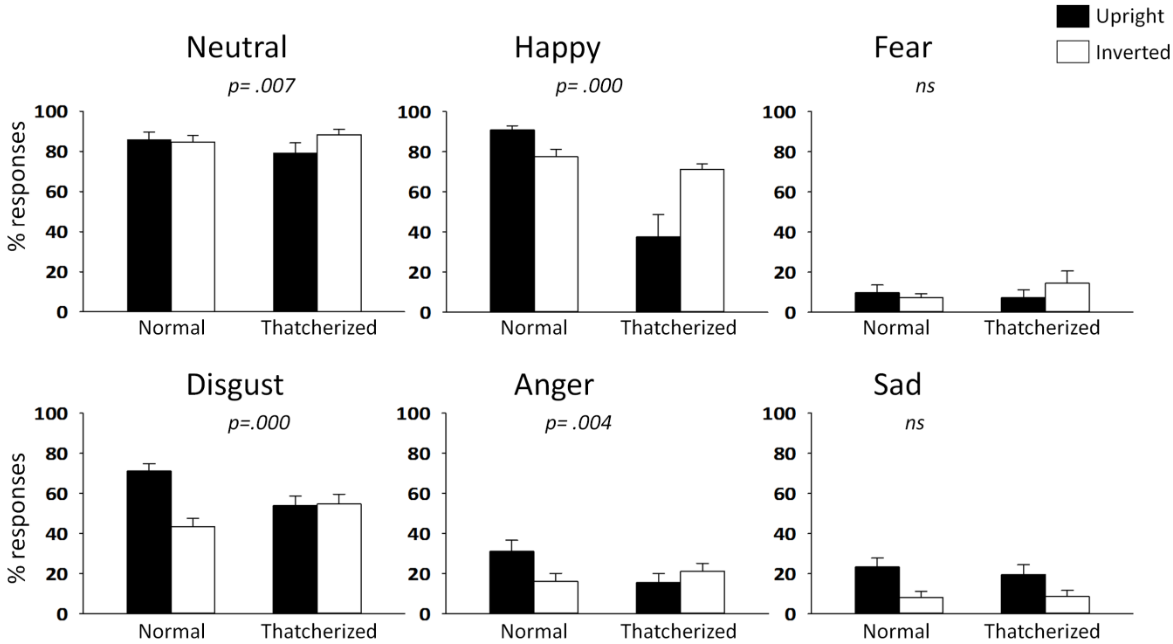

Figure 4.6: *Recognition of facial expression in the mouth region. Normal and thatcherized images were presented in an upright or inverted orientation. There was a significant interaction between the orientation of the image and whether the image was normal or thatcherized. This effect was due to lower recognition of inverted compared to upright normal faces, but higher recognition of inverted compared to upright thatcherized faces. The p-values for the interactions are shown for each emotional expression. Error bars represent ± standard error across participants.*

To investigate the patterns of errors, a confusion matrix was generated (Figure 5). This shows how participants responded to different emotional expressions. The pattern of incorrect responses was not obviously different for normal or thatcherized images. Rather, it appears that thatcherized and inverted images had a lower number of correct responses. For example, the correlation in correct performance between upright normal and inverted normal was $r = .92$ ($p < 0.001$). Similarly, the correlation in correct performance between upright normal and upright thatcherized was $r = .89$ ($p < 0.001$). Finally, the correlation between upright thatcherized and inverted thatcherized was $r = .92$ ($p < 0.001$). Together, this suggests that the effects of inversion and thatcherization reflect a lower number of correct responses rather than a different pattern of response.

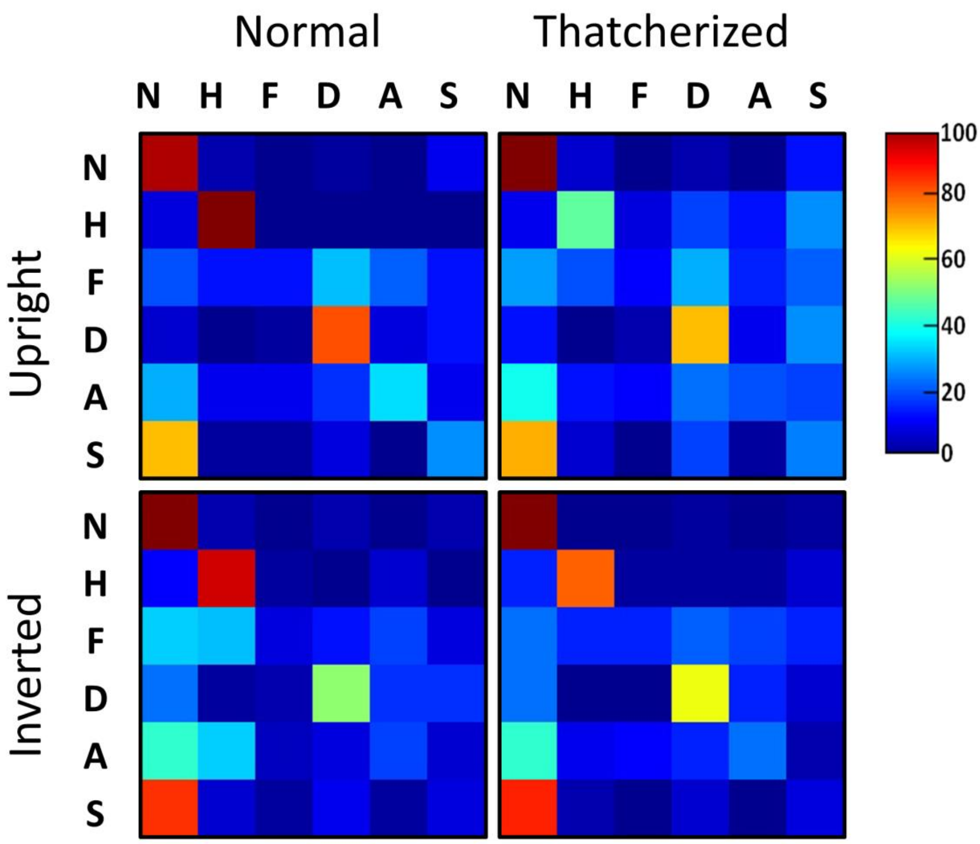

Figure 4.7: *Confusion matrices for the presented and perceived emotional expressions in the mouth region. The y-axis represents the expression that was presented and the x-axis represents the expression that was reported. Correct performance is shown along the diagonal elements, whereas errors or confusion are shown on the off-diagonal elements. Colour bar represents accuracy in %.*

Reaction Time (mouth region)

A 3 way ANOVA with Expression (neutral, happy, fear, disgust, anger, sad), Condition (normal, thatcherized) and Orientation (upright, inverted) was performed on the reaction time data from the mouth region in Experiment 2 (Table 3). There was a significant effect of Orientation ($F_{1,9}$ = 27.3, p < 0.001). This was due to lower RT for upright (1258 ± 24 ms) compared to inverted (1583 ± 39 ms) faces. There was an effect of Expression ($F_{5,45}$ = 13.8, p < 0.001). This was due to differences in RT across different expressions (neutral: 1049 ± 37 ms, happy: 1153 ± 37, Fear: 1731 ± 65 ms, Disgust: 1284 ± 41 ms, Anger: 1715 ± 71 ms, Sad: 1591 ± 73 ms). There was not any significant effect of Condition ($F_{1,9}$ = 1.8, p = .21). There was also no significant interaction of Condition * Orientation ($F_{1,9}$ = 4.6, p = .06), Expression * Condition ($F_{5,45}$ = 1.3, p = .30) or Expression * Orientation ($F_{5,45}$ = 3.0, p = .07). The interaction between Expression * Condition * Orientation was also not significant ($F_{5,45}$ = 2.9, p = .11).

Table 4.4: *Average reaction time values for correct responses to emotional expression when only the mouth region of the face was visible in Experiment 2.*

	Normal		Thatcherized	
	Upright	Inverted	Upright	Inverted
Neutral	922.1 ± 52.8	1084.0 ± 71.9	1017.6 ± 45.8	1171.6 ± 123.9
Happy	999.2 ± 42.2	1209.4 ± 92.3	1125.7 ± 66.2	1276.1 ± 96.1
Fear	1750.2 ± 124.6	1897.0 ± 132.9	1291.4 ± 90.4	1985.4 ± 172.1
Disgust	1057.3 ± 49.5	1299.0 ± 62.4	1288.1 ± 95.9	1492.7 ± 119.8
Anger	1513.5 ± 102.2	1977.6 ± 190.6	1525.8 ± 128.4	1842.6 ± 143.2
Sad	1280.5 ± 119.4	1771.2 ± 194.5	1320.9 ± 70.9	1989.7 ± 202.9

2.1.5 Discussion

The aim of this experiment was to determine the effect of inversion on the recognition of normal and thatcherized facial expressions. Inversion of normal faces reduced the recognition of some facial expressions (disgust, anger, sad), but had no effect on the recognition of other expressions (neutral, happy, fear). In contrast, thatcherization of faces reduced the recognition of all expressions. However, in contrast to normal faces, there was a benefit of inversion for the majority of thatcherized expressions; for some expressions (neutral, happy, fear), there was an improved recognition, whereas for other expressions (disgust, anger) there was an attenuation of the inversion effect found in normal faces. A similar pattern of results was found when only the eyes or mouth was visible. This suggests that a disruption to configural processing does not explain the Thatcher illusion.

A variety of behavioural evidence has shown that the perception of facial identity is affected by the inversion of the image (Rossion and Boremanse, 2008; Valentine, 1988; Tanaka and Farah, 1993; Tanaka and Farah, 1991; Yin, 1969). In contrast, studies of facial expression have only reported small effects of inversion, with the recognition of some emotions being completely unaffected (Calvo and Nummenmaa, 2008; PrKachin, 2003; Birgit, Seidel, Kainz and Carbon, 2009; McKelvie, 1995; Fallshore and Bartholow, 2003). Our results showed that inversion affected the recognition of some facial expressions (disgust, anger, sad), but it had no significant effect on the recognition of other expressions (neutral, happy, fear). The dissociation in the effect of inversion on identity and expression suggests that different representations underpin these aspects of face processing. This is consistent with a variety of evidence that suggests these facial attributes are processed along parallel processing streams (Haxby, Hoffman and Gobbini, 2000; Young and Bruce, 2011; Bruce and Young, 2012; Harris, Young and Andrews, 2014).

In contrast to inversion of the whole face, the local inversion of facial features in a thatcherized face had a marked effect on the recognition of all facial expressions. Given the effect of inversion on normal faces, the prediction was that there should be some reduction in the recognition of facial expressions in inverted Thatcherized faces. In contrast, we found that there was a benefit of inversion for thatcherized faces in five of the six expressions. For expressions that showed no effect of inversion in normal faces (neutral, happy, fear), there was an increased recognition of inverted compared to upright thatcherized faces. On the other hand, expressions in which there was a reduction in recognition following inversion (disgust, anger) showed no inversion effect for thatcherized faces.

So, what explains the different effect of inversion on normal and thatcherized faces? One possible explanation is that the orientation of the eyes and mouth in an inverted, thatcherized face is in the correct orientation. So, if the recognition of facial expression is based solely on the orientation of the expressive features of the face, then the features may be more recognizable in the typical orientation. However, this explanation would predict that the recognition of expression in inverted thatcherized images should be equivalent to upright normal faces. The results show that recognition of facial expression in inverted, thatcherized faces is typically lower than upright, normal faces.

Another possible explanation for the improved recognition of facial expression in inverted thatcherized faces could be the way that facial expression is encoded. A variety of evidence suggests that the perception of facial expression can be based on either a continuous (Woodworth & Schlosberg, 1954; Russell & Bullock, 1985) or a categorical (Darwin, 1998; Ekman, 1972) representation. In a recent study, we provided a neural explanation for these findings by showing that a face-selective region in the superior temporal sulcus (STS) had a continuous representation of facial expression, whereas the face-selective region of the amygdala had a more categorical representation of facial expression (Harris, Young and Andrews, 2012). It is possible, therefore, that these representations may be differentially affected by inversion. We provided partial support for this possibility in a recent study in which we showed that STS was sensitive to the orientation of thatcherized faces (Psalta, Young, Thompson and Andrews, 2014). In contrast, the categorical representation of expression in regions such as the amygdala may have a coarser scale that is less sensitive to orientation (Vuilleumier, Armony, Driver and Dolan, 2003). For example, an increase in contrast in the mouth region could indicate happiness, whereas an increase in contrast in the eye region could indicate fear. Differences in the effect of inversion on each expression may reflect differential sensitivity of the key visual information that is diagnostic of these different facial expressions. From this perspective, the reduced recognition of facial expression in upright thatcherized faces could result from interference between different neural representations of facial expression. When the faces are inverted the orientation-sensitive representation that gives rise to the grotesque expression is attenuated, but the categorization of the facial expression continues to be processed since it is less orientation-sensitive.

The effect of inversion on the perception of facial expression seen in the Thatcher illusion is widely attributed to disruption of configural processing (Bartlett and Searcy, 1993; Rhodes, Brake and Atkinson, 1993; Lewis and Johnston, 1997; Leder, Candrian, Huber and Bruce, 2001; Boutsen and Humphreys, 2003; Boutsen, Humphreys, Praamstra and Warbrick, 2006). To address whether the effects that we have observed could also be explained by the configural properties of the face, we repeated the experiment with only the mouth region or the eye region visible. If the pattern of results can be explained by configural processing, we would expect that they would be abolished when only the isolated features are visible and there is no configural information. However, we found a similar interaction between the effect of inversion on normal and thatcherized images. When only the eye region was shown, there was a significant interaction between the effect of thatcherization and the effect of inversion for two expressions (neutral and fear). This interaction occurred because inversion of neutral or fear faces resulted in a reduction in the recognition of normal faces, but an increased recognition of thatcherized faces. When only the mouth region was shown, there was a significant interaction between the effect of thatcherization and inversion on three expressions (neutral, happy, disgust). Inversion resulted in a reduction in recognition in normal happy faces, but an increased recognition in thatcherized happy faces. Inversion had no effect on normal neutral faces, but increased recognition of thatcherized neutral faces. Finally, inversion had a significant reduction on the recognition of normal disgust faces, but had no effect on the recognition of thatcherized disgust faces. The differences in which expressions showed an interaction between orientation and thatcherization for the eye and mouth region reflect the relative importance of these regions for different expressions. Indeed, overall recognition of facial expressions also varied as a function of facial feature. For example, the recognition of fear was more accurately recognized from the eye region, whereas disgust and happy were more easily recognized from the mouth region.

Our findings are consistent with recent studies showing a lack of evidence for configural processing of upright thatcherized faces, as defined by RT-based (Donnelly, Cornes and Menneer, 2012) and accuracy-based (Mestry, Menneer, Wenger and Donnelly, 2012) measures. In Experiment 2, the only cue to the orientation of the face was the jaw line for the mouth region and the eyebrows or the bridge of the nose for the eye region. Nevertheless, it appears that these cues are sufficient to signal the critical orientation cues that influence our perception of the facial features. The presence of interactions between orientation and thatcherization when only the eye or mouth regions were shown suggests that inversion is disrupting the local coding of the expressive features of the face. The findings suggest that low-level image discrimination of faces can be influenced by the context in which the face is perceived. This fits with a recent study that demonstrated how the global properties of natural images (including faces) can influence low-level feature detectors (Neri, 2011; 2014). It is possible that the inability to detect image differences may reflect changes to the feedback from higher to lower visual regions.

In conclusion, we show that the perception of facial effect of inversion on normal faces differs for each expression. There was a significant effect of inversion on some expressions, but little or no effect on the recognition of other expressions. In contrast to inversion, thatcherization of images significantly reduced recognition across all emotional expressions. Interestingly, however, we found that inverting thatcherized images actually improved recognition of some facial expressions. We suggest that this paradoxical improvement in face perception with inversion may provide insights into the way that different visual information is represented for the processing of different aspects of face perception.

Chapter 5

5.1 THE THATCHER ILLUSION IS NOT RESTRICTED TO GROTESQUE EXPRESSIONS

5.1.1 Abstract

The aim of this chapter was to determine whether the marked effect of inversion in the Thatcher illusion is specific to grotesque expressions. To address this question, composite images were generated by transposing the mouth and eyes from one face onto another face. This generated pairs of images posing the same facial expression, but with different facial features. Next, we used a matching task, in which participants were asked to report whether two simultaneously presented whole face images were identical or different. We found that participants were able to discriminate original and composite versions of the same face when they were presented in an upright configuration. However, when the images were inverted the ability to discriminate between images was significantly reduced. These results suggest that the effect of inversion found in the Thatcher illusion is not specific to grotesque expressions, but reflects a more general orientation-specific encoding of expressive features.

5.1.2 Introduction

Our ability to perceive and recognize a face is impaired when it is inverted (Yin, 1969). The Thatcher Illusion provides a compelling example of the effect of inversion on face perception (Thompson, 1980). In this illusion, a local inversion of the eyes and mouth cause a face to look grotesque. However, when the thatcherized face is inverted, the image no longer looks grotesque. Despite this clear effect of inversion on the perception of faces, the precise cognitive mechanisms that underpin the Thatcher illusion remain unclear (Bartlett and Searcy, 1993; Valentine, 1988; Murray, Yong and Rhodes, 2000; Talati, Rhodes and Jeffery, 2010).

In contrast to the Thatcher illusion, there appears to be a much smaller effect of inversion on the recognition of normal facial expressions (Calvo and Nummenmaa, 2008; PrKachin, 2003; Birgit, Seidel, Kainz and Carbon, 2009; McKelvie, 1995; Fallshore and Bartholow, 2003). Indeed, a number of studies have shown that the recognition of some expressions, particularly positive emotions, are not affected by inversion (McKelvie, 1995; PrKachin, 2003; Calvo and Nummenmaa, 2008, Fallshore and Bartholow, 2003).

The difference in the effect of inversion on the perception of thatcherized and normal facial expressions may reflect differences in the task. The Thatcher illusion involves an inability to discriminate between a normal and a thatcherized image on a matching task (Thompson, 1980; Lewis and Johnston, 1997; Bartlett and Searcy, 1993; Murray, Yong and Rhodes, 2000; Rotshtein, Malach, Hadar, Graif and Hendler, 2001; Maurer, Le Grand and Mondloch, 2002). In contrast, studies of recognition involve matching each image to an internal representation of different facial expressions (McKelvie, 1995; Fallshore and Bartholow, 2003; PrKachin, 2003). So, it remains unclear whether a similar effect of inversion would be apparent for normal facial expressions if matching task was used.

The aim of this study was to determine whether the inversion effect shown by the Thatcher illusion is specific to grotesque expressions or whether it is also apparent for normal expressions. To address this question, composite face images were generated by replacing the mouth and eyes from one face image with the same features from a different face. Participants were asked to discriminate between face images in the upright and inverted orientation. If the Thatcher illusion is specific to grotesque expressions, then we would expect that the ability to discriminate between original and composite versions of the same face will not be affected by inversion. However, if the Thatcher illusion reflects a more general orientation-specific encoding of expressive features, then we would expect inversion to have a significant effect.

5.1.3 Materials and Methods

5.1.3.1 Participants

Twenty eight participants took part in the study (18 Female; mean age 19.94, ± 1.4). The study was approved and conducted following the guidelines of the Ethics committee at the University of York, Psychology Departments. Participants were students from the University of York who had normal or corrected to normal vision. The participants viewed the monitor at a distance of approximately 57 cm.

5.1.3.2 Stimuli

Face stimuli were selected from the Facial Expressions of Emotion Stimuli and Tests (FEEST) set (Young, Perrett, Calder, Sprengelmeyer and Ekman, 2002). There were four individuals posing six expressions (neutral, happy, fear, disgust, anger, sad). Composite images were generated using image editing software. Composite images were generated by replacing the eyes and mouth from one image with the same features from a different face (Figure 1). The features that were replaced were always posing the same expression.

5.1.3.3 Procedure

Participants were presented simultaneously with two whole face images (7 x 11^{o}) to the left and right of a fixation cross. The centre of each image was 5^{o} from the fixation cross. Images were presented for 800 ms and participants were asked to indicate whether the images were completely identical or different in any way. There were 4 experimental conditions (Figure 2A,B):

(i) normal-normal, same Identity; two identical images of a normal face.

(*ii) normal-composite, same identity;* normal face and composite face of the same person.

(iii) normal-normal, different Identity; normal face images of two different people.

(iv) normal-composite, different identity; a normal face and composite face of two different people.

There were 24 trials for each condition giving a total of 96 trials per run. There were two runs. In each run, images were either presented upright or inverted.

Figure 5.1: *Examples of normal and composite images from the six different expressions used in this study. Faces are shown in their original (top) and composite configurations (bottom).*

5.1.4 Results

Accuracy on the matching task was analysed by a 3-Way ANOVA with Condition (normal-normal, normal-composite), Orientation (upright, inverted) and Identity (same, different). This revealed a significant effect of Condition ($F_{1,27}$ = 11.9, p < 0.01), Orientation ($F_{1,27}$ = 31.5, p < 0.001) and Identity ($F_{1,27}$ = 53.9, p < 0.001). There was also a significant interaction of Condition * Orientation * Identity ($F_{5,55}$ = 20.7, p < 0.001). To investigate this interaction, the effects of Condition * Orientation were performed independently on same identity and different identity trials.

Figure 2C shows % correct responses for upright and inverted images from the same identity. A 2 x 2 ANOVA with Condition (*normal-normal*, *normal-composite*) and Orientation (*upright*, *inverted*) shows that there was a significant effect of Condition ($F_{1,27}$= 25.0, p < 0.001) and Orientation ($F_{1,27}$ = 67.2, p < 0.001). There was also a significant interaction between Condition * Orientation ($F_{1,27}$ = 20.0, p < 0.001). The interaction reflects the fact that accuracy in the *normal-composite* condition was significantly lower than the *normal-normal* condition when the faces were *inverted* (*t(27)* = 5.9, $p < 0.001$).

Figure 2D shows % correct responses for upright and inverted images with different identities. There was a significant effect of Condition ($F_{1,27}$ = 14.8, p = 0.001), but no significant effect of Orientation ($F_{1,27}$ = 3.6, p = .07). The interaction between Condition * Orientation ($F_{1,27}$ = 3.4, p = .08) was also not significant. The effect of Condition was due to a small increase in the *normal-composite* condition (95.8 ± 1.2 %) compared to the *normal-normal* condition (91.8 ± 2 %). The difference in the pattern of data for the different identity faces presumably reflects the fact that participants were able to use a variety of cues from the different identity faces (internal and external cues) to determine whether the two images were different.

Next, reaction times on the matching task (Figure 2F,G) were analysed with a 3-Way ANOVA with Condition (normal, normal-composite), Orientation (upright, inverted) and Identity (same, different) as the main factors. This revealed an effect of Orientation ($F_{1,27}$ = 16.5, $p < 0.001$), but no significant effects of either Identity ($F_{1,27}$ = 3.5, p = .07) or Condition ($F_{1,27}$ = 1.7, p = .21). There was also no significant interaction of Identity * Condition * Orientation ($F_{1.27}$ = .7, p = .42). There were no other significant interactions (Identity * Condition ($F_{1,27}$ = .22, p = .88), Identity * Orientation ($F_{1,27}$ = .13, p = .73), Condition * Orientation ($F_{1,27}$ = 1.1, p = .31).

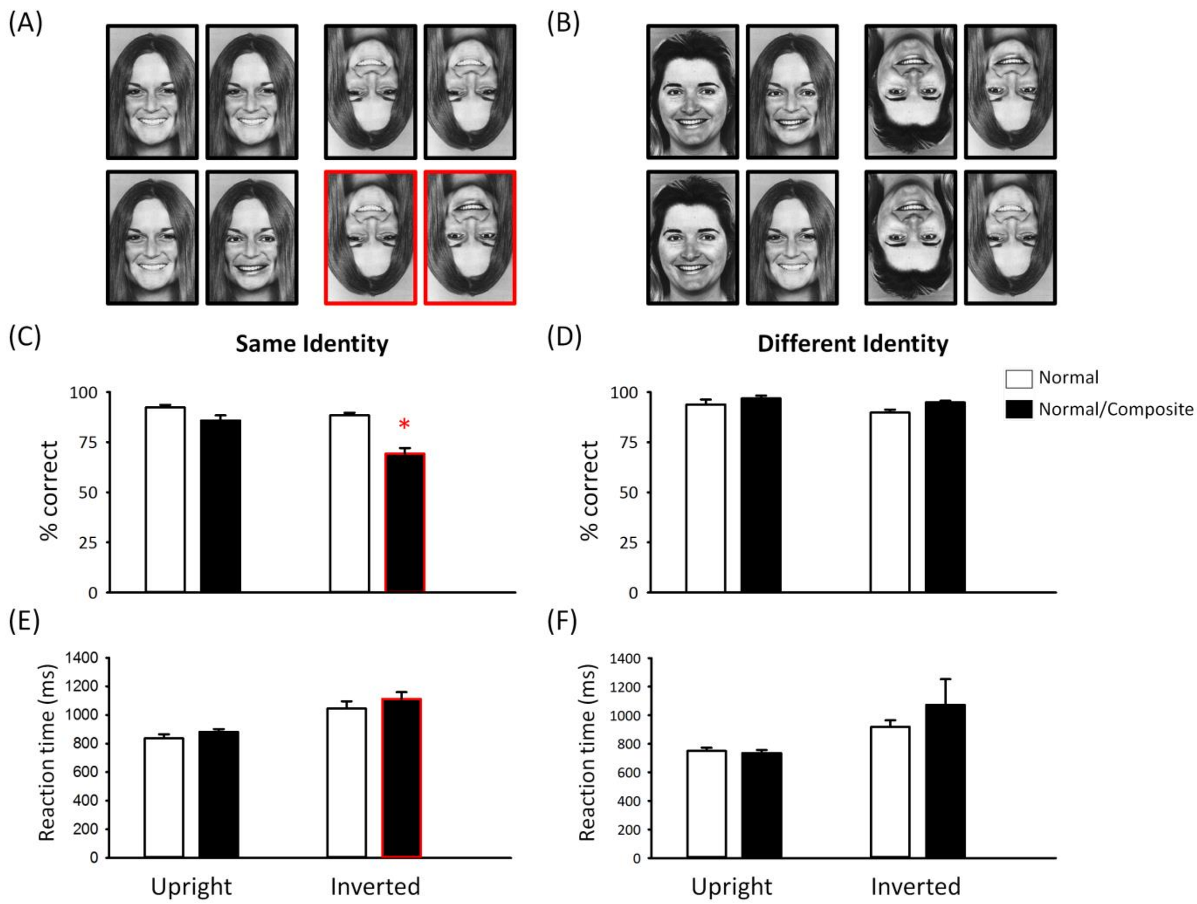

Figure 5.2: *Examples of face pairs of faces with (A) the same identity image or (B) different identities were presented in the upright or inverted orientation. Faces could both be normal (top), or one normal and one composite (bottom). Participants were asked to report whether the faces were identical or different. % correct performance was determined for (C) same identity and (D) different identity faces. There was a significant reduction in the discrimination between the normal and composite faces with the same identity (red) when they were inverted compared to when they were upright. Reaction time was determined for (E) same identity and (F) different identity faces. Error bars represent ± S.E.M, *P < 0.001.*

5.1.5 Discussion

The aim of the present study was to determine whether the effect of inversion on face perception demonstrated by the Thatcher illusion is specific to grotesque expressions. Composite face images were generated by transposing the mouth and eyes from one face onto another face. Using a matching task, we found that the ability to discriminate between an original face and a composite face that only differed in the eyes and mouth was easily performed when the faces were upright. However, the ability to discriminate the same pair of images was significantly reduced when they were inverted. These results suggest that the Thatcher illusion is not specific to grotesque expressions, but reflects a more general orientation-specific encoding of expressive features.

Previous studies that have looked at the effect of inversion on the perception of normal facial expressions have not found large effects (Calvo and Nummenmaa, 2008; PrKachin, 2003; Birgit, Seidel, Kainz and Carbon, 2009; McKelvie, 1995; Fallshore and Bartholow, 2003). Indeed, the recognition of some expressions, particularly positive emotions, are reported not to be affected by inversion (McKelvie, 1995; Calvo and Nummenmaa, 2008, Fallshore and Bartholow, 2003). On the surface, these findings do not fit with our results that show that the ability to discriminate the expressive features of a face is significantly attenuated by inversion. However, a possible reason for the discrepancy between our results and those of previous studies may be found in the experimental design. In expression recognition paradigms, participants are required to match an image to an existing internal representation. It is possible, therefore, that the information that is necessary to elicit an appropriate categorical judgement may not require a precise representation. For example, an increase in brightness in the mouth area could indicate happiness, whereas an increase in brightness in the eyes could indicate fear. Furthermore, this mechanism may not be orientation sensitive. In contrast, the matching paradigm used in this study relies on the ability to make fine perceptual discriminations of the image. Our results suggest that this fine-scale discrimination in faces is orientation sensitive.

The effect on inversion on the ability to discriminate facial expressions is surprising given the simple nature of the task. Participants were only asked to indicate whether the images were identical or different in any way. However, the results show that the ability to determine whether the features of a face were different was significantly impaired when the faces were inverted. This finding suggests that low-level image discrimination of faces can be influenced by the context in which the face is perceived. This fits with a recent study that demonstrated how the global properties of natural images (including faces) could influence low-level feature detectors (Neri, 2011; 2014). It is possible that the inability to detect image differences from inverted faces may reflect feedback from higher to lower visual regions.

In conclusion, we have shown that the Thatcher illusion is not specific to grotesque expressions. Rather, we show that the ability to discriminate changes in the expressive features of the face (mouth and eyes) is greater in upright compared to inverted faces. This suggests that the Thatcher illusion reveals a more general orientation-sensitivity to facial features.

Chapter 6

6.1 THE EFFECT OF THATCHERIZATION ON JUDGEMENTS OF FACIAL IDENTITY

6.1.1 Abstract

The Thatcher illusion demonstrates the orientation-sensitivity of the processes underlying the perception of facial expression, but it is not clear whether thatcherization has a similar effect on judgements of facial identity. To address this issue, we compared performance on an identity matching task with normal and thatcherized faces. Despite, the dramatic effect on the appearance of the faces, we found no effect of thatcherization on the ability to judge facial identity. However, there was a significant effect of inversion on judgements of facial identity. Moreover, in contrast to judgements of facial expression (see Chapter 5), there was no interaction between the effects of inversion and thatcherization. These results demonstrate that the thatcherization of faces specifically affects the perception of facial expression and provides further support for different processes underlying the perception of identity and expression.

6.1.2 Introduction

The majority of studies that have investigated the effect of inversion on face processing have focussed on identity. A variety of evidence has shown that judgements of facial identity are impaired when faces are turned upside down (Yin, 1969; Valentine, 1988). These behavioural findings have been complemented by neuroimaging studies that have investigated the effect of face inversion on processing in face related areas (Haxby et al., 1999; Kanwisher, Tong and Nakayama, 1998; Yovel and Kanwisher, 2004; 2005; Mazard, Schiltz and Rossion, 2006). For example, fMR-adaptation studies have shown that the fusiform face area (FFA) is the primary neural source of the face inversion effect, with a smaller response to inverted compared to upright faces. Other studies using the fMR-adaptation paradigm have also found reduced adaptation to facial identity in the FFA with inverted faces (Yovel and Kanwisher, 2004; Mazard, Schiltz and Rossion, 2006; Schiltz and Rossion, 2006).

The effect of inversion on the perception of facial expression is clearly shown in the Thatcher illusion. Turning the eyes and the mouth upside-down relative to the rest of the face gives rise to a grotesque facial expression when the face is upright (Thompson, 1980; Bartlett and Searcy, 1993; Parks, Coss and Coss, 1985). However, when the image is inverted the grotesque appearance is no longer visible. The Thatcher illusion appears to demonstrate a degree of independence between the processing of facial identity and expression. The identity of a thatcherized face can be recognized when the face is upside down, albeit with some difficulty, whereas the ability to perceive the grotesque facial expression is completely lost. Inversion appears to be having a differential effect on the processing of facial expression and identity. However, despite the anecdotal evidence for thatcherization having a minimal effect on the recognition of identity, no studies have investigated the effect of the thatcherization on the perception of facial identity.

The aim of this study was to explore the effect of thatcherization on the perception of facial identity. Using a matching paradigm, we asked participants to judge whether two simultaneously presented face images were of the same identity or different. We predicted that disruption to the configuration of the internal features of the face should affect the recognition of facial identity. Based on previous studies, we also predicted that inversion would also have an effect on the recognition of identity. In chapter 4, we showed that inversion improved the recognition of facial expression in thatcherized images. We predicted that a similar effect may occur for familiar faces as inversion would attenuate the perception of the grotesque expression that is clear visible in upright faces.

6.1.3 Materials and Methods

6.1.3.1 Participants and stimuli

18 participants took part in the behavioural experiment (14 Female; mean age, 26 ± 2). All participants were right-handed and had normal to corrected-to-normal vision. Written consent was obtained for all participants and the study was approved by the York Neuroimaging Centre Ethics Committee. Visual images (11 x 7˚) were presented ~57 cm from the subjects' eyes.

Face images were taken from 8 familiar identities (4 male, 4 female). There were 8 images for each identity. All images had a frontal pose. Faces were thatcherized by inverting the mouth and eyes regions. Normal and thatcherized images were also inverted by 180^{o}. The familiarity of the faces was confirmed by a post-test in which each subject was asked to indicate whether the names of the identities used in the experiment were familiar and whether they could mentally associate the name with a picture of the face. 87% (± 1.1) of participants reported that the names were familiar and that they could associate a name with a face.

6.1.3.2 Design

A matching experiment was used to determine the ability of the participants to recognize the identity of familiar faces. In each trial, participants viewed two images that were presented successively and had to indicate by a button press whether the two identities were the same or a different person. The two images were always different. So, in a same identity trial, two different images of the same identity were used. Each image was presented for 800ms and images were separated by an interval of 200ms. In contrast to chapter 3, 4, 5 of this thesis in the current chapter the two images were presented successively rather than simultaneously. The use of the successive comparisons allowed as investigating whether successful discrimination could also be achieved independently of the use of the image presentation.

There were 4 stimulus conditions (Figure 1):

(i) normal-normal, upright; two upright normal face images.

(*ii) normal-normal, inverted;* two inverted normal face images *(iii) normal-thatcherized, upright;* one normal and one thatcherized face, both upright

(*iv) normal-thatcherized, inverted;* one normal and one thatcherized face, both inverted

There were 64 trials for each condition, giving a total of 256 trials for each participant.

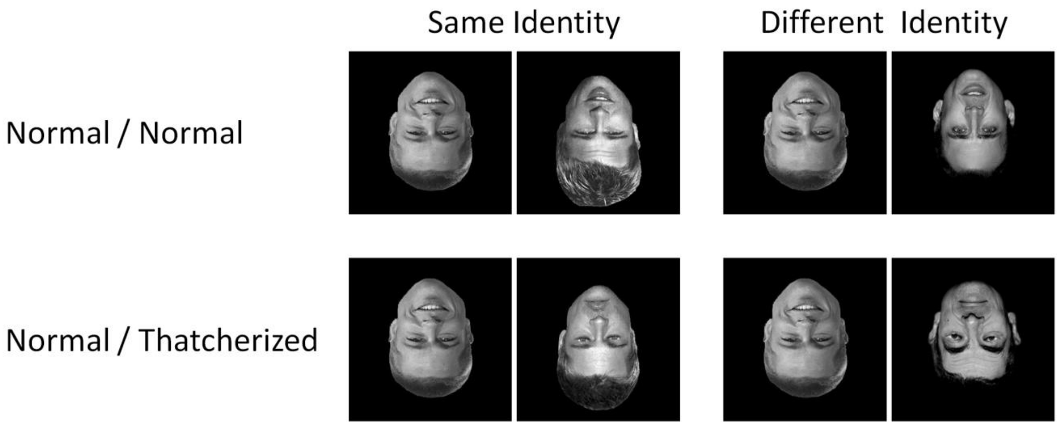

Figure 6.1: *Example of the conditions used in the study. Images were shown in a normal (top row) or thatcherized configuration (bottom row) of the same (left) and different (right) identity. Invert page for the upright view of images.*

6.1.4 Results

Accuracy judgements are shown in Figure 2A. A 2 x 2 ANOVA was performed with Condition (*normal-normal, normal-thatcherized*) and Orientation (*upright, inverted*) as the main factors. There was a significant effect of Orientation ($F_{1,17}$ = 21.1, p = 0.001) that was due to the higher recognition of *upright* (95.1 ± 0.8 %) compared to *inverted* faces (86.4 ± 2.0 %). There was no significant effect of Condition ($F_{1,17}$ = 1.7, *p* = 0.22) and there was no significant interaction between Condition * Orientation ($F_{1,17}$ = 0.9, *p* = .36).

Reaction time judgements are shown in Figure 2B. A 2 x 2 ANOVA was carried out, with Condition (*normal-normal, normal-thatcherized*) and Orientation (*upright, inverted*) as the main factors. There was a significant effect of Orientation ($F_{1,17}$ = 23.4, $p < 0.001$) due to slower reaction times for *inverted* (1123.0 ± 33.3 ms) compared to *upright* faces (947.4 ± 51.8 ms). There was also a significant effect of Condition ($F_{1,17}$ = 4.6, *p* = 0.05). The significant effect of Condition was due to faster reaction time in the *normal-normal* condition (1018.1 ± 43.5 ms) compared to *normal-thatcherized* condition (1052.3 ± 41.5 ms). There was no significant interaction between Condition * Orientation ($F_{1,17}$ = 1.2, *p* = .30).

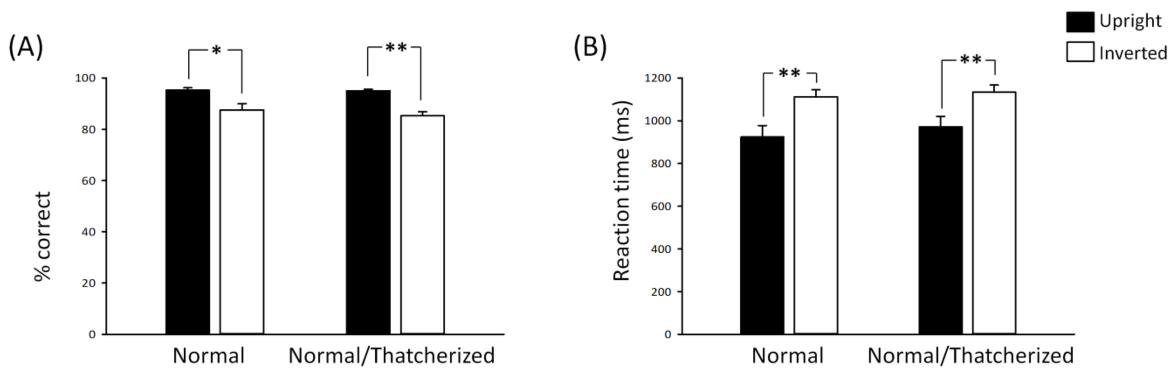

Figure 6.2: *(A) Accuracy and (B) reaction time to responses on an identity matching experiment. Pairs of faces in each trial could both be normal (Normal), or one could be normal and the other thatcherized (Normal/Thatcherized). The images could have the same identity or different identities. Participants were asked to report whether the identity of the faces was the same or different. Error bars represent ± standard error across participants, *P < 0.001. Values that are significantly different are indicated by ** P < 0.001 and * P < 0.01.*

6.1.5 Discussion

The aim of this study was to determine the effect of thatcherization on the recognition of facial identity. Participants viewed two images and had to judge whether they belonged to the same identity. In contrast to judgements of facial expression, thatcherization of the images had no significant effect on judgements of identity. In contrast, there was a significant effect of inversion.

The lack of an effect of thatcherization on the recognition of facial identity does not fit with models of face processing that suggest the importance of the configuration of the internal features of the face for recognition (Valentine 1991; Maurer, Le Grand and Mondloch, 2002; Yovel and Kanwisher 2004). These models suggest that with the ability to make use of differences in internal features improves as faces become familiar. For example, behavioural studies have shown that internal features are more salient than external features when recognizing familiar faces but that perceivers make use of both internal and external features when matching unfamiliar faces (Ellis, Shepherd and Davies, 1979; Young, Hay, McWeeny, Flude, and Ellis, 1985; O'Donnell and Bruce 2001; Bonner, Burton and Bruce, 2003). Despite the clear importance of the internal features in the perception and recognition of faces, other studies have shown that face recognition can occur in situations in which information from the internal features is degraded (Burton, Bruce and Hancock, 1999).

Other studies have suggested that successful face recognition depends on the integration of information from the internal and external features of the face (Young, Hellawell and Hay, 1987; Andrews, Davies-Thompson, Kingstone and 2010;

Axelrod and Yovel, 2010). The importance of these interactions between the internal and external features of the face is clearly illustrated in the Presidential Illusion (Sinha and Poggio 1996), which appears to show an image of the Bill Clinton and Al Gore. However, closer inspection reveals that the internal features of the former President and Vice-President are identical; Bill Clinton's eyes, nose, and mouth have been digitally superimposed onto Al Gore's face! Nevertheless, the external features of Al Gore and the appropriate context are salient enough for us to misperceive this composite image as Al Gore (see also Sinha and Poggio, 2002). A similar illusion that combines the internal and external features of David Cameron and Nick Clegg, shows that this illusion is not restricted to US politicians (Andrews and Thompson, 2010). Together, these results show that successful face recognition can tolerate significant degradation of the internal features.

The lack of an effect of thatcherization on the perception of facial identity contrasts with the dramatic effect of this manipulation on the perception of facial expression (Chapter 4). These findings confirm the idea that the processing of facial identity and expression occur independently. This dissociation is consistent with a variety of evidence that facial identity and expression are processed along parallel processing streams (Haxby, Hoffmann and Gobbini, 2000; Young and Bruce, 2011). For example, Haxby and colleagues (2000) proposed a neural model of face processing in which the processing of faces occurs along two parallel pathways: an inferior pathway projects to fusiform gyrus and is involved in processing invariant aspects of the face such as identity; a superior pathway projects to the superior temporal sulcus and is involved in the processing of changeable aspects of faces such as expression.

Consistent with previous studies, we found that inversion had an effect on judgements of facial identity (Valentine, 1988; Diamond and Carey, 1986; Yin, 1969; Rossion, 2008). For example, Yin (1969) investigated that recognition memory of faces and other mono-oriented objects. The results showed that the inverted performance was disproportionately worse for faces than any other object category used in the study. Likewise, Diamond and Carey (1986) using the same experimental paradigm as Yin (1969) and suggested that faces were more vulnerable to inversion than were landscapes. A similar effect of inversion has been shown in neuroimaging studies that have investigated the effect of inversion on the responses of face-selective regions of the fusiform gyrus (Kanwisher, Tong and Nakayama, 1998; Aguirre, Singh and D'Esposito, 1999; Haxby et al., 1999; Yovel and Kanwisher, 2004; 2005; Mazard, Schiltz and Rossion, 2006; Schiltz and Rossion, 2006). Although they differ in the magnitude of the inversion effect, the majority of studies report a decreased response in the FFA to inverted faces. These studies also report reduced fMR-adaptation to facial identity in the FFA with inverted compared to upright faces (Yovel and Kanwisher, 2004; Mazard, Schiltz and Rossion, 2006; Schiltz and Rossion, 2006).

The effect of inversion on judgements of facial identity in this study (~9%) was smaller than reported in previous studies of faces (23% in experiment 3 of Diamond and Carey, 1986; 18% in Susilo, Rezlescu and Duchaine, 2013; 22% in experiment 3 of Riesenhuber, Jarudi, Gilad and Sinha, 2004). One possible explanation for the smaller effect of inversion in this study is that the faces used in the current study were familiar, whereas the faces used in other experiments on face inversion are typically unfamiliar. The ability to recognize familiar faces across a variety of changes in illumination, expression, viewing angle, and appearance contrasts with the inherent difficulty found in the perception and matching of unfamiliar faces across similar image manipulations (Bruce, Valentine and Baddeley, 1987; Hancock, Bruce and Burton, 2000). This difference in perception has been incorporated into cognitive models of face processing, which propose that familiar and unfamiliar faces are represented differently in the human visual system (Bruce and Young 1986; Burton, Bruce and Hancock, 1999). So, one explanation for the small effect of inversion on recognition reflects a difference in the way that familiar and unfamiliar faces are represented.

In conclusion, our results show that there was no effect of thatcherization on the perception of facial identity. However, we did find an effect of inversion on judgements of facial identity. These results provide further evidence for the independence of the processing of facial identity and expression.

General Discussion

The perception of upright faces is one of the most developed visual abilities in humans. However, when the face is viewed upside-down, our ability to perceive it drops significantly. This is known as the Face Inversion Effect (FIE). An example of the FIE is the Thatcher illusion (Thompson, 1980). The compelling nature of this illusion was shown through its constant reference throughout the literature and the fact that the original article has been cited more than 300 times (ISI Web of Science). Despite the importance of the Thatcher Illusion for showing the selectivity of face processing, the precise neural processes underlying the phenomenon have remained unclear (Thompson, Anstis, Rhodes, Jeffery and Valentine, 2009). The aim of this thesis was to study the behavioural and neural basis of the Thatcher illusion through a series of linked experiments. Specifically this thesis asked the following questions:

- What are the neural correlates of the Thatcher illusion?
- Does a disruption to configural processing explain the Thatcher Illusion?
- Can inversion affect the recognition of normal facial expressions of emotion?
- Is the Thatcher illusion evident for non-grotesque expressions?
- Does thatcherization of faces affect judgements of identity?

In chapter 2, I compared the response to Thatcherized and normal faces in face-selective regions of the human brain using an fMR-adaptation paradigm. The principle behind the adaptation technique was that the repetition of the same stimuli will lead to habituation and decrease of fMR signal, but the opposite will be observed when a different image is repeated within the block. The sensitivity of the neural representation can then be determined for different changes to the stimulus.

I found that the ability to discriminate between stimuli that alternated between normal and a thatcherized image within the same block was substantially reduced when the images were inverted. In contrast, participants were easily able to make this discrimination when the faces were upright. The release of adaptation in the upright orientation suggested that the underline neural representation were sensitive to this change and this was indicated by the fact that the fMR signal remained at its original increase response, whereas in the inverted orientation the neural representation presented insensitivity. This was due to the inability of the human brain in perceiving the image change and the image was processed as being the same rather than different.

A neural correlate of this behavioral effect was found in a face-selective region that is involved in the processing of facial expression: the STS. I found an increased response in the STS when there was a change in the configuration from a normal to a Thatcherized face. However, there was no difference in response between conditions when the faces were inverted. Finally, I found that the FFA – a region involved in processing facial identity - showed a significant response to changes between normal and Thatcherized faces, but that this sensitivity to Thatcherized images was evident for both upright and inverted faces.

These findings indicated that there was a clear separation between the perception of neural representation of facial identity and expression. I have shown that the perception of expression is strongly dependent on changes observed in facial configuration at the upright orientation, but not at the inverted orientation in the STS. I also indicated that this observation was apparent when the identity was unchanged compared to when the identity was changed. This suggests that the magnitude of the response in the STS was independent from the change in identity and reflects a more general mechanism of expression change within the brain. The preferential response in the STS to sequences which varied in configuration, but not in identity is therefore consistent with the role of this region in processing invariant aspects of faces such as expression. This is consistent with the neural model proposed by Haxby and colleagues (Haxby, Hoffman and Gobbini, 2000) and suggests that STS is sensitive to information associated with expression processing and this information is relatively independent from identity processing. In contrast to the STS, there was an increase response in the FFA when the faces were presented in the inverted orientation as well. Similar to the STS this increase in activation in the FFA was only apparent when the identity of the faces was unchanged within the block. This is likely to reflect the sensitivity of the FFA in processing image changes that are associated with changes in facial identity. This functional dissociation between identity and expression helps shed light on the selective neural processes underlying the perception of faces and provides a possible neural correlate of the Thatcher Illusion.

An interesting approach for future research would be to separately investigate the effect of orientation in normal and thatcherized faces of various emotional expressions. In chapter 2, I only used happy faces to investigate responses of normal and thatcherized faces in face responsive regions. The STS and Amygdala are thought to be of great importance in representing changes in emotional expression (Haxby, Hoffman and Gobbini, 2000). It would be interesting to see whether there is a difference in the processing of various emotional expressions in face perception regions, as well as emotionally related regions like amygdala across normal and thatcherized faces.

In chapter 3 of this thesis, I asked whether the Thatcher illusion is still evident when second-order configural information is absent. To address this issue I measured the magnitude of the Thatcher illusion when only the eye region or only the mouth region was visible. I found that participants were easily able to discriminate a normal face from a thatcherized face when the images were presented upright. However, when the images were inverted, performance was below chance levels. Interestingly, performance on the isolated features revealed similar results to the whole face. This suggests that the Thatcher illusion cannot be explained by a disruption to second-order configural processing. Rather, these results demonstrate that a key component of the Thatcher illusion is to be found in orientation-specific encoding of the expressive features (eyes and mouth) of the face. An interesting approach for future research would be to run an fMRI experiment that will investigate neural responses in regions responsive in face perception using isolated eye and mouth features. This will allow us to draw comparisons between the perception of normal and thatcherized features and investigate orientation-specific encoding in the human brain.

The aim of chapter 4 of this thesis was to determine whether there is an effect of inversion on the judgements of various facial expressions, similar to the one seen in the Thatcher illusion. Previous studies have reported a small effect of inversion on the perception of normal emotional expression. For example, studies suggested that inversion has no effect on judgements of facial expression such as happiness, but a small effect on judgements of negative emotions, such as fear, anger, disgust and sadness (McKelvie, 1995; Calvo and Nummenmaa, 2008). These studies clearly contrast with the substantial effect of inversion found in the Thatcher illusion.

To address this discrepancy in the literature, I compared the recognition of facial expressions in normal and thatcherized faces that were presented in an upright and inverted orientation. The results indicated that the effect of inversion on normal faces had a small and inconsistent effect on the recognition of facial expressions. For example, there was a significant effect of inversion on some expressions (anger and sad), but little effect on other expressions (neutral, happy, fear, disgust). In contrast to inversion, thatcherization of images significantly reduced recognition across most emotional expressions. Interestingly, however, I found that inverting thatcherized images actually improved recognition of some facial expressions (happy, neutral, fear). The results show that recognition of facial expression in inverted, thatcherized faces is always lower than in upright, normal faces and is similar to that in inverted, normal faces.

To address the importance of configural processing in a different paradigm, I asked how thatcherization and inversion would affect the perception of the key expressive features (mouth region or eye region) when shown in isolation. A similar pattern of results was evident when only the mouth region or only the eye region was shown. Again, I found that inversion only had a small and inconsistent effect on the perception of normal facial expressions. However, I found that inversion resulted in an increased recognition of some facial expressions. This improvement in the recognition of emotional expression in thatcherized faces following inversion reflects a reduction in the precision with which the expressive features of the face are encoded and suggests that an orientation-sensitivity to the expressive features in the face may be key to explaining the Thatcher illusion.

In chapter 5, I aimed to determine whether the effect of inversion on face perception demonstrated by the Thatcher illusion is specific to grotesque expressions or whether there is a more general orientation sensitivity in the encoding of facial features. I found that the ability to discriminate between an original face and a composite face that only differed in the eyes and mouth was significantly impaired when the images were inverted. However, the same pair of images was easily discriminated when they were presented upright. These results suggest that the ability to discriminate between two faces was affected by the orientation of the image. Furthermore, I suggest that the Thatcher illusion is not specific to grotesque expressions, but reflects a more general orientation-specific encoding of expressive features like the eyes and the mouth. An interesting future approach to this experiment would be to try to quantify the extent to which changes could promote an inversion effect. Stimuli manipulations could be generated using the morphing technique while measuring participants matching judgements.

The aim of chapter 6, was to determine the effect of inversion and thatcherization on judgements of facial identity. To address this issue, a matching paradigm was used to measure the effect of inversion on the recognition of normal and thatcherized faces. Our results suggested no effect of thatcherization on the ability to judge facial identity, despite the dramatic effect on the appearance of the faces. However, there was a significant effect of inversion in both facial configurations. Moreover, in contrast to judgements of facial expression (see Chapter 4), there was no interaction between the effects of inversion and thatcherization. This dissociation is consistent with a variety of evidence that facial identity and expression are processed along parallel processing streams (Haxby, Hoffman and Gobbini, 2000; Young and Bruce, 2011).

The small effects of thatcherization and inversion on the perception of facial identity contrast with the dramatic effect of these manipulations on the perception of facial expression. Our results reveal that internal feature manipulation did not prevent the successful recognition of the facial identity. In the literature, there is a lot of evidence that suggests that face recognition is achieved through the integration of both internal and external features (Young, Hellawell and Hay, 1987; Andrews, Davies-Thompson, Kingstone and Young, 2010; Axelrod and Yovel, 2010). The importance of the external features of the face is clearly illustrated in experiments in which facial recognition was achieved even when there is no difference in the internal features (Sinha and Poggio, 1996; Andrews and Thompson, 2010). Our results show once more that successful face recognition can tolerate significant degradation of the internal features.

The other significant finding from this experiment was that inversion only had a small effect on face recognition. Previous studies have shown that inversion has a larger effect on judgements of facial identity (Valentine, 1988; Diamond and Carey, 1986; Yin, 1969; Rossion, 2008). One possible explanation might be the difference in which familiar and unfamiliar faces are represented in the human brain. The small effect of inversion in this study might be due to the use of familiar faces, whereas the faces used in other experiments on face inversion are typically unfamiliar. This view is accepted by a variety of experiments that proposed that familiar and unfamiliar faces are represented differently in the human visual system (Bruce and Young 1986; Burton, Bruce and Hancock, 1999). Overall these results, confirm the idea that the processing of facial identity and expression occur through two parallel pathways.

Overall, the findings of the current thesis provide a different perspective on previous theoretical accounts of Thatcher Illusion. For example, the Expression Disruption Theory (Valentine, 1988; Yin, 1969) suggests that inversion has a negative effect in the perception of facial expression. In accordance with this theory, we found that inversion does disrupt the perception of facial expression for some but not all facial expressions. Rather, we find that it is the precise perception of the face that is affected by inversion. As far as the dual processing model (Bartlett and Searcy, 1993) is concerned, this thesis was unable to demonstrate that the perceived normality of the thatcherized faces is due to the disruption of configural processing. This was observed both in experiments performed in chapter 3 and 4 that showed similar pattern of results when only the eyes or mouth was visible. We were not able to address the frame of reference (Rock, 1973) explanation of the Thatcher illusion, since our experimental manipulations did not provide a test of this theory.

In conclusion, this thesis provides a significant contribution to our understanding of the Thatcher Illusion using a combination of neuroimaging and behavioural results. The key findings of this thesis are that the neural basis of the

Thatcher illusion is founded on the orientation-sensitivity of face-selective regions which are involved in the processing of facial expression. Behavioural findings suggest that the perception of the Thatcher illusion is still evident in the absence of configural information. This challenges previous interpretations of the Thatcher illusion that are based on a disruption of configural processing. Finally, the selectivity of the Thatcher illusion to the processing of expression is shown by the lack of effect of thatcherization on the processing of facial identity.

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