Facial expression aftereffect and its association with autistic traits in obscured faces

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TECHNOLOGICAL
UNIVERSITY**

**FACIAL EXPRESSION AFTEREFFECT AND
ITS ASSOCIATION WITH AUTISTIC TRAITS
IN OBSCURED FACES**

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**CHENGWEN LUO
SCHOOL OF SOCIAL SCIENCE
2017**

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Table of Content

Acknowledgement	I
Table of Content	III
List of Figures and Tables.....	VI
Publications.....	VIII
Abstract.....	IX
CHAPTER I: Introduction and literature review	- 1 -
1.1 How are faces processed in the neural system?	- 4 -
1.2 The brain structure for facial emotion processing	- 7 -
1.3 Perceptual completion: empirical approaches and neural representations	- 9 -
1.4 Adaptation paradigm and the facial expression aftereffect.....	- 15 -
1.5 Autistic traits and face adaptation.....	- 19 -
1.6 Outline of the thesis	- 23 -
Chapter II: Facial emotion aftereffect to obscured faces by bubbles technique	- 25 -
2.1 Experiment 1.1	- 26 -
2.1.1 Method	- 26 -
2.1.2 Results.....	- 33 -
2.2 Experiment 1.2.....	- 38 -
2.2.1 Method	- 38 -
2.2.2 Results.....	- 40 -
2.2.3 Discussion.....	- 42 -

2.3 Experiment 1.3	- 44 -
2.3.1 Method and Results.....	- 44 -
2.3.2 Discussion	- 47 -
2.4 General Discussion	- 48 -
2.4.1 Does attention facilitate adaptation to dynamic images?.....	- 48 -
2.4.2 What are the possible neural pathways for perceiving facial emotions from the bubbled faces?	- 50 -
2.5 Summary of Study I.....	- 53 -
CHAPTER III: Association between autistic traits and emotional adaptation in incomplete faces.....	
3.1 Experiment 2.1	- 58 -
3.1.1. Methods.....	- 59 -
3.1.2 Results and Discussion	- 65 -
3.2 Experiment 2.2.....	- 72 -
3.2.1 Methods.....	- 74 -
3.2.2 Results and Discussion	- 76 -
3.3. Experiment 2.3.....	- 81 -
3.3.1. Methods.....	- 82 -
3.3.2 Results and discussion	- 85 -
3.4 Global Analyses Across Experiments.....	- 90 -
3.5 General Discussion	- 92 -
3.4 Summary of Study II.....	- 97 -
Chapter IV: Neural correlates of perceptual completion and autistic traits.....	- 99 -

4.1 Experiment 3	- 103 -
4.1.1 Methods.....	- 103 -
4.1.2 Data recording and analysis	- 107 -
4.2 Results.....	- 110 -
4.2.1 Behavioral Results	- 110 -
4.2.2 ERP results.....	- 112 -
4.3 Discussion	- 119 -
4.3.1 N170 and face adaptation in obscured faces.....	- 120 -
4.3.2 The association between AQ and perceptual completion	- 122 -
4.3.3 Amodal completion and perceived emotion intensity	- 123 -
4.3.4 The association between AQ and the perceived intensity of emotion	- 124 -
4.4 Summary	- 126 -
Chapter V: Discussion, future directions, and conclusion.....	- 127 -
5.1 General Discussion	- 127 -
5.1.1 The mechanism of facial emotion perception.....	- 128 -
5.1.2 The negative association between AQ and perception of facial emotions.	- 130 -
5.2 Limitations and future directions	- 131 -
5.3 Conclusions.....	- 135 -
References.....	- 137 -

List of Figures and Tables

Figure 1.1 Example of stimuli used to probe perceptual filling-in	13
Figure 2.1 Face stimuli used in experiment 1.1.....	28
Figure 2.2 Trial sequence for the static emotion-unrecognizable adaptation condition in Experiment 1.1.....	32
Figure 2.3 Facial expression aftereffect in Experiment 1.1.....	34
Figure 2.4 Facial expression aftereffect in Experiment 1.2.....	41
Figure 2.5 Control Experiment.	42
Figure 2.6 Transfer of FEA across size and location in Experiment 1.3.....	46
Figure 3.1 Facial stimuli used in Experiment 2.1.....	61
Figure 3.2 Trial sequence for the misaligned occluder (MO) condition.....	64
Figure 3.3 Facial expression aftereffect in Experiment 2.1.....	66
Figure 3.4 Relationship between AQ and FEA magnitude after adapting to occluded static faces for Experiment 2.1	67
Figure 3.5 Facial stimuli used for Experiment 2.2.....	75
Figure 3.6 Facial expression aftereffect in Experiment 2.2.....	77
Figure 3.7 Relationship between AQ and FEA magnitude after adapting to full and occluded flickering faces in Experiment 2.2.....	78
Figure 3.8 Inversion effects and the correlations with AQ score	86
Figure 3.9 Accuracy and perceived emotion intensity of the adaptors.....	88
Figure 4.1 Demonstration facial stimuli used for Experiment 3.1.....	106
Figure 4.2 Trial sequence for AFO condition for Experiment 3.1.....	107

Figure 4.3 Behavioral results for Experiment 3.1.....	111
Figure 4.4 Correlation between overall FEAs and AQ for Experiment 3.1.	111
Figure 4.5 N170 amplitude of happy test faces following different adaptors.	113
Figure 4.6 LPP of happy test faces following different adaptors.	11
Figure 4.7 Correlation between AQ and N170 amplitude change in the right hemisphere.	111
Table 1 Mean correct recognizable and unrecognizable emotional faces.	39

Publications

1. Chapter 2:
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2. Chapter 3:

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Abstract

Objects we see in daily life are often occluded and rarely appear in full form. The present study investigates how people recognize emotions from partially occluded faces. Previous studies have shown that prolonged exposure to a complete emotional face biases the perception of emotion of subsequent faces, the facial expression aftereffect (FEA). However, less is known about the influences of an obscured emotional face to the perception of subsequent facial emotions. People with autism spectrum disorder (ASD) have been found to suffer from compromised ability to process facial emotions. Autistic traits typically exhibited in people with ASD are also demonstrated in neurotypical individuals (NT) to milder degrees, however, the association between autistic traits and the perception of facial emotion in NT is understudied. The present thesis aims to bridge the gap by addressing the following questions: (1) Can the perception of facial emotion be biased by prolonged exposure to partially obscured emotional faces? (2) How autistic traits are associated with the perception of facial emotion from these faces? (3) What are the possible neural mechanisms of the association between autistic traits and FEAs. Three studies were carried out to address these questions.

Study 1 was carried out to answer the first question. The recognizability of the facial emotion was manipulated by partially occluding different areas of the faces. We then manipulated the dynamics, the location, and size of the preceding face (the adaptor) to infer the contribution of local versus high-level information to the perception of facial emotion. Results indicate that for static conditions,

significant FEAs were only observed when participants could recognize the emotion conveyed by the adaptors (Experiment 1.1). However, the dynamic facial videos generated significant FEAs regardless of recognizability (Experiment 1.2). The FEAs also survived locational shift of the adaptor, suggesting high-level adaptation of facial emotion and possible activation of both dorsal and subcortical pathways (Experiment 1.3).

The second study tested the association between autistic traits and FEAs. In Experiment 2.1, we occluded the adapting faces with aligned or misaligned bars, and measured the autistic traits of participants with Autism-Spectrum Quotient (AQ). Both conditions produced significant FEAs, with FEAs and autistic traits negatively correlated. In Experiment 2.2, we manipulated the holistic perception levels by flickering the viewable facial parts in different synchronization. Results again showed significant FEAs in all conditions, however, the association between autistic traits and FEAs was abolished.

The third study further explored the association between AQ and FEAs in obscured emotional faces using simultaneous behavioral and EEG recordings. Results showed that the N170 suppression was stronger if the preceding adaptors could be more holistically perceived. We observed a positive correlation between autistic traits and N170 suppression, suggesting that high autistic traits were associated with reduced holistic perception in obscured faces. The late positive potential (LPP), an indicator of emotion processing, were suppressed when emotion of test faces was the same as of the adaptor's. The LPP suppression of the test faces was largest when the adaptors had the strongest completion cues. Autistic

traits were negatively associated with perceived emotional intensity of the obscured face with intermediate completion cues.

Taken together, the thesis has investigated the perception of facial emotion from partially occluded faces in neurotypical individuals with a range of autistic traits. Results show that prolonged exposure to obscured faces produces FEA, although the magnitude of FEA is subject to autistic levels. Increasing autistic level is associated with smaller perceptual bias after adapting to static partially obscured faces. Possible explanations are that people with high AQ suffer from compromised ability to integrate viewable facial parts into a holistic construct and reduced emotion intensity perception. To the best of our knowledge, this is the first study that has been carried out to examine the emotion adaptation in NT with a range of autistic traits. In addition to that, we used both behavioral and physiological approaches which provide a more comprehensive understanding of the perception of facial emotion under impoverished conditions. It also sheds lights on possible training schemes that could help to improve the quality of life in people with high autistic traits.

CHAPTER I: Introduction and literature review

Objects we see in our daily life are mostly incomplete. For instance, an item could be partially occluded by itself or by neighboring objects. Despite that images projected to the retina are mostly fragmented due to the opaque nature of occluders, we nevertheless perceive the surroundings as coherent. Such filling-in of missing information is called amodal completion (Kanisza & Gerbino, 1982) or perceptual filling-in/completion (Weil & Rees, 2011). The present study aims to investigate how people recognize objects when information provided are incomplete, focusing on emotion perception from obscured faces.

Faces play a crucial role in social interactions (Bruce, Desimone, & Gross, 1981; Perrett, Rolls, & Caan, 1982). People who are better at decoding emotional cues are more likely to succeed in negotiation and report positive feelings in interpersonal relations than those less skilled ones (Elfenbein, Der Foo, White, Tan, & Aik, 2007; Robert Stephen Feldman, Philippot, & Custrini, 1991). Even though the spatial layout of all faces shares a great similarity, two eyes horizontally align above the nose which is above the mouth in the middle, most of us are still able to individualize hundreds of faces. Faces seen in daily life rarely appear in full form but are often occluded by spectacles, sunglasses, hats, scarfs and/or other accessories. However, when looking at a face with glasses, we rarely notice that facial information is incomplete due to occlusion or distortion by spectacles.

Numerous studies have been conducted regarding the amodal perception of face identities (Harris & Aguirre, 2008) and face viewpoints (Chen, Liu, Chen, &

Fang, 2009; Chen, Zhou, Yang, & Fang, 2010; Fang & He, 2005; Harris & Aguirre, 2008; Yokoyama, Noguchi, Tachibana, Mukaida, & Kita, 2014). These studies can be broadly divided into two categories based on their research purposes. One category aims to examine the neural process of the perception of occluded faces, such as the time course of the filling-in and the brain areas involved (Chen et al., 2009; Chen et al., 2010; Harris & Aguirre, 2008). The other category uses obscured faces as an approach to studying the contribution of holistic versus local information in face perception (Fang & He, 2005; Harris & Aguirre, 2008; Yokoyama et al., 2014).

The interest in studying the contribution of different information in the perception of various facial attributes arises because of the abundance of information we can tell from a simple glance of a face, such as identity, emotional status, ethnicity, age, attractiveness and even health condition (Kalick, Zebrowitz, Langlois, & Johnson, 1998). These judgments are made based on different facial cues, for instance, age can be reflected by skin condition alone, i.e. local information; whereas the perception of attractiveness depends on the whole face, i.e. holistic information (Abbas & Duchaine, 2008). A typical approach to disentangle the contribution of local features from holistic information is by manipulating the perceptual completion levels of incomplete faces via adaptation. Adaptation refers to the phenomenon that our perception can be biased by previous experience, for instance, prolonged exposure to a happy face (the adaptor) makes a previously perceived neutral face appear sad: the facial expression aftereffect (FEA) (Gibson, 1933; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster &

MacLeod, 2011). If a perceptually-completed obscured facial adaptor produces a larger FEA than its non-completed counterparts with identical local information, it indicates contribution of holistic information in the perception of the particular facial attribute (Fang & He, 2005; Harris & Aguirre, 2008; Yokoyama et al., 2014). Using this approach, it has been shown that perception of face identity, viewpoint, and gender rely on both local and holistic information (Fang & He, 2005; Harris & Aguirre, 2008; Yokoyama et al., 2014).

However, the perception of emotion from obscured faces is far from well understood, and the findings are mixed (Butler, Oruc, Fox, & Barton, 2008; Meaux & Vuilleumier, 2016; Xu, Dayan, Lipkin, & Qian, 2008). The present thesis aims to investigate the perception of facial emotion from obscured faces by answering the following questions: (1) what information is critical for the perception of emotion from occluded faces? (2) People with Autism Spectrum Disorder (ASD) suffer from compromised ability in face perception and information integration (Happé & Frith, 2006), will autistic traits be associated with the emotion perception of obscured faces in neurotypical individuals? (3) What are the possible neural mechanisms for the association between the autistic traits and FEAs? In the following sections, I will begin the literature review by delineating the neural mechanism for face perception (section 1.1 and 1.2) and amodal completion (Section 1.3). Subsequently, I will review the adaptation research paradigm and facial expression aftereffect (Section 1.4); followed by a summary of studies that have been carried out to examine the relationship between autistic traits and face

adaptation (Section 1.5). Lastly, I will outline the three studies presented in the dissertation and their significance (Section 1.6).

1.1 How are faces processed in the neural system?

The visual system processes information in a hierarchical approach (Felleman & Van Essen, 1991). Most visual information projected to the retina is sent to the primary visual cortex (V1) via the lateral geniculate nucleus (LGN) and then processed in a feed-forward fashion. Neurons at low-level cortices (e.g. V1) have small receptive fields and are tuned to process simple features of stimuli, such as orientation or curvature (Hubel & Wiesel, 1965). High-level neurons gather information from those in the lower levels and process more complex stimuli via larger receptive fields (Hubel & Wiesel, 1965; Parul, 2013). The cortices are connected in a way that different attributes of visual information are processed by distinctive pathways (Kafaligonul, Breitmeyer, & Ögmen, 2015; Van Essen & Gallant, 1994). For instance, the ventral pathway, a.k.a. the ‘what’ pathway, processes information related to object recognition. The dorsal pathway, also known as the ‘where’ pathway, processes visually guided action, attention, and relative location/orientation (Ungerleider, 1982). The dorsal pathway also hosts object-sensitive areas, patients with occipitotemporal cortex damage (the ventral pathway) can nevertheless use information of object that is beyond their conscious awareness to guide hand movements to grasp the target (Goodale, Milner, Jakobson, & Carey, 1991). In addition to the feed-forward processing of visual information (from the retina to the LGN, and further to the primary visual cortex and other higher-level visual cortices), there are other pathways involved. For

instance, evidence has shown that a small proportion of the fibers from the retina take a secondary route bypassing the LGN and V1, reach other brain areas via the superior colliculus (SC) and the pulvinar (LeDoux, 1996; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). There are extensive interconnections/ 'short-cuts' between cortical and subcortical pathways (Pessoa & Adolphs, 2010). For instance, LGN has direct connections with the V2 and V4 (Yukie & Iwai, 1981); pulvinar and amygdala also extensively connects with visual cortices (such as V1, V2, and V4) (Pessoa & Adolphs, 2010).

The neural system for face perception has been under intense debate, and there are two main models proposed (Haxby & Gobbini, 2011; Kanwisher, McDermott, & Chun, 1997). One model suggests that all facial information is propagated to a structure dedicated for face perception, the Fusiform Face Area (FFA) in the temporal cortex (Kanwisher et al., 1997). However, other researchers suggest that the FFA is an area that processes information requiring expertise, but not for face perception alone (Gauthier, Skudlarski, Gore, & Anderson, 2000; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002). As the FFA has been reported to be activated to a similar extent as faces when experts were processing objects of expertise (e.g. car or birds) (Gauthier et al., 2000).

The other model proposes that faces are processed by a distributed neural system (Haxby, Hoffman, & Gobbini, 2000), with a core system analyzes face-specific information, and an extended system works in conjunction with the core system to extract face-related information. The core system includes inferior occipital gyrus (OFA), the FFA, the posterior region of superior temporal sulcus

(pSTS) and adjacent regions that are significantly activated by faces. The FFA responds preferentially to invariant aspects of faces, such as identity; whereas the pSTS responds preferentially to changeable aspects of faces, such as expressions, eye gaze, and speech-related movements (Haxby et al., 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998). Evidence of dissociable pathways for the perception of emotion and identity comes from single neuron recordings, imaging, and lesion studies. For instance, selective attention to identity modulates the neural responses in the FFA but not the STS; whereas selective attention to eye gaze only modulates activities in the STS but not the FFA (Hoffman & Haxby, 2000). Removing the STS lead to deficits in the perception of eye gaze and facial expressions, but spares the ability to process identity (Eacott, Heywood, Gross, & Cowey, 1993; Kanwisher & Moscovitch, 2000; Young, Newcombe, & De Haan). On the contrary, prosopagnosia patients showed the opposite pattern, with impaired recognition of identity but preserved the perception of emotion and other facial attributes (Damasio, Damasio, & Van Hoesen, 1982; Tranel, Damasio, & Damasio, 1988). The extended system retrieves face-related information after the facial information being analyzed by the core system. For instance, if the identity of the face is familiar, an automatic process will occur to retrieve information related to this individual, such as his personality traits and shared memories (Gobbini & Haxby, 2007; Todorov & Uleman, 2002).

1.2 The brain structure for facial emotion processing

For the perception of facial emotions, besides of the detailed analytical feed-forward processing by the cortical pathway, other regions, such as the medial prefrontal cortex, the orbitofrontal cortex (OFC), the limbic system (e.g. the amygdala, the anterior cingulate cortex) have been found to be sensitive to emotional stimuli (Etkin, Egner, & Kalisch, 2011; Phan, Wager, Taylor, & Liberzon, 2002; Protopopescu et al., 2005). These structures do not respond equally to all facial emotions. For instance, the amygdala responds maximally to negative emotions, such as fear (Phan et al., 2002), whereas the prefrontal cortex is generally sensitive to all emotions (Kawasaki et al., 2001).

Abundant research has argued for a fast-but-coarse processing in the subcortical pathways. For instance, Maior et al. (2010) also reported that some pulvinar neurons differentially responded to emotions in a short latency (<100 ms). however, some cortical structures, such as the OFC, show comparable or even faster reaction time towards emotional stimuli than that of the amygdala (Tsao, Freiwald, Tootell & Livingstone, 2006; Etkin et al., 2011; Kawasaki et al., 2001; Morrison, Saez, Lau, & Salzman, 2011; Pessoa & Adolphs, 2010). For instance, Morrison and colleagues (2011) found that the amygdala responded faster to aversive information, whereas the OFC reacted more quickly to rewarding/positive information in monkey studies.

Perception of emotion does not always reach consciousness. A typical example is that patients with cortical blindness who suffer from vision loss due to damages of visual cortex, could still be able to recognize/differentiate emotional

information falling into the blindsight (Burra et al., 2013; Van den Stock et al., 2011). This may be partly because a small proportion of the fibers from the retina take a secondary route and reaches the amygdala via the superior colliculus (SC) and the pulvinar, i.e. a subcortical pathway (LeDoux, 1996; Williams et al., 2004), although other ‘short-cuts’ between the LGN and emotion-sensitive regions may also contribute to the processing of emotions (Pessoa & Adolphs, 2010). Emotions could be rendered beyond conscious awareness by various manipulations. A recent review paper has summarized two major types of qualitatively different operations (Tamietto & De Gelder, 2010). The ‘attentional unawareness’ refers to the situation that unawareness of emotion was due to lack of attention allocated to the targets. For instance, in daily life, we are only able to consciously perceive a very small fraction of sensory inputs due to limited attentional resources, and only those with high importance or saliency reach awareness. The neural responses to those unattended stimuli are suppressed by top-down modulations to increase the signal-to-noise-ratio by which facilitates the processing of the important/salient objects. In this case, the suppressed emotional stimuli are processed mainly by subcortical structures, such as the amygdala, and cortices that have direct connections with these areas, such as part of the OFC. On the other hand, the ‘sensory unawareness’ refers to situations that the signal strength of stimuli ‘is insufficient to evoke cortical activity in visual areas..., (but) can trigger activity in subcortical visual structures, such as the superior colliculus, that have a lower threshold of activation’ (Tamietto & De Gelder, 2010, P698). Typical examples include backward masking

and binocular rivalry. In this case, it has been suggested that the subcortical pathways play a dominant role in the processing of undetected affective stimuli.

The subcortical pathways modulate neural activities in the cortical pathways via connections between the cortical and subcortical regions (Armony & Vuilleumier, 2013). For instance, it has been consistently reported that FFA neural responses to fearful faces are larger than neutral faces. This suggests that fear processed by the subcortical pathway has increased visual attention, which enhances face processing in the FFA (Vuilleumier & Pourtois, 2007). Amygdala lesions could lead to comparable FFA activation regardless of the valence of facial emotions (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004).

To summarize, faces are processed by distributed systems, with a core system that analyzes different domains of facial information, and an extended system that retrieves related information of the face, with possible connections between the two systems. Facial emotions could also be processed by cortical and subcortical regions. Here, we ask how our brain responds to partially occluded emotional faces. Does it simply ignore the missing parts, or fill-in the missing information? These questions will be reviewed in the following section.

1.3 Perceptual completion: empirical approaches and neural representations

The whole is greater than the sum of its parts, the gist of Gestalt perception, guiding the way we perceive and interpret (Heider, 1977). The ‘law of closure’ is one of the most important rules of the Gestalt theory, and it refers to the tendency

to perceive incomplete shapes as a complete whole. For instance, when looking at a dog behind picket fence, we can perceptually complete the missing parts that are occluded by the fence and nevertheless perceive it as a dog instead of fragments. The ability of the visual system to overcome various obstacles and make sense of the surroundings have intrigued researchers for decades (Ehrenstein, Spillmann, & Sarris, 2003; Palmer, 1999; Rump, Giovannelli, Minshew, & Strauss, 2009).

There are two main approaches to induce the perceptual completion, stereoscopic display and pictorial occlusion (Beller, 1971; Kanizsa, 1979; Nakayama et al., 1989). The stereoscopic display creates a visual disparity between the two eyes via binocular fusion and thus leads to a 3D perception which mimics the natural settings (Harris & Aguirre, 2008; Nakayama et al., 1989). Pictorial occlusion, on the other hand, is achieved by applying opaque occluders in front of objects on a 2D basis and can be achieved both monocularly and binocularly (Johnson & Olshausen, 2005; Rauschenberger, Liu, Slotnick, & Yantis, 2006). Pictorial occlusion, compared to the stereo display, includes features such as T-junctions where continuous edges of the occluding object intersect with the edges of the occluded, but lack direct depth information. Thus, perceptual completion induced by the pictorial occlusion might require extra time for the attribution of ownership of fragmented surfaces, i.e. to decide whether a certain surface belongs to the occluder or the occluded (Pessoa & De Weerd, 2003).

However, pictorial occlusion has nevertheless been widely used to study amodal completion due to its simplicity and ubiquity in daily life, typical scenarios including viewing photos and watching surveillance videos (Bushnell, Harding,

Kosai, & Pasupathy, 2011; Pratt & Sekuler, 2001; Rauschenberger et al., 2006). More importantly, several approaches have been applied to reduce cognitive efforts for the attribution of border ownership, such as introducing motion to the occluded objects (Brown & Weisstein, 1991; Meyer & Dougherty, 1987; Vezzani, Kramer, & Bressan, 2014). Elements sharing a common motion or destination are more likely to be grouped together and perceived as a unitary item, the law of common fate. The motion thus makes the assignment of border-ownership effortlessly. Flickering images between low and high luminance could efficiently induce depth perception. Studies have shown that we tend to perceive flickering regions localized behind the depth panel of the non-flickering regions (Schwab & Nusbaum, 2016; Wong & Weisstein, 1984). Using a square-wave flickering pattern, the frequency for optimal depth perception is around 6-8 HZ (Schwab & Nusbaum, 2016; Wong & Weisstein, 1984). Compared to static pictorial occlusion, combining pictorial occlusion with kinetic information seems to be a convenient and powerful approach to study perceptual completion (Bair & Movshon, 2004; Kiritani, 1999; Lin & He, 2012; Sekuler & Murray, 2001; Wagemans & d'Ydewalle, 1989).

How does the brain process obscured objects? One theory hypothesized that the recognition of obscured targets followed a feature-matching approach (Bülthoff & Edelman, 1992; Fukushima, 1980; Marr & Nishihara, 1978). The brain does not fill-in the missing information, and people recognize the target by matching available information with features of the object template in the mental representation. If this is the case, one would expect similar response patterns and

reaction time in recognizing the target regardless of its relative location to the occluder, as long as the available information is kept constant. Whereas mounting evidence suggested otherwise (Chen et al., 2009; Chen et al., 2010; Fang & He, 2005; Fang, Murray, & He, 2007; Hazenberg, Jongsma, Koning, & van Lier, 2014; Hegdé, Fang, Murray, & Kersten, 2008; Kim, Feldman, & Singh, 2012; Weigelt, Singer, & Muckli, 2007). For instance, Murray and colleagues (2001) reported different response patterns when perceiving amodally completed and non-completed object. The study used a priming-match paradigm (Figure 1.1), and participants were told to attend to the dark-colored shape during the priming stage (left column, i.e. a full circle or a notched circle). Immediately after the disappearance of the prime, they were required to judge whether a subsequent image (full/notched circle) had the same shape as of the attended one in the priming stage. Reaction time was recorded and compared among conditions. Results showed in the right column. (a) When the prime was a full circle, reaction time to a subsequent full circle was shorter than to a notched circle, suggesting the perception of a full circle in the priming stage. (b) When the prime was a notched circle misaligned with the square, reaction time to a subsequent notched circle was shorter than to a full circle, indicating the perception of a notched circle in the priming stage. (c) When the prime was a notched circle aligned with the square, results depends on the presentation duration of the prime (Rauschenberger et al., 2006). When the prime was displayed briefly, such as 50ms, participants showed faster reaction time to subsequent notched circles, indicating a perception of a notched circle at the priming stage. Only when the prime was displayed long

enough (e.g. 250ms), the reaction time was faster to subsequent full circles despite that the local image of the prime was notched, indicating a perception of a full circle at the priming stage (Rauschenberger et al., 2006). The response patterns in condition (c) indicate that perceptual completion takes time. The time-course of completion process varies from experiment to experiment, probably due to different levels of complexity and the amount of occlusion of test stimuli (Anaki, Boyd, & Moscovitch, 2007; Chen et al., 2009; Murray, Sekuler, & Bennett, 2001). Discrepancies in reaction time and physiological responses have not only been reported in studies employing pictorial occlusion, but have also been reported in those using stereoscopic display (Chen et al., 2009; Chen et al., 2010; Harris & Aguirre, 2008; Yokoyama et al., 2014).

Figure 1.1 The priming-match paradigm (Adopted from Murray Sekuler, & Bennett, 2001). The left column shows three types of prime. Participants were told to attend to the dark-colored shape (a full or notched circle). Immediate after the disappearance of the prime, participants **were asked to judge** whether a following image (full/notched dark circle) had the same shape as of the prime. Results in the right column show that: (a) When the prime was a full circle, reaction time to subsequent full circles was shorter than to notched ones; (b) When the prime was a notched circle misaligned with the square, reaction time to subsequent notched circles was shorter than to full circles; (c) When the prime was a notched circle aligned with the square. Results depend on the duration of the prime. If the duration was brief (e.g. 50 ms), participants showed faster reaction time to notched circles. However, when the prime was displayed long enough (e.g. 250 ms), the reaction time was faster to full circles, indicating occurrence of perceptual filling-in.

Increasing evidence indicates that extra cognitive steps are involved in the brain when people perceive obscured images. Then a subsequent question comes, which brain areas are responsible for the filling-in of missing information? Some researchers have suggested that the filling-in is achieved in retinotopic visual areas (Gerrits & Vendrik, 1970; Júnior, Rosa, Gattass, & Rocha-Miranda, 1992), with 'a point-for-point representation of filled-in regions in retinotopic areas' (Weil & Rees, 2011). For instance, single cell recordings showed similar activation pattern in V2 between presenting an illusory bar and a real bar. However, a slight change which disrupted the perception of the illusory bar would not activate neurons in that area (Peterhans & von der Heydt, 1989). This model is known as the 'isomorphic model' which suggest that filling-in is automatic and less subject to attentional loads (Cohen & Grossberg, 1984; Gerrits & Vendrik, 1970; Sasaki & Watanabe, 2004).

The 'symbolic model', however, suggests that the interpolation occurs at high cortical areas and is subject to attentional loads (Chen et al., 2010; Dennett, 1991; Gregory, 1972; Lin & He, 2012). For instance, when facial fragments were presented behind occluders (FBO), low-level visual cortices, such as V1 and V2, showed lower Blood-oxygen-level dependent (BOLD) activation compared to those presented in front of the occluders (FIO) (Chen et al., 2010). However, in high-level cortical areas (LOC, OFA, and FFA), FBO and full faces showed similar BOLD activation, and both were stronger than the FIO (Chen et al., 2010). The results have well demonstrated that when perceiving perceptually completed occluded objects, the early visual cortices are suppressed compared to its non-completed counterpart with identical local information. Whereas activations of

higher visual cortices are enhanced. Using a psychophysical approach, Lin and He (2012) found larger motion aftereffects when the adapting object could be perceived as coherent. Selective attention systematically modulated the magnitude of motion aftereffects, indicating that ‘perceptual completion relies heavily on later mechanisms in support of the symbolic model’ (Lin, & He, 2012).

To summarize, increasing evidence suggests the occurrence of filling-in when perceiving obscured objects. Time-course of the process depends on the complexity and nature of the stimuli (Pessoa & De Weerd, 2003), and the loci of this process are still controversial.

1.4 Adaptation paradigm and the facial expression aftereffect

As mentioned previously, adaptation refers to the phenomenon that sustained exposure to an object systematically biases the perception of a subsequent object of the same category (Gibson, 1933). It can tap neuronal populations at different cortical levels, and thus has been referred to as ‘psychologist’s micro-electrode’ (Frisby, 1979; Kohn, 2007). Several theories have been proposed to explain the physiological mechanisms of visual adaptation, and one of the most widely accepted theories is the ‘neuronal fatigue’ (see the review: Kohn, 2007; Sanchez-Vives, Nowak, & McCormick, 2000). Neurons respond preferentially to their preferred stimulus pattern. The fatigue hypothesis suggests that prolonged exposure to the preferred stimuli fatigues the neuronal population, and thus the habituated neurons become less responsive when their preferred stimuli reappear (Eggermont, 1985).

One approach to probe the low- versus high-level adaptation is to examine tolerance of translational invariance (Afraz & Cavanagh, 2008; Webster, 2015; Zhao & Chubb, 2001). More specifically, low-level adaptation is retinotopic and the aftereffect cannot survive a locational shift between test and adapting stimuli (Afraz & Cavanagh, 2008; Zhao & Chubb, 2001). Such location-dependent aftereffects are observed in simple geometric shapes. This is because simple shapes are processed by neurons with small receptive fields in early visual cortex (Angelucci, Levitt, & Lund, 2002; Cavanaugh, Bair, & Movshon, 2002). For instance, adaptation to a curve habituates a group of neurons in V2 (Levitt, Kiper, & Movshon, 1994; Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989). While the receptive field of a V2 cell is around 3 degrees, a 5-degree locational change of the test curve will shift its retinal projection outside of the receptive field of the neurons that have been habituated. In other words, the image of the test curve would be projected to a new group of neurons in V2. Thus, no curvature aftereffect is observed. On the contrary, neurons at higher-cortical levels, such as those located in inferior temporal cortex (IT), have a receptive field of around 10 to 30 degrees (Fujita, 2002; Gross, Rocha-Miranda, & Bender, 1972; Op De Beeck & Vogels, 2000). Therefore, the activation of these neurons is more tolerant to locational shifts between adapting and test stimuli (Afraz & Cavanagh, 2008; Ito, Tamura, Fujita, & Tanaka, 1995; Zhao & Chubb, 2001).

The face aftereffect is one of the most studied examples of high-level adaptation (Webster, 2012; Webster, 2015; Webster, Kaping, Mizokami, & Duhamel, 2004). It has been reported in many facial attributes, such as identity,

expression, ethnicity, face viewpoint, gender, and attractiveness (Adams, Gray, Garner, & Graf, 2010; Afraz & Cavanagh, 2008; Fang & He, 2005; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Webster & MacLeod, 2011; Webster & Maclin, 1999; Yokoyama et al., 2014). The perception of face identity, gender and viewpoint rely heavily on holistic information (Happé & Frith, 2006). Besides that they are processed by high-level visual cortexes, their aftereffects also survive locational and size change between the adapting and test stimuli (Afraz & Cavanagh, 2008; Rhodes, Jeffery, Clifford, & Leopold, 2007; Rhodes et al., 2011; Zhao & Chubb, 2001). Other supporting evidence includes larger face viewpoint and gender aftereffects in perceptually completed face than non-completed counterparts (Yokoyama et al., 2014).

Because many facial dimensions require holistic processing, it does not necessarily indicate that the perception of facial emotion shares the same mechanism. Anatomically, the perception of face identity, viewpoint and expression shares overlapping yet distinctive neural pathways (Haxby & Gobbini, 2011; Haxby et al., 2000; Hoffman & Haxby, 2000). Face viewpoint is processed in the right FFA and the lateral occipital cortex (LO) (Fang et al., 2007); facial identity in the FFA, and facial emotion in the pSTS (Haxby & Gobbini, 2011; Haxby et al., 2001; James V Haxby, Elizabeth A Hoffman, & M Ida Gobbini, 2000).

The contribution of low-level (local) and high-level (holistic) information in the perception of facial emotion is in debate (Matsumiya, 2014; Xu et al., 2008). For instance, Flack and colleagues (2005) found that pSTS was activated similarly

to aligned and misaligned emotional faces, indicating feature-based processing of facial expression in pSTS (Flack et al., 2015). However, studies employing the face inversion paradigm reported otherwise. It has been widely accepted that the processing of upright faces primarily relies on holistic information, whereas the perception of inverted faces is feature-based processing (Bartlett & Searcy, 1993; Yin, 1969). Previous studies reported inversion effect of facial expression, indicating that the processing of facial emotion also depends on holistic information (Bimler, Skwarek, & Paramei, 2013; Haxby et al., 1999; Leube et al., 2003), although the finding was not consistently reported (Lipp, Price, & Tellegen, 2009; Savage & Lipp, 2015).

However, from the perspective of a feature-based adaptation of facial emotion, indeed, an emotional face could be decomposed into a series of local features. For example, a happy face could be a combination of an upward facing concave curve, two crescent-shaped eyes, and a distinct contrast pattern, all of which could generate aftereffects (for a review see Kohn, 2007). Recognition and adaptation of some emotions, such as sad/happy, could be achieved by the mouth alone (Gosselin & Schyns, 2001; Schyns, Petro, & Smith, 2007; Xu et al., 2008). Therefore, it is possible that face aftereffects (at least for facial expression) ‘... need not reflect specific processes of face processing’ (Webster & Maclin, 1999). Conversely, studies have also reported that the FEA does not require a strict retinotopic overlap between the test and adaptor, although the retinal distance between the two determines the magnitude (Matsumiya, 2014). Fox and colleagues (2007) tried to minimize local adaptation by using emotional faces from different

identities and still observed a diminished FEA compared to that generated by faces with the same identity, suggesting an identity-independent ‘semantic’ adaptation (Fox & Barton, 2007).

Taken together, the adaptation paradigm is a powerful tool for probing the contribution of local versus holistic information in face perception, especially when combining techniques that manipulate perceptual completion levels. While the perception of face viewpoint, identity, and gender relies on both local features and holistic representation, cues for facial emotion recognition are in debate. Importantly, in the realm of face perception, substantial individual differences have been reported (Martin, Berry, Dobranski, Horne, & Dodgson, 1996; Poljac, Poljac, & Wagemans, 2013). The following section will review the possible influence of autistic traits on face perception and adaptation.

1.5 Autistic traits and face adaptation

The Autism Spectrum Disorders (ASD) are characterized by a wide range of deficits in social skills, communication, attention, and a higher tendency to avoid eye contact (Association, 2003; Behrmann, Thomas, & Humphreys, 2006). People with ASD were less accurate in judging/labeling facial expression compared to those age-matched controls (Feldman, McGee, Mann, & Strain, 1993; Feldman et al., 1991), and IQ-matched controls (Braverman, Fein, Lucci, & Waterhouse, 1989). Such deficits could be due to decreased attention to emotional faces (Calder, Lawrence, & Young, 2001), reduced perception of emotion intensity (Smith, Montagne, Perrett, Gill, & Gallagher, 2010), and increased attention to a particular region of the face (Dawson, Webb, & McPartland, 2005). However,

other studies applying similar approaches failed to replicate these findings when controlling for verbal IQ (Loveland, Pearson, Tunali-Kotoski, Ortegon, & Gibbs, 2001; Tracy, Robins, Schriber, & Solomon, 2011). Imaging studies, on the other hand, have consistently reported weaker responses in emotion-focus areas in ASD participants than matched controls, such as the amygdala (i.e. the subcortical pathway) (Kleinhans et al., 2011; Pierce, Müller, Ambrose, Allen, & Courchesne, 2001). On the contrary, ASD patients tend to show larger activation in the areas associated with intention allocation to facial emotions, with a greater focus on specific features (Critchley et al., 2000; Wang, Dapretto, Hariri, Sigman, & Bookheimer, 2004).

Despite the well-observed physiological differences, ASDs showed comparable performance in behavioral tasks such as labeling basic emotions, suggesting that their deficit probably lies in automatic processing but not the cognitive evaluation of emotions (Wang et al., 2004, Kleinhans et al., 2011; Pierce et al., 2001). The idea explains the mixed findings in behavioral studies investigating facial emotion processing in those with ASD, since the deficits are more likely to reveal through tasks involving implicit processing of facial emotions rather than those employing explicit processing (Critchley et al., 2000).

Recent studies have indicated that people with ASD exhibit atypical face aftereffects. For example, Pellicano and colleagues (2007; 2013) reported smaller identity and eye gaze aftereffects in autistic children compared with matched neurotypical controls (NT). Rutherford and colleagues (2012) found that while people with ASD and neurotypical controls (NT) showed comparable FEAs to

happy faces, the ASD group exhibited smaller FEAs to sad faces. More importantly, adapting to negative emotions (e.g. fear, anger, and disgust) evoked negative afterimages (e.g. fear and sad) in people with ASD, in contrast to NT who produced positive aftereffects (e.g. happy), suggesting abnormal processing of emotions in ASD. More recent work, however, reported otherwise. Cook and colleagues (2014) demonstrated comparable FEAs between autistic adults and NT controls. Similarly, Walsh and colleagues (2015a; 2015b) found no group differences in the sizes of identity and figural aftereffects between high-functioning ASD adults and matched controls.

It has been hypothesized that ASD participants may only exhibit seemingly intact emotion adaptation aftereffects due to the atypical processing of faces (Cook et al., 2014). Those with ASD could have developed the use of compensatory face processing strategies to counter any experienced difficulties: for example, non-holistic, whereby they extract facial information from individual facial features rather than processing the face as a coherent whole (Joseph & Tanaka, 2003; Klin, Jones, Schultz, Volkmar, & Cohen, 2002). Support for this suggestion comes from evidence that the mouth appears to abnormally drive emotion perception in those with ASD (Neumann, Spezio, Piven, & Adolphs, 2006; Spezio, Adolphs, Hurley, & Piven, 2007) and their subclinical relatives (Adolphs, Spezio, Parlier, & Piven, 2008). In these cases, seemingly neurotypical face adaptation aftereffects might be due to them perceiving faces from the mouth region.

Rather than being a single phenotype, autism spreads across a large spectrum, from severe autism at one extreme (the ASD) to Asperger's Syndrome and extend

continuously into neurotypical individuals who also share certain traits with autistic subjects (Baron-Cohen, 1997; Frith, 1991). The Autism-spectrum Quotient (AQ) is a self-administered questionnaire designed to measure autistic tendencies in the general population (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). It should be stressed, though, that it is far from clear whether those with ASD (and their subclinical relatives) perceive facial emotion in a similar way as subclinical individuals with high autistic traits. The possibility that there is a diminishing ability to perceive emotion in a holistic fashion as autistic traits increase in the neurotypical population is certainly, however, of interest. Such a finding would infer that those with ASD are not abnormal in their emotion perception *per se*, but merely utilizing a neurotypical face processing strategy that is similar to those that are subclinically high in autistic traits.

These studies, however, allowed participants to look at fully viewable faces. As mentioned above (section 1.2), people with ASD and their relatives may use non-holistic strategies to process facial emotion. By partially obscuring the face, our participants will be required to perceive emotion through amodal completion of the viewable face parts into a gestalt percept. We anticipate that such a paradigm will reveal an association between emotion adaptation and autistic traits that previously went unobserved. By contrast, if no association between AQ and FEA to obscured faces were to be found, then it would imply that holistic perception of facial emotion does not diminish in the form of FEA across increasing levels of autistic traits.

1.6 Outline of the thesis

This thesis aims to study how people infer facial emotion from partially obscured faces and its association with autistic traits. Three studies were conducted and will be illustrated in the following three chapters. In the second chapter, we investigated whether adaptation to obscured emotional faces could lead to FEAs and how does recognizability of facial adaptors influence FEAs. In the third chapter, we examined the relationship between autistic traits and FEAs in neurotypical population. Particularly, we used obscured faces with different amodal completion levels to achieve a more comprehensive understanding of the contribution of local versus holistic information to facial emotion perception. The fourth chapter explored the neural correlates of autistic traits, perceptual completion, and the FEAs in obscured emotional faces using simultaneous EEG and behavioral recordings.

The present thesis could enrich the literature by disentangling the contribution of facial features (local) and holistic information in FEA. Examining the perception and processing of emotional faces under impoverished conditions could help to achieve a more comprehensive understanding of face perception from an ecological approach, and provide theoretical guides for computation vision. Importantly, studying the association between autistic traits and facial emotion perception help to understand of the underlying mechanism of facial recognition deficit in people with high autistic traits. To the best of our knowledge, this is the first study that has been carried out to examine the emotion adaptation in NT with a range of autistic traits, using both behavioral and physiological approaches.

Possible training schemes and intervention therapies could also be proposed to help to improve the quality of life in people with autism.

Chapter II: Facial emotion aftereffect to obscured faces by bubbles technique

Adaptation to a face with a particular expression can induce a repulsive bias in the emotion perception of a subsequent neutral face, the facial expression aftereffect (FEA) (Hsu & Young, 2004; Webster et al., 2004). The FEA has been widely reported in fully viewable faces; however, a mouth or even a simple curve could also generate FEAs (Xu et al., 2008). This finding suggests that the FEA do not require a full face as an adaptor. However, an emotional face could be decomposed into a series of local features as mentioned, all of which could generate aftereffects (Kohn, 2007). Therefore, it is possible that the FEA reflects low-level adaptation. However, other studies observed FEAs when the local information was minimized by changing the identities of the adapting and test faces (Fox & Barton, 2007). Although it has been argued that the change of identity may not well reduce the local aftereffect, as the curvature of the mouth and orientation of lines for the same emotion is independent of identity (Butler et al., 2008). Nevertheless, local information, such as the mouth, could generate FEAs. One important question remains: do other parts of the face contribute to the FEA, and if so, under what circumstances?

To address this question, we used the bubbles technique (Gosselin & Schyns, 2001) to manipulate the face features visible during adaptation. By varying the position and size of small apertures, or “bubbles”, through which part of the stimulus is visible, one can identify/locate the most informative features in the

stimulus (Gosselin & Schyns, 2001). For facial expression, placing bubbles near the mouth region makes emotion, e.g. happy or sad, more identifiable than placing the bubbles over other face regions (Chen & Chen, 2010; Gosselin & Schyns, 2001). In the current study, we used adaptors in which bubbles were placed either over the emotion-recognizable mouth regions or over the emotion-unrecognizable regions away from the mouth, in order to determine the contribution of different facial features to the judgment of facial expression and FEAs. Specifically, we aimed to determine whether FEAs occur after adapting to static, emotion-unrecognizable bubbled-face images (Experiment 1), whether FEAs occur following adaptation to video-sequences of emotion-unrecognizable bubbled-faces (Experiment 2), and whether FEAs are affected by the size and location of the bubbled faces during adaptation (Experiment 3). The results of the study have enabled us to determine the extent to which the visual system is able to integrate information about the facial expression that on its own is below the threshold for perceiving facial expression.

2.1 Experiment 1.1

2.1.1 Method

Subjects

A total of seven participants (five males and two females, average age: 26.7 years), with normal or corrected-to-normal vision, participated in the study. All participants were naïve to the purpose of the study. The study was approved by the Institutional Review Board at Nanyang Technological University, Singapore.

Apparatus and Research Stimuli

Stimuli were presented on a 17-inch Samsung monitor (SyncMaster 793MB) with a refresh rate of 85 Hz and a spatial resolution of 1024×768 . The monitor was controlled by an iMac Intel Core i3 computer. A chin rest was fixed at 75 cm from the monitor, making each pixel subtend 0.024° . Luminance was measured by a Minolta LS-110 photometer. Experiments were run in Matlab R2010a using Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Face images were obtained or derived from the Karolinska Directed Emotional Faces database (KDEF) (Lundqvist, 1998).

Test stimuli. Happy, sad, and neutral emotion face images of the same person were taken from the KDEF database. The faces were cropped to a size of $2.50^\circ \times 3.02^\circ$ to ensure that they only included facial features. We used MorphMan 4.0 (STOIK Imaging, Moscow, Russia) to generate the intermediate facial expressions in steps of 0.05 by morphing the happy and neutral faces, and the neutral and sad faces. Twenty-one faces with equal-step changes were generated, with happiness ranging from 0 (sad) to 1 (happy) in proportions of 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8 and 0.9. Example stimuli are shown in Fig 2.1.

Figure 2.1 Face stimuli used in experiment 1.1

a. Test stimuli (varying from sad to happy). **b.** Examples of emotion-recognizable bubbled faces. **c.** Examples of emotion-unrecognizable bubbled faces.

Adapting stimuli. We developed four sets of adapting stimuli: the sad face and three sets of bubbled faces derived from the sad face. The three sets of adaptors were: 1. mouth only; 2. emotion-unrecognizable static faces and 3. emotion-recognizable static faces. To minimize adaptation aftereffects generated by local information, we enlarged the size of the adapting stimuli from $2.50^\circ \times 3.02^\circ$ to $2.98^\circ \times 3.50^\circ$.

For the mouth only adaptor, we first added a gray mask onto the original photo, and then punctured the mask in the mouth region using a Gaussian aperture. For the emotion-unrecognizable and recognizable static faces, we generated 180 adaptors by applying the bubbles technique to the happy and sad faces (i.e. 90 images for each emotion). Specifically, four Gaussian apertures with a radius of 8 pixels and a fuzzy coefficient of 3 units (to blur the bubble surroundings, similar to

the standard deviation of a Gaussian function) were randomly positioned on the two emotional faces. Next, we ran a pre-experiment (described in detail in the “*pre-experiment*” section in *Procedure*) to determine which of the bubbled faces were emotion-recognizable and which were emotion-unrecognizable. Based on the results of the pre-experiment, we then selected the emotion-recognizable faces as those judged $> 94.4\%$ in the accuracy as emotion-recognizable, and the emotion-unrecognizable faces as those judged between 43.3% and 55% in the accuracy as emotion-unrecognizable. We randomly selected nine faces from each category (see examples in Figure 2.1b & c). In the category of unrecognizable faces, the nine faces we selected were those with subtle emotional cues, such as eyes, but the information was too limited plus placed in the peripheral and therefore, people cannot tell the emotion. In this case, we have 36 faces in total (in each category: emotion $\times$ recognizability $\times$ number of faces = $2 \times 2 \times 9$).

Stimulus arrangement. A black fixation cross (0.62 cd/m^2) was presented on a white background (69.89 cd/m^2) throughout the experiments. The fixation cross consisted of a vertical and a horizontal line subtending 0.34° and 0.048° , respectively. All visual stimuli were presented on the right side of the fixation cross at distances detailed below.

Procedure

We used the constant stimuli and two-alternative-forced-choice (2-AFC) research paradigm in all experiments.

Pre-experiment. (static face recognizability test). This experiment classified the static bubbled faces into emotion-recognizable and emotion-unrecognizable

categories. Six subjects participated in this test. There was a total of 180 bubbled faces, half of which were happy faces and half sad faces. Participants were instructed to maintain their fixation on the cross throughout the experiment. Stimuli appeared for 4 s and participants judged the facial expression as happy or sad via a key press. If participants did not decide within 3 s after the stimulus disappeared, the face was classified as unrecognizable.

All except 4 trials out of the total of 3240 produced responses within 3 s. From the results, we identified 36 static faces divided into 4 categories: static recognizable happy; static recognizable sad; static unrecognizable happy; and static unrecognizable sad. The mean accuracy for static recognizable images was 98.2%, and for unrecognizable ones 51.03%. We also calculated response bias (c) ranging from -1 to 1, with positive values suggesting a conservative tendency and 0 suggesting no bias. D-prime measures sensitivity, a score of 0 suggests an inability to differentiate happy and sad. In the 2AFC task, a score of 0.75 is often used to define the threshold, although other values may also be used (Harvey Jr, 2003). The sensitivity was roughly normal-distributed according to the Shapiro-Wilk test (all $ps > .05$). The sensitivity of discriminating the sad unrecognizable static faces (the adapting faces) were: $d' = 0.23$, and the bias $c = 0.088$. One-sample t -tests of the d' revealed no difference from 0 ($t_{(5)} = 2.38$, $p > .05$), indicate no discriminability in facial emotion for the sad unrecognizable static faces.

Experiment 1 determined whether the recognizability of the adapting facial expression affected the FEA. The test stimulus was the full face taken from the face

set (section *Test Stimuli*). There were five conditions: 1. full face adaptor (F); 2. mouth-only face adaptor (M); 3. static-recognizable face adaptor (SR); 4. static-unrecognizable face adaptor (SU); and, 5. no-adaptor baseline (N). For the static-recognizable and static-unrecognizable face adaptation conditions, one of the nine adapting faces from the corresponding group appeared as the adaptor. The adapting face varied from trial to trial in random order. The center-to-center distances from the fixation cross to the stimuli were 3.84° and 3.24° for the adaptor and test, respectively. This difference, together with the stimulus size difference ($2.98^\circ \times 3.50^\circ$ for the adaptor vs. $2.50^\circ \times 3.02^\circ$ for the test), was designed to minimize the effects of localized, low-level contrast and luminance adaptation.

The five conditions were tested in a randomized block design, and the order of the test stimuli and adaptors was also randomized. Each condition was tested in two sessions. Within each session, the test stimuli were repeated 10 times. Each with-adaptation session typically lasted for 10 mins, and the baseline session took 3 mins. Participants had a ten-minute break between sessions to prevent carry-over effect (subjects may experience aftereffect after the adapting stimulus disappears) between two consecutive sessions.

Participants were required to maintain eye fixation on the central cross throughout the entire session. For the with-adaptation conditions, the adapting stimulus appeared and lasted for 4 s. After a 506 ms inter-stimulus-interval, the test stimulus was displayed for 200 ms, followed by a 50 ms beep to remind participants to respond (Figure 2.2). The screen remained blank until they responded. No feedback was given at any time.

Figure 2.2 Trial sequence for the static emotion-unrecognizable adaptation condition in Experiment 1.1. Example is condition “SU”. Subjects fixated on the cross and pressed the space bar to initiate a trial block. After 506 ms, the adapting face appeared for 4 s. After a 506 ms inter-stimulus-interval (ISI), a test face appeared for 200 ms. A beep was played to remind subjects to press the appropriate key to report a happy or sad expression of the test face. In actual experiments, the fixation cross was always at the center of the screen.

Data analysis. Psychometric functions of the proportion of happy response trials as a function of stimuli proportion of happiness were fitted for each subject with the Sigmoidal (logistic) function in the form of $f(x) = 1/[1+e^{-a(x-b)}]$, where b is the test-stimulus parameter corresponding to 50% of the psychometric function [point of subjective equality (PSE)] and $a/4$ is the slope of the function at the PSE. We used a two-tailed paired t -test to compare subjects’ PSEs or the slopes for different conditions in the experiment. Aftereffect was measured as the difference between the PSE of an adaptation condition and the PSE of the corresponding baseline condition. We used the convention that repulsive aftereffects were negative. Analyses were performed in Matlab.

2.1.2 Results

The results from one naïve subject are shown in Figure 2.3a. The Figure plots the proportion of happy responses as a function of the stimuli's proportion of happiness. The black curve is the baseline condition without adaptation (N). After adapting to the saddest face, the psychometric function for the full face adaptor shifted to the left – this is the expected FEA(Hsu & Young, 2004; Webster et al., 2004). Adapting to the mouth-only image also produced a significant FEA, as noted in previous work (Xu, Dayan, Lipkin, & Qian, 2008b). However, new findings were observed for the bubbled face adaptors: the static emotion-recognizable adaptors produced a small facial expression aftereffect, whereas the static emotion-unrecognizable adaptors produced no aftereffect. Figure 2.3b shows the average FEAs across the seven subjects for all four conditions. Each FEA was calculated as the difference between the adaptation and baseline PSEs, and the error bars are standard errors of means (SEM) of the average FEAs calculated across subjects. Shapiro-Wilk test showed that FEAs were normally distributed (all $ps > .10$). Two-tailed paired t -tests were conducted on the differences between the adaptation and baseline PSEs, and the resulting p -values are shown. Figure 2.3b shows that all FEAs were significant, except the static emotion-unrecognizable FEAs. We also compared the mouth, and full face or emotion-recognizable FEAs, and the differences were significant or marginally significant ($p = .0023$ and $p = .056$, respectively). We then conducted a post hoc power analysis to see whether there is enough power to detect the difference. The powers for face, mouth, static recognizable and static unrecognizable face adaptation conditions (F, M, SR, and

SU) were 0.83, 0.62, 0.55 and 0.03, respectively, which were in line with their significance levels.

Figure 2.3 Facial expression aftereffect in Experiment 1.1. Psychometric functions from a naïve subject on facial emotion judgment (happy vs. sad). The five curves represent baseline condition (no adaptor, solid black circle, N), adaptation to a full sad face (dashed red star, F), adaptation to a sad mouth (dash-dot magenta cross, M), adaptation to a set of static recognizable faces (dashed blue triangle, SR), and adaptation to a set of static unrecognizable faces (dotted green square, SU). **b.** Summary of data from all seven participants. The error bars represent the SEM.

In this experiment, we measured the FEA in full test faces using adaptors with different amounts of available emotional information. Adapting to a single face part, for which subjects were unable to recognize the emotion, did not generate a significant FEA. As the information was presumably too limited to activate the relevant perceptual mechanisms and thus participants were not able to consciously aware of the expression. How does this square with the results of studies that have manipulated awareness using methods other than bubbles? Three of these methods are crowding, continuous flash suppression (CFS) and masking.

First, the effect of crowding on adaptation. He et al. (1996) and Rajimehr et al. (2003) found that adapting to a crowded stimulus did not reduce an aftereffect in perceived orientation. However Blake et al. (2006) showed that provided the crowded adaptor was low in contrast, a reduction in the orientation aftereffect caused by crowding could be obtained, suggesting that the high contrast adapting stimuli in the experiment by He et al. (1996) and Rajimehr et al. (2003) remained at saturation point even when crowded. For more complex features such as faces, adapting to a crowded face reduces the FEA (Liu, Ong, & Xu, 2012; Xu, Liu, Dayan, & Qian, 2012). Crowding mainly affects the ability to identify the details of the target rather than its visibility or presence (Whitney & Levi, 2011). In the present study subjects could see the static emotion-unrecognizable face adaptors but could not identify their emotion, and we did not find significant FEAs, in line with Xu et al. (2012) who also used static faces as adaptors.

Second, masking on adaptation. Of most relevance here is the paradigm in which an aftereffect is measured using an adaptor whose visibility is reduced or eliminated by a masking stimulus but which nevertheless continues to produce an aftereffect. Sweeny et al. (2011) measured a shape aftereffect using an adaptor shape whose visibility could be reduced by a mask in the same eye (termed monoptic masking) or obliterated by a mask in the other eye (termed dichoptic masking). The adaptor shape was an open- or closed-curved oval shape and subjects were instructed to adjust a test oval or circle to a particular shape, with the degree of adjustment indicating the size of the aftereffect. The mask consisted of scrambled lines. Sweeny et al. (2011) found a double dissociation for the open and

closed adaptor curves, with the dichoptic masking eliminating the closed- but not open-curve aftereffect, and monocular masking eliminating the open- but not closed-curve aftereffect. These results suggest that the closed-curve but not open-curved aftereffects depend on the subject's being aware of the adaptor. Sweeny et al.'s findings are pertinent because an open curve is similar to the curve of a mouth whereas a closed curve describes the outline contour of a face. This is arguably consistent with our finding that the FEA, which is based on adaptation of features such as the curve of the mouth, does not depend on visual awareness of those adaptor features.

Third, continuous flash suppression (CFS) on adaptation. In this paradigm, subjects are typically presented with a static stimulus in one eye and a series of rapidly changing stimuli in the other eye, resulting in suppressed perception of the static stimulus [18]. Moradi et al. (2005) showed that reducing the visibility of the adapting face decreased the face identity aftereffect (distinct from the facial emotion aftereffect, i.e. FEA), and when the adapting face was invisible, the identity aftereffect vanished. Therefore, for face identity aftereffects, awareness of the adapting face appears to be necessary. Previous studies on the facial expression aftereffect (FEA) using continuous flash suppression have produced mixed results. Adams et al. (2010) found that FEAs survived the effects of CFS, suggesting that FEAs are not dependent on awareness of the adapting face (Adams et al., 2010). On the other hand, Yang et al. (2010) found in an initial experiment that FEAs did not survive CFS, suggesting that FEAs do depend on awareness of the adapting face. However, Yang et al. went on to show that the reduction in FEA caused by

the CFS was probably caused by inattention. However, we did not measure the attention allocation of the participants during the experiment, although the abrupt onset when the stimuli appeared could grab attention automatically (Peelen, Heslenfeld & Theeuwes). However, the duration of the adaptor was around 4 seconds, therefore, it is possible that the FEAs might be associated with participants' attention differences to these faces (Rhodes et al., 2011).

To summarize this section: the findings from the studies above using crowding, masking or CFS are mixed with respect to the need for awareness of the adaptor emotion for producing FEAs, with most studies supporting the idea that awareness is not necessary, as we find here. It is worth emphasizing however that in all three of the above methods the adaptor stimulus was physically complete when presented, so any reduction or abolition of perception must have been caused by competition between images, or rather between their neural representations (Keysers & Perrett, 2002). However, with the bubbles technique, the adaptor is physically incomplete when presented. Therefore, the discrepancies between previous studies and ours regarding whether or not awareness of the adaptor emotion is necessary to produce FEAs might ultimately be a consequence of the difference in the nature of the visual input, though for what precise reason is unclear. Since the human brain prioritizes dynamic stimuli over static ones, we conducted experiment 2 by adapting the subjects to dynamic bubbled-face to examine FEA.

2.2 Experiment 1.2

2.2.1 Method

Subjects The same 7 subjects from Experiment 1 participated in this study, four of which participated in the control experiment.

Stimuli

Test stimuli. The same set of test faces as experiment 1.

Adapting stimuli. We categorized the bubbled faces into 4 emotion/recognizability categories (e.g., sad recognizable) in Experiment 1, with a total of 36 faces (differ in emotion and location of the bubbles). To create the dynamic adaptors in Experiment 2, nine faces from the same category (e.g. sad emotion-recognizable) were combined into a video sequence in a random order. Only the sad emotion was used as adaptor. Thus, we have the two adapting videos: 1. dynamic emotion-unrecognizable video (DU), with all nine faces selected from the sad emotion-unrecognizable group; and 2. dynamic emotion-recognizable video (DR), with all nine faces from the sad emotion-recognizable group.

Procedure

Dynamic face video recognizability test. This test examined whether participants were able to recognize the facial emotions of the adaptors. All 7 subjects participated in this test after they had completed experiment 2. The procedure for the dynamic recognition task was the same as for the static recognition task, except for the duration. In this task, each facial frame was presented for 435 ms with no between-frame interval such that the whole sequence took 3.92 s. Participants indicated whether they perceived a happy or sad face via a

key press. Table 1 summarizes the results. The mean accuracy of the unrecognizable sad dynamic faces was 50.71%, which is close to chance performance, whereas the mean accuracy of the ‘unrecognizable’ dynamic happy face videos was above chance at 72.86%. To fully capture the discriminability of emotional faces by the participants, we calculated the d-prime (d') and response bias (c). Our results for the unrecognizable sad adaptors were: $d' = 0.627$ and bias $c = 0.295$. One-sample t -tests of the d' revealed a marginally significant difference from 0 ($t_{(6)} = 2.3$, $P = .06$), indicating participants are more sensitive in discriminating the two emotions in unrecognizable dynamic settings compared with static ones ($d' = 0.23$). Taking response bias into account, participants may have a tendency to respond to the stimuli as happy.

Table 1. Mean correct recognizable and unrecognizable emotional faces.

	Dynamic happy videos	Dynamic sad videos
Recognizable	91.43%	87.14%
Unrecognizable	72.86%	50.71%

Experiment 2 examined the FEAs generated by dynamic adaptors. The procedure was identical to Experiment 1, except that the adaptor was a dynamic sequence of bubbled faces instead of a static bubbled face. In both conditions, each of the nine facial frames was displayed sequentially for 435 ms in a random order, and thus the duration for a dynamic adaptor in each trial was 3.92 s. The sequence of faces varied from trial to trial. We compared the aftereffect from the dynamic adaptor with that of the static adaptor from the previous experiment.

Control experiment. Four of the above seven subjects also participated in the following control experiment. The dynamic face video adaptor was comprised of nine faces, and hence contained more facial expression information than the static face adaptation condition. To examine whether the aftereffect difference between the dynamic and static face adaptors was caused by this information difference, we performed a control experiment in which the adaptors were single composite faces constructed by combining bubbled faces from the dynamic condition. To construct such composite face, we first recorded the locations of all the bubbles of the nine selected faces from each category, then superimposed the bubbles and finally punctured them through a gray-masked face. We did this for the sad-unrecognizable, sad-recognizable, happy-unrecognizable, and happy-recognizable faces. We then tested the ability of the subjects to discriminate the facial expressions of the above four composite faces. The procedure was identical to the pre-experiment, except the face presentation duration was 435 ms in task one and 3.92 s in task two. The 435 ms duration was the same as that of a single frame in the dynamic video, and the 3.92 s duration equaled that of the entire dynamic video. We then tested subject performance using the composite face with bubbles from all sad-unrecognizable faces as the adaptor, and the adaptation durations were either 435 ms or 3.92 s.

2.2.2 Results

In experiment 2, dynamic sequences of emotion-unrecognizable and emotion-recognizable bubbled faces were used as adaptors. Note that the adaptation duration was similar to the static face adaptation (3.92 s) and the data were

collected from the same subjects in Experiment 1. Subject performance under these conditions was compared with the static face adaptation conditions (SR and SU) from the Experiment 1 (Figure 2.4). The results from one naïve subject (the same as in Figure 2.3a) are shown in Figure 2.4a. Interestingly, adapting to emotion-unrecognizable dynamic faces shifted the curve similarly to that of the other three adaptation conditions from the baseline condition. Figure 2.4b shows the mean FEAs across seven subjects. Except for the static unrecognizable face adaptation condition (SU), all other adaptation conditions produced significant FEAs. The powers for SR, DR, SU and DU were 0.55, 0.82, 0.03 and 0.85, respectively, in line with the significance of FEAs.

Figure 2.4 Facial expression aftereffect in Experiment 1.2.

a. Psychometric functions from a naïve subject on facial emotion judgment (happy vs. sad). The five curves represent baseline condition (no adaptor, solid black circle, N), adaptation to static emotion-recognizable face (blue dashed thin open triangle, SR), adaptation to dynamic emotion-recognizable face video (blue dashed thick filled triangle, DR), adaptation to static emotion-unrecognizable face (green dotted thin open square, SU), and adaptation to dynamic emotion-unrecognizable face video (green dotted thick filled square, DU). **b.** Summary of data from all seven participants. The error bars represent the SEM.

Control experiment. Does the dynamic face video contain more information than the static face? We then tested the subjects' ability to discriminate the composite faces, and also measured FEAs using the composite faces as adaptors. In the discrimination task, subjects had to judge facial expression of the composite face. The face image was presented for 435 ms or for 3.92 s. Results revealed that discrimination depended on face stimulus duration (See Figures 2.5a & 2.5b). In general, longer display duration led to higher accuracy, but longer adaptation duration affected the unrecognizable faces more than recognizable faces.

Figure 2.5 Control experiment.

a. Judgment accuracy for short display (435 ms) of the single composite face for happy-recognizable (red bar) is 90.0%, 89.2% for sad-recognizable (blue bar), 71.2% for happy-unrecognizable (orange bar), and 48.3% for sad-unrecognizable (green bar). **b.** Judgment accuracy for long display (3.92 s) of the single composite face (99.4%, 98.6%, 87.5%, and 81.9% for happy-recognizable, sad-recognizable, happy-unrecognizable, and sad-unrecognizable, respectively). **c.** FEAs from adapting to sad-unrecognizable faces at short adaptation duration (435 ms) and long adaptation duration (3.92 s), and baseline condition (0-f). The error bars represent the SEM.

Adapting to the composite unrecognizable faces revealed that FEAs were also duration dependent (Figure 2.5c). Adapting to sad-unrecognizable composites at short adaptation durations (435 ms) did not generate a significant FEA ($p = 0.831$), whereas adapting to the same composite face at longer duration (3.92 s) did

generate a significant FEA ($p = 0.008$). Although it seems that the higher the classification accuracy in the adapting composite faces, the larger the facial expression aftereffect, the correlation between the two is not significant ($r = -0.35$, $p = 0.395$).

2.2.3 Discussion

Although prolonged exposure to static emotion-unrecognizable face did not bias the perception of the emotion of subsequent faces (measured by FEA), the dynamic counterpart did. As dynamic adaptors contained more information on facial expression than the single face adaptors, we performed a control experiment that collapsed all face parts from the dynamic sequence into a single face. When the composite face was presented for the same frame duration as the static adaptors (435 ms), it did not produce a significant FEA. However, when presented for the 3.92s duration of the dynamic adaptor, the composite face did produce a significant FEA.

Therefore, FEAs from the dynamic visual adaptors most likely have resulted from the temporal integration of the sequence of briefly presented faces (435 ms per frame). We appear to be able to integrate the parts of faces into a whole across time. In our everyday visual experience of moving objects, we typically store information from previous images in a visual buffer and then combine them with incoming images (Anaki et al., 2007; Treisman, 1999). Perceptual integration of this sort will generate a different pattern of brain activation compared with a static scene with the same (or even more) information. Using square apertures to reveal a

background image, such as a face or building, James et al. (James, Huh, & Kim, 2010) reported stronger and more sustained brain activation when viewing an aperture of changing images compared with a static scene.

Perceptual integration across time appears to be mediated by brain regions such as the right occipitotemporal and middle cingulate cortical areas (Kadosh, Walsh, & Kadosh, 2010; Lee, Anaki, Grady, & Moscovitch, 2012). It has been shown that dynamic face videos activate the right posterior superior temporal sulcus (pSTS) and right anterior STS (aSTS), whereas static face images from these same face videos activate the right fusiform face area (FFA) and the right occipital face area (OFA) (Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011). It is possible that the dynamic bubbled face videos used in our experiment not only activated face processing regions such as the STS and the inferior temporal cortex, but also regions responsible for image integration, such as the right occipitotemporal cortex and middle cingulate cortex. Further investigations of the brain regions involved in dynamic bubbled face adaptation are needed.

2.3 Experiment 1.3

2.3.1 Method and Results

We examined whether the FEAs generated by dynamic emotion-unrecognizable faces transferred across size and location. For size, we used adapting faces that were larger, the same size or smaller than the test face. Because the total number of conditions was relatively large ($n = 7$), we only presented the average data across subjects.

Results are shown in Figure 2.6a. The black bar is the baseline no-adaptor condition (N), the solid magenta bar is the large adaptor presented at the same location as the test face (S_{big}), the solid blue bar is the same adaptor presented at the same location as the test face (S_{same}), and the solid green bar is the small adaptor presented at the same location as the test face (S_{small}). Shapiro-Wilk test showed that FEAs were normally distributed (all $ps > .09$). Both larger and same-sized adaptors generated significant FEAs ($p = 0.02$ and $p = 0.0057$, respectively), but the smaller adaptor did not. Thus, the FEA produced by the dynamic emotion-unrecognizable adaptors appeared to be dependent on the relative size of the adaptor and test faces.

We next examined location specificity. Using the same-sized adaptor and test, we positioned the dynamic adaptor below the fixation point such that there was no overlap between the adaptor and test. We also applied the same manipulation to the larger and smaller adaptors. The results from the seven subjects are shown in Figure 2.6a. The dashed magenta, blue, and green bars are the larger, same-sized and small adaptors, respectively (L_{big} , L_{same} , and L_{small}) presented at the below-fixation-point location. Both larger and same-sized adaptors generated significant FEAs ($p = 0.045$ and $p = 0.011$), but the smaller adaptor did not ($p = 0.451$). Comparing FEAs from different locations, the two magenta bars (solid vs. dashed, S_{big} vs. L_{large}), two blue bars (solid vs. dashed, S_{same} vs. L_{same}), and two green bars (solid vs. dashed, S_{small} vs. L_{small}) were of similar magnitude. Therefore, the relative location of the adaptor and test did not matter for FEAs produced by dynamic

emotion-unrecognizable adaptors. This differed from our previous findings using static face adaptors(Xu et al., 2008, and 2012).

Figure 2.6 Transfer of FEA across size and location with dynamic face adaptation.

a. Average FEAs from all seven participants, calculated as mean PSE shift from baseline (N, black). The first three bars are for larger-, same-, and smaller-sized adaptors compared to tests (magenta – S_{big}, blue - S_{same}, and green - S_{small} solid hatched bars). The next three bars are the same conditions but at a lower location (magenta – L_{big}, blue - L_{same}, and green - L_{small} dotted hatched bars). The error bars indicate SEMs. The *p*-values were obtained from paired *t*-tests. **b.** Size and location conditions, blue curve: adaptor and test at the same location; green curve adaptor at a lower location than the test.

Figure 2.6b shows the effects of size and location on aftereffect. The blue curve is for the dynamic adaptor and test faces at the same location; the green curve is for dynamic adaptor below the test face. The two curves are parallel for the smaller and same-sized adaptor and test, but cross when the adaptor is larger than the test. The interaction between size and location was not significant ($p = .527$).

To summarize the results of Experiment 3, FEAs using dynamic unrecognizable adaptors depended on the relative size (small vs. same/large) but not the location of the adaptor and test.

2.3.2 Discussion

We measured the FEA in full test faces using adaptors in which only parts of the face were visible at any one time. Adapting to a single face part, for which subjects were unable to recognize the emotion, did not generate a significant FEA, but when a temporal sequence of different emotion-unrecognizable face parts was used as the adaptor, FEAs were significant. Moreover, FEAs from the dynamic adaptor sequences were independent of the relative locations of the adaptor and test, though not entirely independent of their relative size.

Our dynamic adaptors, which consisted of sequences of face parts, contained more information on facial expression than the single face adaptors. A control experiment that collapsed all face parts from the dynamic sequence into a single face, presented for the same frame duration as the static adaptors (435 ms), failed to produce a significant FEA. However, when presented for the dynamic adaptor duration of 3.92s, the composite face did produce a significant FEA. The reason for this was that subjects were only able to accurately identify the emotion of the composite face in the 3.92 s duration condition, as revealed in the control experiment.

Therefore, FEAs from the dynamic visual adaptors must have resulted from the temporal integration of the sequence of briefly presented faces (400 ms per frame). We appear to be able to integrate the parts of faces into a whole across time. In our everyday visual experience of moving objects, we typically store information from previous images in a visual buffer and then combine them with incoming images (Anaki et al., 2007; Anaki & Moscovitch, 2007; Treisman, 1999).

Perceptual integration of this sort will generate a different pattern of brain activation compared with a static scene with the same (or even more) information. Using square apertures to reveal a background image, such as a face or building, James et al. (2010) reported stronger and more sustained brain activation when viewing an aperture of changing images compared with a static scene.

Perceptual integration across time appears to be mediated by brain regions such as the right occipitotemporal and middle cingulate cortical areas (Kadosh et al., 2010; Lee et al., 2012). It has been shown that dynamic face videos activate the right posterior superior temporal sulcus (pSTS) and right anterior STS (aSTS), whereas static face images from these same face videos activate the right fusiform face area (FFA) and the right occipital face area (OFA) (Pitcher et al., 2011). It is possible that the dynamic bubbled face videos used in our experiment not only activated face processing regions such as the STS, but also regions responsible for image integration, such as the right occipitotemporal cortex and middle cingulate cortex. Further investigations of the brain regions involved in dynamic bubbled face adaptation are needed.

2.4 General Discussion

2.4.1 Does attention facilitate adaptation to dynamic images?

When viewing a novel scene, people first distribute their attention across the scene before homing in on the object of interest (Desimone & Duncan, 1995; Wu, Libertus, Meyerhoff, & Woldorff, 2011). Focal spatial attention is then allocated to the target, facilitating categorization and additional processing (Treisman, 1999). In our study, each frame of the dynamic face revealed very limited information about

the sadness. To gain information on the entire dynamic video, subjects had to pay attention to the dynamic adapting stimulus. Perception of dynamic images can induce greater and more sustained attention compared with static images (Kessler et al., 2011; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004). Therefore, it is possible that attention remained at a high level across the presentation of dynamic bubble faces. This possibility invites future studies on eye movement patterns when viewing dynamic face videos.

In our experiments, since we did not monitor eye movements during face adaptation, subjects may have not always fixated on the point position and instead looked at the dynamic faces directly. This would have had two consequences: first, it would have increased the accuracy for judging the static and dynamic faces during adaptation, and second it would have reduced the adaptation aftereffect which increases with adapting stimulus eccentricity (Gheorghiu, Bell, & Gurnsey, 2011). These may be the reasons why we did not observe a strong correlation between the judgment accuracy of the adapting stimulus and the FEA. However, we do not know whether subjects tended to break fixation more in the dynamic than the static faces, or if they did so equally to both.

Our previous study (Xu et al., 2008) observed position specificity in FEAs generated by static simple curves or real face adaptors. In the current study, the FEA generated by dynamic bubble faces survived location and size changes, indicating the involvement of different mechanisms from the ones involved in static face adaptation. The involvement of different mechanisms may imply top-down influence such as attention. The role of attention in adaptation-driven

aftereffects is controversial. Some studies reporting that attention reduces aftereffects, while others have indicated that it enhances them (Rezec, Krekelberg, & Dobkins, 2004; Rhodes et al., 2011; Sarter, Givens, & Bruno, 2001; Shibui, Izawa, Harashima, & Shigemasa, 2003). Our study supports the latter.

2.4.2 What are the possible neural pathways for perceiving facial emotions from the bubbled faces?

Affective stimuli could be detected in a non-conscious, fast but coarse fashion (LeDoux, 1996; Williams et al., 2004). There are two main approaches that can render the target objects unrecognizable, as mentioned in section 1.2. One approach applies a dual-task paradigm and exhausts attentional resources by requiring participants focusing on an attention-absorbing task, and the second irrelevant task may fail to reach consciousness due to insufficient attention. Such operation has been referred to as the ‘unattentional awareness’. However, if the irrelevant task is an emotional stimulus (e.g. a fearful face), participants are more likely to correctly ‘guess’ the emotion conveyed. In this circumstance, both the cortical (e.g. portions of the OFA) and subcortical pathways (e.g. amygdala) are involved in the processing of the unconsciously perceived emotional stimuli (Tamietto & De Gelder, 2010). The other approach, known as the ‘sensory unawareness’ refers to situations that the signal strength of the stimulus ‘is insufficient to evoke cortical activity in visual areas..., (but) can trigger activity in subcortical visual structures, such as the superior colliculus, that have a lower threshold of activation’, and typical examples include backward masking and

binocular rivalry (Tamietto & De Gelder, 2010, P698). For instance, when eye-whites from a fearful face was rendered invisible using backward masking, the amygdala still responded to it even though participants were not aware of the expression (Whalen et al., 2004). Patients with cortical blindness, which refers to vision loss due to damage of striate cortex, could nevertheless recognize/differentiate facial or body emotional information without consciously perceiving them (Burra et al., 2013; Whalen et al., 2004). When stimuli were presented at the blind visual field, bilateral subcortical regions, and the right FFA were activated. Single unit recordings in monkeys and clinical patients reinforced the involvement of subcortical areas in the rapid face and facial emotion processing (Maior, Hori, Tomaz, Ono, & Nishijo, 2010; Rutishauser et al., 2011). Some pulvinar neurons could differentially respond to emotions in a short latency (<100 ms) (Maior et al., 2010). Testing on neurosurgical patients with implanted depth electrodes, half of the tested amygdala neurons responded to faces or parts of faces. About 10% responded differently to emotions, gender or identity. For the face-selective neurons, about 1/3 responded to bubbled faces, about 1/4 to whole faces, about 1/7 to eye cutouts and 1/5 to mouth (all in comparison to a face-scrambled baseline) (Rutishauser et al., 2011).

Although it has been suggested that affective stimuli rendered invisible due to the 'sensory unawareness' are predominantly processed by the subcortical pathways (Tamietto & De Gelder, 2010), evidence for cortical processing also exists (e.g. Jiang & He, 2006; Cumming & Park, 1997; Masson, Busetini & Miles, 1997). For instance, the STS has been found robustly react to invisible fearful face

rendered through binocular rivalry (Jiang & He). Likewise, V1 that typically responds to visual disparity could also be activated by anticorrelated random-dot stereograms which do not evoke a perception of depth (Cumming & Park, 1997). This disparity-vergence is processed by cortical pathways (Celebrini & Newsome, 1995).

In our study, we rendered the emotional faces unrecognizable by masking the majority of the critical areas for the perception of facial emotions, and the adaptors were presented in the peripheral visual fields thus made it more difficult to judge the emotions based on very limited affective cues. It is thus reasonable to assume that our bubbled faces (at least) activated subcortical regions, which did not support conscious awareness of the emotion recognition but could detect salient facial features and contribute to the FEAs. Furthermore, the subcortical regions, such as superior colliculus, could send information to the pulvinar which further projects to the extrastriate cortex and induces FEAs (Krauzlis, Lovejoy, & Zénon, 2013; Tamietto & De Gelder, 2010).

In addition, viewing the incomplete bubbled faces may activate the amodal completion process. In a study conducted by Lin and He (2012) (Lin & He, 2012), they found that prolonged exposure to leftward/rightward moving diamond displayed behind circular apertures would bias the perception of a subsequent stimulus to the other end. Particularly, the adaptation aftereffect survived even when there was no overlap between the adapting and test stimuli. Previous studies found that amodal completion occurs faster in moving images compared to static

ones (Sekuler & Murray, 2001). This could also partly explain stronger FEA in the dynamic unrecognizable condition besides of increased attention.

2.5 Summary of Study I

To summarize, study I showed that adaptation to obscured faces whose emotion was recognizable could lead to FEAs, regardless of the dynamics. However, FEAs to emotion-unrecognizable faces depends on the dynamics of the adaptor, and could be generated by the dynamic, but not the static emotion-unrecognizable faces. Significant FEAs in the former case might be due to increased attention, enhanced amodal completion strength and extensive pathways for the processing of facial emotion that is beyond conscious awareness, especially for the subcortical pathways. In addition, the FEAs survived the size change between the adaptor and the test faces, indicating the contribution of holistic information in the perception of facial emotion. However, there are substantial individual differences as revealed in the large error bars in the results section. The following chapter examines the possible association between autistic traits and FEA to obscured emotional faces.

There are a few limitations of the current study. Firstly, we did not use an eye tracker to monitor eye movements to ensure participants fixate on the central cross throughout the whole experiment. Secondly, the discrimination of the dynamic video was conducted afterward, where a tendency toward conservative judgment was observed. However, this result alone cannot nullify our findings, since there was no response bias in the initial discrimination test. The bias

developed later may be due to the long-lasting effect of adaptation (Carbon & Ditye, 2012).

CHAPTER III: Association between autistic traits and emotional adaptation in incomplete faces

The previous chapter showed that adapting to expression-recognizable partial faces biased judgments of subsequent facial emotions regardless of the dynamics. Surprisingly, the FEAs persisted even when the emotion conveyed by the adaptor was unrecognizable, although only in the dynamic condition. The FEAs in the dynamic unrecognizable condition was tolerant to locational change between the adaptor and test faces, indicating the contribution of holistic information in facial emotion perception. In both cases, the visual system somehow manages to overcome the missing information and nevertheless influence our sensation. However, there are substantial individual differences in the FEAs in our previous study. It is partly because of discrepancies of the participants' abilities to group and utilize the available emotional information. In this study, we are interested in whether FEAs are associated with the ability of face (emotion) processing and object integration in obscured emotional faces.

Autism Spectrum Disorder (ASD) is typically characterized by a wide range of social and communication impairments, including deficits in facial expression perception (Behrmann et al., 2006). However, the existence of emotion perception impairment in ASD is still a topic of heated debate (Bird & Cook, 2013; Harms, Martin, & Wallace, 2010), with some authors speculating that they might not even exist at all (Bird & Cook, 2013). Autistic traits have been widely accepted as a continuous construct with ASD at one extreme, and from there extending

continuously into the neurotypical population (Baron-Cohen, 1997; Frith, 1991). These traits can be measured using a self-administered questionnaire, the Autism-spectrum Quotient (AQ) (Baron-Cohen et al., 2001). This tool has been used to examine possible associations between autistic traits and particular cognitive processes, including those of face processing (Ewbank et al., 2014; Rhodes, Jeffery, Taylor, & Ewing, 2013), with increasing levels of autistic traits linked to reduced processing of facial identity and selectively poorer face recognition (Rhodes et al., 2013).

As mentioned in section 1.5. Adults with high autistic traits might exhibit seemingly intact face perception due to the atypical processing of faces (Cook et al., 2014). Those with ASD could have developed the use of compensatory strategies to counter any experienced deficits (Lahaie et al., 2006). For example, they may extract facial emotion by focusing on specific facial features (i.e. non-holistic perception) rather than processing the face as a coherent whole (Joseph & Tanaka, 2003; Klin et al., 2002). Another possibility is that the recognition of full-blown emotional faces is very easy, and thus their performance in differentiating any possible deficits reach a ceiling effect (M. J. L. Smith et al., 2010). All of these studies, however, allowed participants to view full faces. By manipulating the visibility of the adapting faces, we might reveal the face processing strategies across the continuum of autistic traits in adults during face adaptation.

It has been suggested that amodal/perceptual completion, the ability to infer a stimulus's full form when it is partially obscured (Kasai & Murohashi, 2013; Michotte, Thines, & Crabbe, 1964), is related to processing in the Lateral

Occipital Complex (Hegd et al., 2008; Lerner, Hendler, & Malach, 2002). Previous studies have shown that LOC exhibits abnormal neural responses (Hubl et al., 2003) and volumetric differences (Ecker et al., 2012; Nickl-Jockschat et al., 2012) in people with ASD. By partially obscuring the emotional faces, participants will be required to perceive emotion through amodal completion of the viewable face parts into a gestalt percept (Nakayama et al., 1989; Yokoyama et al., 2014). We hypothesized that people with high AQ may use non-holistic strategies to process facial emotion, and they were to exhibit diminished FEA to happy faces when the most informative region, the mouth, is deleted, then it would imply that they have a greater reliance upon featural information when processing facial expressions. People with low AQ may tend to use a more holistic approach when perceiving the obscured emotional faces, and therefore, might exhibit larger FEAs compared to high AQ scorers. We thus anticipate that such a paradigm will reveal an association between emotion adaptation and autistic traits. By contrast, if there were no association between AQ and FEA to obscured faces, then it would imply that those high in autistic traits have similar abilities at processing faces holistically in comparison to those with low levels of such traits.

In the current study, we sought to answer two questions: 1) Does the FEA to obscured faces reveal a previously unidentified association with autistic traits in NT adults? 2) Is there any difference in FEAs between obscured adapting faces that could be amodally completed compared to those could not? We designed the following two experiments to answer the two questions. In the first experiment, we manipulated the face occlusion by aligned or misaligned bars for the adapting faces.

As misaligned bars disrupt the holistic perception of the adapting faces, we expect dissociation between the two manipulations for high autistic traits subjects. In our second experiment, we adapted subjects to happy faces occluded by bars; however, we also manipulated amodal completion by flickering the contrast of viewable parts in a synchronized or asynchronized fashion. We examined whether synchronized flickering facial parts generated FEA and whether asynchronization impairs amodal completion and thus adaptation. As in our first experiment, we were also interested in how our manipulations might affect any possible association between AQ and FEA.

3.1 Experiment 2.1

In the previous experiment, we adapted our participants to happy faces that were partially occluded by aligned or misaligned opaque bars (Fig 3.1). We anticipate that the aligned bars should facilitate a coherent perception of the adapting face due to its fairly natural display. If participants are able to fill-in the missing facial parts in high-level cortical areas, and form a global representation of the faces, then the FEA should consist of the viewable local (i.e., viewable featural information, such as the eyes) and global (i.e., ability to infer emotion by grouping viewable parts together into a whole percept) components of the aftereffect. Those high in autistic traits have been associated with diminished abilities in global perception (Brosnan, Scott, Fox, & Pye, 2004; Kasai & Murohashi, 2013). We therefore anticipate that the holistic component in our FEA will diminish as autistic traits increase due to diminishing abilities in the amodal completion of the

viewable parts coherently. In our misaligned condition, however, we anticipate that the unnatural positioning of the bars will disrupt the holistic perception of the adapting face for all participants. Prior work has shown such unnatural items are more difficult to process than those that are occluded in a natural way, and thus lead to reduced amodal completion strength (Johnson & Olshausen, 2005; Kasai & Murohashi, 2013; Murray et al., 2001). We, therefore, expect no association to be found between autistic traits and FEA in this condition.

3.1.1. Methods

Subjects Thirty subjects (14 males, mean age: 26.5 ± 2.5 years) from Nanyang Technological University consented to participate in both experiments presented here. All subjects had normal or corrected-to-normal vision. The study was approved by the Institutional Review Board at Nanyang Technological University, Singapore.

Apparatus and Stimuli Visual stimuli were presented on a 17-inch Philips CRT monitor controlled by iMac Intel Core i3 computer, with a refresh rate of 85 Hz and resolution of 1024×768 pixels. A chin rest was fixed at a distance of 75 cm from the monitor. Thus each pixel subtended a visual angle of 0.024° . The luminance values below were measured with a Minolta LS-110 photometer. Experiments were conducted in Psychophysics Toolbox extensions in Matlab R2010a (Brainard, 1997). During the experiment, eye movements were recorded by Mobile Eye-XG (Applied Science Laboratories) with a sampling rate of 30 HZ.

A black fixation cross (1.04 cd/m^2) was presented at the center of a white screen (51.20 cd/m^2) throughout the experiment, subtending a vertical and a

horizontal angle of 0.34° and 0.048° , respectively. We selected three facial images with happy, neutral and sad expressions of the same person from the Karolinska Directed Emotional Faces database (Lundqvist, 1998). All stimuli used in the experiments were derived from the three pictures, of the same size ($3^\circ \times 3.53^\circ$). The stimuli were shown on the right side of the fixation with a center to center distance 3.85° horizontally and 0° vertically.

Test stimuli. A set of intermediate facial images with emotion ranging from happy to sad were generated by morphing the happy face with the neutral face, and the neutral with the sad face, using MorphMan 4.0 (STOIK Imaging, Moscow, Russia). All images were grayscaled and ovally cropped with a size of $3^\circ \times 3.53^\circ$ to remove external features. A total of 21 images were created in incremental steps of 0.05, with 0 representing the saddest face and 1 the happiest face. Images with proportions equal to 0.3, 0.35, 0.40, 0.45, 0.50, 0.55 and 0.60 were used as test faces (Fig 1c) in both experiments (29.22 cd/m^2).

Adapting stimuli. There were four types of adaptor faces. Static full face (Static_F) was merely the intact smiling face image. Flickering full face (Flicker_F) was generated by alternating a low-luminance happy face (24.37 cd/m^2) with an identical but high-luminance face (44.56 cd/m^2) in a square wave fashion, the Michelson Contrast between the two faces was 0.29 (Michelson, 1927). Each phase displayed for 106 ms (9.4HZ) with a total duration of 2.12 seconds. The ‘aligned occluder’ (AO) adaptor (Figure 3.1c) was generated by applying three gray bars (24.32 cd/m^2) on top of the static happy face. The three bars were placed over the mouth, on the forehead, and between the eyes and mouth region with equal

distances between the parallel bars. Previous studies have shown that a simple misalignment of occluders and partial object could disrupt/reduce the holistic perception (Johnson & Plshausen, 2005; Kellman, Yin & Shipley, 1998). Thus, our ‘misaligned occluder’ (MO) face was created in a similar way as AO, except that the three bars were moved aside in an unnatural position to disrupt coherent perception (Figure 3.1d).

(a) Static happy full face, Static_F

(b) Flickering full face, Flick_F

(c) Aligned occluder (AO)

(d) Misaligned occluder (MO)

(e) Test faces

Figure 3.1 Facial stimuli used in Experiment 2.1.

(a). *Static happy full face, Static_F*. The facial image was kept constant with participants perceiving it as a single static happy face during the adaptation period. **(b).** *Flickering full face, Flick_F*. The face alternated between high- and low-luminance with each luminance frame lasting 106 ms. **(c).** Static aligned occluder face, AO; **(d).** Static misaligned occluder face, MO; **(e)** Test faces, proportion of happiness ranged from 0.3 to 0.6.

Autism-Spectrum Quotient (AQ). The AQ is a self-administered tool with 50 items measuring autistic traits on a continuous basis (Baron-Cohen et al., 2001). Participants rate statements on five subscales (social skill, attention switching, attention to detail, communication, and imagination) on a four-point Likert scale from definitely agree, slightly agree, slightly disagree to definitely disagree (see Appendix 1 for example items). These rated responses were then coded in the AQ scoring system. The internal consistency of items in the five domains was moderate to high in British samples (Cronbach's alpha coefficients for Communication = .65; Social skills, = .77; Imagination = .65; Attention to detail = .63; Attention Switching = .67). The total AQ score ranges from 0 to 50, with higher values indicating greater autistic tendencies. The factor structure of the AQ is reported to be consistent across western and eastern cultures and the Cronbach's coefficients for the five subscales also vary from moderate to high in Asian countries (Lau et al., 2013; Rump et al., 2009; Wakabayashi et al., 2007). We, therefore, use it as a measure of autistic phenotype in the present study.

Procedure

We used a two-alternative forced choice paradigm in all experiments. This experiment measured the effect of face occlusion on FEA. The adapting faces were either the full faces (static/ flickering) or obscured (aligned or misaligned occlude) faces, while the test faces were fully viewable. Throughout the experiment, participants were required to maintain their fixation on the central cross. We used an eye tracker (ASL Mobile Eye XG; Applied Science Laboratories, Waltham, MA)

with a sampling rate of 30 HZ to ensure eye fixation throughout the whole experiment. There were five conditions in total presented in a randomized block design: 1) a baseline condition with no adaptor (baseline); 2) adapting to the AO; 3) adapting to the MO; 4) adapting to the Flicker_F; adapting to the 5) Static_F. These conditions were run in separate blocks with two blocks per condition. Different random orders of the total 10 blocks were used for different subjects. Over the two blocks for each condition, each test face was repeated 20 times. Each block was separated by a 5-min break to avoid any carryover effects from the previous adaptor into the next block.

At the beginning of each block, the eye-tracker was calibrated and validated with a 9-point calibration system with an accuracy of 1°. Participants started each block of the trials by fixating on the cross and then pressing the space bar (Fig 2). After an initial 506 ms, the adaptor appeared for 2 seconds, followed by a 200 ms inter-stimulus-interval (ISI). The test face was then presented for 141 ms. Participants judged the emotion of the test face to report happy or sad via a key press. This response ended the trial and commenced the next one after a 1 s intertrial interval (ITI). Then the adaptor re-appears, indicating the start of a new trial. Subjects received no feedback on their performances at any time.

Figure 3.2 Trial sequence for the misaligned occluder (MO) condition.

The adapting face first appeared for 2 s, followed by a 200 ms inter-stimulus-interval (ISI), a test face then appeared for 141 ms. A beep played immediately afterwards to prompt a response. Subjects had to press either the “A” or “S” key to indicate a perception of a happy or sad expression. After a 1-s Inter-trial-interval (ITI), the next trial began. Experimental parameters for all conditions and experiments are detailed in the Methods.

Data analysis

To measure FEA, we first calculated the percentage of happy responses from each individual for each test face. The percentage of happy responses was plotted against the proportions of happiness in the morphed test face. The results were then fitted with a sigmoidal function in the form of $f(x) = 1/[1+e^{-a(x-b)}]$, where b equals to 50% point of the psychometric function [the point of subjective equity (PSE)] indicating chance performance, and $a/4$ determines the slope and indicates the response sensitivity. The aftereffect was calculated by subtracting the PSE of the baseline (no adaptation) from the adaptation condition(s) of interest. We conducted a two-tailed paired samples t -test to compare the PSEs between particular

comparisons of conditions. The relationship between aftereffects and autistic traits (AQ) was measured by Pearson correlation. All analyses were performed in Matlab.

The eye tracking data were analyzed in the following steps. We calculated the proportion of time when participants broke fixation during the experiment. By using the in-built algorithm from the software ASL Results, we measured the total amount of time when participants' gaze fell out 1° from the fixation point for each condition (corrected for head motion). The duration of breaking fixation was then divided by the total amount of time of that particular condition, by which we get the proportion of breaking fixation (PBF). In order to examine breaking of fixation in each adaptation condition in a similar way as we do with our aftereffect magnitudes, we subtracted the PBF of the baseline condition from the condition of interest.

3.1.2 Results and Discussion

Descriptive statistics of AQ

The AQ score ranges from 8 to 30 (Mean = 19, SD = 6.0) among the recruited participants. The Skewness and Kurtosis of the AQ were .43 and .83 respectively, both within acceptable ranges of parametric analysis (George & Mallery, 2010). Previous studies have shown that men tend to have higher AQ than women (e.g. Baron-Cohen, et al., 2001), however, there was no significant gender difference in the AQ score in our participants ($t(28) = -.725$, $p = .47$), possibly due to the sampling effect. The Shapiro-Wilk test showed that the FEAs for the FEAs were normally distributed (both $ps > .41$).

Face emotion aftereffects and AQ

We compared the effects of amodal completion in aligned and misaligned faces on facial expression adaptation in Experiment 1, and its relation to the autistic traits of our subjects. The FEA was calculated by subtracting the PSE (50% happy/sad responses) of the baseline from the adaptation conditions (as indicated in Figure 3.3 b&c). Results showed significant FEAs after adapting to all faces (all $ps < .001$). The FEA difference between the AO and MO is not significant ($p = .49$), nor was the difference between the static and flickering full face ($p = .18$). The differences between the obscured and complete faces, however, were significant (all $ps < .01$).

Figure 3.3 Facial expression aftereffect in Experiment 2.1.

(a). Summary of data from all 30 participants. AO, aligned occluder adaptor; MO, misaligned occluder adaptor. Error bars indicate SEMs and p -values were obtained by paired t -tests. (b) Psychometric curves from a naïve subject with low AQ score. (c) Psychometric curves from a naïve subject with high AQ score.

Figure. 3.4. Relationship between AQ and FEA magnitude for Experiment 2.1. (a). AO, aligned occluder adaptor; and (b) MO, misaligned occluder adaptor; (c) Static_F, static full face adaptor; and (d) Flicker_F, flickering full face adaptor. In this figure, facial expression aftereffect was plotted as a function of individual AQ. The correlations were significant for obscured face conditions, but not for full face adaptor conditions.

We then looked into any possible association between FEA and autistic traits as measured by AQ scores: we found significant correlations between the two in both the aligned ($r(30) = -.55$, $p = .002$, Figure 3.4a) and misaligned conditions ($r(30) = -.38$, $p = .04$, Figure 3.4b). These negative correlations in both aligned and

misaligned occluded conditions indicate that the increasing autistic traits are associated with smaller FEA magnitudes in subjects. However, the correlations were abolished when the adapting faces were complete, regardless of dynamics, $r(30) = .10, p = .59$ and $r(30) = -.11, p = .56$ for static and flickering full face respectively (Figure 3.4 c & d).

We used two types of obscured adaptors (AO and MO) in this experiment. In the AO face condition, the occluding bars were aligned on the face. We had hypothesized that apparently neurotypical levels of emotion adaptation aftereffects in ASD were likely due to non-holistic processes. We, therefore, wondered whether diminishing holistic perception of emotional faces might express itself as autistic traits increased in a neurotypical population, as shown by FEA to partially obscured faces. In condition MO, we expected that the misalignment between the occluders and the partial objects disrupted amodal completion, as widely reported in previous work (e.g. Murray, Sekuler & Bennett, 2001; Johnson & Olshausen, 2005). Thus the association between FEA and AQ would be abolished. However, this was not the case. One possible reason was that the stimuli in prior work were mostly simple geometric shapes or objects, and thus simple misalignments between the occluders and partial objects could disrupt amodal completion. However, the stimuli we used were high-level faces, and such manipulation may not be enough to disrupt the holistic processing of the emotional faces.

The negative correlations between AQ and FEA (Figure 3.4) for both AO and MO suggest that our participants scoring high in AQ may be less efficient in grouping emotional information from the viewable face parts of the adaptors, and

thus produced diminished or nonexistent FEA. This finding is consistent with the ‘weak central coherence’ theory which posits a diminished ability for global integration in people with high AQ (Happé & Frith, 2006). Those high in autistic traits perform better on tasks involving local processing, but worse on tasks that rely on holistic processing (Brosnan, et al., 2004; Happé & Frith, 2006). Our results suggest that seemingly neurotypical emotion adaptation aftereffects in ASD are likely due to the non-holistic processing of facial emotion; those high in AQ were probably unable to produce FEA in the present experiment due to the occluded bars disrupting the view of the mouth’s curve in our adaptors. Instead, any aftereffects being produced by our participants may be due to their ability to amodally infer emotion holistically from the partially viewable face parts: an ability that seems to diminish as levels of autism increase (Happé & Frith, 2006; Sucksmith, Roth, & Hoekstra, 2011).

Emotion Sensitivity and AQ

In addition to emotion adaptation aftereffects, we examined our participants’ abilities to discriminate the test faces’ emotions. As earlier mentioned, there is still some debate as to whether emotion recognition abilities are related to autistic traits. To test this, we calculated participants’ sensitivity at judging emotion by extracting the slope of the psychometric curve ($a/4$, details in *Data Analysis* section); steeper slopes indicate increasingly superior abilities in categorizing test faces’ emotions. Results showed no significant difference in the sensitivity after adapting to all these conditions (all $ps > .10$). We then correlated these values indexing emotion

recognition with AQ and found no significant association in the baseline ($r(30) = -.11$, $p = .57$, Fig. 3.4b), nor AO ($r(30) = -.28$, $p = .13$), and the full face adaptor conditions. We found that AQ was not correlated with sensitivity of emotion for any condition (both $ps > .10$). Curiously, the correlation between sensitivity in MO and AQ was significant ($r(30) = -.51$, $p = .004$), with increasing levels of AQ associated with diminishing sensitivity at judging the emotion of test faces. Adapting to an unnatural setting (misaligned occluded face) may disrupt subsequent sensitivity to emotion recognition in those high in AQ. Why this might be the case seems at present unclear, but the corner of the misaligned bar would be over the mouth of the subsequently presented test face. Our high AQ participants may have been more susceptible to the low-level adaptation of this feature which then disrupted their attempts at discerning emotion from the test faces' mouth region. By contrast, our low AQ participants were likely judging emotion in a holistic fashion and so were not affected by adaptation to the misaligned bar.

It was unclear from prior research whether levels of autism can modulate emotion processing. Low functioning autistic children have difficulties in identifying emotional faces' expressions (Gross, 2004; Tantam, Monaghan, Nicholson, & Stirling, 1989; Weeks & Hobson, 1987). Other studies, however, have found no evidence of such an impairment in basic emotion recognition of static (Adolphs, Sears, & Piven, 2001; Baron-Cohen, Spitz, & Cross, 1993; Grossman, Klin, Carter, & Volkmar, 2000; Volkmar, Sparrow, Rende, & Cohen, 1989), or dynamic facial expressions (Gepner, Deruelle, & Grynfeldt, 2001) in autism. A recent meta-analysis of 16 studies found that ASD individuals had

difficulties in the recognition of five basic emotions (sad, anger, surprise, fear and disgust) but did not have difficulties in recognizing happiness (Uljarevic & Hamilton, 2013). Remarkably, even in a neurotypical sample, we have found that levels of autism can modulate happy emotion perception, as shown through emotion adaptation aftereffects. In contrast, autistic traits were associated with the ability to explicitly categorize the emotions of the test faces in the misaligned condition, but not in the baseline and aligned conditions. Thus, it suggests that adaptation to the misaligned occluders increasingly disrupts sensitivity to facial emotion as AQ increases.

Eye tracking results

The overall PBF was 2.34%, indicating that participants maintained fixation on the vast bulk of trials. We subtracted the PBF of each condition from its corresponding baseline and performed a one-way ANOVA (repeated measures). Results showed that PBFs were similar across all conditions ($F(3, 76) = 1.21, p = .29$). Pearson correlations conducted between PBF and AQ showed that AQ score was not correlated with the PBFs in any condition (all $ps > .10$). Overall, it seems that the association between AQ and FEA was not due to attention. It should be stressed, however, that our measure for attention was rather limited in what it can inform us, and it might be the case that our low AQ participants paid more covert attention, that is attention without moving the eyes from fixation, to the obscured adapting faces. It thus invites further investigation into this question.

In Experiment 2.1, we observed an association between FEA and AQ in both AO and MO conditions. A possible reason for the association between FEA and AQ in the MO condition was that simple misalignments between the occluders and viewable facial parts on a 2D basis were not effective enough to disrupt the holistic processing. Therefore, we further manipulated the amodal completion strength in Experiment 2.2 by flickering the viewable facial parts in different synchronization.

3.2 Experiment 2.2

In Experiment 2, we created two face images, differing in luminance, from a single face identity and alternated the display of the two images in a video sequence as adaptors. The “Law of Common Fate” suggests that elements undergoing synchronous luminance change facilitate binding and are more likely to be considered as a unitary item (Levinthal & Franconeri, 2011). Based on that assumption, we manipulated the synchronization between the luminance of the unoccluded facial parts (e.g., eyes, nose and chin) to either increase or decrease amodal completion. In one adaptor condition, we flickered the adapting faces’ viewable parts in synchrony between high and low contrast rapidly (i.e., 106 ms high contrast followed by 106 ms of low contrast). This should facilitate the binding of the adapting faces as a single percept across all participants by which increase the perception of the face parts as a greater whole. We expect the synchronized flickering would, therefore, lead to greater levels of emotion adaptation relative to adaptation in the first experiment. Previous studies have

reported comparable contrast sensitivity for flickering stimuli between those with ASD and NT controls (Bertone, Mottron, Jelenic, & Faubert, 2005; Pellicano, Gibson, Maybery, Durkin, & Badcock, 2005). If our low AQ participants were already binding the face parts efficiently in Experiment 1, then this manipulation should have little/small effect on them. By contrast, those higher in AQ might have been experiencing diminished adaptation aftereffects in Experiment 1 purely due to reduced levels of holistic perception of the face parts' emotion. If this were the case, then synchronized flickering should facilitate the binding of the face features as indexed by an increase in emotion adaptation in these individuals. This should have the effect of abolishing the association between AQ and FEAs.

Of course, this flickering manipulation will also arguably have the effect of increasing our participants' attention towards the adapting face too. To counter possible attentional effects, we will need to test our participants using a face where contrast flickering still occurred to attract attention, but binding was instead disrupted. To accomplish this, we have another condition where participants were to adapt to an asynchronous flickering condition where only two of the four face parts were luminance flicked. We hypothesized that if those low in AQ were able to holistically process the partially occluded adaptors in Experiment 1, then asynchronous flickering should disrupt this ability. In contrast, those high in AQ were likely unable to holistically process the partially viewable adaptors in Experiment 1 anyway as shown by their non-existent FEA. Thus, this asynchronous flickering manipulation will abolish the association between AQ and FEA, due to all participants finding it difficult to bind the face parts into a single

percept to process emotion. The FEA in this condition should, therefore, be smaller than the FEA produced in the aligned condition in Experiment 1.

Finally, to our knowledge, no prior study has actually examined an association between emotion adaptation to fully viewable faces and autistic traits in a neurotypical population; an oversight we set out to resolve. We anticipated that the correlation between emotion adaptation and FEA would be abolished due to those higher in autistic traits being able to produce aftereffects from the mouth region in the full face. Such a finding would support recent work in ASD populations in suggesting that levels of autism are not associated with emotion adaptation aftereffects when the whole face is in view (Cook et al., 2014). We also included another flickering luminance condition, this time using a fully viewable face. If flickering does not lead to any attention related increases in emotion perception, then there should be no difference in FEA between the fully viewable static and flickering conditions. If, however, luminance contrasts were to result in increased emotion adaptation due to increased attentional processing, then we should see greater emotion adaptation aftereffects in this condition relative to the static face that is fully viewable.

3.2.1 Methods

Subjects

The same 30 participants from Experiment 1 participated in Experiment 2.

Stimuli and procedure

Experiment 2 employed the same set of test faces from Experiment 1, but the adapting faces were manipulated in a different way. We created two sets of happy

adaptors (Figure 3.5). The synchronized flickering occluded face (SFO) was created by applying the three occluders aligned over the Flicker_F adaptor; in this adaptor, all face parts flickered congruently. The asynchronous flickering occluded face was the same as the SFO except that the eye and chin regions were always kept at low-luminance between consecutive video frames, we term it as partial flickering occluded face (PFO). We expected the lack of flickering in the eye and chin regions combined with alternate flickering in the nostril and forehead regions would disrupt amodal completion. In total, we have two sets of face adaptors: synchronized flickering occluded face (SFO) and partial flickering occluded face (PFO). The experimental procedure was identical to Experiment 1. There were three conditions in total: adapting to (1) SFO, (2) PFO, and (3) no-adaptor (the baseline). All conditions were run in separate and randomized blocks, which were repeated as in Experiment 1.

Figure 3. 5 Face adaptors used in Experiment 2.2.

(a). *Synchronized flickering occluded face, SFO.* This was generated by adding three occluders onto the flickering full face (Flick_F). **(b).** *Partial flickering occluded face, PFO.* This set was generated in the same way as the synchronized flickering occluded face, except that the eye and chin regions remained at low-luminance throughout while the nostril and forehead flickered between low- and high-luminance in consecutive frames.

3.2.2 Results and Discussion

We manipulated the dynamics and available information in Experiment 2. The Shapiro-Wilk test shows that the FEAs in experiment 2 were normally distributed (all $ps > .24$). Results are shown in Figure 3.6. Adapting to the synchronous flickering occluded face (SFO) generated significant FEA ($t(29) = -6.00, p < .001$), and so does adapting to the asynchronous flickering occluded face (PFO) ($t(29) = -2.80, p = .005$). Moreover, we observed a significant difference in FEA between the two occluded face SFO and PFO, $t(29) = 2.5, p = .007$. This is expected due to the “Law of Common Fate” (Levinthal & Franconeri, 2011), as asynchronous flickering interferes with amodal completion by the incongruently flickering facial parts. Thus, we observed a significant difference in FEA between the two occluded face adaptors. Results for low and high autistic traits subjects are shown in Figure 3.6b and 3.6c. We also compared the FEAs generated by the SFO and PFO with the FEA by AO (Experiment 1), however, the differences were not significant (both $ps > .30$).

Pearson correlations between FEA and AQ are demonstrated in Figure 3.7. In contrast to Experiment 1, FEA magnitudes did not correlate with individual AQ in the two flickering conditions (SFO, $r(30) = -.12, p = .52$; PFO, $r(30) = -.07, p = .70$). These results indicate that the alternate flickering manipulation (asynchronous flickering) abolished FEA in both the low and high AQ participants. The fact that there were no correlations with AQ in any of the conditions suggests that the ability to temporally integrate flickering faces holistically is not diminished by increasing autistic traits.

Figure 3.6 Facial expression aftereffect in Experiment 2.2.

(a). Summary of data from all 30 participants. Baseline, no adaptor; AO SFO, synchronized flickering occluded face adaptation; PFO, asynchronized partial flickering occluded face adaptation. **(b)** Psychometric functions from a naïve subject with low AQ score. **(c).** Psychometric functions from a naïve subject with high AQ score.

We were also interested in whether there was any relationship between the FEA and AQ across each condition in Experiment 2. Pearson correlations between FEAs and AQ are displayed in Figure. 3.7. In contrast to Experiment 1, the FEA magnitudes did not correlate with individual AQ in any condition (SFO, $r(30) = -.12$, $p = .52$; AFO, $r(30) = .07$, $p = .70$). Furthermore, correlations between FEA and AQ subscales were not significant. These results indicate that both the flickering manipulations abolished the relationship between AQ and FEA to partially occluded faces. Similarly, allowing participants to fully view adapting faces also abolished any relationship between AQ and FEA.

In Experiment 2, we had expected that people with high AQ could benefit more from flickering in synchrony in comparison to the FEA to the static, aligned condition in Experiment 1. Similarly, those low in AQ would probably experience no/little benefit from such manipulation due to ceiling effects in their ability to glean emotion from the occluded adaptor. To test for any differences in these

conditions across experiments that may not have been apparent in our ANOVA or correlations, we subtracted the FEA for the static aligned condition in Experiment 1 from the synchronous flickering condition's FEA for each participant and found a significant correlation between these values and AQ (Fig. 3.7c, $r(30) = .47$, $p = .009$). This suggests that the emotion perception benefits of synchronous flickering as indexed by FEA relative to the aligned adaptor in Experiment 1 were greater for high AQ participants, in comparison to low AQ participants who seemed to exhibit diminished FEA to synchronized flickering. These converse effects across high and low AQ participants can, therefore, explain why the association between AQ and FEA in Experiment 1 was abolished in the synchronous condition. This improvement in emotion processing in high AQ participants may be through the temporal integration of consecutive frames as dynamic facial stimuli which activate the regions of the brain involved in facial movement and emotion, such as the STS (Winston, Henson, Fine-Goulden, & Dolan, 2004).

We had also predicted that asynchronous flickering would disrupt emotion perception of the adaptors in those with low AQ, and thus they would exhibit smaller FEA relative to their FEAs to the aligned adaptor in Experiment 1. To examine this, we subtracted the FEA in the AFO condition from those in the static aligned condition in Experiment 1. We found a significant negative correlation between these values and AQ ($r(30) = -.51$, $p = .004$, Fig. 3.7d), thus indicating that asynchronous flickering increasingly disrupted emotion perception as indexed by FEA as AQ decreased. For example, Figure 3.7f shows that disrupting the grouping

of stimulus parts through asynchronous flickering seems to have little effect on those high in AQ, but severely impacts upon emotion perception in those low in AQ, leading them to exhibit smaller FEA than in the aligned condition in Experiment 1. The “Law of Common Fate” (Levinthal & Franconeri, 2011) therefore seems to have differential effects across AQ depending upon the experimental manipulations.

Fig. 3.7 Relationship between AQ and FEA magnitude after adapting to occluded flickering faces. In the first four figures, aftereffect amplitudes were plotted as a function of individual AQ. Adapting to the: **(a)** Synchronized flickering occluded face (SFO condition); **(b)** Partial flickering occluded face (PFO condition). In the last two figures, aftereffect differences were plotted as a function of AQ. **(c)** Aftereffect difference between SFO and AO. **(d)** Aftereffect difference between PFO and AO.

Emotion Sensitivity, Attention and AQ

As in the case of Experiment 1, we decided to examine our participants' sensitivity in perceiving emotion in the test faces after adaptation by performing a correlation on the slope values of the psychometric curves at PSE and AQ. We found that AQ was not correlated with sensitivity of emotion for any condition (all p s > .23). This suggests that participants' sensitivity in judging the emotion of the test faces was similar across all levels of autistic traits regardless of adaptation condition.

In Experiment 2, flickering might draw the attention of those high in AQ more than those with low AQ. The overall PBF in experiment 2 was 1.94%, and was similar to the PBF in Experiment 1 ($t(29)=.89, p = .38$). The PBF in the baselines were comparable between experiment 1 and 2 ($t(29)=1.64, p = .11$). We subtracted the PBF of each condition from its corresponding baseline and performed a one-way ANOVA (repeated measures). Results showed that PBFs were similar across all conditions ($F(3.28, 95.16) = .51, p = .69$, Greenhouse-Geisser corrected as Mauchly's sphericity test had been violated, $\chi^2(14) = 44.32, p < .001$). We then examined the relationship between attention on fixation, AQ, and FEA. As in Experiment 1, we did not observe a significant correlation between AQ and the tendency to break fixation (PBF) in general ($r(30) = .20, p = .30$), nor AQ with PBF in any condition (all p s > .13). The tendency to break fixation for each condition relative to baseline was also not correlated with the FEA induced by the two occluded flickering conditions (PFO and SFO, $r(30) = .16, p = .26$ and $r(30) = -.04, p = .83$, respectively). This suggests that FEA was not associated with the

breaking of fixation. Similarly, there did not seem to be any relationship between this drawing of attention by the adaptor and AQ. Therefore, the lack of association between AQ and FEA in Experiment 2 cannot be explained by increased attention in the high AQ participants.

Finally, it may also be that increasing levels of AQ are associated with decreasing abilities to explicitly recognize the emotion conveyed by the adaptors in both Experiment 1 & 2. We therefore decided to ask our participants to recognize the emotion of our adaptors from the previous experiments, along with additional versions created using a sad face.

3.3. Experiment 2.3

We have argued that increasing AQ is associated with diminishing FEA in Experiment 1 due to increasingly weaker holistic processing. To provide more direct evidence for this suggestion, we decided to use the face inversion task to index holistic processing of our adapting faces across AQ. If the inversion effects for our adapting faces in Experiment 1 become smaller as AQ increases, then this could be taken as evidence that those high in AQ experience decreased holistic perception of the adapting faces' emotions. Such cases must therefore rely more heavily upon featural information when perceiving emotion. We chose this task because at least in comparison to the composite task, it keeps the canonical configuration of the faces intact similar to our adapting faces, albeit upside down.

An alternative interpretation for why AQ is associated with FEA in Experiment 1 is that those high in AQ have reduced perception of the adapting faces' emotional

intensity; for example, low AQ participants may perceive the same faces as being happier than high AQ participants, thus leading to greater adaptation aftereffects. This association is then abolished in Experiment 2, due to high AQ participants perceiving the adapting faces' emotions as being more intense, and thus making their judgments more similar to low AQ participants. In this perspective, perception of the adaptors' emotional intensity can explain our findings rather than increased holistic processing *per se*. To test this, we asked our participants to rate the emotional intensity of the adapting faces used in Experiments 1 & 2.

Finally, it may also be that increasing levels of AQ are associated with decreasing abilities to explicitly recognize the emotion conveyed by the adaptors in Experiment 1. We therefore decided to ask our participants to recognize the emotion of our adaptors from the previous experiments, along with additional versions created using a sad face.

3.3.1. Methods

Subjects

A number of months after the first two experiments, we invited all of our participants to return for Experiment 3. Due to many having graduated, only 19 could participate, so we recruited a further 3 new participants to take part, making a total of 22 participants (10 males, mean age 26.2 ± 2.57 years). As before, we asked our new participants to complete the AQ. Eye tracking data was recorded during all tasks. Participants were informed to respond as accurately and quickly as possible during the inversion tasks, whereas for the recognition and intensity tasks, they

merely had to respond as accurately as they could. Participants completed the emotion recognition task before the intensity judgment task, and the order was randomized together with the rest two tasks, with Participants had a 3-minute break between consecutive tasks.

Stimuli and procedure

Inversion Task: Fully Viewable Faces

Face inversion is thought to disrupt the holistic processing of facial emotion, with any differences in response times between upright and inverted faces believed to crudely index a participant's ability to holistically process a face. Under such circumstances, a smaller inversion effect suggests greater employment of featural processing. Thus, if the inversion effect were to diminish as AQ increases, then this would suggest that high AQ participants had reduced levels of holistic processing for that particular face. We therefore decided to ask participants to judge the emotion of fully viewable, upright or inverted, sad and happy faces (4 faces) presented in the same location as where the adaptors were presented during Experiments 1 and 2, while participants fixated on a central cross. Each face was randomly presented 10 times with a total of 40 trials overall for each participant.

Inversion Task: Occluded Faces

The present task was the same as the previous one, except we asked participants to rate faces that had been partially occluded in the same way as the aligned occluder adaptor in Experiment 1. As featural processing of the mouth is

disrupted in these faces, we anticipate that the face inversion effect should diminish as AQ increases.

Emotion Recognition Task

In our first task, we tested whether AQ was associated with the recognizability of the emotions conveyed by the adaptors. Participants were required to judge the emotion of the 6 adaptor types (AO, MO, Static_F, Flicker_F, SFO, PFO) while maintaining their fixation on the central cross throughout. There were 12 faces, half of which were the original happy versions of the adaptors used in the previous experiments with the other half sad, taken from the same identity as the adaptors. Each face appeared in a randomized order for 5 times, thus a total of 60 trials for each participant. The location and duration of the stimuli were the same as the adaptors used in previous experiments (2 s), with participants judging their facial expression as happy or sad via a key press. After pressing the key, participants had a 500 ms inter-trial interval until the start of the next trial.

Emotional Intensity Task

Upon completion of the recognition test, participants judged the perceived emotional intensity of the faces used in the Emotion Recognition Task using a 7-point Likert Scale, with 1 representing the lowest intensity and 7 the highest. The paradigm was the same as the Emotion Recognition Task, except participants had to judge the faces' emotional intensity instead. There were 60 trials for each participant.

3.3.2 Results and discussion

Inversion Task: Fully Viewable Faces

The mean accuracy for upright faces was 97.96%, and 93.41% for inverted faces. To investigate the inversion effect, we performed a paired samples *t*-test between the two face viewpoints (upright vs inverted). The upright faces were identified more accurately than their inverted counterparts ($t(21) = 2.71, p = .01$, Figure 3.8a). The mean correct responses' reaction times for upright and inverted faces were 0.60 s and 0.68 s, respectively. The same *t*-test was performed on reaction times for inversion effect. Again, reaction times also revealed an inversion effect, with upright faces identified faster than inverted ($t(21) = 7.64, p < .001$, Figure 3.8c).

We quantified the inversion effect for both the accuracy and response times by subtracting the upright measures from the inverted responses. These inversion effects showed no associations with AQ (all $ps > .54$, Figure 3.8b & d). This is perhaps unsurprising, as the mouth region is still in view for all participants and can strongly assist in recognition judgments.

Inversion Task: Occluded Faces

The mean accuracy for upright and inverted occluded faces was 93.41% and 86.14%, respectively. The upright faces were identified more accurately than their inverted counterparts ($t(21) = 2.21, p = .04$, paired *t*-test, Figure 3.8a). This is interesting as it suggests the presence of a holistic effect in the occluded faces.

Figure 3.8. Inversion effects and the correlations with AQ score. **(a).** Accuracy for the inversion tasks. Error bars show mean ± 1.0 SEM; **(b).** The correlation between the accuracy inversion effect (AIE) and AQ scores. AIE was calculated by subtracting the accuracy of the inverted faces from the accuracy of the upright faces. **(c).** Reaction time for the inversion tasks. Error bars show mean ± 1.0 SEM; **(d).** The correlation between the reaction time inversion effect (RTIE) and AQ scores. RTIE was calculated by subtracting the reaction time of the upright faces from the reaction time of the inverted faces.

Response times for upright and inverted faces were 0.70 s and 0.81 s, respectively. Reaction times were faster for upright faces than the inverted ($t(21) =$

6.42, $p < .001$, paired t -test, Figure 3.8c). To examine whether there was an association between holistic processing and AQ, we correlated the inversion effect with AQ. These analyses again showed no associations for either the response times or accuracy (both $ps > .16$, Fig. 8b & d). Overall, these results suggest that it is not entirely clear that the relationship between FEA and AQ in Experiment 1 was due to diminishing levels of holistic processing as autistic traits increased, at least as indexed by the inversion effects.

Emotion Recognition Task

Results showed that participants were able to easily recognize the emotions of all adaptors, with accuracy ranging from 86.36% (happy MO) to 100% (happy PFO), and an overall mean accuracy of 95.15%. We averaged the happy and sad emotions together and performed an ANOVA on the recognizability of the different conditions (static full, dynamic full, static occluded aligned, static occluded misaligned, occluded synchronized and unsynchronized). This analysis revealed a significant main effect ($F(3.36,60.52) = 6.21$, $p = .001$, $\eta^2 = .23$) (Fig. 9a). Pairwise comparisons with Bonferroni corrections revealed no differences in the recognition of the occluded aligned and misaligned adapting facial types in Experiment 1 (the accuracy for the AO and MO were 91.36% and 89.09%, respectively, $p = 1.00$). No differences were found among any pair of the 4 adapting facial types in Experiment 2 either (the mean accuracy for SFO was 96.82%, PFO 96.82%, Static_F 99.09%, and Flicker_F 97.73%, all $ps = 1.00$). Pearson correlations found no association between AQ and recognition accuracy of

the types of faces (all $ps > .30$). This suggests that the association between AQ and FEA in Experiment 1 was not due to diminishing recognition abilities of the adaptor's emotion as autistic traits increase.

Figure 3.9. **(a).** Accuracy for the emotion recognition task. Aligned occluded (AO), Misaligned occluded (MO); Synchronized flickering occluded face (SFO condition), Partial flickering occluded face (PFO condition), Static full face (Static_F condition), Flickering full face (Flick_F condition). Error bars show mean ± 1.0 SEM; **(b).** The correlation between overall accuracy of the adaptors used in experiments and the FEAs. The blue circle indicates aligned occluded face used as adaptor in Experiment 1; **(c).** Perceived emotion intensity of the different types of adaptors; **(d).** The correlation between perceived emotion intensity of the adaptors used in experiments and the FEAs.

Using Bonferroni-corrections for multiple comparisons, we examined the recognition accuracies of the adaptor types used in Experiment 1 & 2. These analyses revealed that the static occluded faces (AO & MO) were judged less accurately than the occluded flickering faces (SFO & PFO) ($t(21) = -3.89, p = .002$) and the fully viewable faces (Static_F & Flicker_F) ($t(21) = -3.50, p = .007$). The accuracy of the fully viewable faces were similar to the two occluded flickering adaptors ($t(21) = -.93, p = 1.00$).

Pearson correlations found no association between the judgment accuracy of the faces and AQ (all $ps > .12$), again indicating that basic recognizability of the adaptors was not related to AQ. FEA was not correlated with recognizability of the adapting faces either ($r(114) = .15, p = .11$, Figure 3.9b). However, these interpretations should be taken with caution as ceiling effects may mask a relationship that is not apparent from such a basic task.

Emotional Intensity Task

We performed the same ANOVA on the intensity task by averaging happy and sad emotions to see if there were any differences in the perceived intensity for the different facial types (AO, MO, SFO, PFO, Static_F and Dynamic_F). These results showed a significant main effect ($F(2.65, 55.55) = 66.03, p < .001, \eta^2 = .76$, Fig 3.9c). Bonferroni-corrected comparisons indicated that perceived intensity was highest for the fully viewable faces compared to the occluded faces (all $ps < .001$), regardless of dynamic information (mean intensity for Static_F and Flicker_F were 6.07 and 6.14 respectively, with no differences between them, $p =$

1.00). This suggests that the larger FEA in the two fully viewable face conditions in Experiment 2 could have been due to their emotions being perceived as more intense.

The perceived intensity for the aligned condition was higher than that of the misaligned (mean intensity for aligned was 4.20 and for misaligned was 3.38, $p = .01$). Perceived intensity between the two occluded dynamic faces was comparable (SFO: 4.46 and PFO: 4.34, $p = 1.00$). Both two occluded dynamic faces were judged to be more intense than that of the misaligned (all $ps < .001$).

AQ was not correlated with the perceived intensity of any facial type (all $ps > .34$). These results suggest that the association between AQ and FEA in Experiment 1 was not due to differences in our participants' perceptions of the adapting faces' emotional intensity. However, a significant correlation was observed between FEAs and the perceived intensity of all of the adapting faces ($r(114) = .32$, $p < .001$, Fig 3.9d), indicating that FEA is strongly dependent upon the emotional intensity of faces.

3.4 Global Analyses Across Experiments

We manipulated the adapting stimuli to either facilitate or disrupt holistic perception of emotion in the above experiments. To investigate the effects of different manipulations on FEA, we analyzed the data of the 19 participants from all 3 experiments. In Experiments 1 and 2, we were interested in whether these manipulations tapped into differences in the holistic perception of emotion. We first conducted a global analysis using a multilevel mixed-effects regression to

predict the FEAs from all conditions based on the different factors (e.g., intensity rating, accuracy, eye tracking results, inversion effect and AQ). The results showed that the perceived intensity was a significant predictor for FEA ($\beta = .011, p < .001$). To separately look at the effects in individual conditions, a series of stepwise multiple regressions were performed, with FEA from each condition as a dependent variable and the corresponding intensity rating, accuracy, eye tracking results, inversion effect and AQ as independent variables. If our manipulations were effective and influenced different aspects of facial emotion perception, then we would expect to find FEAs to be predicted by different factors. We found that for Experiment 1, AQ was the only significant predictor for the FEA in the AO condition ($\beta = -.002, p = .001$), and explained a significant proportion of variance ($R^2 = .50, F(1, 17) = 16.91, p = .001$). For the FEA in the MO condition, occluded face accuracy inversion effect was the only significant predictor ($\beta = -.07, p = .02$) and explained .27 of the overall variance. For Experiment 2, no factor could significantly predict FEA in the SFO, PFO, Static_F conditions (all $ps > .20$); but the full-face accuracy inversion effect seemed to predict the FEA in the Flicker_F condition ($\beta = -.22, p = .04$). Thus, our findings support the suggestion that our various manipulations led to different predictors for FEA.

To summarize, the perception of emotional intensity in the adapting faces seems to account for the differences in FEA across all conditions in Experiments 1 and 2: the fully viewable faces which produced the largest FEA were also perceived as conveying emotion more intensely. However, the way in which our

adapting stimulus manipulations affected subsequent FEA are heterogeneous: AQ was the only significant predictor for FEA in aligned occluded face adaptation; whereas the emotion recognizability inversion effect (a holistic processing index) was the only significant predictor for FEA in misaligned occluded face adaptation in Experiment 1. In Experiment 2, only the accuracy inversion effect for the fully viewable face significantly predicted the FEA in the Flicker_F condition. The other index of holistic processing, the response-time face inversion effect, failed to predict FEA, nor clearly confirm our hypothesis that the FEA in Experiment 1 was due to diminishing holistic perception of the adapting faces as AQ increases. Also, analysis of our eye-tracking data showed that none of our findings across the tasks appeared to be due to any relationship with AQ and attention, as indexed by breaking of fixation (all correlations' $ps > .31$).

3.5 General Discussion

It has been hypothesized that seemingly neurotypical FEA in ASD adults may purely be due to atypical (i.e., non-holistic) face processing strategies (Cook, et al., 2014). By contrast, neurotypical individuals are believed to produce FEA mainly through the holistic processing of the adapting face's emotion. The present study set out to test whether this hypothesis held true across varying levels of autistic traits in a neurotypical population, with those high in such traits expected not to produce adaptation aftereffects when required to process emotion in a holistic manner. To accomplish this, we used opaque bars to partially occlude the adapting faces. This meant that any emotion adaption aftereffects would need to be produced

through amodal completion of the adapting face's emotion into a coherent, holistic percept. We hypothesized that this ability would diminish as autistic traits increased, and thus produce similarly diminishing FEA.

As we predicted, FEA to the partially occluded faces were indeed associated with autistic traits in Experiment 1. This association was abolished in Experiment 2 when participants could fully view the face; possibly due to increasingly greater reliance upon the happy face's mouth to process emotion as autistic traits increased. Similarly, contrast flickering of the faces also abolished the association between AQ and FEA due to synchronous flickering boosting FEA for high AQ participants, and flickering diminishing FEA for low AQ participants. In our final experiment, we find evidence that any relationship between FEA and AQ in the aligned occluded condition could not be explained by differences in either the recognizability of the adaptors' emotions, nor in their perceived intensity. While we had hypothesized that the relationship between AQ and FEA in Experiment 1 was due to diminishing abilities to code emotion from the adaptors in a holistic fashion, we failed to clearly show this with our face inversion task.

Why is it that higher AQ scores are associated with FEA to the obscured adaptors in Experiment 1? It has been suggested that those with ASD are known to have impaired grouping, or holistic perception, of complex stimuli (Bertone, et al., 2005; Sucksmith, et al., 2011). In the inversion task in Experiment 3, however, it is not entirely clear that as autistic traits increase, then so too does the ability to code emotion from the occluded adaptors in a holistic fashion decrease. Does this therefore mean that the relationship between AQ and FEA is not related to holistic

face perception? We do not believe so. First, this lack of a clear relationship may be due to the fact that the face inversion task itself relies upon unnatural face processing strategies (i.e., those used during inversion) as a way indexing holistic face perception. As earlier mentioned, it is still unclear whether inversion merely disrupts holistic processing in a quantitative (Sekuler, Gaspar, Gold, & Bennett, 2004) or qualitative (Rossion, 2008) fashion, thus the face inversion effect may not be a true index of holistic perception of emotion. Our occlusion paradigm, however, is arguably a better way of testing holistic perception over inversion and composite tasks as it keeps the face's parts in their canonical formation. Thus, under such circumstances, participants' emotion perception of the adapting faces must be due to the fairly natural strategies used in daily life. We therefore believe that the relationship between AQ and FEA in Experiment 1 is actually a better index of holistic processing than one yielded from inversion or composite paradigms.

Lastly, in Experiment 2 we found evidence to support prior work (e.g. Cook, et al., 2014) in suggesting that levels of autism in adulthood are not associated with FEA after adapting to a fully viewable face: as a group, those with both high and low AQ produced comparable FEA in both of these conditions. It is a common finding that adapting to fully viewable faces leads to FEA in neurotypical participants (Webster, et al., 2004). Why then can participants high in AQ also generate FEA? One possible explanation is that people with high AQ tend to gaze away from the eye region and spend more time looking at the mouth (Kliemann, Dziobek, Hatri, Steimke, & Heekeren, 2010). In addition, the mouth is typically the most informative region for the perception of happy emotions (Schyns, et al., 2007;

Chen & Chen, 2010). Our previous findings showed that low-level visual stimuli, such as a curved line or a mouth, are sufficient to produce FEA (Xu, et al., 2008). Therefore, high AQ participants may have a greater tendency to focus on the mouth region, and thus generate FEA based on local mouth adaptation without any global representation of the face. However, the most informative facial areas for other facial expressions (e.g., angry, surprise, fear) and identity are not the same; therefore, extrapolating this possibility to other types of emotion adaptation should be done with caution. However, the fact that our high AQ participants generated FEA to the occluded flickering faces may indicate some ability at being able to extract emotion as a gestalt percept. These dynamic faces may require a different neural network that is sensitive to facial motion (e.g., posterior superior temporal sulcus (pSTS) and anterior STS (aSTS), Pitcher et al., 2011), in comparison to static faces which might be reliant upon the fusiform gyrus and the occipital face area.

We found that neither the recognizability nor the perceived emotional intensity of the adapting faces can explain the association between FEA and AQ in the aligned condition in Experiment 1. Emotional intensity was, however, linked to the magnitude of the FEA across all adaptation conditions. For example, the fully viewable faces' emotions were rated as being more intense than their obscured counterparts, and thus produced larger aftereffects. This is to our knowledge the first time that the perceived emotional intensity of adapting faces has been shown to produce differential magnitudes of FEA. We also generally found no association between autistic traits and emotion recognition abilities, at least in the baseline

conditions. These findings corroborate recent suggestions that levels of autism are not related to emotion recognition (Bird & Cook, 2013).

This final finding may appear at odds with the relationship we have observed between FEA and AQ. However, FEA is measured by visual adaptation, a behavioral technique which probes the short-term plasticity of visual perception, where our judgments of the test faces are influenced by our prior exposure to the adapting faces. This technique is distinct from purely recognizing the emotion of faces. In addition to the aftereffect, visual adaptation has at least two more consequences: renormalization (extreme stimuli become less extreme after adaptation) and sensitivity (increase sensitivity to stimuli that are similar to the adaptor). Therefore, visual adaptation can reveal subtle differences in emotion perception between conditions where recognition alone can fail (Liu et al., 2014). However, intact emotion recognition may only be occurring in the high AQ participants purely due to increased reliance upon the mouth region to judge emotion. If the test faces had their mouths obscured, we would anticipate a relationship between AQ and emotion recognition to emerge.

The fact that that we did find a strong correlation between emotion recognition performance and AQ in the misaligned condition is unusual, particularly as there were no differences between the FEA across the two conditions in Experiment 1. Adapting to misaligned bars must increasingly disrupt emotion recognition strategies when judging the test faces as AQ increases. As those high in AQ appear to judge emotion mainly from the mouth region, it is therefore likely that the corner of the misaligned bar impairs subsequent perception of emotion from the mouth.

These findings warrant further investigation as they will surely reveal components of emotion perception and recognition that are both distinct and shared with varying levels of autism.

3.4 Summary of Study II

By manipulating the perceptual completion levels of emotional faces, we have provided the first evidence for an association between autistic traits and facial expression aftereffects in NT adults. The association exists only in static obscured adapting faces, but abolished when the adaptors were full faces or obscured flickering faces. Synchronous luminance changes of a partially viewable face appear to facilitate facial emotion processing compared to the asynchronized flickering condition. However, one would argue that the FEAs between the two could be due to the variance of luminance; since in the SFO, all parts flicker while only half of facial frames flicker in the PFO. We tested this possibility in the following study by adding an alternate flickering condition (AFO) where all facial parts flicker in an asynchronized fashion. Furthermore, synchronously flickering facial parts seem to benefit the perception of facial emotion in those high in autistic traits, suggesting that emotion processing may involve distinct cortical pathways to some degrees for static and flickering faces, and is related to autistic traits.

Our results of a negative association between autistic traits and FEA may due to several possibilities: (1) People with high autistic traits have compromised ability to integrate information and thus lead to decreased holistic face perception; (2) Reduced intensity perception of facial emotions in people with high AQ may

also contribute to their smaller FEAs to static obscured faces. However, the association of AQ and FEA is abolished in flickering obscured ones regardless of synchronization. Possible reasons and the neural mechanism will be explored in the next study.

Chapter IV: Neural correlates of perceptual completion and autistic traits

In the previous study, we have shown that increasing autistic traits (AQ) are associated with reduced FEAs to obscured static faces, but the relationship is abolished when they flicker, regardless of the synchronization. For the synchronized flickering occluded condition (SFO), those high-AQ participants seem to benefit more from such manipulation than those with low AQ scores. The benefit may come from an enhanced holistic face configuration processing. For the asynchronized partial flickering condition (PFO), the abolished association between AQ and FEAs could be due to that the manipulation of asynchronized flickering disrupted the holistic perception in all participants regardless of the AQ scores. To examine the neural correlates of perceptual completion, the FEA, and AQ, we thus simultaneously recorded behavioral and electroencephalogram (EEG) responses.

This study focused on two ERP components, the N170 and Late Positive Potential (LPP). N170 is a negative deflection, and peaks at around 130-200ms (Bötzel, Schulze, & Stodieck, 1995). Its amplitude is larger to faces compared to non-facial stimuli, and thus is considered as an indicator of face detection (Eimer, 2000, 2011; Joyce & Rossion, 2005; Rossion et al., 2002). At least two possibilities have been raised to explain a larger N170 amplitude to faces compared to objects (Eimer, 2011; Luck & Kappenman, 2011). One theory suggests that faces elicit larger postsynaptic activities compared to non-facial stimuli (Eimer, 2011). The

other theory suggests a greater synchronization of neural activity when processing faces compared to non-facial stimuli, and therefore a smaller inter-trial latency jitter leads to larger averaged amplitudes (Eimer, 2011; Luck & Kappenman, 2011).

The N170 reflects holistic encoding of the facial configuration (Eimer, 2011; Sagiv & Bentin, 2001). For instance, inverted faces elicit larger N170 than upright faces, the face inversion effect (FIE) (Rossion et al., 1999). The reasons for the FIE is still inconclusive. One hypothesis suggests that the processing of upright and inverted faces involves distinct mechanisms. Perception of upright face relies on holistic information, whereas perceiving inverted face depends on featural information (Rossion et al., 2000; Vizioli, Foreman, Rousselet, & Caldara, 2009). Another hypothesis indicates that processing inverted faces recruits additional mechanisms at an early stage, and thus the greater cognitive efforts lead to augmented N170 responses (Sadeh & Yovel, 2010).

Repeated viewing of a facial emotion results in a repulsive shift in the perception of subsequent emotional faces, the FEA. Physiologically, repetition of the same stimulus leads to reduced neural activities, the repetition suppression (Grill-Spector, 2006). For instance, when people view a face repeatedly, the neural responses in the fusiform face area (FFA) gradually decrease, as reflected by a reduction of the N170 amplitude (Ewbank, et al., 2014; Amihai, et al., 2011). Such reduction reflects 'categorical adaptation', as the preceding facial adaptor 'fatigues' the neuronal population that respond preferentially to facial configuration (i.e. FFA), and therefore the firing rate of the affected neuronal populations is decreased when new faces appear (Grill-Spector, 2006; Grill-Spector, Henson, & Martin,

2006). In contrast, if the preceding stimuli are non-faces, the FFA neurons are less activated, and thus the suppression will be smaller when subsequent faces appear (Amihai, Deouell, & Bentin, 2011; Eimer, 2011; Eimer, Gosling, Nicholas, & Kiss, 2011; Schinkel, Ivanova, Kurths, & Sommer, 2014).

The component LPP reflects an evaluative stage of information processing and is typically observed in the centroparietal area from 300ms to 600ms (Schupp, Flaisch, Stockburger, & Junghofer, 2006; Luck & Kappenman, 2011). It is an indicator of emotion perception. The amplitude of LPP is modulated by the perceived intensity of emotions, and is larger to affective faces/images than those with neutral emotions (Hajcak, MacNamara, & Olvet, 2010; Hajcak & Olvet, 2008; Keil et al., 2002; Keil et al., 2003). Two possible models have been proposed for an increased LPP to affective stimuli. The ‘enhanced attention model’ suggests that emotional information automatically attracts more attention compare to neutral information, and therefore are processed more efficiently (Keil et al., 2003; Moratti, Saugar, & Strange, 2011; Sabatinelli, Bradley, Lang, Costa, & Versace, 2007; Zeelenberg, Wagenmakers, & Rotteveel, 2006). The ‘global inhibition model’ suggests that the enhanced LPP reflects greater efforts to suppress processing of other information whenever emotional stimuli are presented (Bocanegra & Zeelenberg, 2009; Knyazev, 2007).

Repetition suppression also exists in LPP when repeatedly presenting stimuli with the same emotion (Codispoti, Ferrari, & Bradley, 2006; Olofsson & Polich, 2007; Wang et al., 2016). For instance, adaptation to a happy face suppresses the LPP of subsequent happy faces, and the habituation has been observed cross-

modally, from auditory to visual, suggesting a high-level ‘semantic adaptation’ (Butler et al., 2008; Wang et al., 2016). The LPP reflects the perception of emotion, and has been widely used in studying abnormalities in emotion processing in clinical settings, such as patients anxiety disorders (Richards, Holmes, Pell, & Bethell, 2013), depression (Kayser, Bruder, Tenke, Stewart, & Quitkin, 2000) and schizophrenia (Strauss et al., 2013; Streit, Wölwer, Brinkmeyer, Ihl, & Gaebel, 2001).

In this study, we tested the neural correlates of perceptual completion, the FEAs, and autistic traits. The stimuli were generated in the same way as Experiment 2 in the previous study: happy adapting faces occluded by three bars, and the holistic perception levels were manipulated by flickering the viewable facial parts in different synchronization. Particularly, we added an alternate-flickering face (AFO, Figure 4.1e). In AFO, the facial luminance was incoherent in any adjacent facial parts and all flicker between consecutive frames. The purpose of adding this condition is twofold. Firstly, AFO can serve as a control condition. In the previous chapter, we found a larger FEA in the obscured synchronized flickering condition (SFO, Figure 4.1 c) than the partial flickering condition (PFO, Figure 4.1 d). However, one might argue that all the facial parts flicker in SFO, whereas only half flicker in PFO, thus the FEA difference between the two conditions might not be due to various completion levels, but is because of the local contribution of the facial parts that flicker in SFO but not PFO. Thus, we added the AFO in which the local information was identical to the SFO to ensure that any FEA difference was not due to the discrepancies in local information.

Secondly, we were interested if there would be any FEA difference between the AFO and PFO conditions. Although holistic perception in both conditions may have been disrupted, half of the facial frames in PFO have a coherent luminance; whereas the luminance in the AFO condition is incoherent in any given frame. We are interested in whether there is a difference in the perceptual completion levels and perceived emotional intensity between the two conditions.

For the behavioral data, we calculated the perceptual biases (FEAs). For the EEG data, we calculated the mean amplitudes of N170 and LPP of happy and sad test faces for each condition. Behaviorally, we expected larger FEAs after adapting to the SFO compared to those generated by the AFO and the PFO. For the EEG results, we anticipated that adaptation to the baseline (full face) lead to the strongest N170 suppression of test faces. For test faces adapted to the three occluded adaptors, a larger N170 suppression indicates a greater level of perceptual completion. We thus expect smaller N170 amplitudes for test faces adapted to the SFO than those adapted to the PFO or AFO. We also expected to replicate previous findings of the LPP suppression. Finally, we calculated the correlation between AQ, the behavioral and physiological results to investigate whether and how AQ was associated with the holistic perception of occluded facial emotions.

4.1 Experiment 3

4.1.1 Methods

Subjects

Sixteen naïve local subjects took part in the experiment (9 males and 7 females, university students), with an age range of 21-28 years and a mean of 23.

All subjects had a normal or corrected-to-normal vision and were right-handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants were provided with written consent. The protocols of the study were approved by the Institutional Review Board at Nanyang Technological University, Singapore and University of Macau, China.

Apparatus and Stimuli

Visual stimuli were presented on a 23-inch Dell LED monitor (with a refresh rate of 60 Hz and resolution of 1920×1080 pixels) at a viewing distance of 75 cm, and the luminance below was measured with a Minolta LS-110 photometer. The experiments were conducted in E-prime (Psychology Software Tools, Pittsburgh). During the experiment, a black fixation cross was presented at the center of a white screen throughout the experiment. We first selected a person's sad, happy and ambiguous emotions from Taiwanese Facial Expression Image Database (TFEID) (Chen & Yen, 2007). They were grayscaled and ovally cropped to a size of $3.58^\circ \times 4.2^\circ$ to remove external features. All stimuli used in the experiments were derived from the three pictures and all stimuli were shown on the left side of the fixation.

Test stimuli We generated a set of intermediate facial images with emotion gradually vary from happy to sad by morphing the happy face with the neutral face, and the neutral with the sad face using MorphMan 4.0 (STOIK Imaging, Moscow, Russia). A total of 21 images were created in steps of 0.05, with 0 representing the saddest face and 1 the happiest face. Images with proportions equal to 0.1, 0.35, 0.4, 0.45, 0.5, 0.55, 0.6 and 0.9 were used as test faces (Figure 4.1.a) in the experiment.

Adapting stimuli We generated four adaptors (Figure 4.1.b-e). 1) *Baseline*: a neutral full flickering face, which was generated by alternating a low-luminance neutral face (26.46 cd/m^2) with an identical but high-luminance face (45.59 cd/m^2) in a square wave fashion, the Michelson Contrast between the low and high luminance was 0.32 (Michelson, 1927). 2) *Synchronized-flickering occluded happy face (SFO)*. It was generated by alternating a happy face between low and high luminance. Three gray bar occluders (24.82 cd/m^2) were then placed on top of the flickering face as in the previous study. 3) *Partial-flickering occluded happy face (PFO)*. The face was also occluded by three bars as in SFO. However, only half of the facial parts in the PFO condition flicker (i.e. the forehead and nostril flicker, but the eye and chin regions were kept at low-luminance between consecutive video frames). We expect that such manipulation can partially disrupt amodal completion. (4) *Alternate-flickering occluded happy face (AFO)*. All facial parts flickers in AFO, however, the forehead and nostril region flicker in the same phase, while the eye and chin region flicker in counter-phase. Thus, the luminance in any given frame was incoherent.

Figure 4.1 Demonstration facial stimuli used in Experiment 3. 1.

(a). Test faces, proportion of happiness ranges from 0.1 to 0.9. **(b).** *Baseline*, a neural full face flicker between low- and high-luminance without break in between, duration of each frame was 100ms. **(c).** *Synchronized-flickering occluded happy face (SFO)*. Generated by alternating a happy face between low and high luminance without break in between, three occluders were then applied onto the face. All facial frames have coherent luminance **(d).** *Partial-flickering occluded happy face (PFO)*. The dashed lines are for illustration purposes. The nostril and the forehead flicker, whereas the eye and chin remained low-luminance across frames. The luminance was incoherent in half of the facial frames. **(e).** *Alternate-flickering occluded happy face (AFO)*. All facial parts flickers in AFO, however, the forehead and nostril flicker in the same phase, while the eye and chin flicker in counter-phase. The luminance in any given facial frame was incoherent.

Procedure

All participants were adapted to the four conditions in separate blocks in a randomized order. Each condition consisted of 26 repetitions for each test face and thus 208 trials in total. After each block, participants were given a 10-min break to avoid any carry-over effect from the previous block into the next one.

Participants initiated each block by fixating on the cross and then pressing the space-bar (Figure 4.2). In each trial, the adaptor first appeared for 3.2 seconds, followed by a 500ms inter-stimulus-interval (ISI). The test face then appeared for 150ms. Participants had to judge the emotion of the test face as either happy or sad via a key press on a standard keyboard. The next trial began right after the response with no feedback.

Figure 4.2 Trial sequence for AFO condition for Experiment 3.1.

The trial began with subjects fixating on the cross which lasted for 500ms. Adapting face appears for 3.2 s, followed by a 500ms inter-stimulus-interval (ISI), a test face then appeared for 150 ms. A beep played immediately afterwards to prompt a response. Subjects had to press either the “A” or “S” key to indicate a perception of a happy or sad expression.

4.1.2 Data recording and analysis

Psychophysical data

We measured FEAs by sorting the responses into fraction of ‘happy’ for each test face for the four conditions separately. The test faces were parameterized according

to the proportion of happiness in the morphed faces. Same analyses were used as previous studies.

Electrophysiological data

EEG recording. EEG was recorded from 64 Ag/AgCl active electrodes (BioSemi Active Two system, the Netherlands) organized according to the international standard 10-20 system. Additional two EOG electrodes were placed 3 cm below the eye and the outer canthus to measure vertical and horizontal eye movements, respectively. Electrode impedances were kept below 10 K Ω . EEG was digitized at 1024 HZ. Participants were asked to minimize blinking, body movement, swallowing, and other movements.

EEG preprocessing. All analyses were performed offline in MATLAB with the EEGLAB 13.4.4b toolbox (Delorme and Makeig, 2004). Datasets were down-sampled to 512 HZ and were filtered between 0.05 and 30 with a basic FIR filter. The continuous EEG signal was then re-referenced to a common average and epoched in an interval of -100 to 800 ms with the onset of test face at 0; all epoched data were linear detrended. Following the analyses used by Miyakoshi (2010), we visually inspected the epochs to remove irregular noise, and we then used an automatic artifact rejection to detect remaining abnormal epochs by joint probability and kurtosis, with a rejection threshold at 5 SD (implemented in EEGLAB; for detail, Delorme, Sejnowski, & Makeig, 2007). The data were then submitted to independent component analysis (ICA), using the *runica* algorithm (Makeig, Bell, Lee, Jung, & Enghoff, 2000). ICA components that carried ocular and muscle movements artifacts were identified by ADJUST and removed after

visual inspection (Mognon, Jovicich, Bruzzone, & Buiatti, 2011). Automatic data rejection was performed again with joint probability and kurtosis of 5 SD, and a second ICA was run on the pruned data. The same rejection procedure was conducted again to achieve a final decomposition.

EEG analyses We analyzed two components: the face-sensitive N170, and the emotion component LPP. For the N170, the mean amplitudes of test faces were calculated in a pre-selected time window from 150ms - 190ms at electrodes in the occipitotemporal areas (left hemisphere: P5, P7, P9, PO3, PO7, and O1; right hemisphere: P6, P8, P10, PO4, PO8 and O2). For the LPP, previous studies showed a maximal centroparietal distribution (Schupp et al., 2004; Schupp et al., 2006). We thus calculated the LPP in preselected time segments, from 300ms – 600ms at electrodes in the centroparietal area (C1, CZ, C2, CP1, CPZ, CP2).

Previous work has shown that the LPP is sensitive to the valence of emotion. Adaptation to a happy face suppresses the LPP of a subsequent happy face, but enhances that of a sad test face (Wang et al., 2016). Thus the ERP components were analyzed based on the valence of test faces: happy (proportion of happiness: 0.9 and 0.6), sad (proportion of happiness: 0.1 and 0.35), and ambiguous faces (proportion of happiness: 0.4, 0.45, 0.5, and 0.55).

Previous research has well documented that the N170 reflects holistic face processing (Eimer, 2011; Sagiv & Bentin, 2001). We thus compared the mean amplitudes of test faces' N170 in each condition to examine the perceptual completion levels of the adaptors using three sets of Two-Way repeated-measures ANOVA (hemisphere: left VS. right; adaptor type: baseline, SFO, PFO, and AFO)

based on the valence of test faces. The first set was the N170 responses of happy test faces after adapting to different conditions. The second and third sets were N170 responses to ambiguous and sad test faces. All post hoc *t*-tests were Bonferroni corrected. To measure the perceived intensity of emotion, we calculated the mean amplitude of the LPP for test faces, again based on valence, and performed a one-way repeated-measures ANOVA. A series of correlations between AQ, PSE, and neural change were then conducted.

4.2 Results

4.2.1 Behavioral Results

The results from a naïve subject are shown in Fig. 4.3a. Adapting to the SFO lead to the most rightward shift in the psychometric curve relative to baseline, indicating adaptation to SFO (happy emotion) leads to the most frequent perception of sad emotions in the test phase. Psychometric curves of PFO and AFO also shifted rightward to a smaller degree. Shapiro-Wilk test showed that FEAs were normally distributed (all *ps* > .10). Fig 3b summarizes the mean PSEs from all 16 participants. Planned paired-sample *t*-test showed that adaptation to SFO leads to the largest FEA ($p = .0014$), followed by PFO ($p = .0194$) and AFO ($p = .0229$). A significant difference was observed between the synchronized condition and the two asynchronized conditions (SFO and PFO, $p = .0429$; SFO and AFO, $p = .0024$), but not between the PFO and AFO ($p > .80$).

Figure 4.3 Behavioral results in Experiment 3.1.

(a). Psychometric functions from a naïve subject. Baseline: a neural full face. SFO: Synchronous flickering occluded face; PFO: Partial flickering occlude face; AFO: Alternate flickering occluded face. **(b)** Summary of data from all 16 participants. Error bars indicate SEMs and p -values were obtained by paired t -tests.

AQ and PSE

We performed Pearson correlations between PSEs and AQ scores. Overall, PSE diminished as AQ increased ($r(48) = -.36, p = .012$), indicating that higher autistic traits were associated with smaller FEAs. However, the negative correlation between AQ and PSE was not significant when performed for each condition, although was marginal in the PFO condition ($r(16) = -.452, p = .079$).

Figure 4.4 Correlation between overall FEA and AQ score in Experiment 3.1. SFO: Synchronized-flickering occluded face; PFO: Partial-flickering occlude face; AFO: Alternate-flickering occluded face.

4.2.2 ERP results

N170 is suppressed after adaptation to full face and SFO

The N170 peaks bilaterally at the occipitoparietal area, and maximizes in the right hemisphere, consistent with previous studies (Eimer, 2011; Rossion & Jacques, 2008). Three sets of two-way ANOVA analyses (laterality: left vs. right $\times$ adaptor type: baseline, SFO, PFO, and AFO) were conducted based on the valence of test faces.

The first set examined the N170 of happy test faces after adapting to the four types of faces (Figure 4.5). Results revealed significant main effects for both factors: hemisphere ($F(1,15) = 33.35, p < .001$) and adaptor type ($F(3,13) = 14.94, p < .001$). The interaction between the two was also significant ($F(3,45) = 3.24, p = .031$). N170 amplitudes were larger in the right hemisphere compared to the left. However, our results do not necessarily indicate a right hemisphere advantage in the processing of face because all stimuli were always displayed at the left side of the fixation cross and thus would be projected to the right hemisphere. The post-hoc *t*-test revealed that the N170 in the left hemisphere were not significantly different between conditions (all $ps > .25$). In the right hemisphere, adapting to the baseline (full face) and the SFO led to the strongest N170 suppression in subsequent faces, and the difference between the two was not significant ($p > .11$). For test faces following occluded adaptors, the N170 attenuation was stronger when the preceding facial parts flickered in synchrony (i.e., SFO), compared to the asynchronized conditions (both $ps < .05$). No difference was observed between

PFO and AFO ($p > .90$). Therefore, our results indexed that SFO was processed in a more holistic manner compared to PFO and AFO.

Figure 4.5 The N170 amplitude of happy test faces following different adaptors.

(a). Left hemisphere: The N170 of happy test faces after adapting to baseline, SFO, PFO and AFO. **Baseline:** full face with neutral emotion. **SFO:** Synchronized-flickering occluded face; **PFO:** Partial-flickering occluded face; **AFO:** Alternate-flickering occluded face. The emotion of the three obscured faces is happy. **(b).** Right hemisphere: The N170 of happy test faces after adapting to the four types of faces. **(c)** Mean amplitude of N170 in the left hemisphere, time window 150-190ms, and **(d)** Mean amplitude of N170 in the right hemisphere, time window 150-190ms.

The N170 of the sad and ambiguous test faces were similar to that of the happy faces. For the sad test faces, both factors hemisphere ($F(1,15) = 39.83$; $p < .001$)

and adaptor type ($F(3,45) = 26.18$; $p < .001$) showed significant main effects, and the two-way interaction was not significant ($F(3,45) = 2.41$; $p = .079$). For the sad test faces, Post-hoc t -test revealed that in the left hemisphere, the N170 mean amplitude was comparable between the baseline and the SFO ($p = .81$). Comparisons among the N170 of test faces adapting to occluded faces revealed similar magnitudes between the SFO condition and the AFO condition ($p > .5$), and both of which were smaller than PFO ($p < .01$). In the right hemisphere, a similar pattern has been observed. Adaptation to baseline leads to greatest N170 suppression, followed by SFO, and the difference between the two was significant ($P=.01$). Adaptation to SFO lead to stronger N170 suppression in subsequent test faces compared to those adapting to PFO ($p = .069$), and AFO ($p = .005$). No difference was observed between PFO and AFO ($p = 1.00$).

For the ambiguous test faces, the main effects for hemisphere ($F(1,15) = 38.03$; $p < .001$) and adaptor type ($F(3,45) = 24.10$; $p < .001$) were significant, but not the interaction ($F(3,45)=1.91$; $p = .142$). In the left hemisphere, similarly, adapting to baseline lead to strongest N170 suppression to test faces compared to those following the occluded faces (all $ps < .05$). Differences between SFO, PFO and AFP were not significant (all $ps > .10$). For the right hemisphere, again, adaptation to baseline resulted in greatest N170 suppression compared to the rest three conditions (all $Ps < .01$). While there is a trend for a smaller N170 magnitude after adapting to SFO compared to PFO and AFO, the effect did not persist after the Bonferroni correction (for PFO, $p = .061$ and $.366$ before and after Bonferroni correction, respectively; for AFO, $p = .012$ and $.073$ before and after Bonferroni

correction, respectively). No difference was observed between PFO and AFO ($p = 1.00$). However, previous studies suggest that Bonferroni correction is over-conservative, and given that our ANOVA analysis has two factors with 2 and 4 levels for each factor, the Bonferroni correction deflates the α (in our case is $\alpha/n=.00625$) (Benjamini, & Hochberg 1995; Perneger, 1998). Therefore, we adopted the False Discovery Rate (FDR) and examined again. Results indicate that the difference between the AFO and SFO becomes significant (test = 1), but not between SFO and PFO (test = 0).

FEAs and neural suppression in N170 are partially correlated

To measure the possible link between FEAs and face configuration adaptation, Pearson correlations were conducted between FEAs and the N170 suppression for each condition. Since the emotional valence of test faces does not influence N170 responses, we thus combined the N170 suppression of happy, sad and neutral faces. No significant correlation was observed in any condition for the left hemisphere (all $ps > .27$). For the right hemisphere, we found a marginal correlation between the FEA and N170 suppression in condition PFO ($r(16) = -.482, p = .058$), but not in SFO ($r(16) = -.318, p = .23$) and AFO ($r(16) = -.137, p = .613$). Note that N170 is a negative deflection; a smaller value of N170 change reflects a greater absolute difference from the baseline. Therefore, the negative correlation between the FEA and N170 suppression in PFO indicates that increasing FEAs are associated with larger N170 suppression in that condition.

Adaptation to happy emotion suppressed LPP to subsequent happy faces

LPP is an endogenous ERP component and reflects evaluative processing (Luck & Kappenman, 2011). To examine the influence of the adaptors with different completion levels to the emotion perception of subsequent faces, we performed three sets of one-way ANOVA repeated-measures based on the valence of test faces. In the first set, we compared the LPP suppression of happy test faces after adapting to various conditions. The results replicated previous findings (Wang et al., 2016). The main effect of adaptor type was significant ($F(3,45) = 4.76, p = .012$). Overall results were shown in Figure 4.6, the LPP magnitude of happy test faces was smaller after adapting to the SFO than those adapted to the baseline ($p = .051$) and the AFO ($p = .030$), but was comparable to PFO ($p = .64$). No difference was observed between the baseline, the PFO, and the AFO (all $ps > .5$). For ambiguous and sad test faces, the main effect for adaptor type was not significant (both $ps > .05$).

Figure 4.6 LPP of happy test faces following different adaptors.

(a). LPP for happy test faces after adapting to different conditions. Baseline: fully-viewable face, neutral emotion; SFO: Synchronized-flickering occluded face, happy emotion; PFO: Partial-flickering occlude face, happy emotion; AFO: Alternate-flickering occluded face, happy emotion. (b) Amplitude plot of LPP to happy test faces, from time window 300-600ms.

FEA and neural suppression in LPP are partially correlated

We performed Pearson correlations between FEAs and the LPP suppression of test faces after adapting SFO, PFO, and AFO. For condition SFO, the correlation between LPP suppression and the FEAs were not significant (happy test faces: $r(16) = -.33, p = .212$, sad test faces: $r(16) = .063, p = .816$), although was marginal for ambiguous test faces ($r(16) = .44, p = .088$). This finding is possibly because that the FEA was calculated by subtracting Point of Subjective Equity (PSE) where the emotion was uncertain, which made the ambiguous faces most subjected to be biased. For condition PFO, a similar correlation was observed. The correlation between FEA and LPP suppression not significant (happy: $r(16) = .17, p = .528$, sad: $r(16) = .054, p = .843$, and for ambiguous: $r(16) = .432, p = .095$). For condition AFO, the LPP suppression was not correlated with any type of facial emotion (all $ps > .5$).

AQ is correlated with neurophysiological responses

We performed Pearson correlations between AQ and N170/LPP amplitude change relative to the baseline where significant main effects were found. The purpose of doing so is to examine the neural correlates of the perceptual completion of the emotional face and the influence of autistic traits to FEA. We first calculated the N170 change of test faces after adapting to SFO, PFO, and AFO against the baseline. The correlations between AQ and N170 change were then performed cross emotions for each condition.

The results are shown in Figure 4.7. In the left hemisphere, AQ was not correlated with N170 change to test faces in any condition (all p s $> .10$). In the right hemisphere, the association between AQ and N170 change was observed in condition PFO ($r = .709, p = .002$) and marginal in AFO ($r = .45, p = .077$), but not in SFO ($r = -.14, p = .62$). Note that N170 is a negative deflection; thus a smaller value of N170 change reflects a larger absolute value, which indicates greater difference from the baseline. Our finding of a positive association between AQ and N170 change in PFO suggest that people with high AQ tend to have smaller N170 differences in test faces after adapting to PFO compared to baseline. Similar interpretation goes for the association between AQ and N170 change for condition AFO. The results could be interpreted in two possible ways.

Figure 4.7 Correlation between AQ and N170 amplitude change in the right hemisphere.

(a). N170 magnitude change to test faces across happy, ambiguous and sad emotions in the left hemisphere, from left to right: correlation between AQ and N170 change following SFO, PFO and AFO, respectively. (b). N170 magnitude change to test faces across happy, ambiguous and sad emotions in the right hemisphere, from left to right: correlation between AQ and N170 change following SFO, PFO and AFO, respectively.

One possibility is that people with high AQ performed better in perceiving face configuration of PFO and AFO compared to those low with AQ scores. In other words, the holistic perception of the two adaptors is stronger in people with high AQ. However, this is unlikely since when looking at a face, people with ASD tend to focus on local cues (specific face feature) instead of the holistic information (Brosnan, Scott, Fox, & Pye, 2004; Grelotti, Gauthier, & Schultz, 2002). Another possibility is that people with high AQ may have reduced the holistic perception of full faces, and therefore, the difference in face configuration perception between full face and partial face is not as prominent as those low AQ scorers. Details will be illustrated in the discussion.

For the correlation between AQ and LPP suppression, we only analyzed it for happy test faces. As adapting to the four types of adaptor lead to significant LPP difference in happy, but not sad and ambiguous test faces. For happy test faces, a negative association was observed in condition PFO ($r = -.64, p = .008$), but not in SFO ($r = -.18, p = .512$) and AFO ($r = .22, p = .41$).

4.3 Discussion

The present study examined the neural correlates of perceptual completion, autistic traits and the FEAs in neurotypical individuals with a range of autistic levels. We manipulated the synchronization of viewable flickering facial parts to either increase or disrupt the holistic face perception. Behaviorally, consistent with previous studies, we found significant FEAs after adapting to all obscured faces, and the magnitude was largest when the adaptor had the strongest completion cue.

Autistic traits were negatively associated with FEAs, and were mostly driven by the PFO. For the ERP results, we observed the largest N170 suppression of test faces adapted to the full-face baseline, indicating the strongest 'categorical adaptation'. Suppression was second largest for test faces adapted to SFO and smallest in the two asynchronized conditions. Increasing FEAs were associated with larger N170 suppression in PFO, and AQ negatively associated with N170 amplitude change in PFO. For LPP, adapting to SFO suppressed the LPP to happy test faces, but the effect was not observed in PFO and AFO. Increasing FEA was positively correlated with LPP suppression in SFO and PFO, but not in AFO. The results are discussed below.

4.3.1 N170 and face adaptation in obscured faces

N170 is an ERP component reflecting face configuration perception (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Prior exposure to faces reduces the N170 magnitude of subsequent faces (Amihai et al., 2011; Schweinberger & Neumann, 2016). Source analyses have indicated that the N170 reflect the activities in the FFA (Deffke et al., 2007). Prior exposure to the preceding face lead to neuronal fatigue of FFA and thus a smaller activity when subsequent faces appear (i.e. larger suppression). Based on our results of the N170 suppressions following different adaptors, it is reasonable to expect that the FFA activities were strongest when viewing full face, followed by the SFO, and were weakest in AFO and PFO. This speculation was supported by a recent fMRI study by Chen and colleagues (2010). In their experiment, participants viewed a set of full faces and occluded faces with

perceptual completion manipulated. Identical facial fragments were either stereoscopically displayed in front of occluders (IO, perceptual completion disrupted) or behind occluders (BO, perceptual completion intact). Results showed strongest activities in Occipital Face Area (OFA) and FFA when viewing full faces, weaker when viewing the BO, and the weakest in IO. The finding has been replicated in other studies (Fang & He, 2005; Harris & Aguirre, 2008). Our study is arguably consistent with previous research, indicating that varying the synchronization of viewable parts is an effective approach to manipulate perceptual completion levels.

The N170 response showed a hemispheric difference, and the suppression was stronger in the right hemisphere compared to the left. The difference could possibly be due to hemispheric preferences in processing local and holistic facial information. Left hemisphere has been reported to be more involved in analytical featural processing, while the right hemisphere preferentially processes holistic information (Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Júnior, Sousa, & Fukusima, 2014). Therefore, a right hemispheric advantage in processing human faces has been proposed (Kanwisher et al., 1997; Rossion, Schiltz, & Crommelinck, 2003). However, as mentioned previously, our results do not necessarily support the right hemispheric advantage in face processing since all the stimuli were always displayed on the left side of the fixation cross. Future studies could present stimuli in the center to eliminate such concerns.

4.3.2 The association between AQ and perceptual completion

Our study showed that people with high AQ tend to have smaller N170 difference in test faces between PFO and baseline conditions. Similar results were also observed in condition AFO, but not in SFO. As mentioned in the results section, such findings are probably not due to an increased completion level in PFO and AFO in those with high AQ, but more likely to be the results of decreased holistic perception in the full face (baseline).

Faces tend to be processed in a holistic manner in neurotypical individuals (Valérie Goffaux & Rossion, 2006; Yokoyama et al., 2014). For people with low AQ scores, adaptation to a full face leads to strong ‘categorical adaptation’, thus a large reduction in N170 when subsequent faces appear (Amihai et al., 2011; Eimer, 2011; Eimer et al., 2011; Schinkel et al., 2014). However, the holistic processing for PFO and AFO was disrupted due to asynchronized flickering. Therefore, we observed large N170 difference to subsequent faces adapted to PFO and AFO relative to those adapted to baseline. On the other hand, people with high AQ suffer from reduced holistic perception, even to full faces (Dawson et al., 2005; Joseph & Tanaka, 2003). Therefore, the N170 habituation to subsequent faces could be weaker after adapting to baseline (full face) compared to those with low AQ scores. Meanwhile, the holistic perception in PFO and AFO were disrupted, thus we observed a smaller N170 difference between test faces appear after PFO/AFO and those appear after the baseline.

From what has been discussed above, people with low AQ showed greater N170 differences between baseline and asynchronized conditions, while those with

high scores showed smaller differences, and therefore we observed that increasing AQ was associated with smaller N170 difference. Why was the association abolished in SFO? This is probably because flickering facial parts in synchrony increased perceptual completion, and mimicked the perception of a full-face baseline. Therefore, the difference of SFO and baseline was minimized across participants regardless of AQ scores.

4.3.3 Amodal completion and perceived emotion intensity

Adapting to the SFO leads to the strongest LPP suppression to subsequent happy faces compared to those following the AFO and the baseline, suggesting the highest perceived emotional intensity. The results replicated previous studies examining emotion adaptation in fully viewable faces (Codispoti et al., 2006; Olofsson & Polich, 2007; Wang et al., 2016). Mean amplitudes of LPP are similar in test faces following AFO and baseline, indicating that emotional influence of AFO resembles that of a neutral face. However, we nevertheless observed the behavioral differences, the FEA, as reported in the results section (4.3.1). Previous studies have suggested that FEAs, if using faces from the same identity, is consisted of (at least) two components: identity adaptation and an identity-independent ‘semantic emotion’ adaptation (Fox & Barton, 2007). Our results of a significant FEAs in AFO are probably due to both facial identity adaptation and local adaptation (e.g. local curvature).

LPP suppression was similar between condition PFO and SFO, suggesting similar perceived emotional intensity in the two conditions. However, their

perceptual completion levels are different. One possibility is that facial completion does not affect the perceived emotional intensity. However, this is unlikely as LPP responses to test faces are different between AFO and SFO. Alternatively, half of the facial frames in PFO have congruent luminance, it is possible some participants may be able to view them as coherent and thus perceived the emotional intensity to a similar degree as the SFO. Supporting evidence has shown that happiness could be recognized as fast as 23-28ms (Martinez & Du, 2010), in the present study, the duration of the (coherent) frames was sufficient (100 ms) for people to recognize the emotion. However, to the best of our knowledge, it seems that no study has been carried out to examine the influence of presentation duration to the perceived emotional intensity, and future work may be conducted to bridge the gap.

4.3.4 The association between AQ and the perceived intensity of emotion

Interestingly, AQ was associated with the LPP suppression of happy test faces adapted to the PFO, but abolished when they appear after the AFO and SFO. The results indicate that increasing AQ is related to decreased perceived emotional intensity in partial faces with intermediate completion cues. Previous studies reported an impaired subcortical pathway for the perception of emotion in people with ASD, indicating a compromised ability for the ‘fast-but-coarse’ processing (Kleinhans et al., 2011). In our study, the luminance-congruent facial frame in PFO was a coherent occluded happy face and was briefly displayed (100ms), then masked/interfered by the luminance-incongruent frame. Therefore, the perceived intensity could be subject to the different degrees of involvement of subcortical

pathways, as influenced by AQ scores (Kleinmans et al., 2011; Pierce et al., 2001). In addition, the perceptual completion level of the luminance-congruent facial frames is modulated by AQ. For those with low AQ, increased perceptual completion facilitates emotion intensity perception despite that the most salient (diagnostic) feature for happy face recognition was largely covered. On the contrary, those with high AQ had reduced intensity perception due to heavy reliance on non-diagnostic local feature (as we covered the mouth).

The compensatory strategies for relying on local feature has also been widely observed (Bölte, Holtmann, Poustka, Scheurich, & Schmidt, 2007; Doi et al., 2013; Kliemann et al., 2010). It partially explained the inconsistent findings in the literature examining FEAs among people with ASD and neurotypical individuals with various autistic levels. Recognition of different emotion relies on various cues, for instance, happiness could be recognized based on the mouth alone, whereas recognition of other emotions may depend on a combination of several features, e.g. lower forehead and eyebrows for anger; nose and mouth for disgust (Gosselin & Schyns, 2001; Smith, Cottrell, Gosselin, & Schyns, 2005). People with ASD have a stronger preference for avoiding eyes and focus on the mouth region when looking at faces (Boraston, Blakemore, Chilvers, & Skuse, 2007; Dalton et al., 2005; Joseph & Tanaka, 2003). Therefore, comparable FEA might be observed if using fully-viewable faces whose emotion could be differentiated by a single feature. Such possibility explains the comparable FEA between ASD and normal controls in anger-disgust FEA in Cook's finding (2014), as the mouth alone is enough to differentiate anger and disgust. However, for emotions recognition which requires

integration of several facial features, the FEA may show abnormal trends, such as found in Rutherford's study (2012) which involved the discrimination of 6 basic emotions.

4.4 Summary

In study 3, we investigated the neural correlates between autistic traits and perceptual completion in obscured emotional faces in neuro-typical participants. Our results have indicated that flickering facial parts in different synchronization is a useful tool to study perceptual completion. We also replicated previous research that prolonged exposure to faces could lead to 'categorical adaptation' to subsequent faces, as reflected by reduced N170 amplitude. Importantly, the suppression was strongest in test faces adapted to full-face baseline, weaker in those adapted to SFO, and weakest in those adapted to FPO and AFO. In addition, AQ negatively correlated with the ability to perceive faces holistically.

Consistent with previous literature, we observed high-level emotional adaptation, as reflected by LPP suppression of happy test faces after adapting to the SFO. AQ negatively correlated with perceived emotion intensity in the PFO, which could be due to the different degrees of involvement of subcortical processing and/or the difference in perceptual completion level. For people with high AQ, it is possible that they used a feature-based local processing as a compensatory strategy for facial emotion perception. Our results shed light on the current inconsistent findings in the literature regarding face aftereffect in people with ASD.

Chapter V: Discussion, future directions, and conclusion

5.1 General Discussion

Using psychophysics, eye-tracking and EEG recordings, a series of experiments were carried out to examine the perception of emotion from obscured faces and its relation to autistic traits in neurotypical individuals. In the first study, we manipulated the recognizability, dynamics, location and size of the adaptors to investigate how obscured faces influences FEAs. Results showed that FEAs to static bubbled faces depended on the recognizability of the adaptor, and were observed only when participants could recognize the emotion. However, FEAs to dynamic facial videos were not subject to the recognizability of emotion and survived a locational change of the adapting faces, suggesting possible activation of dorsal and subcortical pathways.

The second study further tested the contribution of local and holistic information to facial expression perception by manipulating the completion strength of obscured emotional faces. Particularly, we examined the association between autistic traits and FEAs. The completion levels of the adaptor were manipulated by using both static and flickering obscured faces. Results showed that increasing autistic traits were associated with smaller FEAs in static obscured faces. The correlation, however, was abolished when the preceding adaptor was full faces (regardless of the dynamics), or obscured flickering faces.

In the third study, to further understand the possible neural mechanism of perceptual completion in obscured emotional faces and its relations with AQ, we

simultaneously recorded behavioral and EEG responses. Results showed that adapting to full face (baseline) lead to the largest N170 suppression in test faces, followed by those adapted to the obscured face with the strongest completion cue (SFO), and were least suppressed in AFO and PFO. People with higher AQ have a smaller N170 change in test faces after adapting to PFO than those adapted to the baseline. The LPP to subsequent happy faces was also suppressed after prolonged exposure to SFO. AQ was positively associated with LPP suppression in happy test faces after adapting to PFO. Taken together, the findings from the three studies have the following implications in facial emotion perception.

5.1.1 The mechanism of facial emotion perception

Facial emotion could be processed with and without our conscious awareness. For emotional faces that could be consciously processed, it mainly follows a hierarchical feed-forward processing approach where the fine details are analyzed (Felleman & Van Essen, 1991; Rhodes et al., 2007; Xu et al., 2008). The extensive interconnections of the brain, however, allow more complicated networks for the processing of affective stimuli (Tamietto & De Gelder, 2010; Pessoa & Adolphs, 2010). For emotions that fail to be consciously perceived, it may nevertheless influence subsequent behavioral and physiological responses (Jiang & He, 2006; Merikle, Smilek, & Eastwood, 2001; Morris, Ohman, & Dolan, 1998; Tamietto & De Gelder, 2010). As mentioned previously, the rendering of unconsciousness could be due to qualitatively different operations (Tamietto & De Gelder, 2010). If the unawareness of stimuli is due to the ‘attentional unawareness’,

both subcortical and/or cortical processing may contribute to the processing of the stimuli. On the other hand, if it is due to ‘sensory unawareness’, the subcortical pathways may play a more important role in the processing of the undetected stimuli.

In the first study, FEAs were observed after adapting to the dynamic emotion-unrecognizable videos and survived locational change in the dynamic unrecognizable conditions. The manipulation in this case was the ‘sensory awareness’ since most emotional cues were obscured and the signal was not strong enough to elicit conscious awareness of the emotions conveyed by the adaptor displayed in the peripheral visual field. The FEAs could be mainly due to activation of the dorsal pathway and subcortical pathway, especially the amygdala (Maior et al., 2010).

The FEA involves local, holistic and high-level semantic representations (Fox & Barton, 2007; Matsumiya, 2014; Wang et al., 2016). Previous studies showed that adaptation to a convex curve or a mouth could lead to FAE, suggesting the contribution of local features to emotion perception (Xu et al., 2008). FEA survived substantial locational shift between test and adapting stimuli (Matsumiya, 2014), and remained significant when the identity of the emotional face was changed, suggesting holistic and semantic adaptation (Fox & Barton, 2007). Furthermore, FEAs could even be generated cross-modally by happy voice (Wang et al., 2016). Our second and third studies partially replicated these findings and supported the contribution of holistic information to FEA. Test faces adapted to SFO (strongest completion cues) showed larger N170 suppression compared to

other adaptors with the same local features. In addition, we found LPP suppression when the emotion of adapting faces matches with test faces.

5.1.2 The negative association between AQ and perception of facial emotions.

Previous studies reported mixed findings regarding FEAs in people with ASD (Cook et al., 2014; Fiorentini, Gray, Rhodes, Jeffery, & Pellicano, 2012; Rutherford et al., 2012; Walsh et al., 2015a; Walsh et al., 2015b). A possible explanation for the inconsistency, as reflected by study 2 and 3, is the recruitment of different facial features in these tasks and varying degrees of holistic perception required. From the results of our experiments, it seems that people with high AQ suffer from a compromised ability in holistic perception and a reduced perception of emotional intensity in obscured faces. Therefore, whether a deficit could be revealed or not is stimulus-dependent. For experiments using facial emotions that do not require integration and could be recognized based on a local feature alone, no deficit might be revealed. Partially occluding emotional faces, especially covering regions that are critical for the recognition of the emotion, could be a useful tool to nullify the compensatory mechanism.

Flickering viewable facial parts abolished the association between AQ and FEAs, as reflected by study 2 and study 3, regardless of synchronization. People with high AQ seem to benefit more from such manipulation. Previous research indicated that facial perception deficits in people with ASD might be a result of reduced social motivation to engage with social-emotional stimuli (Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012; Grelotti et al., 2002). Therefore, the

increased exogenous attention evoked by flickering could help to direct attention to the faces. If this is the case, training programs and intervention therapies might be useful to help ASD children to develop social communication skills (Rhodes et al., 2011).

Finally, increasing autistic traits might be associated with reduced automatic processing of facial emotion. Although previous studies reported that people with ASD have impaired cognitive evaluation and reduced automatic processing (Tracy et al., 2011), others suggested that cognitive assessment was intact. For instance, people with ASD showed comparable behavioral performance in facial-emotion-related task with neurotypical individuals, but activation in subcortical regions (such as the amygdala, FFA, pulvinar and superior colliculus) were reduced (Cook et al., 2014; Kleinhans et al., 2011; Pierce et al., 2001; Press, Richardson, & Bird, 2010; Yerys et al., 2015). Our EEG results in Study 3 also showed that increasing AQ was associated with reduced LPP suppression in test faces adapted to the PFO, but not SFO and AFO. It is possible that automatic evaluation processing deficit in people with high AQ is associated with reduced emotion intensity perception. Fast processing of faces also occurs in cortical pathways (Tsao, Freiwald, Tootell & Livingstone, 2006), however, its relation with ASD is less known.

5.2 Limitations and future directions

The current thesis has investigated how people infer facial emotion from obscured faces and its association with autistic traits. There are some limitations

for the work presented. For instance, number of participants in experiment 3 was relatively small. Although previous EEG studies examining face perception have used similar or even smaller numbers of participants (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Marcus Streit, Wölwer, Brinkmeyer, Ihl, & Gaebel, 2000). Nevertheless, our results could be more convincing (especially for some marginal significant p values) with a larger sample size. In addition, the spread of the AQ score in experiment 3 was not very representative of the distribution of the general population. Participants were postgraduate students from University of Macau, with a medium and high AQ scores (from 15 to 28). Future studies could expand the AQ range and recruit people with clinically diagnosed ASD to further explore the possible link between face perception and autistic traits.

Study 1 and 2 showed larger FEAs in dynamic adaptor than static ones. A possible reason is that enhanced exogenous attention increased adaptability of the entire cortical pathways, and thus larger FEAs (Rhodes et al., 2011). Another possibility is that exogenous attention facilitated amodal completion process and amplified FEA (Davis & Driver, 1997; Moore, Yantis, & Vaughan, 1998). Based on Study 1 and 2, we could not disentangle the contribution of the two possibilities. To deal with this problem, Study 3 added a control condition (AFO) in which facial parts were interleaved between the low and high luminance in any give facial frame. The local information of AFO is the same with the synchronized flickering adaptor (SFO), and results showed that FEA was smaller after adapting to AFO than SFO, supporting the second explanation. Future work, however, may be conducted to investigate the influence of attention to amodal completion.

In our study, the test and adapting faces were from the same identity. Therefore, FEAs observed consisted of both identity and emotion aftereffects. However, we expect a similar FEA pattern if the identity of the two are not matched, although smaller (Fox & Barton, 2007). Previous studies have suggested that aftereffect increases logarithmically with the duration of adapting stimuli and decays exponentially with that of the test faces. Therefore, by increasing the duration of the adaptor or decreasing that of the test face, we might still get substantial FEAs as observed in the current work. In addition, we used happy and sad emotions to study emotion perception in obscured faces and its relation with autistic traits, future work could be conducted with other emotions, such as fear and anger, due to their evolutionary importance.

Furthermore, previous studies have shown other-race effect in face perception, which refers to impaired recognition of faces from other races (Chance & Goldstein, 1996; Lindsay, Jack, & Christian, 1991; Natu, Raboy, & O'Toole, 2011; Vizioli, Rousselet, & Caldara, 2010). The other-race effect is usually accompanied by the belief that faces from other race look alike (Vizioli et al., 2010), probably because of unfamiliarity and lack of motivation to individualize those faces (Zhao, Hayward, & Bülthoff, 2014). In a recent study, Vizioli and colleagues (2010) reported abolished N170 repetition suppression when using other-race faces. For facial expression recognition, it has long been suggested that facial expressions are universal for humankind (Ekman, Sorenson & Friesen, 1969; Ekman, 1971). However, increasing evidence shows that people from eastern and western countries pay attention to different aspects of facial features (Ito, Masuda

& Li, 2013; Yuki, Maddux & Masuda, 2007). However, the other-race effect would be reduced or even eliminated when training is provided for a short period of time (Goldstein & Chance, 1985; Tanaka & Pierce, 2009) or participants have lived in an integrated culture for several years (Bruce & Young, 2012; Chiroro & Valentine, 1995). In this thesis, study 1 and study 2 used Caucasian faces as test stimuli, and participants were Caucasians and Chinese-ethnicity students who had been exposed frequently to Caucasians faces for more than five years. In the third study, the participants and test stimuli were all from Chinese ethnicity.

For the measurement of autistic traits, self-report questionnaire was conducted in neurotypical individuals (university students). Although it has been widely suggested that autistic trait is a continuous construct (Baron-Cohen et al., 2001), it should be stressed that it is far from clear whether those with ASD (and their subclinical relatives) perceive facial emotion in a similar way as subclinical individuals merely high in autistic traits. The possibility that diminishing ability to perceive emotion in a holistic fashion as autistic traits increase in neurotypical population is certainly, however, of interest. Therefore, it should be cautious to extrapolate our findings to the whole population. Future studies could extend the AQ range to the clinically diagnosed ASD patients to see whether the association between AQ and FEA/ERP responses in neurotypical individuals still holds for those ASD patients.

Lastly, our studies have shown a negative association between the perception of facial emotion and AQ in obscured faces. We have argued that this is possibly because people with high AQ experience greater difficulty in integrating

available facial parts and forming a holistic representation of facial emotions. However, as mentioned earlier, the ‘weak central coherence’ theory suggests that the integration deficits also exhibit in other non-face objects, therefore, it raises another question: could the impaired facial emotion perception from obscured faces essentially a result of difficulty in integrating complex stimuli? Previous studies have shown that repetition suppression of face/geometry shapes is negatively correlated with autistic traits (Ewbank et al., 2014). However, we cannot directly compare the suppression between the two and draw a conclusion due to difference of the stimuli (e.g. complexity difference, one condition is complex faces and the other is simple shapes). Future research could be conducted using greebles and faces.

5.3 Conclusions

In conclusion, the studies presented in the thesis investigated how neurotypical individuals infer emotion from partially obscured faces and its association with autistic traits. Three studies have been conducted using psychophysics, eye tracking and EEG measures. It contributes to our understanding of facial emotion perception in several ways: (1) Our emotion perception can be biased without conscious awareness. The findings attest that facial emotion could be processed via both cortical and subcortical pathways. For emotions that fail to reach conscious awareness, especially when caused by sensory unawareness, the subcortical pathway may have played substantial roles in the perception of such affective stimuli. (2) Emotion perception relies on both local and holistic

information. Therefore, adaptation to obscured faces with strongest completion cue could lead to the largest FEA compared to non-completed counterparts. (3) Neurotypical individuals with high AQ is associated with smaller FEA, and possibly due to impaired holistic processing and reduced intensity perception.

To the best of our knowledge, it is the first study that has reported a negative association between autistic traits and facial emotion aftereffect in neurotypical individuals. Our findings offer an explanation as to why those with ASD have been shown to evince neurotypical emotion adaptation aftereffects: it is likely due to featural processing, probably of the mouth region. The autistic traits are negatively associated with the perceptual completion levels and perceived emotion intensity of obscured faces. One possible reason could be due to different degrees of involvement of subcortical processing as modulated by autistic levels. It also sheds light on potential training schemes that could help to improve the quality of life in people who demonstrate a high level of autistic traits.

References

- Abbas, Z.-A., & Duchaine, B. (2008). The role of holistic processing in judgments of facial attractiveness. *Perception*, 37(8), 1187-1196.
- Adams, W. J., Gray, K. L., Garner, M., & Graf, E. W. (2010). High-level face adaptation without awareness. *Psychological Science*, 21(2), 205-210.
- Adolphs, & Ralph. (2006). Perception and Emotion: How We Recognize Facial Expressions. *Current Directions in Psychological Science*, 15(5), 222-226. doi: 10.1111/j.1467-8721.2006.00440.x
- Adolphs, R., Spezio, M. L., Parlier, M., & Piven, J. (2008). Distinct face-processing strategies in parents of autistic children. *Current Biology*, 18(14), 1090-1093.
- Afraz, S.-R., & Cavanagh, P. (2008). Retinotopy of the face aftereffect. *Vision Research*, 48(1), 42-54.
- Amaral, D. G., & Price, J. (1984). Amygdalo - cortical projections in the monkey (Macaca fascicularis). *Journal of Comparative Neurology*, 230(4), 465-496.
- Amihai, I., Deouell, L. Y., & Bentin, S. (2011). Neural adaptation is related to face repetition irrespective of identity: a reappraisal of the N170 effect. *Experimental brain research. Experimentelle Hirnforschung. Experimentation cerebrale*, 209(2), 193-204. doi: 10.1007/s00221-011-2546-x
- Anaki, D., Boyd, J., & Moscovitch, M. (2007). Temporal integration in face perception: evidence of configural processing of temporally separated face

parts. *J Exp Psychol Hum Percept Perform*, 33(1), 1-19. doi: 10.1037/0096-1523.33.1.1

Anaki, D., & Moscovitch, M. (2007). When a face is (or is not) more than the sum of its features: Configural and analytic processes in facial temporal integration. *Visual Cognition*, 15(6), 741-763. doi: 10.1080/13506280601130883

Angelucci, A., Levitt, J. B., & Lund, J. S. (2002). Anatomical origins of the classical receptive field and modulatory surround field of single neurons in macaque visual cortical area V1. *Progress in brain research*, 136, 373-388.

Armony, J., & Vuilleumier, P. (2013). *The Cambridge handbook of human affective neuroscience*: Cambridge University Press.

Association, A. P. (2003). *Diagnostic and Statistical Manual of Mental Disorders: DSM-5*: ManMag.

Bair, W., & Movshon, J. A. (2004). Adaptive temporal integration of motion in direction-selective neurons in macaque visual cortex. *J Neurosci*, 24(33), 7305-7323. doi: 10.1523/JNEUROSCI.0554-04.2004

Baron-Cohen, S. (1997). *Mindblindness: An essay on autism and theory of mind*: MIT press.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The autism-spectrum quotient (AQ): Evidence from asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of autism and developmental disorders*, 31(1), 5-17.

- Bartlett, J. C., & Searcy, J. (1993). Inversion and configuration of faces. *Cognitive psychology*, 25(3), 281-316.
- Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Cognitive Brain Research*, 17(3), 613-620.
- Behrmann, M., Thomas, C., & Humphreys, K. (2006). Seeing it differently: visual processing in autism. *Trends Cogn Sci*, 10(6), 258-264. doi: <http://dx.doi.org/10.1016/j.tics.2006.05.001>
- Beller, H. K. (1971). Priming: effects of advance information on matching. *Journal of Experimental Psychology*, 87(2), 176.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the royal statistical society. Series B (Methodological)*, 289-300.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8(6), 551-565.
- Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2005). Enhanced and diminished visuo-spatial information processing in autism depends on stimulus complexity. *Brain*, 128(10), 2430-2441.
- Bimler, D. L., Skwarek, S. J., & Paramei, G. V. (2013). Processing Facial Expressions of Emotion: Upright vs. Inverted Images. *Frontiers in Psychology*, 4, 54. doi: 10.3389/fpsyg.2013.00054
- Bird, G., & Cook, R. (2013). Mixed emotions: the contribution of alexithymia to the emotional symptoms of autism. *Translational psychiatry*, 3(7), e285.

- Blake, R., Tadin, D., Sobel, K. V., Raissian, T. A., & Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proceedings of the National Academy of Sciences of the United States of America*, 103(12), 4783-4788. doi: 0509634103
- Bocanegra, B. R., & Zeelenberg, R. (2009). Emotion improves and impairs early vision. *Psychological science*, 20(6), 707-713.
- Bölte, S., Holtmann, M., Poustka, F., Scheurich, A., & Schmidt, L. (2007). Gestalt perception and local-global processing in high-functioning autism. *Journal of autism and developmental disorders*, 37(8), 1493-1504.
- Boraston, Z., Blakemore, S. J., Chilvers, R., & Skuse, D. (2007). Impaired sadness recognition is linked to social interaction deficit in autism. *Neuropsychologia*, 45(7), 1501-1510. doi: 10.1016/j.neuropsychologia.2006.11.010
- Bötzel, K., Schulze, S., & Stodieck, S. R. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental brain research*, 104(1), 135-143.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial vision*, 10, 433-436.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433-436.
- Braverman, M., Fein, D., Lucci, D., & Waterhouse, L. (1989). Affect comprehension in children with pervasive developmental disorders. *Journal of autism and developmental disorders*, 19(2), 301-316.

- Brosnan, M. J., Scott, F. J., Fox, S., & Pye, J. (2004). Gestalt processing in autism: Failure to process perceptual relationships and the implications for contextual understanding. *Journal of Child Psychology and Psychiatry*, 45(3), 459-469.
- Brown, J. M., & Weisstein, N. (1991). Conflicting figure-ground and depth information reduces moving phantom visibility. *Perception*, 20(2), 155-165.
- Bruce, C., Desimone, R., & Gross, C. G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *Journal of neurophysiology*, 46(2), 369-384.
- Bruce, V., & Young, A. W. (2012). *Face perception*: Psychology Press.
- Bülthoff, H. H., & Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. *Proceedings of the National Academy of Sciences*, 89(1), 60-64.
- Burra, N., Hervais-Adelman, A., Kerzel, D., Tamietto, M., De Gelder, B., & Pegna, A. J. (2013). Amygdala activation for eye contact despite complete cortical blindness. *The Journal of Neuroscience*, 33(25), 10483-10489.
- Bushnell, B. N., Harding, P. J., Kosai, Y., & Pasupathy, A. (2011). Partial occlusion modulates contour-based shape encoding in primate area V4. *The Journal of Neuroscience*, 31(11), 4012-4024.
- Butler, A., Oruc, I., Fox, C. J., & Barton, J. J. (2008). Factors contributing to the adaptation aftereffects of facial expression. *Brain research*, 1191, 116-126.
- Calder, A. J., Lawrence, A. D., & Young, A. W. (2001). Neuropsychology of fear and loathing. *Nature Reviews Neuroscience*, 2(5), 352-363.

- Calder, A. J., Young, A. W., Keane, J., & Dean, M. (2000). Configural information in facial expression perception. *Journal of Experimental Psychology: Human Perception and Performance*, 26(2), 527.
- Calvo, M. G., Fernández-Martín, A., & Nummenmaa, L. (2013). A smile biases the recognition of eye expressions: Configural projection from a salient mouth. *The Quarterly Journal of Experimental Psychology*, 66(6), 1159-1181.
- Carbon, C.-C., & Ditye, T. (2012). Face adaptation effects show strong and long-lasting transfer from lab to more ecological contexts. *Frontiers in Psychology*, 3, 3.
- Cavanaugh, J. R., Bair, W., & Movshon, J. A. (2002). Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. *Journal of neurophysiology*, 88(5), 2530-2546.
- Celebrini, S. I. M. O. N. A., & Newsome, W. T. (1995). Microstimulation of extrastriate area MST influences performance on a direction discrimination task. *Journal of Neurophysiology*, 73(2), 437-448.
- Censi, S., Simard, M., Mottron, L., Saint-Amour, D., & Bertone, A. (2013). Assessing lateral interactions within the early visual areas of adults with autism. *Journal of Vision*, 13(9), 837-837.
- Chance, J. E., & Goldstein, A. G. (1996). The other-race effect and eyewitness identification.
- Chen, J., Liu, B., Chen, B., & Fang, F. (2009). Time course of amodal completion in face perception. *Vision Research*, 49(7), 752-758. doi: <http://dx.doi.org/10.1016/j.visres.2009.02.005>

- Chen, J., Zhou, T., Yang, H., & Fang, F. (2010). Cortical dynamics underlying face completion in human visual system. *The Journal of Neuroscience*, 30(49), 16692-16698.
- Chen, L.-F., & Yen, Y.-S. (2007). Taiwanese facial expression image database. Available: <http://bml.ym.edu.tw/download/html>. Brain Mapping Laboratory, Institute of Brain Science, National Yang-Ming University, Taipei, Taiwan.
- Chen, M.-Y., & Chen, C.-C. (2010). The contribution of the upper and lower face in happy and sad facial expression classification. *Vision Research*, 50(18), 1814-1823.
- Chevallier, C., Kohls, G., Troiani, V., Brodtkin, E. S., & Schultz, R. T. (2012). The social motivation theory of autism. *Trends Cogn Sci*, 16(4), 231-239.
- Chiroro, P., & Valentine, T. (1995). An investigation of the contact hypothesis of the own-race bias in face recognition. *The Quarterly Journal of Experimental Psychology*, 48(4), 879-894.
- Codispoti, M., Ferrari, V., & Bradley, M. M. (2006). Repetitive picture processing: autonomic and cortical correlates. *Brain research*, 1068(1), 213-220.
- Cohen Kadosh, K., Walsh, V., & Cohen Kadosh, R. (2010). Investigating face-property specific processing in the right OFA. *Social Cognitive and Affective Neuroscience*. doi: 10.1093/scan/nsq015
- Cohen, M. A., & Grossberg, S. (1984). Neural dynamics of brightness perception: Features, boundaries, diffusion, and resonance. *Perception & psychophysics*, 36(5), 428-456.

- Cook, R., Brewer, R., Shah, P., & Bird, G. (2014). Intact facial adaptation in autistic adults. *Autism Res*, 7(4), 481-490. doi: 10.1002/aur.1381
- Critchley, H. D., Daly, E. M., Bullmore, E. T., Williams, S. C., Van Amelsvoort, T., Robertson, D. M., . . . Howlin, P. (2000). The functional neuroanatomy of social behaviour. *Brain*, 123(11), 2203-2212.
- Dalton, K. M., Nacewicz, B. M., Johnstone, T., Schaefer, H. S., Gernsbacher, M. A., Goldsmith, H., . . . Davidson, R. J. (2005). Gaze fixation and the neural circuitry of face processing in autism. *Nature neuroscience*, 8(4), 519-526.
- Damasio, A. R., Damasio, H., & Van Hoesen, G. W. (1982). Prosopagnosia: Anatomic basis and behavioral mechanisms. *Neurology*, 32(4), 331-331.
- Davis, G., & Driver, J. (1997). Spreading of visual attention to modally versus amodally completed regions. *Psychological science*, 8(4), 275-281.
- Dawson, G., Webb, S. J., & McPartland, J. (2005). Understanding the nature of face processing impairment in autism: insights from behavioral and electrophysiological studies. *Developmental neuropsychology*, 27(3), 403-424.
- Deffke, I., Sander, T., Heidenreich, J., Sommer, W., Curio, G., Trahms, L., & Lueschow, A. (2007). MEG/EEG sources of the 170-ms response to faces are co-localized in the fusiform gyrus. *Neuroimage*, 35(4), 1495-1501. doi: 10.1016/j.neuroimage.2007.01.034
- Delorme, A., Sejnowski, T., & Makeig, S. (2007). Enhanced detection of artifacts in EEG data using higher-order statistics and independent component analysis. *Neuroimage*, 34(4), 1443-1449.

- Dennett, D. C. (1991). *Consciousness Explained*. Boston (Little, Brown and Co) 1991.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual review of neuroscience*, 18(1), 193-222.
- Dhall, A., Goecke, R., Joshi, J., Wagner, M., & Gedeon, T. (2013). *Emotion recognition in the wild challenge 2013*. Paper presented at the Proceedings of the 15th ACM on International conference on multimodal interaction.
- Doi, H., Fujisawa, T. X., Kanai, C., Ohta, H., Yokoi, H., Iwanami, A., . . . Shinohara, K. (2013). Recognition of facial expressions and prosodic cues with graded emotional intensities in adults with Asperger syndrome. *Journal of autism and developmental disorders*, 43(9), 2099-2113.
- Eacott, M., Heywood, C., Gross, C., & Cowey, A. (1993). Visual discrimination impairments following lesions of the superior temporal sulcus are not specific for facial stimuli. *Neuropsychologia*, 31(6), 609-619.
- Eggermont, J. J. (1985). Peripheral auditory adaptation and fatigue: A model oriented review. *Hearing Research*, 18(1), 57-71. doi: [http://dx.doi.org/10.1016/0378-5955\(85\)90110-8](http://dx.doi.org/10.1016/0378-5955(85)90110-8)
- Ehrenstein, W., Spillmann, L., & Sarris, V. (2003). Gestalt Issues in Modern Neuroscience. *Axiomathes*, 13(3-4), 433-458. doi: 10.1023/B:AXIO.00000007203.44686.aa
- Eimer, M. (2000). The face - specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*, 11(10), 2319-2324.

- Eimer, M. (2011). The face-sensitive N170 component of the event-related brain potential. *The Oxford handbook of face perception*, 329-344.
- Eimer, M., Gosling, A., Nicholas, S., & Kiss, M. (2011). The N170 component and its links to configural face processing: a rapid neural adaptation study. *Brain research*, 1376, 76-87.
- Ekman, P., Sorenson, E. R., & Friesen, W. V. (1969). Pan-cultural elements in facial displays of emotion. *Science*, 164(3875), 86-88.
- Ekman, P., & Friesen, W. V. (1971). Constants across cultures in the face and emotion. *Journal of personality and social psychology*, 17(2), 124.
- Elfenbein, H. A., Der Foo, M., White, J., Tan, H. H., & Aik, V. C. (2007). Reading your counterpart: The benefit of emotion recognition accuracy for effectiveness in negotiation. *Journal of Nonverbal Behavior*, 31(4), 205-223.
- Etkin, A., Egner, T., & Kalisch, R. (2011). Emotional processing in anterior cingulate and medial prefrontal cortex. *Trends in cognitive sciences*, 15(2), 85-93.
- Ewbank, M. P., Rhodes, G., von dem Hagen, E. A., Powell, T. E., Bright, N., Stoyanova, R. S., . . . Calder, A. J. (2014). Repetition suppression in ventral visual cortex is diminished as a function of increasing autistic traits. *Cerebral Cortex*, bhu149.
- Fang, F., & He, S. (2005). Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. *Neuron*, 45(5), 793-800.

- Fang, F., Murray, S. O., & He, S. (2007). Duration-dependent fMRI adaptation and distributed viewer-centered face representation in human visual cortex. *Cerebral Cortex*, 17(6), 1402-1411.
- Feldman, R. S., McGee, G. G., Mann, L., & Strain, P. (1993). Nonverbal affective decoding ability in children with autism and in typical preschoolers. *Journal of Early Intervention*, 17(4), 341-350.
- Feldman, R. S., Philippot, P., & Custrini, R. J. (1991). Social competence and nonverbal behavior.
- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1(1), 1-47.
- Fiorentini, C., Gray, L., Rhodes, G., Jeffery, L., & Pellicano, E. (2012). Reduced face identity aftereffects in relatives of children with autism. *Neuropsychologia*, 50(12), 2926-2932.
- Flack, T. R., Andrews, T. J., Hymers, M., Al-Mosaiwi, M., Marsden, S. P., Strachan, J. W., . . . Young, A. W. (2015). Responses in the right posterior superior temporal sulcus show a feature-based response to facial expression. *Cortex*, 69, 14-23.
- Fox, C. J., & Barton, J. J. (2007). What is adapted in face adaptation? The neural representations of expression in the human visual system. *Brain research*, 1127, 80-89.
- Frisby, J. (1979). *Seeing: Illusion, Brain and Mind*. Oxford: Oxford Univ. Press.
- Frith, U. (1991). *Autism and Asperger syndrome*: Cambridge University Press.

- Fujita, I. (2002). The inferior temporal cortex: architecture, computation, and representation. *Journal of neurocytology*, 31(3-5), 359-371.
- Fukushima, K. (1980). Neocognitron: A self-organizing neural network model for a mechanism of pattern recognition unaffected by shift in position. *Biological cybernetics*, 36(4), 193-202.
- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature neuroscience*, 3(2), 191-197.
- George, D., & Mallery, P. (2010). *SPSS for Windows Step by Step: A Simple Guide and Reference 18.0 Update*: Prentice Hall Press.
- Gepner, B., Mestre, D., Masson, G., & de Schonen, S. (1995). Postural effects of motion vision in young autistic children. *Neuroreport*, 6(8), 1211-1214.
- Gerrits, I. H., & Vendrik, A. (1970). Simultaneous contrast, filling-in process and information processing in man's visual system. *Experimental brain research*, 11(4), 411-430.
- Gheorghiu, E., Bell, J., & Gurnsey, R. (2011). Why do shape aftereffects increase with eccentricity? *Journal of Vision*, 11(14), 18-18.
- Gibson, J. J. (1933). Adaptation, after-effect and contrast in the perception of curved lines. *Journal of Experimental Psychology*, 16(1), 1-31.
- Gobbini, M. I., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces. *Neuropsychologia*, 45(1), 32-41.

- Goffaux, V., Hault, B., Michel, C., Vuong, Q. C., & Rossion, B. (2005). The respective role of low and high spatial frequencies in supporting configural and featural processing of faces. *Perception*, 34(1), 77-86.
- Goffaux, V., & Rossion, B. (2006). Faces are "spatial"--holistic face perception is supported by low spatial frequencies. *Journal of Experimental Psychology: Human Perception and Performance*, 32(4), 1023.
- Goldstein, A. G., & Chance, J. E. (1985). Effects of training on Japanese face recognition: Reduction of the other-race effect. *Bulletin of the Psychonomic Society*, 23(3), 211-214.
- Goodale, M. A., Milner, A. D., Jakobson, L., & Carey, D. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349(6305), 154-156.
- Gosselin, F., & Schyns, P. G. (2001). Bubbles: a technique to reveal the use of information in recognition tasks. *Vision Research*, 41(17), 2261-2271.
- Gregory, R. L. (1972). Cognitive contours. *Nature*.
- Grelotti, D. J., Gauthier, I., & Schultz, R. T. (2002). Social interest and the development of cortical face specialization: What autism teaches us about face processing. *Developmental psychobiology*, 40(3), 213-225.
- Grill-Spector, K. (2006). Selectivity of adaptation in single units: implications for fMRI experiments. *Neuron*, 49(2), 170-171.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn Sci*, 10(1), 14-23.

- Gross, C. G., Rocha-Miranda, C. E. d., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the Macaque. *Journal of neurophysiology*, 35(1), 96-111.
- Gross, T. F. (2004). The perception of four basic emotions in human and nonhuman faces by children with autism and other developmental disabilities. *Journal of abnormal child psychology*, 32(5), 469-480.
- Grossman, J. B., Klin, A., Carter, A. S., & Volkmar, F. R. (2000). Verbal bias in recognition of facial emotions in children with Asperger syndrome. *Journal of Child Psychology and Psychiatry*, 41(3), 369-379.
- Hajcak, G., MacNamara, A., & Olvet, D. M. (2010). Event-related potentials, emotion, and emotion regulation: an integrative review. *Developmental neuropsychology*, 35(2), 129-155.
- Hajcak, G., & Olvet, D. M. (2008). The persistence of attention to emotion: brain potentials during and after picture presentation. *Emotion*, 8(2), 250.
- Happé, F., & Frith, U. (2006). The weak coherence account: detail-focused cognitive style in autism spectrum disorders. *Journal of autism and developmental disorders*, 36(1), 5-25.
- Harms, M. B., Martin, A., & Wallace, G. L. (2010). Facial emotion recognition in autism spectrum disorders: a review of behavioral and neuroimaging studies. *Neuropsychology review*, 20(3), 290-322.
- Harris, A., & Aguirre, G. K. (2008). The representation of parts and wholes in face-selective cortex. *Journal of Cognitive Neuroscience*, 20(5), 863-878.
- Harris, J. (2014). *Sensation and perception*. London: SAGE.

- Harvey Jr, L. O. (2003). Detection sensitivity and response bias. *Psychology of Perception. Psychology*, 4165.
- Haxby, J. V., & Gobbini, M. I. (2011). *Distributed neural systems for face perception*: The Oxford Handbook of Face Perception.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, 293(5539), 2425-2430.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4(6), 223-233.
- Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, 22(1), 189-199.
- Hazenbergh, S. J., Jongsma, M. L., Koning, A., & van Lier, R. (2014). Differential familiarity effects in amodal completion: Support from behavioral and electrophysiological measurements. *Journal of Experimental Psychology: Human Perception and Performance*, 40(2), 669.
- He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, 383(6598), 334-337. doi: 10.1038/383334a0
- Hegd, J., Fang, F., Murray, S. O., & Kersten, D. (2008). Preferential responses to occluded objects in the human visual cortex. *Journal of Vision*, 8(4), 16.
- Heider, F. (1977). Cited in Dewey, RA 2007. *Psychology: An introduction*.

- Hobson, R. P. (1986). The autistic child's appraisal of expressions of emotion. *Journal of Child Psychology and Psychiatry*, 27(3), 321-342.
- Hoffman, E. A., & Haxby, J. V. (2000). Distinct representations of eye gaze and identity in the distributed human neural system for face perception. *Nature neuroscience*, 3(1), 80-84.
- Hsu, S., & Young, A. (2004). Adaptation effects in facial expression recognition. *Visual Cognition*, 11, 871-899.
- Hubel, D. H., & Wiesel, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *Journal of neurophysiology*, 28(2), 229-289.
- Hubl, D., Bölte, S., Feineis-Matthews, S., Lanfermann, H., Federspiel, A., Strik, W., . . . Dierks, T. (2003). Functional imbalance of visual pathways indicates alternative face processing strategies in autism. *Neurology*, 61(9), 1232-1237.
- Ito, M., Tamura, H., Fujita, I., & Tanaka, K. (1995). Size and position invariance of neuronal responses in monkey inferotemporal cortex. *Journal of neurophysiology*, 73(1), 218-226.
- Ito, K., Masuda, T., & Man Wai Li, L. (2013). Agency and facial emotion judgment in context. *Personality and Social Psychology Bulletin*, 39(6), 763-776.
- James, T. W., Huh, E., & Kim, S. (2010). Temporal and spatial integration of face, object, and scene features in occipito-temporal cortex. *Brain Cogn*, 74(2), 112-122. doi: 10.1016/j.bandc.2010.07.007

- Jiang, Y., & He, S. (2006). Cortical responses to invisible faces: dissociating subsystems for facial-information processing. *Current Biology*, 16(20), 2023-2029.
- Johnson, J. S., & Olshausen, B. A. (2005). The recognition of partially visible natural objects in the presence and absence of their occluders. *Vision Research*, 45(25), 3262-3276.
- Joseph, R. M., & Tanaka, J. (2003). Holistic and part - based face recognition in children with autism. *Journal of Child Psychology and Psychiatry*, 44(4), 529-542.
- Joyce, C., & Rossion, B. (2005). The face-sensitive N170 and VPP components manifest the same brain processes: the effect of reference electrode site. *Clinical Neurophysiology*, 116(11), 2613-2631.
- Júnior, M. F., Rosa, M., Gattass, R., & Rocha-Miranda, C. E. (1992). Dynamic surrounds of receptive fields in primate striate cortex: a physiological basis for perceptual completion? *Proceedings of the National Academy of Sciences*, 89(18), 8547-8551.
- Júnior, R. d. M., Marinho de Sousa, B., & Fukusima, S. (2014). Hemispheric specialization in face recognition: From spatial frequencies to holistic/analytic cognitive processing. *Psychology & Neuroscience*, 7(4), 503.
- Kafaligonul, H., Breitmeyer, B. G., & Ögmen, H. (2015). Feedforward and feedback processes in vision. *Frontiers in Psychology*, 6, 279. doi: 10.3389/fpsyg.2015.00279

- Kalick, S. M., Zebrowitz, L. A., Langlois, J. H., & Johnson, R. M. (1998). Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question. *Psychological science*, 9(1), 8-13.
- Kanisza, G., & Gerbino, W. (1982). Amodal completion: Seeing or thinking. *Organization and representation in perception*. Erlbaum, Hillsdale, NJ.
- Kanizsa, G. (1979). *Organization in vision: Essays on Gestalt perception*: Praeger Publishers.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, 17(11), 4302-4311.
- Kanwisher, N., & Moscovitch, M. (2000). *The Cognitive Neuroscience of Face Processing: A Special Issues of Cognitive Neuropsychology*: Psychology Press.
- Kasai, T., & Murohashi, H. (2013). Global visual processing decreases with autistic-like traits: A study of early lateralized potentials with spatial attention. *Japanese Psychological Research*, 55(2), 131-143. doi: 10.1111/jpr.12014
- Kawasaki, H., Adolphs, R., Kaufman, O., Damasio, H., Damasio, A. R., Granner, M., . . . Howard, M. A. (2001). Single-neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. *Nature neuroscience*, 4(1), 15-16.
- Kayser, J., Bruder, G. E., Tenke, C. E., Stewart, J. E., & Quitkin, F. M. (2000). Event-related potentials (ERPs) to hemifield presentations of emotional

- stimuli: differences between depressed patients and healthy adults in P3 amplitude and asymmetry. *International Journal of Psychophysiology*, 36(3), 211-236.
- Kellman, P. J., Yin, C., & Shipley, T. F. (1998). A common mechanism for illusory and occluded object completion. *Journal of Experimental Psychology: Human Perception and Performance*, 24(3), 859.
- Keil, A., Bradley, M. M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P. J. (2002). Large - scale neural correlates of affective picture processing. *Psychophysiology*, 39(5), 641-649.
- Keil, A., Gruber, T., Müller, M. M., Moratti, S., Stolarova, M., Bradley, M. M., & Lang, P. J. (2003). Early modulation of visual perception by emotional arousal: evidence from steady-state visual evoked brain potentials. *Cognitive, Affective, & Behavioral Neuroscience*, 3(3), 195-206.
- Kessler, H., Doyen-Waldecker, C., Hofer, C., Hoffmann, H., Traue, H. C., & Abler, B. (2011). Neural correlates of the perception of dynamic versus static facial expressions of emotion. *GMS Psycho-Social-Medicine*, 8, Doc03. doi: 10.3205/psm000072
- Keysers, C., & Perrett, D. I. (2002). Visual masking and RSVP reveal neural competition. *Trends Cogn Sci*, 6(3), 120-125.
- Kim, S. H., Feldman, J., & Singh, M. (2012). Curved apparent motion induced by amodal completion. *Atten Percept Psychophys*, 74(2), 350-364. doi: 10.3758/s13414-011-0237-0

- Kiritani, Y. (1999). Perceptual causality in the amodal completion of kinetic structures. *Psychological research*, 62(4), 255-260.
- Kleinhans, N. M., Richards, T., Johnson, L. C., Weaver, K. E., Greenson, J., Dawson, G., & Aylward, E. (2011). fMRI evidence of neural abnormalities in the subcortical face processing system in ASD. *Neuroimage*, 54(1), 697-704.
- Kliemann, D., Dziobek, I., Hatri, A., Steimke, R., & Heekeren, H. R. (2010). Atypical reflexive gaze patterns on emotional faces in autism spectrum disorders. *The Journal of Neuroscience*, 30(37), 12281-12287.
- Klin, A., Jones, W., Schultz, R., Volkmar, F., & Cohen, D. (2002). Visual fixation patterns during viewing of naturalistic social situations as predictors of social competence in individuals with autism. *Archives of general psychiatry*, 59(9), 809-816.
- Knyazev, G. G. (2007). Motivation, emotion, and their inhibitory control mirrored in brain oscillations. *Neuroscience & Biobehavioral Reviews*, 31(3), 377-395.
- Kohn, A. (2007). Visual Adaptation: Physiology, Mechanisms, and Functional Benefits. *Journal of neurophysiology*, 97(5), 3155-3164. doi: 10.1152/jn.00086.2007
- Kozyrev, V., Silveira, L. C. L., & Kremers, J. (2007). Linking lateral interactions in flicker perception to lateral geniculate nucleus cell responses. *The Journal of physiology*, 581(3), 1083-1100.

- Krauzlis, R. J., Lovejoy, L. P., & Zénon, A. (2013). Superior colliculus and visual spatial attention. *Annual review of neuroscience*, 36.
- Krolak-Salmon, P., Henaff, M. A., Tallon-Baudry, C., Yvert, B., Guenot, M., Vighetto, A., . . . Bertrand, O. (2003). Human lateral geniculate nucleus and visual cortex respond to screen flicker. *Annals of Neurology*, 53(1), 73-80. doi: 10.1002/ana.10403
- Lahaie, A., Mottron, L., Arguin, M., Berthiaume, C., Jemel, B., & Saumier, D. (2006). Face perception in high-functioning autistic adults: evidence for superior processing of face parts, not for a configural face-processing deficit. *Neuropsychology*, 20(1), 30.
- Lau, W. Y.-P., Gau, S. S.-F., Chiu, Y.-N., Wu, Y.-Y., Chou, W.-J., Liu, S.-K., & Chou, M.-C. (2013). Psychometric properties of the Chinese version of the Autism Spectrum Quotient (AQ). *Research in Developmental Disabilities*, 34(1), 294-305. doi: <http://dx.doi.org/10.1016/j.ridd.2012.08.005>
- LeDoux, J. (1996). The Emotional Brain Simon Schuster. *New York*, 384.
- Lee, Y., Anaki, D., Grady, C. L., & Moscovitch, M. (2012). Neural correlates of temporal integration in face recognition: an fMRI study. *Neuroimage*, 61(4), 1287-1299. doi: 10.1016/j.neuroimage.2012.02.073
- Lerner, Y., Hendler, T., & Malach, R. (2002). Object-completion effects in the human lateral occipital complex. *Cerebral Cortex*, 12(2), 163-177.
- Leube, D. T., Yoon, H. W., Rapp, A., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. (2003). Brain regions sensitive to the face inversion effect: a

- functional magnetic resonance imaging study in humans. *Neurosci Lett*, 342(3), 143-146.
- Levinthal, B. R., & Franconeri, S. L. (2011). Common-fate grouping as feature selection. *Psychological science*, 0956797611418346.
- Levitt, J. B., Kiper, D. C., & Movshon, J. A. (1994). Receptive fields and functional architecture of macaque V2. *J Neurophysiol*, 71(6), 2517-2542.
- Lin, Z., & He, S. (2012). Emergent filling in induced by motion integration reveals a high-level mechanism in filling in. *Psychological science*, 23(12), 1534-1541.
- Lindsay, D. S., Jack, P. C., & Christian, M. A. (1991). Other-race face perception. *Journal of applied psychology*, 76(4), 587.
- Lipp, O. V., Price, S. M., & Tellegen, C. L. (2009). No effect of inversion on attentional and affective processing of facial expressions. *Emotion*, 9(2), 248.
- Liu, P., Ong, J., & Xu, H. (2012). Top and bottom half faces influence equally and interact nonlinearly in face-identity adaptation. *Journal of Vision*, 12(9), 623-623.
- Tsao, D. Y., Freiwald, W. A., Tootell, R. B., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science*, 311(5761), 670-674.
- Loveland, K. A., Pearson, D. A., Tunali-Kotoski, B., Ortegon, J., & Gibbs, M. C. (2001). Judgments of social appropriateness by children and adolescents

- with autism. *Journal of autism and developmental disorders*, 31(4), 367-376.
- Luck, S. J., & Kappenman, E. S. (2011). *The Oxford handbook of event-related potential components*: Oxford university press.
- Lundqvist, D. (1998). The Karolinska Directed Emotional Faces - KDEF. from Department of Clinical Neuroscience, Psychology section, Karolinska Institutet
- Luo, C., Wang, Q., Schyns, P. G., Kingdom, F. A. A., & Xu, H. (2015). Facial Expression Aftereffect Revealed by Adaption to Emotion-Invisible Dynamic Bubbled Faces. *PloS one*, 10(12), e0145877.
- Maier, R. S., Hori, E., Tomaz, C., Ono, T., & Nishijo, H. (2010). The monkey pulvinar neurons differentially respond to emotional expressions of human faces. *Behavioural brain research*, 215(1), 129-135.
- Makeig, S., Bell, T., Lee, T., Jung, T., & Enghoff, S. (2000). EEGLAB: ICA toolbox for psychophysiological research. *WWW Site, Swartz Center for Computational Neuroscience, Institute of Neural Computation, University of San Diego California* < www.sccn.ucsd.edu/eeglab.
- Marr, D., & Nishihara, H. K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. *Proceedings of the Royal Society of London B: Biological Sciences*, 200(1140), 269-294.
- Martin, R. A., Berry, G. E., Dobranski, T., Horne, M., & Dodgson, P. G. (1996). Emotion perception threshold: Individual differences in emotional sensitivity. *Journal of Research in Personality*, 30(2), 290-305.

- Martinez, A., & Du, S. (2010). How fast can we recognize facial expressions of emotion? *Journal of Vision*, 10(7), 607-607.
- Masson, G. S., Busetini, C., & Miles, F. A. (1997). Vergence eye movements in response to binocular disparity without depth perception. *Nature*, 389(6648), 283-286.
- Matsumiya, K. (2014). Retinotopy of Facial Expression Adaptation. *Multisensory research*, 27(2), 127-137.
- Meaux, E., & Vuilleumier, P. (2016). Facing mixed emotions: Analytic and holistic perception of facial emotion expressions engages separate brain networks. *Neuroimage*, 141, 154-173. doi: 10.1016/j.neuroimage.2016.07.004
- Merikle, P. M., Smilek, D., & Eastwood, J. D. (2001). Perception without awareness: Perspectives from cognitive psychology. *Cognition*, 79(1), 115-134.
- Meyer, G. E., & Dougherty, T. (1987). Effects of flicker-induced depth on chromatic subjective contours. *Journal of Experimental Psychology: Human Perception and Performance*, 13(3), 353.
- Michelson, A. (1927). *Studies in Optics*.: U. of Chicago Press.
- Michotte, A., Thines, G., & Crabbe, G. (1964). Amodal completion and perceptual organization (Tr.). *Louvein: Studia Psychologica*.
- Mognon, A., Jovicich, J., Bruzzone, L., & Buiatti, M. (2011). ADJUST: An automatic EEG artifact detector based on the joint use of spatial and temporal features. *Psychophysiology*, 48(2), 229-240.

- Moore, C. M., Yantis, S., & Vaughan, B. (1998). Object-based visual selection: Evidence from perceptual completion. *Psychological science*, 9(2), 104-110.
- Moradi, F., Koch, C., & Shimojo, S. (2005). Face adaptation depends on seeing the face. *Neuron*, 45(1), 169-175. doi: 10.1016/j.neuron.2004.12.018
- Moratti, S., Saugar, C., & Strange, B. A. (2011). Prefrontal-occipitoparietal coupling underlies late latency human neuronal responses to emotion. *The Journal of Neuroscience*, 31(47), 17278-17286.
- Morris, J. S., Ohman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, 393(6684), 467-470. doi: 10.1038/30976
- Morrison, S. E., Saez, A., Lau, B., & Salzman, C. D. (2011). Different time courses for learning-related changes in amygdala and orbitofrontal cortex. *Neuron*, 71(6), 1127-1140.
- Murray, R. F., Sekuler, A. B., & Bennett, P. J. (2001). Time course of amodal completion revealed by a shape discrimination task. *Psychonomic Bulletin & Review*, 8(4), 713-720.
- Nakayama, K., Shimojo, S., & Silverman, G. H. (1989). Stereoscopic depth: its relation to image segmentation, grouping, and the recognition of occluded objects. *Perception*, 18(1), 55-68.
- Natu, V., Raboy, D., & O'Toole, A. J. (2011). Neural correlates of own-and other-race face perception: Spatial and temporal response differences. *Neuroimage*, 54(3), 2547-2555.

- Neumann, D., Spezio, M. L., Piven, J., & Adolphs, R. (2006). Looking you in the mouth: abnormal gaze in autism resulting from impaired top-down modulation of visual attention. *Social cognitive and affective neuroscience*, 1(3), 194-202.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97-113.
- Olofsson, J. K., & Polich, J. (2007). Affective visual event-related potentials: arousal, repetition, and time-on-task. *Biological psychology*, 75(1), 101-108.
- Op De Beeck, H., & Vogels, R. (2000). Spatial sensitivity of macaque inferior temporal neurons. *Journal of Comparative Neurology*, 426(4), 505-518.
- Palmer, S. (1999). Gestalt perception. *The MIT encyclopedia of the cognitive sciences*, 344-346.
- Parul, I. (2013). *Glaucoma: Basic and Clinical Perspectives*: Future Medicine Ltd.
- Peelen, M. V., Heslenfeld, D. J., & Theeuwes, J. (2004). Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *Neuroimage*, 22(2), 822-830.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, 10, 437-442.
- Pellicano, E., Gibson, L., Maybery, M., Durkin, K., & Badcock, D. R. (2005). Abnormal global processing along the dorsal visual pathway in autism: a possible mechanism for weak visuospatial coherence? *Neuropsychologia*, 43(7), 1044-1053.

- Pellicano, E., Jeffery, L., Burr, D., & Rhodes, G. (2007). Abnormal adaptive face-coding mechanisms in children with autism spectrum disorder. *Current Biology*, 17(17), 1508-1512.
- Pellicano, E., Rhodes, G., & Calder, A. J. (2013). Reduced gaze aftereffects are related to difficulties categorising gaze direction in children with autism. *Neuropsychologia*, 51(8), 1504-1509.
- Perrett, D., Rolls, E., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. *Experimental brain research*, 47(3), 329-342.
- Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: from a'low road'to'many roads' of evaluating biological significance. *Nature reviews neuroscience*, 11(11), 773-783.
- Pessoa, L., & De Weerd, P. (2003). *Filling-in: From perceptual completion to cortical reorganization*: Oxford University Press.
- Peterhans, E., & von der Heydt, R. (1989). Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps. *The Journal of Neuroscience*, 9(5), 1749-1763.
- Perneger, T. V. (1998). What's wrong with Bonferroni adjustments. *BMJ: British Medical Journal*, 316(7139), 1236-1238.
- Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. *Neuroimage*, 16(2), 331-348.

- Pierce, K., Müller, R.-A., Ambrose, J., Allen, G., & Courchesne, E. (2001). Face processing occurs outside the fusiform face area in autism: evidence from functional MRI. *Brain*, *124*(10), 2059-2073.
- Pitcher, D., Dilks, D. D., Saxe, R. R., Triantafyllou, C., & Kanwisher, N. (2011). Differential selectivity for dynamic versus static information in face-selective cortical regions. *Neuroimage*, *56*(4), 2356-2363. doi: 10.1016/j.neuroimage.2011.03.067
- Poljac, E., Poljac, E., & Wagemans, J. (2013). Reduced accuracy and sensitivity in the perception of emotional facial expressions in individuals with high autism spectrum traits. *Autism*, *17*(6), 668-680.
- Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebral Cortex*, *14*(6), 619-633.
- Pratt, J., & Sekuler, A. B. (2001). The effects of occlusion and past experience on the allocation of object-based attention. *Psychonomic Bulletin & Review*, *8*(4), 721-727.
- Press, C., Richardson, D., & Bird, G. (2010). Intact imitation of emotional facial actions in autism spectrum conditions. *Neuropsychologia*, *48*(11-3), 3291-3297. doi: 10.1016/j.neuropsychologia.2010.07.012
- Protopopescu, X., Pan, H., Altemus, M., Tuescher, O., Polanecsky, M., McEwen, B., . . . Stern, E. (2005). Orbitofrontal cortex activity related to emotional processing changes across the menstrual cycle. *Proceedings of the National*

Academy of Sciences of the United States of America, 102(44), 16060-16065.

Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *The Journal of Neuroscience*, 18(6), 2188-2199.

Rajimehr, R., Montaser-Kouhsari, L., & Afraz, S. R. (2003). Orientation-selective adaptation to crowded illusory lines. *Perception*, 32(10), 1199-1210.

Rauschenberger, R., Liu, T., Slotnick, S. D., & Yantis, S. (2006). Temporally unfolding neural representation of pictorial occlusion. *Psychological science*, 17(4), 358-364.

Rezec, A., Krekelberg, B., & Dobkins, K. R. (2004). Attention enhances adaptability: evidence from motion adaptation experiments. *Vision Res*, 44(26), 3035-3044. doi: 10.1016/j.visres.2004.07.020

Rhodes, G., Jeffery, L., Clifford, C. W., & Leopold, D. A. (2007). The timecourse of higher-level face aftereffects. *Vision Res*, 47(17), 2291-2296. doi: 10.1016/j.visres.2007.05.012

Rhodes, G., Jeffery, L., Evangelista, E., Ewing, L., Peters, M., & Taylor, L. (2011). Enhanced attention amplifies face adaptation. *Vision Research*, 51(16), 1811-1819.

Rhodes, G., Jeffery, L., Taylor, L., & Ewing, L. (2013). Autistic traits are linked to reduced adaptive coding of face identity and selectively poorer face recognition in men but not women. *Neuropsychologia*, 51(13), 2702-2708.

- Rhodes, G., Jeffery, L., Watson, T. L., Clifford, C. W., & Nakayama, K. (2003). Fitting the mind to the world face adaptation and attractiveness aftereffects. *Psychological science*, 14(6), 558-566.
- Richards, A., Holmes, A., Pell, P. J., & Bethell, E. J. (2013). Adapting effects of emotional expression in anxiety: evidence for an enhanced late positive potential. *Social neuroscience*, 8(6), 650-664.
- Richler, J. J., Tanaka, J. W., Brown, D. D., & Gauthier, I. (2008). Why does selective attention to parts fail in face processing? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 34(6), 1356.
- Rossion, B., Delvenne, J.-F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., & Guérit, J.-M. (1999). Spatio-temporal localization of the face inversion effect: an event-related potentials study. *Biological psychology*, 50(3), 173-189.
- Rossion, B., Gauthier, I., Goffaux, V., Tarr, M. J., & Crommelinck, M. (2002). Expertise training with novel objects leads to left-lateralized facelike electrophysiological responses. *Psychological science*, 13(3), 250-257.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito - temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face - specific processes in the human brain. *Neuroreport*, 11(1), 69-72.

- Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *Neuroimage*, 39(4), 1959-1979.
- Rossion, B., Schiltz, C., & Crommelinck, M. (2003). The functionally defined right occipital and fusiform “face areas” discriminate novel from visually familiar faces. *Neuroimage*, 19(3), 877-883.
- Rump, K. M., Giovannelli, J. L., Minshew, N. J., & Strauss, M. S. (2009). The development of emotion recognition in individuals with autism. *Child development*, 80(5), 1434-1447.
- Rutherford, M., Troubridge, E. K., & Walsh, J. (2012). Visual afterimages of emotional faces in high functioning autism. *Journal of autism and developmental disorders*, 42(2), 221-229.
- Rutherford, M. D., Troubridge, E. K., & Walsh, J. (2012). Visual afterimages of emotional faces in high functioning autism. *J Autism Dev Disord*, 42(2), 221-229. doi: 10.1007/s10803-011-1233-x
- Rutishauser, U., Tudusciuc, O., Neumann, D., Mamelak, A. N., Heller, A. C., Ross, I. B., . . . Adolphs, R. (2011). Single-unit responses selective for whole faces in the human amygdala. *Current Biology*, 21(19), 1654-1660.
- Sabatinelli, D., Bradley, M. M., Lang, P. J., Costa, V. D., & Versace, F. (2007). Pleasure rather than salience activates human nucleus accumbens and medial prefrontal cortex. *Journal of neurophysiology*, 98(3), 1374-1379.

- Sadeh, B., & Yovel, G. (2010). Why is the N170 enhanced for inverted faces? An ERP competition experiment. *Neuroimage*, 53(2), 782-789. doi: 10.1016/j.neuroimage.2010.06.029
- Sagiv, N., & Bentin, S. (2001). Structural encoding of human and schematic faces: holistic and part-based processes. *Journal of Cognitive Neuroscience*, 13(7), 937-951.
- Sanchez-Vives, M. V., Nowak, L. G., & McCormick, D. A. (2000). Membrane mechanisms underlying contrast adaptation in cat area 17 in vivo. *J Neurosci*, 20(11), 4267-4285.
- Sarter, M., Givens, B., & Bruno, J. P. (2001). The cognitive neuroscience of sustained attention: where top-down meets bottom-up. *Brain research reviews*, 35(2), 146-160. doi: [http://dx.doi.org/10.1016/S0165-0173\(01\)00044-3](http://dx.doi.org/10.1016/S0165-0173(01)00044-3)
- Sasaki, Y., & Watanabe, T. (2004). The primary visual cortex fills in color. *Proceedings of the National Academy of Sciences*, 101(52), 18251-18256.
- Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., & Matsumura, M. (2004). Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study. *Cognitive Brain Research*, 20(1), 81-91.
- Savage, R. A., & Lipp, O. V. (2015). The effect of face inversion on the detection of emotional faces in visual search. *Cogn Emot*, 29(6), 972-991. doi: 10.1080/02699931.2014.958981

- Schinkel, S., Ivanova, G., Kurths, J., & Sommer, W. (2014). Modulation of the N170 adaptation profile by higher level factors. *Biological psychology*, 97, 27-34.
- Schupp, H. T., Flaisch, T., Stockburger, J., & Junghofer, M. (2006). Emotion and attention: event-related brain potential studies. *Prog Brain Res*, 156, 31-51. doi: 10.1016/s0079-6123(06)56002-9
- Schwab, E. C., & Nusbaum, H. C. (2016). *Pattern Recognition by Humans and Machines: Visual Perception* (Vol. 1): Academic Press.
- Schweinberger, S. R., & Neumann, M. F. (2016). Repetition effects in human ERPs to faces. *Cortex*, 80, 141-153.
- Schyns, P. G., Petro, L. S., & Smith, M. L. (2007). Dynamics of visual information integration in the brain for categorizing facial expressions. *Current Biology*, 17(18), 1580-1585.
- Sekuler, A. B., & Murray, R. F. (2001). AMODAL COMPLETION: A CASE STUDY IN. *From fragments to objects: Segmentation and grouping in vision*, 130, 265.
- Shibui, S., Izawa, K., Harashima, H., & Shigemasa, K. (2003). Adaptation to the facial expressions of emotion in the realistic face. *Perception*, 32, 173-174.
- Smith, M. J. L., Montagne, B., Perrett, D. I., Gill, M., & Gallagher, L. (2010). Detecting subtle facial emotion recognition deficits in high-functioning autism using dynamic stimuli of varying intensities. *Neuropsychologia*, 48(9), 2777-2781.

- Smith, M. L., Cottrell, G. W., Gosselin, F., & Schyns, P. G. (2005). Transmitting and decoding facial expressions. *Psychological science*, 16(3), 184-189.
- Spezio, M. L., Adolphs, R., Hurley, R. S., & Piven, J. (2007). Abnormal use of facial information in high-functioning autism. *Journal of Autism and Developmental Disorders*, 37(5), 929-939.
- Strauss, G. P., Kappenman, E. S., Culbreth, A. J., Catalano, L. T., Lee, B. G., & Gold, J. M. (2013). Emotion regulation abnormalities in schizophrenia: cognitive change strategies fail to decrease the neural response to unpleasant stimuli. *Schizophrenia bulletin*, 39(4), 872-883.
- Streit, M., Wölwer, W., Brinkmeyer, J., Ihl, R., & Gaebel, W. (2000). Electrophysiological correlates of emotional and structural face processing in humans. *Neurosci Lett*, 278(1), 13-16.
- Streit, M., Wölwer, W., Brinkmeyer, J., Ihl, R., & Gaebel, W. (2001). EEG-correlates of facial affect recognition and categorisation of blurred faces in schizophrenic patients and healthy volunteers. *Schizophrenia research*, 49(1), 145-155.
- Sucksmith, E., Roth, I., & Hoekstra, R. (2011). Autistic traits below the clinical threshold: re-examining the broader autism phenotype in the 21st century. *Neuropsychology review*, 21(4), 360-389.
- Sweeny, T. D., Grabowecky, M., & Suzuki, S. (2011). Awareness becomes necessary between adaptive pattern coding of open and closed curvatures. *Psychol Sci*, 22(7), 943-950. doi: 10.1177/0956797611413292

- Tamietto, M., & De Gelder, B. (2010). Neural bases of the non-conscious perception of emotional signals. *Nature Reviews Neuroscience*, 11(10), 697-709.
- Tan, X., & Triggs, B. (2010). Enhanced local texture feature sets for face recognition under difficult lighting conditions. *IEEE transactions on image processing*, 19(6), 1635-1650.
- Tanaka, J. W., & Pierce, L. J. (2009). The neural plasticity of other-race face recognition. *Cognitive, Affective, & Behavioral Neuroscience*, 9(1), 122-131.
- Tantam, D., Monaghan, L., Nicholson, H., & Stirling, J. (1989). Autistic children's ability to interpret faces: A research note. *Journal of Child Psychology and Psychiatry*, 30(4), 623-630.
- Todorov, A., & Uleman, J. S. (2002). Spontaneous trait inferences are bound to actors' faces: evidence from a false recognition paradigm. *Journal of personality and social psychology*, 83(5), 1051.
- Tracy, J. L., Robins, R. W., Schriber, R. A., & Solomon, M. (2011). Is emotion recognition impaired in individuals with autism spectrum disorders? *Journal of autism and developmental disorders*, 41(1), 102-109.
- Tranel, D., Damasio, A. R., & Damasio, H. (1988). Intact recognition of facial expression, gender, and age in patients with impaired recognition of face identity. *Neurology*, 38(5), 690-690.
- Treisman, A. (1999). Solutions to the binding problem: progress through controversy and convergence. *Neuron*, 24(1), 105-110, 111-125.

- Uljarevic, M., & Hamilton, A. (2013). Recognition of emotions in autism: a formal meta-analysis. *Journal of autism and developmental disorders*, 43(7), 1517-1526.
- Ungerleider, L. G. (1982). Two cortical visual systems. *Analysis of visual behavior*, 549-586.
- Van den Stock, J., Tamietto, M., Sorger, B., Pichon, S., Grézes, J., & de Gelder, B. (2011). Cortico-subcortical visual, somatosensory, and motor activations for perceiving dynamic whole-body emotional expressions with and without striate cortex (V1). *Proceedings of the National Academy of Sciences*, 108(39), 16188-16193.
- Van Essen, D. C., & Gallant, J. L. (1994). Neural mechanisms of form and motion processing in the primate visual system. *Neuron*, 13(1), 1-10.
- Veazzani, S., Kramer, P., & Bressan, P. (2014). Stereokinetic effect, kinetic depth effect, and structure from motion: The Oxford Handbook of Perceptual Organization. Oxford University Press, Oxford, UK.
- Vizioli, L., Foreman, K., Rousselet, G. A., & Caldara, R. (2009). Inverting faces elicits sensitivity to race on the N170 component: A cross-cultural study. *Journal of Vision*, 10(1), 15-15.
- Vizioli, L., Rousselet, G. A., & Caldara, R. (2010). Neural repetition suppression to identity is abolished by other-race faces. *Proceedings of the National Academy of Sciences*, 107(46), 20081-20086.

- von der Heydt, R., & Peterhans, E. (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *The Journal of Neuroscience*, 9(5), 1731-1748.
- Vuilleumier, P., & Pourtois, G. (2007). Distributed and interactive brain mechanisms during emotion face perception: evidence from functional neuroimaging. *Neuropsychologia*, 45(1), 174-194.
- Vuilleumier, P., Richardson, M. P., Armony, J. L., Driver, J., & Dolan, R. J. (2004). Distant influences of amygdala lesion on visual cortical activation during emotional face processing. *Nature neuroscience*, 7(11), 1271-1278.
- Wagemans, J. (2015). *The Oxford Handbook of Perceptual Organization*: Oxford University Press.
- Wagemans, J., & d'Ydewalle, G. (1989). The effects of kinetic occlusion and categorization on amodal completion: A comment on Gerbino and Salmasso (1987). *Acta psychologica*, 72(3), 281-293.
- Wakabayashi, A., Baron-Cohen, S., Uchiyama, T., Yoshida, Y., Tojo, Y., Kuroda, M., & Wheelwright, S. (2007). The autism-spectrum quotient (AQ) children's version in Japan: a cross-cultural comparison. *Journal of autism and developmental disorders*, 37(3), 491-500.
- Walsh, J., Maurer, D., Vida, M. D., Rhodes, G., Jeffery, L., & Rutherford, M. (2015a). Norm-based coding of facial identity in adults with autism spectrum disorder. *Vision Research*, 108, 33-40.

- Walsh, J., Vida, M. D., Morrissey, M. N., & Rutherford, M. (2015b). Adults with autism spectrum disorder show evidence of figural aftereffects with male and female faces. *Vision Research*, 115, 104-112.
- Wang, A. T., Dapretto, M., Hariri, A. R., Sigman, M., & Bookheimer, S. Y. (2004). Neural correlates of facial affect processing in children and adolescents with autism spectrum disorder. *J Am Acad Child Adolesc Psychiatry*, 43(4), 481-490. doi: 10.1097/00004583-200404000-00015
- Wang, X., Guo, X., Chen, L., Liu, Y., Goldberg, M. E., & Xu, H. (2016). Auditory to Visual Cross-Modal Adaptation for Emotion: Psychophysical and Neural Correlates. *Cereb Cortex*. doi: 10.1093/cercor/bhv321
- Webster, M. A. (2012). Evolving concepts of sensory adaptation. *F1000 Biology Reports*, 4, 21. doi: 10.3410/B4-21
- Webster, M. A. (2015). Visual adaptation. *Annual review of vision science*, 1, 547-567.
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, 428(6982), 557-561. doi: 10.1038/nature02420
- Webster, M. A., & MacLeod, D. I. (2011). Visual adaptation and face perception. *Philos Trans R Soc Lond B Biol Sci*, 366(1571), 1702-1725. doi: 10.1098/rstb.2010.0360
- Webster, M. A., & Maclin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review*, 6(4), 647-653.

- Weeks, S. J., & Hobson, R. P. (1987). The salience of facial expression for autistic children. *Journal of Child Psychology and Psychiatry*, 28(1), 137-152.
- Weigelt, S., Singer, W., & Muckli, L. (2007). Separate cortical stages in amodal completion revealed by functional magnetic resonance adaptation. *BMC neuroscience*, 8(1), 70.
- Weil, R. S., & Rees, G. (2011). A new taxonomy for perceptual filling-in. *Brain research reviews*, 67(1), 40-55.
- Whalen, P. J., Kagan, J., Cook, R. G., Davis, F. C., Kim, H., Polis, S., . . . Maxwell, J. S. (2004). Human amygdala responsivity to masked fearful eye whites. *Science*, 306(5704), 2061-2061.
- Whitney, D., & Levi, D. M. (2011). Visual crowding: A fundamental limit on conscious perception and object recognition. *Trends Cogn Sci*, 15(4), 160-168.
- Williams, M. A., Morris, A. P., McGlone, F., Abbott, D. F., & Mattingley, J. B. (2004). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *The Journal of Neuroscience*, 24(12), 2898-2904.
- Winston, J. S., Henson, R., Fine-Goulden, M. R., & Dolan, R. J. (2004). fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. *Journal of neurophysiology*, 92(3), 1830-1839.

- Wong, E., & Weisstein, N. (1984). Flicker induces depth: Spatial and temporal factors in the perceptual segregation of flickering and nonflickering regions in depth. *Perception & psychophysics*, 35(3), 229-236.
- Wu, C. T., Libertus, M. E., Meyerhoff, K. L., & Woldorff, M. G. (2011). The temporal dynamics of object processing in visual cortex during the transition from distributed to focused spatial attention. *J Cogn Neurosci*, 23(12), 4094-4105. doi: 10.1162/jocn_a_00045
- Xu, H., Dayan, P., Lipkin, R. M., & Qian, N. (2008). Adaptation across the cortical hierarchy: Low-level curve adaptation affects high-level facial-expression judgments. *Journal of Neuroscience*, 28(13), 3374-3383. doi: 10.1523/jneurosci.0182-08.2008
- Xu, H., Liu, P., Dayan, P., & Qian, N. (2012). Multi-level visual adaptation: dissociating curvature and facial-expression aftereffects produced by the same adapting stimuli. *Vision Res*, 72, 42-53. doi: 10.1016/j.visres.2012.09.003
- Yerys, B. E., Gordon, E. M., Abrams, D. N., Satterthwaite, T. D., Weinblatt, R., Jankowski, K. F., . . . Vaidya, C. J. (2015). Default mode network segregation and social deficits in autism spectrum disorder: Evidence from non-medicated children. *NeuroImage : Clinical*, 9, 223-232. doi: 10.1016/j.nicl.2015.07.018
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81(1), 141.

- Yokoyama, T., Noguchi, Y., Tachibana, R., Mukaida, S., & Kita, S. (2014). A critical role of holistic processing in face gender perception. *Frontiers in human neuroscience*, 8.
- Young, A., Newcombe, F., & De Haan, E. E, Small, M., & Hay, DC (1993). Face perception after brain injury: Selective impairments affecting identity and expression. *Brain*, 116, 941-959.
- Yuki, M., Maddux, W. W., & Masuda, T. (2007). Are the windows to the soul the same in the East and West? Cultural differences in using the eyes and mouth as cues to recognize emotions in Japan and the United States. *Journal of Experimental Social Psychology*, 43(2), 303-311.
- Yukie, M., & Iwai, E. (1981). Direct projection from the dorsal lateral geniculate nucleus to the prestriate cortex in macaque monkeys. *J Comp Neurol*, 201(1), 81-97. doi: 10.1002/cne.902010107
- Zeelenberg, R., Wagenmakers, E.-J., & Rotteveel, M. (2006). The impact of emotion on perception bias or enhanced processing? *Psychological science*, 17(4), 287-291.
- Zhao, L., & Chubb, C. (2001). The size-tuning of the face-distortion after-effect. *Vision Research*, 41(23), 2979-2994.
- Zhao, M., Hayward, W. G., & Bülthoff, I. (2014). Face format at encoding affects the other-race effect in face memory. *Journal of Vision*, 14(9), 6-6.

Appendix 1: The Autism-Spectrum Quotient

1. I prefer to do things with others rather than on my own.
2. I prefer to do things the same way over and over again.
3. If I try to imagine something, I find it very easy to create a picture in my mind.
4. I frequently get so strongly absorbed in one thing that I lose sight of other things.
5. I often notice small sounds when others do not.
6. I usually notice car number plates or similar strings of information.
7. Other people frequently tell me that what I've said is impolite, even though I think it is polite.
8. When I'm reading a story, I can easily imagine what the characters might look like.
9. I am fascinated by dates.
10. In a social group, I can easily keep track of several different people's conversations.
11. I find social situations easy.
12. I tend to notice details that others do not.
13. I would rather go to a library than to a party.

14. I find making up stories easy.
15. I find myself drawn more strongly to people than to things.
16. I tend to have very strong interests, which I get upset about if I can't pursue.
17. I enjoy social chitchat.
18. When I talk, it isn't always easy for others to get a word in edgewise.
19. I am fascinated by numbers.
20. When I'm reading a story, I find it difficult to work out the characters' intentions.
21. I don't particularly enjoy reading fiction.
22. I find it hard to make new friends.
23. I notice patterns in things all the time.
24. I would rather go to the theater than to a museum.
25. It does not upset me if my daily routine is disturbed.
26. I frequently find that I don't know how to keep a conversation going.
27. I find it easy to "read between the lines" when someone is talking to me.
28. I usually concentrate more on the whole picture, rather than on the small details.
29. I am not very good at remembering phone numbers.
30. I don't usually notice small changes in a situation or a person's appearance.
31. I know how to tell if someone listening to me is getting bored.
32. I find it easy to do more than one thing at once.
33. When I talk on the phone, I'm not sure when it's my turn to speak.
34. I enjoy doing things spontaneously.

- 35. I am often the last to understand the point of a joke.
- 36. I find it easy to work out what someone is thinking or feeling just by looking at their face.
- 37. If there is an interruption, I can switch back to what I was doing very quickly.
- 38. I am good at social chitchat.
- 39. People often tell me that I keep going on and on about the same thing.
- 40. When I was young, I used to enjoy playing games involving pretending with other children.
- 41. I like to collect information about categories of things (e.g., types of cars, birds, trains, plants).
- 42. I find it difficult to imagine what it would be like to be someone else.
- 43. I like to carefully plan any activities I participate in.
- 44. I enjoy social occasions.
- 45. I find it difficult to work out people's intentions.
- 46. New situations make me anxious.
- 47. I enjoy meeting new people.
- 48. I am a good diplomat.
- 49. I am not very good at remembering people's date of birth.
- 50. I find it very easy to play games with children that involve pretending.