Understanding face perception through the contributions of bottom-up and top-down processing : a psychophysical approach

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**UNDERSTANDING FACE PERCEPTION THROUGH THE
CONTRIBUTIONS OF BOTTOM-UP AND TOP-DOWN PROCESSING:
A PSYCHOPHYSICAL APPROACH**

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ABSTRACT

Face perception (recognition of facial expression and face identity in particular) plays a remarkable role in our daily social interaction. This research aims to understand the face-coding mechanism using a psychophysical approach, with three studies using the face adaptation paradigm to investigate face-coding machinery from both bottom-up and top-down perspectives.

Study 1 addressed the holistic nature in face adaptation. Through a series of experiments, it revealed that the facial expression aftereffect produced by a whole face was significantly greater than the simple linear summation of the aftereffects induced by its two components (an isolated mouth part and a mouthless face part). This “gestalt” effect in facial expression adaptation was consistently observed with upright cartoon faces (Experiment 1.1) and upright real faces (Experiment 1.3) but was eliminated in upside-down faces (Experiment 1.2). These findings point to a hierarchical multilevel face-coding framework where neural responses from low-level visual areas are projected via nonlinear functions to higher-level regions in forming the holistic face representation.

Study 2 investigated the different roles of top and bottom half faces in facial expression and face identity adaptation. We used a whole real face and its two size-equivalent components (a top-half face part and a bottom-half face part) as the adaptors in both facial expression and face identity adaptation tests. Results reproduced the gestalt effect in both types of face adaptation and also showed that the bottom-half face part contributed most to facial expression adaptation whereas the top-half face part made major contribution to face identity adaptation. This finding suggests a multidimensional face-coding

framework with dissociable mechanisms, with facial expression and face identity employing distinctive strategies in recruiting facial properties towards the holistic representation.

Study 3 examined the role of attention in face adaptation, by using the orientation pattern of microsaccades to index the deployment of attention during the adaptation. We showed that the facial expression aftereffect remained unaffected when the allocation of attention towards the adapting face was not successfully increased by a brightness-change-detection task, whereas it was remarkably reduced when a target-letter-detection task successfully diverted observers' attention away from the adapting face. This finding demonstrates the prominent influence of top-down attention on facial expression adaptation, pointing to a face-coding framework with adaptive plasticity modulated by top-down mechanisms.

Taken together, findings in this research shed light on a more comprehensive understanding of the neural coding mechanism underlying face perception.

CHAPTER I: INTRODUCTION

Research Background

Face perception is one of the most ecologically important visual skills for human beings. In daily social interaction, face perception not only enables us to recognize different people in identity, gender, ethnicity, etc., but also provides us with dynamic facial properties from the same person, such as facial expression, eye gazing, attractiveness, etc. Retrieval and interpretation of such information via face perception help us infer the internal status of a particular person (such as emotion, health, or even intentions before actions) and eventually facilitate and improve social interaction (Haxby, Hoffman, & Gobbini, 2000, 2002; Sigala & Rainer, 2007).

During the past decades, scholars from many research fields such as psychology and neuroscience have been investigating this crucial visual skill from various aspects (see reviews in Tsao & Livingstone, 2008). For instance, newborns show preference in visually pursuing schematic faces rather than scrambled ones (Johnson, Dziurawiec, Ellis, & Morton, 1991) or gazing at upright schematic faces rather than their inversions (Mondloch et al., 1999). Studies using single-cell recording (Sugase, Yamane, Ueno, & Kawano, 1999), event-related potentials (ERP) (Pegna, Khateb, Michel, & Landis, 2004), and magnetoencephalography (MEG) methods (Liu, Harris, & Kanwisher, 2010) also show that face targets can be registered in extrastriate areas only 100 ms after stimulus onset, which is about 100 ms faster than that for non-face objects (see reviews in Palermo & Rhodes, 2007). Besides perception superiority, processing of face stimuli also reveals specificity in neural mechanisms. MEG and ERP studies show that electromagnetic responses specific to faces are

elicited around 170 ms post-stimulus (referred to as N170/M170) in occipitotemporal cortex (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, Gosling, Nicholas, & Kiss, 2011; Rossion, Joyce, Cottrell, & Tarr, 2003). A substantial body of brain imaging studies with human subjects has identified three face-specific brain regions that show stronger responses to faces than other objects, i.e., the superior temporal sulcus (STS), the lateral fusiform gyrus (also called the fusiform face area, FFA), and the inferior occipital gyrus (also called the occipital face area, OFA) (Haxby, et al., 2002; Kanwisher, McDermott, & Chun, 1997; Winston, Henson, Fine-Goulden, & Dolan, 2004). For instance, stronger hemodynamic responses in terms of blood-oxygen-level dependence (BOLD) signals are observed in the fusiform face area when faces were presented compared to non-face objects (Spiridon & Kanwisher, 2002; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000), or even when subjects just perceived a face compared to when they did not “see” it in bistable stimuli (Andrews, Schluppeck, Homfray, Matthews, & Blakemore, 2002; Hasson, Hendler, Bashat, & Malach, 2001). Using a combination of functional magnetic resonance imaging (fMRI) and single-cell recording methods, Tsao et al. (2006) found in macaques a face-selective region in the superior temporal sulcus (STS) where nearly all (97%) of the visually responsive neurons were strongly face-selective, suggesting the existence of a dedicated cortical area to support face processing in macaques. In a more recent fMRI study by Tsao et al. (2008), macaques showed six discrete face-selective cortical regions along the temporal lobe, including the posterior lateral face patch (PL), the middle face patch in the STS fundus (MF), the middle face patch on the STS lip (ML), the anterior face patch in the STS fundus (AF), the anterior face patch on the STS

lip (AL), and the anterior medial face patch (AM). In contrast, humans showed five face-selective areas, consisting of three previously reported face regions (STS, FFA, and OFA) and two anterior face patch areas (AFP1 and AFP2) located anterior to the fusiform face area in the anterior collateral sulcus. The findings provide further evidence of face-specific neural mechanisms in both non-human primates and human beings.

While existing research has conducted wide-range investigations to uncover the mechanisms underlying face perception, this visual skill remains far from being fully understood (Tsao & Livingstone, 2008). To achieve a more comprehensive understanding of the face-coding machinery, the current research aims to investigate face perception (recognition of facial expression and face identity in particular) from both bottom-up and top-down perspectives using a psychophysical approach, namely the perceptual adaptation paradigm.

Literature Review

Psychophysics and Perceptual Adaptation Paradigm

Psychophysics is a class of research approaches that quantitatively measures how a physical stimulus (input) influences psychological perception (output), by routinely changing the input's strength to check how the perceptual output changes accordingly (Gescheider, 1997; Gibson & Radner, 1937). For vision studies, the perceptual adaptation paradigm is one of the most classic and efficient psychophysical methods (see reviews in Peter & David, 2009). In such a paradigm, the observer is exposed to an adapting stimulus for a prolonged period (e.g., several seconds), resulting in a perception bias when processing subsequent stimuli in a direction opposite to that of the adapting stimulus. This so-called perceptual aftereffect may occur because repetition of a visual stimulus causes an activity reduction in the neuron population responsible for processing stimuli in the specific category of the adapting stimulus (Dowling, 1967; Sperling, 1970). The perceptual adaptation paradigm has been extensively applied to explore the "channels" representing visual information in order to infer selective neural sensitivities to specific stimulus dimensions and reveal the underlying neural coding process (Michel, Corneille, & Rossion, 2010; Rhodes, Watson, Jeffery, & Clifford, 2010; Susilo, McKone, & Edwards, 2010; H. Yang, Shen, Chen, & Fang, 2011).

Early studies have shown perceptual aftereffects for various low-level and middle-level stimuli, such as orientation (Gibson & Radner, 1937; He, Cavanagh, & Intriligator, 1996; Tyler, 1975), color (McCollough, 1965), motion (Huk, Ress, & Heeger, 2001; Tootell et al., 1995), and shape properties (Suzuki, 2003). In recent years, perceptual aftereffects are extensively observed

in more complicated stimuli, such as faces. For instance, adapting to basic emotions like happy, sad, fear, and anger can bias perception of subsequent ambiguous faces away from the adapting emotion (Fox & Barton, 2007; Louie, Bressler, & Whitney, 2007; Webster, Kaping, Mizokami, & Duhamel, 2004). Besides facial expression, aftereffects are found in a wide range of dimensions of face perception, including identity (Eger, Schyns, & Kleinschmidt, 2004; Rhodes et al., 2011), gender (Barrett & O'Toole, 2009; Rhodes et al., 2004; Webster, et al., 2004), age (Lai, Oruç & Barton, 2012; Schweinberger et al., 2010), ethnicity (Webster, et al., 2004), etc.

Given the well-acknowledged notion that perceptual aftereffects can be mapped to corresponding neural tuning properties, the face adaptation paradigm serves as an essential tool for probing face-coding mechanisms underlying specific aspects of face perception (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Sigala & Rainer, 2007). According to a recent review by Webster and Macleod (2011), the importance of the face adaptation paradigm in understanding the processes and dynamics of face perception is three-fold. First of all, the aftereffect found from the face adaptation paradigm reflects the remarkable influence of the viewing context on face perception; the appearance of a specific face dramatically depends on the faces that observers are previously exposed to. It offers a window for researchers to investigate how individuals' cognitive judgments of a variety of facial attributes (e.g., expression and identity) can be modulated by previous exposure, which has profound implications towards a comprehensive understanding of face perception. Second, the face adaptation paradigm enables researchers to dissect the neural representation of information coding for faces by testing how neural

strategies at low-level visual areas can be applied to high-level vision and whether specific coding mechanisms for face perception exist in the visual system. Third, the face adaptation paradigm is also an important platform for researchers to study the process of adaptation itself by exploring how the plasticity manifested for simple sensory attributes is reflected for more complex and ecologically important stimuli.

In the current studies, we aim to employ this important research approach to investigate the mechanism of face perception from both the bottom-up perspective (i.e., how facial components form the holistic face representation and contribute to different aspects of face perception) and the top-down perspective (i.e., how task-based selective attention modulates face adaptation).

Bottom-up Contribution to Face Perception

Compared to simple visual stimuli (e.g., gratings), a face is a complex visual stimulus that consists of multiple facial components, such as forehead, brows, eyes, nose, mouth, cheeks, etc. Regarding this physical specificity of face stimuli, a primary question is: During the retrieval and coding process of information embedded in a face, how do individual facial components contribute to the perceptual representation of the whole face?

Holistic Face Perception

An extensively accepted view is that face perception is a holistic processing, i.e., rather than processing facial components or features independently, the visual system integrates them into a perceptual entirety of

the whole face. Early in the late 19th century, Sir Francis Galton (1883) proposed that “a face stimulus is perceived as whole, at a single glance, rather than as a collection of independent features” (cited in Goffaux & Rossion, 2006, p. 1023), which is believed to be the first public record of the holistic view of face perception. During the past decades, this notion has been testified and supported by a huge body of empirical studies (see reviews in Tsao & Livingstone, 2008), among which there are three main experimental paradigms.

First of all, researchers found that recognition performance was greatly impaired for upside-down faces compared to upright faces. More importantly, deterioration by inversion is disproportionately large for recognition of faces in contrast to non-face mono-oriented objects like houses (Yin, 1969). This so-called facial inversion effect (FIE) (Rakover & Teucher, 1997) is considered one of the most powerful pieces of the evidence for the involvement of specialized mechanisms in face processing (Farah, Tanaka, & Drain, 1995; Rossion & Boremanse, 2008; Valentine, 1988). Researchers argue that deteriorated recognition of upside-down faces is mainly due to the impaired feature-integration process where facial components are integrated into a holistic representation (Farah, et al., 1995; J. W. Tanaka & Farah, 1993). Farah et al. (1995) found that the FIE was eliminated by instructing subjects to encode faces by part decomposition and the effect was obtained in non-face dot patterns when subjects were asked to encode the dots holistically. In another study by Rossion and Boremanse (2008), holistic processing in face perception was found to persist when face stimuli were rotated from 0° to 60° but it dropped dramatically when the rotation reached 90° to 180° (i.e., complete inversion). Rossion and Boremanse (2008) argued that this non-linear

relationship between orientation and holistic face perception suggested that the FIE was mainly due to the failure of applying an experience-based holistic representation to upside-down faces.

The second line of the research evidence for the holistic nature of face perception comes from findings demonstrating that perceptual processing of one facial feature or face part is greatly affected by other features or by the whole face (Goffaux & Rossion, 2006; Schiltz, Dricot, Goebel, & Rossion, 2010; J. W. Tanaka & Farah, 1993; J. W. Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998; J. W. Tanaka & Sengco, 1997). For instance, Tanaka and Farah (1993) found that facial features were better recognized when placed in the background of a face than when presented alone. Meanwhile, recognition of a whole face was also disrupted while altering properties of its facial features (J. W. Tanaka & Sengco, 1997). This so-called whole-part advantage effect reflects the prominent influence of the whole-face background on processing of local facial features and vice versa (Donnelly & Davidoff, 1999; Leder & Carbon, 2006; J. W. Tanaka, Kiefer, & Bukach, 2004; J. W. Tanaka & Sengco, 1997).

Thirdly, the face composite effect, first reported by Young, Hellawell, and Hay (1987), is regarded as another potent marker for the holistic nature of face perception and has been extensively used in a large amount of face studies (de Heering & Rossion, 2008; Jacques & Rossion, 2009; Schiltz, et al., 2010). In a typical face composite task, subjects are presented with two composite faces simultaneously or subsequently. Each of the two faces consists of a top half part and a bottom half part separated by a horizontal gap. The task is to judge whether the two top halves are identical or not. For aligned composite

faces (i.e., the two face halves are vertically aligned), subjects tend to erroneously perceive the identical top parts as “different” when the bottom parts are different. However, the proneness of such mistakes disappears when the two face halves are misaligned. Researchers argue that this phenomenon is a compelling demonstration that face perception is an integrated process where facial features are processed interdependently (Goffaux & Rossion, 2006; Robbins, McKone, & Edwards, 2007; Rossion & Boremanse, 2008).

The holistic notion of face perception also receives support from neurobiological and neuropsychological evidence. Single-cell recording research with non-human primates found that face-sensitive cells in the inferotemporal cortex responded selectively to a whole-face stimulus but not to either an incomplete face with some parts removed (K. Tanaka, 1996) or a scrambled face image (Desimone, Albright, Gross, & Bruce, 1984). Neuroimaging studies with human subjects indicated that the anterior part of the lateral fusiform gyrus was particularly in charge of holistic processing in face perception (Jacques & Rossion, 2009; Rossion et al., 2003; Rossion et al., 2000; Schiltz, et al., 2010). Moreover, electrophysiological studies reported that the face-specific ERP component (N170) was registered earlier with a smaller amplitude in response to upright faces than upside-down faces, indicating the sensitivity of such neural activity to holistic face processing (Eimer, 2000; Itier, Alain, Sedore, & McIntosh, 2007; Letourneau & Mitchell, 2008).

Taken together, studies from various research fields support the notion that faces are holistically processed, suggesting the existence of mutual interactions among individual facial components in forming the whole face representation (Sergent, 1984). The critical question is: how do such

interactions contribute to the holistic face perception? Towards a better understanding of mechanisms underlying face perception, our first study aims to address this question by exploring the extent of holistic processing in face perception from a quantitative approach using the perceptual adaptation paradigm.

Diverse Aspects of Face Perception

Faces carry a variety of information such as identity, expression, age, gender, race, attractiveness, etc. Regarding the diverse aspects of face perception, many researchers have been exploring whether and how facial components contribute to different aspects of face perception (especially facial expression and face identity) in dissociable visual ways in the cognitive system (see reviews in Sigala & Rainer, 2007).

According to an early functional model of face perception (Bruce & Young, 1986), distinctive neural routes account for visual information processing for different aspects of face representation. On the one hand, perception of face identity involves top-down processing via the so-called “face recognition units” (FRUs) that allow matching between the target face and faces seen previously and stored in the memory. Therefore, familiarity of faces can affect the processing of face identity. On the other hand, other aspects of face information such as age, gender, and facial expression are perceived through a so-called “directed visual processing” that only involves structural analysis of visual characteristics in faces. Therefore, processing of such information is independent of face familiarity (Campbell, 1996; Young, McWeeny, Hay, & Ellis, 1986). In a more comprehensive framework, Haxby

and his colleagues (2000) proposed a distributed human neural system where different aspects of face perception are processed by distinctive neural mechanisms. In this framework, information embedded in faces is categorized into two main aspects: the invariant aspect such as face identity and the changeable aspect such as facial expression. These two aspects are processed in distinctive neural submodules, with the invariant aspect in the lateral fusiform gyrus (Kanwisher, et al., 1997; Liu, et al., 2010; McCarthy, Puce, Gore, & Allison, 1997; Tong, et al., 2000) and the changeable aspect in the superior temporal sulcus (Engell & Haxby, 2007; Engell, Haxby, & Todorov, 2007; Puce, Allison, Bentin, Gore, & McCarthy, 1998).

These two models share the idea that facial expression and face identity are processed through functionally and neurologically distinctive pathways in the visual system. This idea receives support from a huge amount of empirical studies. Behavioral research with healthy human subjects observed dissociable response patterns in reaction time tasks for recognition of face identity and facial expression (Campbell, 1996; Pizzamiglio, Zoccolotti, Mammucari, & Cesaroni, 1983). Neuropsychological studies showed that brain injury could cause selective impairments in human's capability of recognizing face identity (Humphreys, Donnelly, & Riddoch, 1993; Shuttleworth Jr, Syring, & Allen, 1982) or perceiving facial expression (Humphreys, et al., 1993; Tranel, Damasio, & Damasio, 1988; Young, Newcombe, Haan, small, & Hay, 1993). Single-cell recording research with non-human primates also found different populations of neurons that selectively responded to either facial expression or face identity (Hasselmo, Rolls, & Baylis, 1989; Rolls, Cowey, & Bruce, 1992).

More recent evidence, however, points to an interaction model of face perception where facial expression and face identity have relatively dissociable rather than fully independent coding mechanisms (Atkinson & Adolphs, 2011; Burton, Bruce, & Johnston, 1990; Calder & Young, 2005). With image-based analysis technique like principle component analysis (PCA), Calder et al. (2001) found that while distinct groups of principle components coded facial expression and face identity, there were also sets of principle components coding both aspects of face perception (Calder, et al., 2001). Meanwhile, Gothard et al. (2007) reported that some neurons in the amygdala selectively responded to facial expressions of certain individuals but not others, or gave responses of different patterns (in terms of firing rates and duration) to different facial expressions by different individuals. Gothard et al. (2007) argued that these findings demonstrated the existence of amygdala neurons coding both facial expression and face identity, or even unique combinations of these two aspects of face perception. Calder and Young (2005) proposed that previous findings of dissociation between facial expression and face identity could be explained by partially independent coding mechanisms in a single multidimensional model of face perception. This is not to argue against the segregation of mechanisms for facial expression and face identity. Instead, this multidimensional framework posits that dissociation of the two aspects of face perception results from the extraction and analysis of different visual cues that carry corresponding information for recognition of facial expression and face identity.

As pointed out by Calder and Young (2005), to achieve an accurate and comprehensive understanding of the conceptual framework for face perception,

researchers should explore how different properties in a single face image are retrieved and processed for different aspects of face perception. Here, our second study aims to address this question from the psychophysical approach by looking at how information from the same adapting face image is distinctively employed to form the holistic representation of facial expression and face identity.

Top-down Modulation on Face Perception

Studies discussed in the first two sections focus mainly on how facial components are processed in forming the final representation of face perception. Such a bottom-up approach in visual perception emphasizes the contribution from stimuli during information processing. Besides the bottom-up processing, the top-down mechanism also plays a critical role in visual perception. Note that the top-down mechanism here implies selective attention that is endogenous, task-based, and goal-dependent (Tsuchiya & Koch, 2009).

Cognitive studies have extensively shown that selective attention has a prominent influence on stimulus processing. For instance, subjects' performance on detection and discrimination tasks was significantly improved when the target appeared at an attended location compared to an unattended location (Handy, Kingstone, & Mangun, 1996; Hawkins et al., 1990; Müller & Findlay, 1988). Consistent with these behavioral observations, studies using single-cell recording on non-human primates demonstrated that paying attention to a target led to increased stimulus-evoked neural activity in brain regions throughout the visual network (Ito & Gilbert, 1999; McAdams & Maunsell, 1999; Motter, 1994; Scholte, Spekreijse, & Roelfsema, 2001). The

attentional effect of amplifying neural responses was also found in studies using electroencephalography (Luck & Hillyard, 1994) and brain imaging (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991).

Regarding the role of attention in perceptual adaptation, previous studies showed that attention could increase aftereffects induced by low-level or middle-level stimuli (Alais & Blake, 1999; Lankheet & Verstraten, 1995; Montaser-Kouhsari & Rajimehr, 2005; Spivey & Spirn, 2000; Suzuki, 2003). For instance, after attending to one of two transparently superimposed motion patterns, the motion aftereffect was selectively enhanced for the attended pattern (Lankheet & Verstraten, 1995). Similar effects were found in adaptation of orientation (Spivey & Spirn, 2000; Suzuki, 2001) and shapes (Suzuki, 2003). These studies demonstrate the profound influence of attention on low-level and middle-level visual processing.

However, there is still limited knowledge on the role of attention in high-level visual adaptation induced by more complex stimuli like faces. Few studies have investigated whether and how selective attention directed to adapting faces can influence face adaptation. Nevertheless, as a closely related issue, whether face adaptation effects demand awareness of the adaptor has been extensively examined in recent years. For instance, when the adaptor was rendered below awareness by inattention blindness or binocular suppression, the face identity-specific aftereffect virtually disappeared whereas the grating orientation-specific aftereffect survived under the same conditions (Moradi, Koch, & Shimojo, 2005). Consistently, for other dimensions of face perception such as facial expression, face shape, race, and gender, the face aftereffects are all virtually eliminated when adapting faces are made invisible (Amihai,

Deouell, & Bentin, 2011; Moradi, et al., 2005; Stein & Sterzer, 2011; E. Yang, Hong, & Blake, 2010; but see Adams, Gray, Garner, & Graf, 2010). These findings point to the same conclusion that occurrence of face adaptation demands awareness of the adaptor.

Nevertheless, these findings cannot simply be generalized to the relationship between attention and face adaption, given that awareness and attention are considered two distinct processes (Koch & Tsuchiya, 2007; Tsuchiya & Koch, 2009). On the one hand, attention can be allocated to objects that cannot be consciously perceived and as a result produce perceptual effects in the absence of awareness of the target (Naccache, Blandin, & Dehaene, 2002; Sato, Okada, & Toichi, 2007). For example, semantic priming effects induced by invisible words emerge only when words are attended to (Naccache, et al., 2002). On the other hand, observers can consciously perceive an object with little top-down attentional processing (Li, VanRullen, Koch, & Perona, 2002; Reddy, Reddy, & Koch, 2006; Reddy, Wilken, & Koch, 2004). For instance, studies using the dual-task paradigm found that when subjects' focal attention was directed to the screen center where a detection or discrimination task was required, they could still perform certain discrimination tasks in peripheral locations, such as distinguishing male from female or famous faces from non-famous faces (Koch & Tsuchiya, 2007). Evidence from physiological studies has also revealed dissociation between attention and awareness (Bahrami, Lavie, & Rees, 2007; Koivisto, Revonsuo, & Lehtonen, 2006; Woodman & Luck, 2003; Wyart, Dehaene, & Tallon-Baudry, 2012; Wyart & Tallon-Baudry, 2008). An ERP study (Woodman & Luck, 2003) found a preserved lateral negativity associated with attentional execution when the target was suppressed from

visibility. In addition, an fMRI study using the dual-task paradigm (Bahrami, et al., 2007) found stronger hemodynamic signals in response to an invisible peripheral object when the central task was easy and sufficient spatial attention was available for processing the peripheral object, compared to when the central task was hard and little attention resource was left for processing the invisible peripheral object. Due to the discrepancy between awareness and attention, findings from previous studies on the relationship between awareness and face adaptation can hardly provide a clear conclusion on whether and how attention modulates face adaptation.

In a recent study, Rhodes et al. (2011) conducted a direct investigation on whether attention could affect face adaptation. In two experiments, they showed amplified face identity aftereffects (Experiment 1) and face distortion aftereffects (Experiment 2) caused by increased attention to the adapting face. These findings provide direct evidence showing that deployment of attentional resources to the adapting face can increase the high-level face signal's strength in calibrating face-specific coding mechanisms. However, the above study only examined the face identity and face distortion aftereffects. It remains unknown whether attention can modulate adaptation of other aspects of face perception like facial expression. As discussed before, many studies have demonstrated that face identity and facial expression are at least partially dissociable with distinctive neural mechanisms. Therefore, to achieve a comprehensive understanding of the face-coding mechanism, it becomes especially important to probe the influence of attention on facial expression adaptation. Meanwhile, in Rhodes et al. (2011)'s study, manipulation of attention during adaptation included only increasing the attentional deployment to the adapting stimulus. It

remains unclear whether and how diverting attention away from the adaptor can affect face aftereffects, although studies on awareness and face adaptation may have provided indirect implications (Moradi, et al., 2005; Stein & Sterzer, 2011; E. Yang, et al., 2010), namely that face adaptation demands awareness of relevant information from the adapting face.

Our third study aims to address these issues to achieve a more comprehensive understanding of how top-down mechanisms in terms of selective attention are employed to generate a face representation (facial expression in particular). Meanwhile, we aim to conduct a comprehensive investigation on attention's role in tuning face adaptation, by directing task-based selective attention to the adapting face or diverting attention away from the adaptor.

Research Framework

To summarize, the current research investigates face perception using psychophysics to determine both bottom-up contributions from facial components (Study 1 and Study 2) and top-down contributions from selective attention. An illustration of the research framework is shown below (Figure 1).

Figure 1. Illustration of the research framework

CHAPTER II:

STUDY 1 – Nonlinear Interactions among Facial Components

Introduction

As reviewed above, studies from various research fields support the notion that faces are holistically processed (see reviews in Tsao & Livingstone, 2008). According to Bradshaw and Wallace (1971), the holistic nature of face processing highlights the importance of the overall structure or the face “gestalt” in face perception. The term “gestalt” originates from the Gestalt theory (Koffka, 1935; Köhler, 1959), positing that “the whole is greater than the sum of its parts”, i.e., while an object can be physically divided into several separate parts, the perceptual output generated by the whole object is different from (probably greater than) the linear summation of the perceptual outputs produced by its individual components. According to Sergent (1984), in face perception the facial parts are not just perceived together but they influence each other so that perception of a whole face is more than the simple summation of perception of its individual parts. This gestalt effect in face perception indicates that there must be nonlinear interactions among individual facial components during the process of forming the whole face representation. However, to the best of our knowledge, few studies have been conducted to test the holistic nature of face perception from this perspective. Therefore, our first study aims to fill this research gap by exploring how faces are holistically processed by testing the gestalt effect in face perception with a psychophysical approach.

As discussed previously, psychophysics serves as a powerful research tool in the study of visual perception. In psychophysics experiments,

researchers test human observers repeatedly with tens or even hundreds of trials and apply psychometric functions to best fit observers' subjective responses to calculate perceptual thresholds of detection or discrimination. Consequently, the psychophysical approach allows researchers to obtain robust and consistent findings even with a small number of observers, especially for studying fundamental visual processing (Anderson & Vingrys, 2001). In particular, the perceptual adaptation paradigm, which is called the “psychophysicist's microelectrode” (Frisby, 1979, p. 89), has proven to be powerful scientific instrument that enables researchers to noninvasively investigate neural channels with selective sensitivities to specific perception dimensions and thus reveal the neural coding mechanism underlying the perceptual processing (Michel, et al., 2010; Rhodes, et al., 2010; Susilo, et al., 2010; H. Yang, et al., 2011). Given the functional significance and methodological advantage of the psychophysical approach, we employed the perceptual adaptation paradigm in Study 1 to more directly address the neural mechanism of the holistic nature in facial expression perception. We used a whole face and its two components (i.e., an isolated mouth part and a mouthless face part) as adaptors in three adaptation conditions, respectively. We measured the perceptual output in terms of aftereffects and hypothesized that the aftereffect induced by the whole face would be larger than the linear summation of the aftereffects induced by its two components, directly reflecting the holistic nature in face perception.

Experiment 1.1: Nonlinear interactions in upright cartoon faces**Method***Subjects*

Eleven Chinese adults (eight female; age range = 21-31 years, $M = 26.1$ years, $SD = 3.14$) participated in this experiment. They were undergraduate or graduate students from Nanyang Technological University, Singapore. Ten of them (except the author) were naïve to the purpose of this study. All subjects were right-handed with reported normal or corrected-to-normal visual acuity. None of them had known neurological or visual disorders. Such criteria for subject recruitment were also applied to the following experiments. Subjects gave signed informed consent before the experiment and received incentives for their participation at a rate of 10 SGD (≈ 7.6 USD) per hour. All experiments were approved by the Ethics Committee of the Division of Psychology, and Institutional Review Board (IRB), Nanyang Technological University, Singapore.

Apparatus and Materials

The experiment was conducted in a silent and dimly lit room. Stimuli were presented on a 17 inch SA MSUNG monitor (SyncMaster 793MB, Malaysia) controlled by an iMac Intel Core i3 computer. The monitor had a spatial resolution of 1024×768 and a refresh rate of 85 Hz. With a chin rest to stabilize the head position, subjects viewed the stimuli from a distance of 75 cm. Each pixel on the screen subtended a visual angle of 0.024° at this distance. All experiments were run in Matlab (V2010a for Mac) with PsychToolbox

(Brainard, 1997; Pelli, 1997). A Minolta LS-110 photometer was used to measure the luminance gamma.

For this experiment, stimuli were a set of black (0.62 cd/m^2) cartoon faces presented on a white (69.89 cd/m^2) background (with a Michelson contrast of 0.98). Each face consisted of three parts: a circle for the face contour, a curve for the mouth, and two dots for the eyes. The face contour had a diameter of 2.4° . All line widths and dot radii were 0.072° . The two eyes were symmetrically placed in the face contour with a center-to-center distance of 0.77° and a vertical distance of 0.39° higher than the contour center. The mouth location was horizontally centered in the face contour, with a vertical distance of 0.39° lower than the contour center. For all the mouth curves, the arc length was the same (0.75°) but the curvature varied from concave to convex (-0.82 , -0.41 , -0.21 , -0.1 , 0 , 0.1 , and 0.21 in units of $1/^\circ$), resulting in facial expressions varying from sad to happy (Figure 2a). We also generated an inverted happy face and an inverted sad face, with the mouth curvature equal to -0.82 and 0.82 , respectively (Figure 2b). An anti-aliasing method (Matthews, Meng, Xu, & Qian, 2003) was employed for all stimuli to make them appear smooth. A black fixation cross consisting of two line segments (0.048° in width and 0.34° in length) was always centrally presented on the white screen.

Figure 2. Cartoon faces as test stimuli in Experiment 1.1. (a) seven upright cartoon faces with the curvature equal to (-0.82, -0.41, -0.21, -0.1, 0, 0.1, and 0.21; (b) the inverted happy and sad faces, with the mouth curvature equal to -0.82 and 0.82, respectively

Design and Procedure

In this experiment, we aim to measure the aftereffects induced by a whole face and its two facial components, respectively. The experiment included three adaptation conditions (termed f-f, c-f, and e-f), where the first letter represents whether the adapting stimulus was the saddest whole face (f), the most concave curve as the isolated mouth part derived from the saddest face (c), or the mouthless face contour (e) (Figure 3), and the second letter represents the test stimuli were whole faces (f) with the mouth part curvature gradually changing from concave to convex (Figure 2a). We note that previous studies have found the mouth part provides major contribution to facial expression perception and even just a mouth-alike curve can produce significant facial expression aftereffects (Harris & Aguirre, 2008; Xu, et al., 2008). Therefore, decomposing the whole face into a mouth curve and a mouthless face part instead of other ways (e.g., one part has a mouth curve with the circle contour and the other part has two eyes only) allows us to better compare the current results with previous findings.

Figure 3. Three adapting stimuli in Experiment 1.1. From left to right: the saddest whole face (f), the most concave curve equal to the mouth part (c), and the mouthless face part (e)

Subjects were also tested on the baseline condition (termed 0-f), in which no adapting stimulus was shown. To ensure that subjects indeed judged the facial expression of the test faces rather than the mouth curvature, we randomly interleaved in each experiment block two kinds of catch trials, using the inverted happy and sad faces (Figure 2b) as the test stimuli. The upright mouthless face (Figure 3, right) was also used as the test stimulus to check subjects' perception on its facial expression.

The procedure is demonstrated in Figure 4. Each block of trials was initiated when the subject pressed the space bar. For each adaptation block, the adapting stimulus was presented for 4 s, followed by an inter-stimulus interval (506 ms). A test face was then presented for 106 ms. After that, a beep (900 Hz) was played for 59 ms to remind subjects to report their perceived facial expression on the test face. Subjects had to make a two-alternative forced-choice (2-AFC) judgment by pressing one of two keys ("a" or "s") to indicate whether the test face was happy or sad. A 1 s blank intertrial interval was then presented before moving to the next trial. For the baseline block without adaptation, no adapting stimulus was presented. The mouth location on the screen was kept the same for all the face stimuli. Subjects were required to

fixate a central cross throughout the block. No feedback was given on their performance at any time.

This experiment employed a block design, with one block for each of the four conditions. Each subject completed two sessions, each consisting of the four blocks in random temporal orders. For each block, trials for different test stimuli were also randomized, with each test stimulus repeating 10 times. Therefore, for the seven test faces, each subject did a total of 140 trials in each of the four conditions. Subjects were asked to rest for at least 10 min between blocks to avoid carry-over effects and all had sufficient practice to feel comfortable with the task before formal data collection.

Figure 4. Trial sequence for the f-f condition in Experiment 1.1

Data Analysis

For each of the four conditions, the fraction of happy responses to each test face was calculated and then plotted against the mouth curvature in test faces. A psychometric curve was generated by fitting data points with a sigmoidal function as $f(x) = 1/[1+e^{-a(x-b)}]$. Here, a represents the curve slope

while b represents the test-stimulus parameter corresponding to the 50% point of the psychometric function, i.e., the point of subjective equality (PSE). Two-tailed paired t tests were used to examine the difference of PSEs between different conditions (Xu, Dayan, Lipkin, & Qian, 2008).

Results

Figure 5 below shows the results from a naïve subject (HU) in Experiment 1.1. For each condition, the fraction of happy responses was plotted as a function of the mouth curvature in test faces. The black curve represents the baseline condition without adaptation (0-f) and the other three curves (red, blue, and green) represent the three adaptation conditions (e-f, c-f, and f-f), respectively. If the curve representing an adaptation condition is shifted to the left of the black curve (the baseline condition), it means that the observer sees happy expression more frequently in test faces after adaptation in that condition and vice versa for right-shifted adaptation curves.

Figure 5. Psychometric functions from a naïve subject (HU) in Experiment 1.1.

0-f: no adaptation baseline (black curve, empty circles); e-f: adaptation to a mouthless face part (red curve, empty triangles); c-f: adaptation to the most concave curve equal to the mouth part in the saddest cartoon face (blue curve, empty diamonds); f-f: adaptation to the saddest cartoon face (green curve, empty squares); The results for the the inverted happy and sad faces and the mouthless face were shown as filled black circles, red triangles, blue diamonds, and green squares, for the 0-f, e-f, c-f, and f-f conditions, respectively.

For each subject, we obtained the PSE of each psychometric curve (i.e., the mouth curvature corresponding to 50% happy responses). For each adaptation condition, we used the PSE shift against that in the baseline condition as an index for the bias magnitude of facial expression perception (i.e., the facial expression aftereffect). After summarizing the results from all 11

subjects, we applied two-tailed paired t tests to compare the facial expression aftereffects between the three adaptation conditions (e-f, c-f, and f-f) and also to compare the aftereffect in the f-f condition with the summation of the aftereffects in the e-f and c-f conditions.

Figure 6. Summary of all 11 subjects' data from Experiment 1.1. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Figure 6 above demonstrates the average PSE shifts in the three adaptation conditions relative to the baseline condition with error bars representing SEMs. A negative value here means more happy responses compared to the baseline condition, i.e., a typical facial expression aftereffect. Results of two-tailed paired t tests showed that the facial expression aftereffect was significant both in the c-f condition (PSE-shift = -0.18, $t(10) = -7.199$, $p < 0.001$) and in the f-f condition (PSE-shift = -0.27, $t(10) = -9.156$, $p < 0.001$), but it was non-significant in the e-f condition (PSE-shift = -0.016, $t(10) = -1.104$, $p = 0.256$). Moreover, the aftereffect in the f-f condition (PSE-shift = -

0.27) was significantly larger than the linear summation of the aftereffects in the c-f and e-f conditions (PSE-shift summation = -0.20), $MD = 0.076$, $t(10) = 3.820$, $p < 0.001$.

For the catch trials with the inverted happiest and saddest faces as the test stimuli, results showed that subjects always gave sad responses (100%) to the inverted saddest face. For the inverted happiest face, subjects gave happy responses at an average of 98.6% of the time, significantly higher than chance (50%), $t(10) = 62.298$, $p < 0.001$. These results indicate that subjects did judge the facial expression rather than the simple curvature of the mouth part (Xu, et al., 2008; Xu, Liu, Dayan, & Qian, 2012).

Finally, for the mouthless face as the test stimulus, subjects gave happy responses at an average of 48.2% of the time, not significantly different from chance (50%), $t(10) = -0.631$, $p = 0.542$, indicating that subjects perceived the facial expression in the mouthless face as neutral.

Discussion

In Experiment 1.1, we used cartoon faces in a face adaptation paradigm to investigate how perceived facial expression was biased by an adaptor consisting of either a whole face or one of its two parts (i.e., an isolated mouth curve and a mouthless face contour). We aim to test whether the perceptual output in terms of the facial expression aftereffect generated by the whole face is greater than the linear summation of the perceptual outputs generated by its two parts, pointing to a direct demonstration of holistic processing in facial expression perception.

First, we found a significant aftereffect induced by a whole face, demonstrating a typical facial expression aftereffect (Webster, et al., 2004), consistent with previous studies using cartoon faces (Xu, et al., 2008; Xu, et al., 2012). The aftereffect induced by the mouth curve was also significant, suggesting that adaptation to a local feature (e.g., the mouth curve) can also bias the perception of facial expression (Harris & Aguirre, 2008). This lends further support for the existence of a strong local component in facial expression perception (Harris & Aguirre, 2008; Xu, et al., 2008).

In addition, the current results showed that the aftereffect in the f-f condition was significantly greater than the summation of the aftereffects in the c-f and e-f conditions, indicating a stronger perception bias induced by the whole cartoon face than the summation of perception bias generated by the isolated mouth curve and the mouthless face part. Physically, the whole cartoon face consisted of the isolated mouth curve and the mouthless face part. However, it produced a larger perceptual output than the summation of the perceptual outputs generated by its two components, revealing a gestalt effect in facial expression adaptation that points to the holistic processing in face representation (J. W. Tanaka & Farah, 1993; Young, et al., 1987).

Hierarchical models of face processing (Riesenhuber, Jarudi, Gilad, & Sinha, 2004; Riesenhuber & Poggio, 2002) propose that responses from units at a specific layer are combined via nonlinear functions while being propagated to the layers at higher levels. Therefore, responses from high-level face neurons must be arisen from a nonlinear function of local facial features coded in low-level regions. In a physiological study (Baker, Baker, Behrmann, & Olson, 2002), investigators trained monkeys to discriminate stimuli made of two linked

parts and recorded single units from inferior temporal gyrus in the cortex (area IT). Results showed that the influence on neural activity by the two linked parts together was greater than that predicted by the additive influence generated by each part separately, providing a possible neural mechanism to support the holistic notion in the Gestalt theory (Koffka, 1935; Köhler, 1959). This mechanism may well explain the present findings of the gestalt effect in facial expression adaptation. While two facial parts as the adaptors were exposed to the observer either simultaneously (i.e., in the f-f adaptation condition) or separately (i.e., in the c-f and e-f adaptation conditions), it is plausible that the same population of neurons at the low-level visual areas responded with equivalent neural activity in the two situations. These neural responses from the low-level regions would then be propagated to the higher levels to generate the perceptual output of face representation. During the propagation, when the two facial parts were simultaneously presented as a whole face in the f-f adaptation condition, it seems likely that nonlinear interactions occurred between responses to the two parts originating from low-level regions. However, it is likely that such interactions were missing when the two facial parts were presented separately in the c-f and e-f conditions. Eventually, this led to the difference between the aftereffect induced by the whole face and the linear summation of the aftereffects induced by its two facial parts. Therefore, the existence of such nonlinear interactions as reflected by the residual aftereffect in face adaptation provides a vivid hallmark for the holistic nature of facial expression representation.

Moreover, since the aftereffect can be quantitatively measured, this approach allows us to quantify both the individual contributions from each

facial part and also the contribution from the nonlinear interactions among facial components. As seen from the results, the magnitude of the aftereffect generated by the mouth part (-.181) was around 66% of that by the whole face (-.273), indicating that the mouth part provides most of the contributions in facial expression perception, consistent with previous findings that individuals rely more on the mouth or the bottom part of faces in recognizing emotion (Gosselin & Schyns, 2001).

In previous studies on face perception, researchers argue that holistic processing is disrupted in perception of upside-down faces (Farah, et al., 1995; Valentine, 1988). Therefore, if the gestalt effect in face adaptation (i.e., the advantage of a whole face over the linear summation of its facial components in producing face aftereffects) was due to the existence of holistic processing in face perception, it should disappear in upside-down faces. To test this hypothesis and further confirm the findings of Experiment 1.1, we extended the experimental paradigm to upside-down faces in Experiment 1.2.

Experiment 1.2: Absence of nonlinear interactions in upside-down cartoon faces

Method

Subjects

Five adults (three female; age range = 21-29 years, $M = 25.8$ years, $SD = 3.11$) from the subject pool in Experiment 1.1 participated in this experiment. Four of them (except the author) were naïve to the purpose of this study. Subjects gave signed informed consent before the experiment and received incentives for their participation at a rate of 10 SGD (≈ 7.6 USD) per hour.

Apparatus and Materials

The apparatus, materials, and relevant parameters were the same as in Experiment 1.1, except that test stimuli were a set of upside-down cartoon faces instead of upright cartoon faces.

The series of upside-down faces were generated with rotating the upright cartoon faces in Experiment 1.1 by 180 ° and thus the curvature of the mouth parts was also reversed. However, facial expression in these upside-down faces still varied gradually from sad to happy (Figure 7a). The upright happiest and saddest faces were also included, with the mouth curvature equal to 0.82 and -0.82, respectively (Figure 7b). The mouth location on the screen was kept the same for all the face stimuli.

Figure 7. Cartoon faces as test stimuli in Experiment 1.2. (a) seven upside-down cartoon faces with the curvature equal to (0.82, 0.41, 0.21, 0.1, 0, -0.1, and -0.21; (b) the upright happy and sad faces, with the curvature equal to 0.82 and -0.82, respectively

Design, Procedure, and Data Analysis

In this experiment, we measured the aftereffects induced by a whole upside-down face and its two facial components, respectively. The experiment included three adaptation conditions (termed f' - f' , c' - f' , and e' - f'), in which the adapting stimulus was the saddest upside-down whole face (f'), the isolated

curve derived from the saddest upside-down face (c'), or the mouthless upside-down face contour (e'), respectively. The apostrophe represents that the faces or face parts were the inverted version of the upright faces or face parts used in Experiment 1.1. As seen in Figure 8, the adapting stimulus in the f' - f' condition (the whole upside-down face) consisted of the adapting stimulus in the c' - f' condition (the isolated upside-down mouth) and that in the e' - f' condition (the upside-down mouthless face).

Figure 8. Three adapting stimuli in Experiment 1.2. From left to right: the saddest upside-down whole face (f'), the most convex curve equal to the upside-down isolated mouthpart (c'), and the upside-down mouthless face part (e')

The test stimuli (Figure 7a) were a continuum of seven upside-down whole faces (f') with the curvature of the mouth part gradually changing from the most convex to concave (0.82, 0.41, 0.21, 0.1, 0, -0.1, and -0.21 in units of $1/^\circ$). Subjects were also tested on the baseline condition (termed 0- f'), in which no adapting stimulus was shown. Similar to Experiment 1.1, to ensure that subjects indeed judged the facial expression of the test faces rather than the mouth curvature, we randomly interleaved in each experiment block two kinds of catch trials, using the upright saddest and happiest faces as the test stimuli (Figure 7b). The upside-down mouthless face (Figure 8, right) was also used as the test stimulus to check subjects' perception on its facial expression. The experiment procedure and data analysis were the same as in Experiment 1.1.

Results

Figure 9 below shows the results from a naïve subject (HU) in Experiment 1.2. For each of the four conditions, the fraction of happy responses was plotted as a function of the mouth curvature in test faces. Here, the mouth curvature in the upside-down cartoon face had the opposite valence compared to that in the original upright face for the same facial expression.

Similar to Experiment 1.1, the black curve is the baseline condition without adaptation ($0-f''$) and the other three curves (red, blue, and green) represent the three adaptation conditions ($e'-f''$, $c'-f''$, and $f'-f''$), respectively. Here, if the curve representing an adaptation condition is shifted to the right of the black curve (the baseline condition), it means that the observer sees happy expression more frequently in the test stimuli (upside-down faces) in that adaptation condition and vice versa for left-shifted adaptation curves.

Figure 9. Psychometric functions from a naïve subject (HU) in Experiment 1.2.

0-f': no adaptation baseline (black curve, empty circles); e'-f': adaptation to an upside-down mouthless part, generated by removing the mouth part from the upside-down saddest cartoon face (red curve, empty triangles); c'-f': adaptation to the most convex curve, i.e., the isolated mouth part derived from the upside-down saddest cartoon face (blue curve, empty diamonds); f'-f': adaptation to the upside-down saddest cartoon face (green curve, empty squares); The results for the upright happy and sad faces and the upside-down mouthless face were shown as filled black circles, red triangles, blue diamonds, and green squares, for the 0-f', e'-f', c'-f', and f'-f' conditions, respectively.

We applied two-tailed paired *t* tests to compare the PSE shifts (i.e., the facial expression aftereffects) in the three adaptation conditions (e'-f', c'-f', and f'-f') and also to compare the PSE shift in the f'-f' condition with the

summation of the PSE shifts in the $e'-f'$ and $c'-f'$ conditions. Figure 10 showed that the facial expression aftereffect was significant both in the $c'-f'$ condition (PSE-shift = 0.13, $t(4) = 3.226$, $p = 0.032$) and in the $f'-f'$ condition (PSE-shift = 0.16, $t(4) = 4.856$, $p = 0.008$), but it was not significant in the $e'-f'$ condition (PSE-shift = -0.008, $t(4) = -0.818$, $p = 0.459$). Moreover, the aftereffect in the $f'-f'$ condition (PSE-shift = 0.16) was not significantly larger than the linear summation of the aftereffects in the $c'-f'$ and $e'-f'$ conditions (PSE-shift summation = 0.12), $MD = 0.04$, $t(4) = 1.725$, $p = 0.16$.

Figure 10. Summary of all five subjects' data from Experiment 1.2. * $p < 0.05$;

** $p < 0.01$; *** $p < 0.001$

It may be argued that the non-significant results in Experiment 1.2 are simply due to the smaller sample size ($n = 5$) compared to that in Experiment 1.1 ($n = 11$). In response to this concern, we re-analyzed the data of the same five subjects in Experiment 1.1. Results revealed that the facial expression aftereffect was significant both in the $c-f$ condition (PSE-shift = -0.13, $t(4) = -$

5.714, $p = 0.005$) and in the f-f condition (PSE-shift = -0.22, $t(4) = -7.342$, $p = 0.002$), but it was not significant in the e-f condition (PSE-shift = -0.005, $t(4) = -0.316$, $p = 0.768$). Moreover, the aftereffect in the f-f condition (PSE-shift = -0.22) was significantly larger than the linear summation of the aftereffects in the c-f and e-f conditions (PSE-shift summation = -0.14), $MD = 0.087$, $t(4) = 3.227$, $p = 0.032$. Therefore, results from the same five subjects replicated the findings in Experiment 1.1 obtained from 11 subjects, which demonstrated that the perceptual output induced by a whole upright face was larger than the summation of the perceptual outputs induced by its two facial parts, pointing to the holistic processing of facial expression perception in upright faces.

Figure 11. Summary of all five subjects' data from Experiment 1.1. * $p < 0.05$;

** $p < 0.01$; *** $p < 0.001$

For the catch trials using upright saddest and happiest faces as the test stimuli, results showed that for the upright saddest face, subjects gave sad responses at an average of 99.5% of the time, significantly higher than chance

(50%), $t(4) = 161.666$, $p < 0.001$. For the upright happiest face, subjects gave happy responses at an average of 99.8% of the time, significantly higher than chance (50%), $t(4) = 199.000$, $p < 0.001$. These results indicate that subjects did judge the facial expression rather than the simple curvature of the mouth (Xu, et al., 2008; Xu, et al., 2012).

For the trials using the mouthless faces as the test stimuli, subjects gave happy responses at an average of 39.5% of the time, with no significant difference from chance (50%), $t(10) = -2.622$, $p = 0.059$, indicating that subjects perceived the facial expression in the mouthless face as neutral.

Discussion

In Experiment 1.2, we used upside-down cartoon faces in a facial expression adaptation task. We aim to test whether the gestalt effect in face adaptation revealed in upright faces in Experiment 1.1 will be observed in upside-down faces.

First, we found significant facial expression aftereffects induced by an upside-down whole face or an isolated mouth part (a curve). This is consistent with previous studies showing upside-down face aftereffects in a variety of dimensions, such as gender (Rhodes, et al., 2004), shape distortion (Rhodes, et al., 2004; Robbins, et al., 2007), and face identity (Leopold, O'Toole, Vetter, & Blanz, 2001).

More importantly, we found that the gestalt effect in facial expression adaptation observed in upright faces (Experiment 1.1) was absent here in upside-down faces, i.e., the aftereffect induced by the upside-down whole face was not significantly larger than the linear summation of the aftereffects

induced by its two facial parts. Previous studies have suggested the existence of distinctive coding mechanisms for processing upright and upside-down faces. For example, Maurer et al. (2002) propose that for upright faces, in addition to processing characteristics of individual facial features, the complex spatial relationship between facial features plays a critical role in the process of encoding. On the contrary, for upside-down faces, encoding individual facial features is of most significance. Similarly, Watson and Clifford (2003) argue that perception of upright faces involves two separate mechanisms: a high-level holistic processing mechanism specialized for face perception and a lower-level part-based processing mechanism for general object recognition. These two mechanisms are likely to be executed by dissociable populations of neurons. While adaptation in upright faces may recruit neural mechanisms in both levels, adaptation in upside-down faces may occur only in low or mid-level regions (Susilo, et al., 2010).

Therefore, in Experiment 1.2, the absence of the gestalt effect in facial expression adaptation for upside-down faces reflects the qualitative difference of perception between upright faces and upside-down faces, i.e., holistic processing exists in the perception of upright faces but it is disrupted for the perception of upside-down faces, consistent with previous findings (Maurer, et al., 2002; Susilo, et al., 2010; Watson & Clifford, 2003).

Materials used in previous experiments were cartoon faces depicted with simple lines and dots. Therefore, it remains unclear whether the findings can be applied to real faces that we are more likely to encounter in daily life. Besides the more pragmatic significance of using realistic face images, it should also be pointed out that the cartoon faces used in the current experiments

have an important characteristic different from real faces: the mouthless face seems to carry little information of facial expression. This is also revealed by the current finding that subjects judged the facial expression in the mouthless face as neutral. Therefore, it appears not surprising that the mouthless face part generated no significant aftereffect, which might at least partially cause the summation of the aftereffects by this part and the isolated mouth curve to be smaller than the aftereffect by the whole face. In contrast, for real faces, it is common that not only the mouth but also other parts like eyes and brows carry facial expression information, e.g., many people frown while feeling sad and squint while feeling happy. This conspicuous discrepancy between cartoon faces and real faces further highlights the necessity of examining whether the current findings with cartoon faces can be generalized to real faces. Experiment 1.3 was conducted to deal with this concern.

Experiment 1.3: Nonlinear interactions in upright real faces

Method

Subjects

Six adults (three female; age range = 25-31 years, $M = 27.5$ years, $SD = 2.26$) from the subject pool in Experiment 1.1 participated in this experiment. Five of them (except the author) were naïve to the purpose of this study. Subjects gave signed informed consent before the experiment and received incentives for their participation at a rate of 10 SGD (≈ 7.6 USD) per hour.

Apparatus and Materials

The apparatus and relevant parameters were the same as in previous experiments. The stimuli were a set of gray-scaled real faces instead of cartoon faces. We first selected three face images (demonstrating happy, neutral, and sad facial expression, respectively) of a male from the Ekman Pictures of Facial Affect (PoFA) database (Ekman & Friesen, 1976). All three images were cropped into a rectangle shape with the hair and neck areas removed. Each image subtended a size of $3.2^{\circ} \times 4.4^{\circ}$ of visual angle at the distance of 75 cm from the display screen. We slightly adjusted the luminance in the three images with Photoshop CS5 (Adobe Systems Incorporated, California, U.S.A.) and the final average luminance values were balanced for the three face images (around 39 cd/m^2). The images were also slightly modified to make the mouth part visually aligned across the three faces. MorphMan 4.0 (STOIK Imaging, Moscow, Russia) was used to generate intermediate facial expressions. We selected 30 markers (six on the eyes, six on the eyebrows, four on the nose, four around the cheeks, and 10 around the mouth) on each of the three source images so as to align critical features among them. Five images with happiness proportions from 0% (saddest) to 50% (neutral) were generated by morphing the sad face with the neutral face, and another five images with happiness proportions from 50% (neutral) to 100% (happiest) were generated by morphing the neutral face with the happy face. Finally, the test stimuli were eight faces with happiness proportions equal to 0%, 12.5%, 25%, 37.5%, 50%, 62.5%, 75%, and 87.5%, respectively (Figure 12).

Figure 12. Real face images as test stimuli in Experiment 1.3

Experiment 1.3 included three adaptation conditions (termed f-f, m-f, and e-f), in which the adapting stimulus was the saddest whole face (f), the isolated mouth retrieved from the saddest face (m), or the mouthless face part with the mouth removed from the saddest face (e), respectively (Figure 13).

Figure 13. Three adapting stimuli in Experiment 1.3. From left to right: the whole real face (f), the isolated mouth part (m), and the mouthless face part (e)

For the isolated mouth stimulus, we first used Photoshop CS5 to manually carve out the mouth from the saddest face image. We then filled the rest of the image with a uniform grey color, of which the luminance was matched with the average luminance of 36 randomly selected points in the face area surrounding the mouth. Therefore, the contrast of this isolated mouth image was equal to that of the original face image. For the mouthless face stimulus, we also carved out the mouth from the saddest face image and filled the scraped area with a technique feature called *Content-Aware Filling* in Photoshop CS5. This technique feature smoothly filled the area around the mouth (all subjects reported seeing no trace of mouth in the mouthless face when they were asked after the experiment). Finally, the mouthless face image

was also used as the test stimulus to check subjects' perception of facial expression on this artificial image.

Design, Procedure, and Data Analysis

The design and procedure in Experiment 1.3 were the same as in previous experiments, except that the test duration was 200 ms rather than 106 ms. Real faces are obviously more complex visual stimuli relative to cartoon faces and this longer test duration was designed to guarantee task performance in general (Xu, et al., 2008). Since there were eight test faces, each subject did a total of 160 trials in two blocks for each of the four conditions. The data analysis was the same as in previous experiments.

Figure 14. Trial sequence for the m-f condition in Experiment 1.3

Results

Figure 15 below shows the results from a naïve subject (JL) in Experiment 1.3.

Figure 15. Psychometric functions from a naïve subject (JL) in Experiment 1.3.

0-f: no adaptation baseline (black curve, empty circles); e-f: adaptation to a mouthless face part, generated by removing the mouth part from the saddest real face (red curve, empty triangles); m-f: adaptation to an isolated mouth derived from the saddest real face (blue curve, empty diamonds); f-f: adaptation to the saddest whole real face (green curve, empty squares); The results for the mouthless face image were shown as filled black circles, red triangles, blue diamonds, and green squares, for the 0-f, e-f, m-f, and f-f conditions, respectively.

Similar to previous experiments, we obtained the PSE of each psychometric curve for each subject. After summarizing the results from all six subjects, we applied two-tailed paired t tests to compare the PSEs in the three adaptation conditions against that in the baseline condition (i.e., the facial

expression aftereffect) and also to compare the PSE shift in the f-f condition with the summation of the PSE shifts in the e-f and m-f conditions. Figure 16 below demonstrates the average PSE shifts in each adaptation condition relative to the baseline condition.

Figure 16. Summary of all six subjects' data from Experiment 1.3. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Results showed that the aftereffect was significant both in the m-f condition (PSE-shift = -0.069, $t(5) = -3.455$, $p = 0.018$) and in the f-f condition (PSE-shift = -0.13, $t(5) = -6.527$, $p = 0.001$) but it was non-significant in the e-f condition (PSE-shift = -0.014, $t(5) = -0.955$, $p = 0.383$). Moreover, the aftereffect in the f-f condition (PSE-shift = -0.13) was significantly larger than the linear summation of the aftereffects in the c-f and e-f conditions (PSE-shift summation = -0.083), $MD = 0.048$, $t(5) = 3.291$, $p = 0.022$.

Finally, for the mouthless saddest face as the test stimulus, subjects gave sad responses at an average of 98.8% of the time, significantly higher than chance (50%), $t(5) = -75.523$, $p < 0.001$, indicating that subjects perceived the facial expression in the mouthless face as sad.

Discussion

In Experiment 1.3, we aim to examine whether the gestalt effect in facial expression adaptation obtained with cartoon faces in Experiment 1.1 can be applied to real faces.

The significant face aftereffect induced by the whole face showed a standard facial expression aftereffect for real faces (Hsu & Young, 2004; Webster, et al., 2004). Meanwhile, the significant aftereffect induced by the isolated mouth as the adaptor showed that perception of facial expression on real faces could also be biased by a local feature or part alone, again indicating a strong local component in facial expression perception (Harris & Aguirre, 2008; Xu, et al., 2008). After adding the aftereffect in the m-f condition to that in the e-f condition, we found the linear summation to be significantly smaller than the aftereffect generated in the f-f condition. This finding again implies that the whole real face produced a bigger aftereffect than the aggregated influence of the isolated mouth part and the mouthless face part, pointing to the existence of nonlinear interactions among the facial components. In other words, we reproduced the gestalt effect in facial expression adaptation with real faces, again supporting the holistic notion of facial expression perception (J. W. Tanaka & Farah, 1993; Young, et al., 1987).

As shown in the results, the mouth part generated a significant aftereffect (-.069) around 55% of that induced by the whole face (-.131), whereas the aftereffect from the mouthless face part failed to reach significance. This again indicates that the mouth part provides most of the contributions in facial expression perception, consistent with Experiments 1.1 and 1.2 using cartoon faces and also findings in previous studies (e.g., Gosselin & Schyns, 2001; Xu, et al., 2008).

CHAPTER III:**STUDY 2 – Distinctive Contribution of Facial Components****Introduction**

As discussed in the first chapter, faces convey a wealth of information including changeable properties such as facial expression and invariant properties such as face identity. Previous researchers have pointed out that the two most important aspects of face perception, facial expression and face identity, employ at least partially dissociable neural mechanisms and can be functionally separated (Bruce & Young, 1986; Burton, et al., 1990; Haxby, et al., 2000). One important way to reveal the possible dissociation between facial expression perception and face identity perception is to explore how facial properties in a single face image are retrieved and processed to form these two aspects of face perception (Calder & Young, 2005). Surprisingly, however, few existing studies have explored the dissociation and interactions between facial expression and face identity from this perspective, especially using psychophysics to directly probe the face-coding mechanism. Therefore, our second study aims to directly address this issue in a systematic investigation of how information from a single face image is recruited to form a holistic representation of facial expression and face identity.

In Study 2 we used the face adaptation paradigm in Study 1 but included both facial expression and face identity tests so as to examine whether and how facial components contributed distinctively to the two dissociable aspects of face perception. In Study 1, a whole face as the adaptor was divided into a mouth part and a mouthless face part. Such a manipulation might have placed a large emphasis on the mouth part, partially enhancing the saliency of this part

as an adaptor in biasing the perception of subsequent stimuli and thus producing a larger aftereffect. This might have resulted in an overestimation of the importance of the mouth part in facial expression adaptation. To exclude such a possibility, we adopted the method used in the classical face composite paradigm (Young, et al., 1987) and divided the adapting face stimulus into two size-equivalent halves: a top-half part and a bottom-half part. We examined the aftereffects induced by these two face halves in order to measure and compare the individual contribution of each face part to the integrated face representation. To perform a more direct comparison, we used the same set of adapting stimuli for the two face adaptation tests.

The research hypothesis in Study 2 is two-fold. First, it was hypothesized that the gestalt effect would be reproduced in both facial-expression and face-identity adaptation, providing further evidence for the holistic processing in face perception. More importantly, we also hypothesized that the same facial part (top-half face or bottom-half face) would cause different patterns of aftereffects, providing a direct demonstration of how facial components are distinctively retrieved and processed towards different aspects of face representation.

Experiments 2.1 and 2.2: Distinctive contributions of facial components in facial expression and face identity

Method

Subjects

Six adults (two female; age range = 22-28 years, $M = 23.3$ years, $SD = 2.33$) participated in Study 2. They were undergraduate or graduate students

from Nanyang Technological University, Singapore. Five of them (except the author) were naïve to the purpose of this study and did not participate in previous experiments in Study 1. Subjects gave signed informed consent before the experiment and received incentives for their participation at a rate of 10 SGD ($\approx$ 7.6 USD) per hour.

Apparatus and Materials

The apparatus and relevant parameters were the same as in previous experiments. We first selected three grayscale face images (Figure 17) from the Karolinska Directed Emotional Faces (KDEF) database (Lundqvist, Flykt, & Ohman, 1998). Among the three images, two of them belonged to one person (a young Caucasian male, named Adam here), showing a sad and a happy facial expression, respectively. The third image depicted another person (also a young Caucasian male, named Sam here) with a happy facial expression. All the images were cropped into an oval shape with the hair and neck areas removed. Each image had a size of $2.5^\circ \times 3.1^\circ$ at the distance of 75 cm from the display screen.

Figure 17. Three original face stimuli in Study 2: sad Adam (left), happy Adam (right top), and sad Sam (right bottom)

Study 2 consisted of two parts: Experiment 2.1 testing facial expression adaptation and Experiment 2.2 face identity adaptation. With MorphMan 4.0, we generated two continua of face images as test stimuli for facial expression and face identity judgments, respectively.

In Experiment 2.1 testing facial expression adaptation, the sad Sam face was morphed with the happy Sam face, producing 21 images with happiness proportions gradually changing from 0% (saddest) to 100% (happiest). Nine of these images were used as test stimuli with happiness proportions equal to 0%, 15%, 30%, 40%, 50%, 60%, 70%, 85%, and 100%.

Similarly, in Experiment 2.2 testing face identity adaptation, another 21 images with the proportion of the Adam identity gradually changing from 0% (original Sam) to 100% (original Adam) were generated by morphing the sad Sam face with the sad Adam face. Nine of the images were selected as test stimuli with the proportions of Adam identity equal to 0%, 15%, 30%, 40%, 50%, 60%, 70%, 85%, and 100% (Figure 18).

Figure 18. Illustration of the two continua of test faces in Study 2. For the top row, faces were generated by morphing sad Adam (the leftmost one) with happy Adam (the rightmost one) for testing facial expression adaptation; for the bottom row, faces were generated by morphing sad Adam (the leftmost one) with sad Sam (the rightmost one) for testing face identity adaptation

Experiment 2.1 and Experiment 2.2 used the same set of three adapting stimuli, i.e., the whole face of sad Sam (f), the top-half face part (t), and the bottom-half face part (b). For the top-half face image, the bottom-half area was filled with a uniform gray color that had the same luminance as the average luminance of the bottom half in the original face image (for the original bottom-half face: mean luminance = 26.13 cd/m^2), and vice versa for the bottom-half face part (for the original top-half face: mean luminance = 27.48 cd/m^2).

Figure 19. Three adapting stimuli in Study 2. From left to right: the whole face of sad Sam (f), the top-half face part (t), and the bottom-half face part (b)

Design, Procedure, and Data Analysis

Each of the two parts in Study 2 included three adaptation conditions, termed $f\text{-}f_{\text{exp}}$, $t\text{-}f_{\text{exp}}$, and $b\text{-}f_{\text{exp}}$ in Experiment 2.1 and $f\text{-}f_{\text{idt}}$, $t\text{-}f_{\text{idt}}$, and $b\text{-}f_{\text{idt}}$ in Experiment 2.2. The first letter represents the adapting stimulus was the whole face (f), the top-half face part (t), or the bottom-half face part (b); the second letter with the subscript represents the test stimuli were whole faces from the stimulus set for testing facial expression (f_{exp}), or from the stimulus set for testing face identity (f_{idt}). A baseline condition without adaptation was also included for each part (termed $0\text{-}f_{\text{exp}}$ for Experiment 2.1 and $0\text{-}f_{\text{idt}}$ for Experiment 2.2).

The procedure in Experiment 2.1 was the same as in Experiment 1.3. For Experiment 2.2, the only difference was that the task was changed to

judging the face identity instead of the facial expression: subjects were required to make a two-alternative forced-choice (2-AFC) judgment by pressing the “a” or “s” key to report whether the test face was Adam or Sam (Figure 20). Since there were nine test faces, each subject did a total of 180 trials in two blocks for each of the four conditions in Experiments 2.1 and 2.2, respectively. Subjects were allowed sufficient time to learn the facial expressions and the face identities of the original faces (Figure 17) and were also given sufficient practice to get familiar and comfortable with the task before formal data collection. Experiments 2.1 and 2.2 were run separately for each subject, with the order of the two parts counterbalanced across subjects.

Figure 20. Trial sequence for the $t-f_{idt}$ condition in Study 2

The data analysis was similar to previous experiments. The fraction of happy (Experiment 2.1) or Adam responses (Experiment 2.2) to each test stimulus was plotted against the test stimuli in terms of the proportion of happiness (Experiment 2.1) or Adam identity (Experiment 2.2).

Results

Figure 21 and Figure 22 below show the results from a naïve subject (JZ) judging facial expression in Experiment 2.1 and face identity in Experiment 2.2, respectively.

In Figure 21, if the curve representing an adaptation condition is shifted to the left of the black curve (the baseline condition), it means that the observer sees happy expressions more frequently in test stimuli after adaptation to the parts or whole of a sad face and vice versa for right-shifted adaptation curves.

Figure 21. Psychometric functions from a naïve subject (JZ) in Experiment 2.1.

0-f_{exp}: no adaptation baseline (black solid curve, circles); t-f_{exp}: adaptation to a top-half face part (red solid curve, triangles); b-f_{exp}: adaptation to a bottom-half face part (blue solid curve, diamonds); f-f_{exp}: adaptation to the saddest whole face (green solid curve, squares)

In Figure 22, if the curve representing an adaptation condition is shifted to the right of the black curve (the baseline condition), it means that the observer sees the identity of Adam less frequently in test stimuli after adaptation to the parts or whole face of Adam and vice versa for left-shifted adaptation curves.

Figure 22. Psychometric functions from a naïve subject (JZ) in Experiment 2.2.

0-f_{idt}: no adaptation baseline (black dash-dotted curve, circles); t-f_{idt}: adaptation to a top-half face part (red dash-dotted curve, triangles); b-f_{idt}: adaptation to a bottom-half face part (blue dash-dotted curve, diamonds); f-f_{idt}: adaptation to the saddest whole face (green dash-dotted curve, squares)

As in previous experiments, we obtained the PSE shift in each adaptation condition against the baseline condition (i.e., the face aftereffect) for each subject in Experiments 2.1 and 2.2, respectively. After summarizing the

results from all six subjects, we applied two-tailed paired t tests to compare the aftereffects between the three adaptation conditions. We also checked the gestalt effect by comparing the aftereffect induced by the whole face (f) to the summation of the aftereffects induced by the top-half face part (t) and the bottom-half face part (b) in Experiments 2.1 and 2.2, respectively. Figure 23 below shows the average PSEs shifts from the baseline condition for each of the three adaptation conditions in Experiments 2.1 and 2.2, respectively.

Figure 23. Comparison of face aftereffects in facial expression adaptation (Experiment 2.1) and face identity adaptation (Experiment 2.2). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

For Experiment 2.1 testing facial expression adaptation, the aftereffect was significant both in the b-f_exp condition (PSE-shift = -0.096, $t(5) = -4.183$, p

= 0.009) and in the $f\text{-}f_{\text{exp}}$ condition (PSE-shift = -0.13, $t(5) = -6.537$, $p = 0.001$), but it was not significant in the $t\text{-}f_{\text{exp}}$ condition (PSE-shift = -0.006, $t(5) = -1.755$, $p = 0.14$). Moreover, the aftereffect in the $f\text{-}f_{\text{exp}}$ condition (PSE-shift = -0.13) was significantly larger than the linear summation of the aftereffects in the $b\text{-}f_{\text{exp}}$ and $t\text{-}f_{\text{exp}}$ conditions (PSE-shift summation = -0.10), $MD = 0.031$, $t(5) = 3.201$, $p = 0.024$.

For Experiment 2.2 testing face identity adaptation, the aftereffect was significant both in the $t\text{-}f_{\text{idt}}$ condition (PSE-shift = 0.079, $t(5) = -9.768$, $p < 0.001$) and in the $f\text{-}f_{\text{idt}}$ condition (PSE-shift = 0.15, $t(5) = 11.083$, $p < 0.001$), but it was not significant in the $b\text{-}f_{\text{idt}}$ condition (PSE-shift = 0.018, $t(5) = 1.350$, $p = 0.235$). Moreover, the aftereffect in the $f\text{-}f_{\text{idt}}$ condition (PSE-shift = 0.13) was significantly larger than the linear summation of the aftereffects in the $b\text{-}f_{\text{idt}}$ and $t\text{-}f_{\text{idt}}$ conditions (PSE-shift summation = 0.097), $MD = 0.055$, $t(5) = 3.505$, $p = 0.017$.

Discussion

In Study 2, we aim to compare how facial components contribute distinctively to two different dimensions of face perception, i.e., facial expression and face identity. We conducted two adaptation experiments (Experiment 2.1 and Experiment 2.2) where subjects were adapted to the same set of three adaptors (Figure 19) but were tested on facial expression and face identity judgments.

First, in Experiment 2.1 testing facial expression adaptation, we found that the aftereffect induced by a whole face was significantly larger than the linear summation of the aftereffects elicited by its two components (i.e., the

top-half face part and the bottom-half face part). This gestalt effect in facial expression adaptation again demonstrates empirical evidence pointing to the holistic nature of facial expression perception, consistent with previous findings (Hsu & Young, 2004; Webster, et al., 2004; Xu, et al., 2008; Xu, et al., 2012). Moreover, the aftereffect induced by the bottom-half-face adaptor was around 72% of that by the whole-face adaptor, suggesting that the bottom-half face part contributed most to the holistic facial expression, consistent with findings from both real faces and cartoon faces in Study 1, and also previous studies reporting that the bottom-half face part, especially the mouth, receives higher reliance in facial expression recognition than other facial parts (Gosselin & Schyns, 2001).

Second, in Experiment 2.2 testing face identity adaptation, we also found the gestalt effect in face adaptation that the aftereffect induced the whole-face adaptor was significantly larger than the linear summation of the aftereffects elicited by its two components (i.e., the top-half face part and the bottom-half face part). This provides additional evidence revealing the holistic property underlying face identity perception, consistent with previous findings (Donnelly & Davidoff, 1999; Goffaux & Rossion, 2006; Michel, et al., 2010; Schiltz, et al., 2010; J. W. Tanaka & Farah, 1993; J. W. Tanaka, et al., 1998). More importantly, unlike the results on facial expression adaptation in Experiment 2.1, for face identity adaptation, it was the top-half face part that elicited a major aftereffect, accounting for about 52% of the aftereffect induced by the whole face. Previous research has shown that eyes play a more prominent role in identity recognition (Ellis, Shepherd, & Davies, 1979; Sekuler, Gaspar, Gold, & Bennett, 2004). Behavioral studies showed that subjects relied strongly on the eye region for face identity discrimination

(O'Donnell & Bruce, 2001; Sekuler, et al., 2004) whereas eye-tracking data revealed that when subjects were scanning face stimuli, they gazed at the stimuli's eyes with longer fixations and higher frequency than other parts (Rizzo, Hurtig, & Damasio, 1987). The current results further support the idea that the top-half face part plays a more critical role in perception of face identity than the bottom-half face part.

Taken together, the observed difference in the aftereffects induced by the top-half part or the bottom-half part between facial expression adaptation and face identity adaptation indicates that the visual system employs distinctive patterns of strategies in recruiting facial characteristics from the face image to generate the two aspects of face perception. This finding provides direct demonstration of dissociable face-coding mechanisms underlying facial expression adaptation and face identity adaptation, in line with a large amount of previous studies (Bruce & Young, 1986; Burton, et al., 1990; Haxby, et al., 2000).

CHAPTER IV:

STUDY 3 – Attentional Modulation on Face Adaptation

Introduction

Study 1 and Study 2 explored bottom-up face-coding mechanisms by addressing the question of how facial components contributed through nonlinear interactions towards the holistic representation of face perception, and how they contributed distinctively to two aspects of face perception, facial expression and face identity. Another important question is how the top-down mechanism is recruited in high-level face perception. Previous research has shown that selective attention can strengthen neural activity (Corbetta, et al., 1991; Ito & Gilbert, 1999; Luck & Hillyard, 1994; McAdams & Maunsell, 1999; Motter, 1994; Scholte, et al., 2001) and improve behavioral performance (Handy, et al., 1996; Hawkins, et al., 1990; Müller & Findlay, 1988). In the psychophysical domain, studies have found that attention can increase perceptual aftereffects for stimuli such as orientation and shapes, demonstrating the attentional influence on low-level and mid-level adaptation (Lankheet & Verstraten, 1995; Montaser-Kouhsari & Rajimehr, 2005; Spivey & Spirn, 2000; Suzuki, 2003). However, there is still limited knowledge about the functional role of attention on high-level adaptation like face adaptation. Our third study aims to probe the face-coding mechanism from a top-down perspective by examining how selective attention modulates face adaptation.

In Experiment 3, we tested facial expression adaptation on real faces in three adaptation conditions: 1) the passive-viewing condition, in which subjects were required to fixate a central cross throughout the experiment block, i.e., the regular adaptation condition as in previous studies. This served as the basic

adaptation condition without extra manipulation on the attention deployment during adaptation; 2) the increasing-attention condition, in which subjects were asked to complete a cognitive task at the adapting face area at the adaptation stage. This was designed to direct subjects' attention towards the adapting stimulus during adaptation; 3) the decreasing-attention condition, in which subjects were asked to complete a cognitive task near the fixation point at the adaptation stage. This was expected to divert subjects' attention away from the adapting stimulus during adaptation.

We first hypothesized that the facial expression aftereffect in the increasing-attention condition would be significantly greater than that in the passive-viewing condition, pointing to the amplified adaptation caused by increased attention to the adapting face. We also hypothesized that the facial expression aftereffect in the decreasing-attention condition would be significantly smaller than that in the passive-viewing condition, pointing to the deteriorated adaptation caused by decreased attention deployed to the adapting face.

Moreover, we employed a video-oculographic method with the eye tracking technique to monitor and record subjects' eye movements in the experiment. With the orientation pattern of microsaccades, we aim to provide a more direct demonstration of the attentional shift during adaptation.

While visually fixating at stationary scenes (e.g., during the adaptation stage), our eyes still continually produce miniature and involuntary ocular motions called fixational eye movements, which can be subdivided into drift, tremor, and microsaccades (Ditchburn & Fender, 1955; Ratliff & Riggs, 1950; Steinman, Haddad, Skavenski, & Wyman, 1973). As the most salient

component in fixational eye movements, microsaccades are ballistic movements with small linear sequence, typical amplitudes between 1' and 25', and an occurrence frequency of once or twice per second (Engbert & Kliegl, 2003). During the past decades, a lot of studies have found that microsaccades are closely related to many kinds of cognitive processing including attention. In a pioneering study using the classical spatial cueing paradigm (Posner, 1980), Engbert and Kliegl (2003) found that onsets of valid visual cues (arrows or colors) presented centrally led to increased occurrence of microsaccades in the corresponding direction. Rolfs et al. (2005) also found the influence of attentional shift on the orientation pattern of microsaccades with peripheral visual cues and auditory cues. Recent years have seen a growing body of evidence demonstrating the remarkable role of the orientation of spatial attention in the direction of microsaccades (Hafed, Lovejoy, & Krauzlis, 2011; Kliegl, Rolfs, Laubrock, & Engbert, 2009; Laubrock, Kliegl, Rolfs, & Engbert, 2010; Rolfs, Engbert, & Kliegl, 2004; Rolfs, et al., 2005). Researchers propose that the orientation of microsaccades can serve as a reliable index for the direction of covert attentional shifts and such empirically measurable dynamics of oculomotor motion can indicate the nature of cognitive processing in the visual system during fixation (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock, Engbert, Rolfs, & Kliegl, 2007; but see Horowitz, Fencsik, Fine, Yurgenson, & Wolfe, 2007; Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2007). Therefore, in Study 3, we aim to examine the orientation pattern of microsaccades during the adaptation stage in order to reflect how deployment of attention to the adapting stimulus affects facial expression adaptation.

Experiment 3: Effects of attention deployed to the adaptor on face adaptation

Method

Subjects

Six adults (three female; age range = 25-32 years, $M = 28.2$ years, $SD = 2.48$) participated in this experiment. They were undergraduate or graduate students from Nanyang Technological University, Singapore. Five of them (except the author) were naïve to the purpose of the current study and did not participate in Study 1 or Study 2. Subjects gave signed informed consent before the experiment and received incentives for their participation at a rate of 15 SGD (≈ 11.4 USD) per hour.

Apparatus and Materials

The apparatus and relevant parameters were the same as in previous experiments, except that subjects' real-time gaze position data were recorded by the EyeLink-II system with a sampling rate of 500 Hz (i.e., 2 ms temporal resolution) and a noise-limited spatial resolution better than 0.01° (SR Research, Osgoode, Ontario, Canada). The experiment was conducted in MATLAB (MathWorks, Natick, MA) with the PsychToolbox (Brainard, 1997; Pelli, 1997) and the EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002). The dominant eye (the right eye for all six subjects in this study) was recorded.

Materials were the same as in Experiment 2.1, except that seven images (instead of nine) were selected from the morphed face set with the happiness proportions equal to 10%, 25%, 40%, 50%, 60%, 75%, and 90%. In this experiment, eye tracking recording (i.e., the set-up process, calibration and

validation) would normally prolong the experiment block and wearing the eye-tracking device would make subjects uncomfortable. Therefore, to avoid exhausting subjects, especially in the adaptation conditions, we decreased the number of test stimuli to reduce the time for each block.

We also used two sets of additional stimuli: 1) For the increasing-attention condition, four new adapting face images were generated by modifying the original image of the adapting face (Figure 17, left). For each new adapting image, one part of the face (i.e., the left eye, the right eye, the left half part of the mouth, or the right half part of the mouth) was made brighter by using the *Dodge Tool* in Photoshop CS5; and 2) For the decreasing-attention condition, a stream of 11 black letters (i.e., X, A, B, E, H, K, L, N, T, U, Z) were used as the target (X) and distractors (the rest) for a target-detection task during adaptation. The font type was Arial and the font size was 24, making each letter subtend a size of around $0.78^{\circ} \times 0.78^{\circ}$ of visual angle.

Design and Procedure

There are three adaptation conditions in this experiment.

1) The passive-viewing condition (Figure 24): This was the same as the full-face adaptation condition in Experiment 2.1, except that the adaptation duration was 2 s instead of 4 s. As with the use of a smaller number of test stimuli, this shorter adaptation was chosen to reduce subjects' fatigue. Before the formal experiment, pilot studies were run to make sure that strong and stable facial expression aftereffects could be obtained with the shorter adaptation duration. In this condition, subjects viewed a face adaptor before

making facial expression judgments of the following test face. They were asked to maintain their fixation at the screen center throughout the experiment block.

Figure 24. Trial sequence for the passive-viewing condition in Study 3

2) The increasing-attention condition (Figure 25): While the adapting face was shown, a brightness change would occur at the left part of the face (i.e., the left eye or the left half of the mouth) or at the right face part (i.e., the right eye or the right half of the mouth). This was done by randomly presenting one of the four new adapting face images to replace the original adapting face for a short duration (106 ms). For each trial, this brightness change occurred once at a random time point during the 2-s adaptation. After the facial expression judgment on the test face, a text was centrally presented asking whether the brightness appeared in the left or right part. Subjects indicated the brightness location (left or right) by pressing the “<” or “>” key with the right hand. This additional task was expected to direct subjects’ attention towards the adapting face in order to increase the allocation of attentional resource to the adapting face.

Figure 25. Trial sequence for the increasing-attention condition in Study 3

3) The decreasing-attention condition (Figure 26): During the adaptation stage, a stream of letters was shown (i.e., the rapid serial visual presentation, RSVP) at the left side close to the fixation with a horizontal distance of 0.73° of visual angle. Subjects were asked to count how many times the target letter (X) had appeared. Following the facial expression judgment on the test face, a text was centrally presented asking whether the target had appeared N times. Subjects had to compare this number N with the actual number of times that the target had appeared and respond *Yes* or *No* by pressing the “>” or “<” key. The target letter was randomly intervened in the letter stream and appeared 0 to 4 times in a trial. For half of the trials in one experiment block, the displayed number N was the same as the actual number of target occurrence. Therefore, subjects should respond *Yes* by pressing the “>” key. For the other half of the trials, the displayed number N was larger than the actual number of target

occurrence by 1. Therefore, subjects should respond *No* by pressing the “<” key. This additional task was expected to divert subjects’ attention away from the adapting face in order to reduce the allocation of attentional resource to the adapting face.

Figure 26. Trial sequence for the decreasing-attention condition in Study 3

A baseline condition (baseline) with no adaptation was also included. Each subject completed two sessions, each with the four conditions in a randomized order. Since there were nine test faces, each subject did a total of 180 trials in two blocks for each of the four conditions in Experiment 3. Subjects had sufficient practice to get familiar with the task before formal data collection.

Eye movements were recorded during the adaptation stage for all conditions. For each experiment block, before the data collection, a nine-point grid calibration was first performed, followed by a nine-point grid validation.

This calibration-and-validation test was repeated once the error magnitude at any of the nine points was more than 1 ° or the mean magnitude of errors for all points exceeded 0.5 °.

Results

Behavioral Data

Results of one-sample t tests showed that the average accuracy in the brightness-change task in the increasing-attention adaptation condition (97.1%) was significantly higher than chance (50%), $t(5) = 43.86$, $p < 0.001$ and the average accuracy in the target-counting task in the decreasing-attention adaptation condition (76.9%) was also significantly higher than chance (50%), $t(5) = 12.57$, $p < 0.001$. These results demonstrated that subjects performed generally well in the tasks.

Figure 27 below shows results from a naïve subject (ZC) in Experiment 3. For each condition, the fraction of happy responses was plotted against the happiness proportion in the test faces. The black curve represents the baseline condition without adaptation (baseline) and the other three curves (red, blue, and green) represent the three adaptation conditions (passive-viewing, increasing-attention, and decreasing-attention), respectively. A leftward shift of the adaptation curve from the baseline curve means that the observer sees happy expression more frequently in test faces after adaptation in that condition and vice versa for the right shift of adaptation curves.

Figure 27. Psychometric functions from a naïve subject (ZC) in Study 3.

baseline: no adaptation baseline (black curve, circles); passive-viewing: regular adaptation without extra tasks at the adaptation stage (red curve, triangles); increasing-attention: brightness changes occur at the adapting face area during adaptation so as to drive attention towards the adaptor (blue curve, diamonds); decreasing-attention: RSVP occurs near the fixation during adaptation so as to divert attention away from the adaptor (green curve, squares).

We applied two-tailed paired t tests to examine the PSE difference between the baseline condition and each of the three adaptation conditions (i.e., the facial expression aftereffect), respectively. Results (Figure 28) showed that the facial expression aftereffect was significant in all three adaptation conditions: passive-viewing, PSE-shift = -0.18, $t(5) = -6.012$, $p = 0.002$; increasing-attention, PSE-shift = -0.17, $t(5) = -5.123$, $p = 0.004$; decreasing-

attention, PSE-shift = -0.08, $t(5) = 3.172$, $p = 0.025$. Results of one-way ANOVA revealed significant difference of the aftereffect size between the three adaptation conditions, $F(2,10) = 12.70$, $p = 0.002$. Ad-hoc analysis of multiple comparison with Bonferroni adjustment revealed no significant difference between the passive-viewing condition (PSE-shift = -0.18) and the increasing-attention condition (PSE-shift = -0.17), $MD = -0.004$, $p > 0.999$. However, the facial expression aftereffects in these two conditions were both significantly larger than that in the decreasing-attention condition (PSE-shift = -0.08): passive-viewing vs. decreasing-attention, $MD = 0.096$, $p = 0.027$; increasing-attention vs. decreasing-attention, $MD = 0.092$, $p = 0.016$.

Figure 28. Summary of all six subjects' data from Study 3. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Eye Movement Data

Each subject completed a total of 2520 trials in six adaptation sessions (two sessions for each adaptation condition). We applied a well-established

algorithm to detect microsaccades that occurred during adaptation. Developed by Engbert and Kliegl (2003), this algorithm relies on the fact that microsaccades can be separated from other types of fixational eye movements (e.g., tremor and drift) by their dynamical overshoot properties. It transforms fixation locations to two-dimensional velocity space and identifies microsaccades via thresholds of minimum duration and peak velocity (see more details in Engbert & Kliegl, 2003). After excluding trials with blinks and saccades, we retrieved 2451 trials (97.2%) from which a total of 15733 microsaccades were identified during the adaptation stage and we focused on horizontal microsaccades (52.6% of all detected microsaccades). These microsaccades were categorized into two types (Rolfs, et al., 2004, 2005): leftward microsaccades were defined as those with an absolute value of the saccade angle (Φ) larger than 135° (i.e., $\Phi > 3\pi/4$ or $\Phi < -3\pi/4$), whereas rightward microsaccades were defined as those with an absolute value of the saccade angle smaller than 45° (i.e., $-\pi/4 < \Phi < \pi/4$). We calculated the frequency of these two types of microsaccades for each of the three adaptation conditions.

For each type of microsaccades, one-way ANOVA was applied to compare the microsaccade occurrence rates between the three adaptation conditions. Result showed that the number of leftward microsaccades per second did not vary across the three adaptation conditions ($n = 0.98, 0.93$, and 0.84 , respectively), $F(2,10) = 1.18$, $p = 0.346$. In contrast, there was a significant difference in the number of rightward microsaccades between the three adaptation conditions, $F(2,10) = 25.63$, $p < 0.001$. Ad-hoc analysis of multiple comparison with Bonferroni adjustment revealed that there was no

significant difference between the passive-viewing ($n = 0.96$) and increasing-attention ($n = 0.85$) conditions, $MD = 0.11$, $p = 0.175$. However, the number of rightward microsaccades per second in these two conditions was both significantly larger than that in the decreasing-attention condition ($n = 0.48$): passive-viewing condition vs. decreasing-attention condition, $MD = 0.48$, $p = 0.002$; increasing-attention condition vs. decreasing-attention condition, $MD = 0.37$, $p = 0.017$.

Figure 29. Comparison of the microsaccade orientation patterns between the three adaptation conditions in Study 3. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Discussion

In Experiment 3, we aim to investigate the top-down mechanism in face perception by examining how task-based attentional deployment modulates facial expression adaptation.

First, when subjects were instructed to detect the change of brightness in the adapting face, more attentional resources were supposed to be deployed towards the adapting face. However, we did not see a significant increase of the facial expression aftereffect in this increasing-attention condition in contrast to the regular adaptation condition. This is at odds with our hypothesis as well as the previous study where Rhodes et al. (2011) found that increasing attentional deployment to the adaptor significantly amplified the face identity aftereffect and the face distortion aftereffect. For the present study, failure to observe an enhanced facial expression aftereffect in the increasing-attention condition might be because attention deployed to the adapting face did not increase at all, indicated by the fact that subjects did not make significantly more microsaccades towards the adapting face. Since the orientation of microsaccades is widely regarded as a reliable index of covert attentional shift (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock, et al., 2007), the comparable amount of microsaccades towards the adapting face in the regular passive-viewing and increasing-attention conditions suggest that attention allocated to the adaptor might not have increased at all in the latter condition. The reason for this might be twofold. On the one hand, the additional task might have been too easy such that subjects did not need to deploy extra attention to complete it. This receives support from the findings that subjects' performance was close-to-ceiling in terms of accuracy ($M = 97.1\%$). However,

this reason alone might not be sufficient since the task was intentionally designed to be similar to the one used in Rhodes et al. (2011)'s study, in which increasing attention to the adaptor was found to amplify face aftereffects significantly. In fact, the task here (differentiating whether the brightness change appeared in the left or the right area of the face) should be more difficult and thus more attention-demanding than the one in Rhodes et al. (2011)'s study (simply detecting whether a brightness change occurred or not). On the other hand, previous studies have shown that face stimuli, especially those with negative emotions, can attract and retain spatial attention (Eastwood, Smilek, & Merikle, 2003; Holmes, Vuilleumier, & Eimer, 2003; Pourtois & Vuilleumier, 2006; Vuilleumier & Schwartz, 2001). In a study with brain-damaged patients, Vuilleumier and Schwartz (2001) found that emotional faces (happy and angry) were less extinguished than neutral faces, suggesting that emotional values in faces could be processed in preattentive visual analysis and modulate the allocation of spatial attention. In another study, Eastwood et al. (2003) found that subjects performed more slowly in a task of counting facial features when the features were placed on negative faces compared to positive or neutral ones. This indicated that negative faces could capture and hold selective attention more effectively than positive and neutral faces. Unlike Rhodes et al. (2011)'s study, where a neutral face was presented as the adaptor, the current experiment used a sad face as the adaptor for the facial expression adaptation task and subjects detected the brightness change occurring on this sad face. This adaptor with negative facial expression might have been able to capture and hold sufficient attention that additional attention was not needed for observers to complete a simple cognitive task in the area where the sad face was presented.

Second, we observed a significantly smaller facial expression aftereffect in the decreasing-attention condition than in the passive-viewing condition. In the former condition, subjects were asked to perform an additional task of counting the occurrence of a target in a stream of rapidly presented letters. These letters appeared at the left to the fixation, the opposite side to that of the adapting face. Therefore, it was intended to divert subjects' attention away from the adaptor. Eye movement data showed that subjects did make significantly less microsaccades towards the adapting face in this condition compared to the regular passive-viewing condition. Since the orientation of microsaccades has been extensively regarded as a reliable index of covert attentional shift (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock, et al., 2007), this provided robust evidence showing that attention deployed to the adapting face was indeed reduced. Therefore, findings here demonstrate that decreasing attention deployed to the adapting face can remarkably deteriorate facial expression adaptation, pointing to the significant role of task-based attention in modulating facial expression adaptation.

It is well known that adaption to simple stimulus properties like shapes or orientation is modulated by attention (Lankheet & Verstraten, 1995; Montaser-Kouhsari & Rajimehr, 2005; Spivey & Spirn, 2000; Suzuki, 2003). In Experiment 3, our results suggest that attention can also modulate adaptation for more complicated stimuli like faces. For simple stimuli, adaptation was processed at low-level or middle-level regions in the visual system (Dowling, 1967; Ferster & Miller, 2000) and therefore the locus of the attentional influence should also be in the lower or middle level along the visual pathway. For face adaptation that recruits high-level coding mechanisms, the modulation

of attention is likely to occur through two possible routes. First, decreasing attention deployed to the adapting face might reduce the signal strength, leading to an attenuated aftereffect. This receives support from two types of face adaptation study. On the one hand, researchers have found that decreasing the adaptation duration, i.e., reducing the signal strength of the adaptor, effectively impaired face aftereffects (Leopold, Rhodes, Müller, & Jeffery, 2005; Rhodes, Jeffery, Clifford, & Leopold, 2007). On the other hand, crowding of the adapting face, leading to the reduction of its visibility and thus its signal strength, also decreased the face aftereffect significantly (Xu, et al., 2012). Second, decreasing the deployment of attention towards the adaptor might have deteriorated the adapting calibration of coding mechanisms. In particular, decreased attention to the adaptor might have reduced the coding efficiency of neurons and the discriminability of stimuli within an adapted population (see reviews in Rhodes, et al., 2011; Webster & MacLeod, 2011).

CHAPTER V: GENERAL DISCUSSION

Summary of Current Findings

Using a psychophysical approach with a face adaptation paradigm, the series of empirical studies reported here probed face-coding mechanisms from both bottom-up and top-down perspectives. For the bottom-up perspective, we investigated in Study 1 how facial components influenced one another to form a holistic face representation, and we investigated in Study 2 how facial components contributed distinctively to different aspects of face perception. For the top-down perspective, we explored in Study 3 the top-down mechanism of face adaptation by testing the influence of task-based deployment of selective attention on face adaptation. Findings from these studies revealed three important characteristics of the face-coding framework for face perception (Figure 30).

A Hierarchical Multilevel Face-Coding Framework

First of all, facial components interact with one another nonlinearly towards a holistic face representation, pointing to a hierarchical multilevel face-coding framework. In Study 1 and Study 2, a gestalt effect was found in face adaptation, namely that the aftereffect produced by a whole face was significantly greater than the linear summation of the aftereffects induced by two facial parts. This gestalt effect in face adaptation directly reflects the holistic notion proposed in the Gestalt theory that “the whole is greater than the sum of its parts” (Koffka, 1935; Köhler, 1959). In existing studies on holistic face processing, researchers have provided much empirical evidence to demonstrate the holistic nature of face perception (see reviews in Tsao & Livingstone, 2008). The face inversion effect (Yin, 1969) shows that inversion

causes a disproportional deterioration of perception in faces compared to other objects, which it is argued is due to configural or holistic processing in face perception (Farah, et al., 1995; Rossion & Boremanse, 2008; Valentine, 1988). The whole-part advantage effect (J. W. Tanaka & Farah, 1993; J. W. Tanaka, et al., 2004; J. W. Tanaka & Sengco, 1997) and the face composite effect both demonstrate the prominent interactions among facial components in face perception (de Heering & Rossion, 2008; Jacques & Rossion, 2009; Letourneau & Mitchell, 2008; Schiltz, et al., 2010; Young, et al., 1987). However, none of these effects directly measure the original holistic notion that “the whole is greater than the sum of its parts” (Koffka, 1935; Köhler, 1959). Recently, several studies directly addressed this notion in face perception but obtained mixed results. With an ideal observer model, Gold, et al. (2012, 2014) measured the psychophysical contrast sensitivities for recognizing a whole face or individual face parts, and found that human observers’ ability of recognizing a whole face was not better than the prediction of their ability of recognizing each individual feature presented in isolation. Therefore, Gold, et al. (2012, 2014) concluded that the perception of a face is not greater than the sum of its parts. In a more recent study, however, when Shen and Palmeri (2014) used the same paradigm in Gold, et al. (2012, 2014)’s experiments but added natural configural variability to the face stimuli, they found that human observers’ recognition of a whole face was better than the predicted sum of performance in recognizing its facial components when shown in isolation. Here, the gestalt effect found in face adaptation in the current research further provides direct evidence to support the holistic notion of face perception, demonstrating that a whole face can induce a significantly larger perceptual output than the simple

linear summation of the perceptual outputs induced by its individual facial components. This result also provides empirical evidence in support of a hierarchical multilevel framework in face-coding. According to the hierarchical model of face processing (Riesenhuber, et al., 2004; Riesenhuber & Poggio, 2002), face-coding involves multiple levels in which neural responses to local facial features in low-level regions are integrated via nonlinear operations while being propagated to higher levels of face-specific processing. This theory receives physiological evidence from non-primates, where neurons in the inferior temporal gyrus (i.e., one of the higher levels in the ventral stream of visual processing) responded to two parts linked together with greater activity than that predicted by the additive neural responses to each part separately (Baker, et al., 2002). In the current research, when two facial parts were presented as adaptors in separate conditions, it is likely that neural responses caused by each of them in low-level visual areas coding local facial features went to higher-level regions, with no integration. However, when the two facial parts were simultaneously presented (i.e., a whole face) as the adaptor, it seems likely that neural responses caused by each of them in low-level regions could be integrated via nonlinear functions while being sent to higher levels. The gestalt effect in face adaptation was observed in upright cartoon faces and real faces for facial expression adaptation and for face identity adaptation but it was eliminated in upside-down faces. This is consistent with previous findings showing the existence of holistic processing along the two face perception dimensions and the disruption of holistic processing in upside-down faces, thus revealing the reliability and robustness of this newly reported effect in face perception.

A Multidimensional Face-Coding Framework with Dissociable

Subsections

Second, facial components contribute distinctively in two different aspects of facial perception (i.e., facial expression and face identity), pointing to a multidimensional face-coding framework with dissociable subsections. In Study 2, we found that for facial expression adaptation, the top-half face part did not induce a significant facial expression aftereffect whereas the bottom-half face part caused a significant facial expression aftereffect amounting to 72% of that induced by the whole face. In contrast, for face identity adaptation, the top-half face part caused a significant face identity aftereffect amounting to 52% of that induced by the whole face, whereas the bottom-half face part failed to induce a significant face identity aftereffect. The finding demonstrates that the bottom-half face part provides the major contribution in facial expression perception whereas the top-half face part plays a leading role in recognition of face identities. It should be noted that the same set of face and facial parts were used as adaptors in the two face adaptation tests. It is likely that these facial parts have stimulated the same populations of neurons in the low-level visual regions in the two face adaptation tasks. However, the neural responses might have gone along different pathways to high-level regions and be assigned with different weights in establishing the ultimate representation of facial expression and face identity. This is finally reflected as different magnitudes of aftereffects induced by different facial parts in the two face adaptation tests. Therefore, findings here provide a direct demonstration that distinctive strategies are employed to recruit information of facial features from a single face image for perception of facial expression and face identity, pointing to the existence of

dissociable pathways and subsections in a multidimensional face-coding framework for the two aspects of face perception.

A Face-Coding Framework with Top-Down Adaptive Plasticity

Third, task-based allocation of selective attention can significantly modulate facial expression adaptation, pointing to the role of top-down mechanisms in the plasticity of the face-coding framework. In Experiment 3, we did not observe an amplified facial expression aftereffect when an additional task at the adapting face area failed to drive more attention to the adaptor, showing that the facial expression adaptation was not influenced by the additional cognitive processing during the adaptation stage when no extra spatial attention was deployed. Meanwhile, when an additional task near the fixation successfully reduced the amount of attentional resources allocated to the adapting face, the facial expression aftereffect was significantly decreased. These findings show a close relationship between the attention deployed to the adapting face and the size of the facial expression aftereffect, demonstrating a remarkable role of attention in the adaptive plasticity of the face-coding framework. This attentional modulation may result from that attentional allocation to the adaptor affects the signal strength of the perceptual input in adaptation. This approach resembles the mechanism that decreasing the signal strength with shorter presentation of the adaptor can significantly reduce the magnitude of face aftereffects (Leopold, et al., 2005; Rhodes, et al., 2007). The possibility of this mechanism also receives support from crowding studies where crowding of the adapting face deteriorates the discriminability of the adapting face and therefore diminishes face adaptation (Xu, et al., 2012).

Meanwhile, the observed attentional modulation on face adaptation might also result from attentional influence on the coding efficiency of neurons and therefore the discriminability of test stimuli within an adapted population (see reviews in Rhodes, et al., 2011; Webster & MacLeod, 2011).

Figure 30. Illustration of a comprehensive face-coding framework revealed in the current research. Red and blue rectangles and arrows represent that two facial parts (top and bottom face halves here) induce neural responses at the low-level vision area, which are then projected to the high-level region. Green double-headed arrows represent nonlinear interactions among low-level neural responses induced by the two facial parts that occur during the propagation the high-level vision area; the line thickness of red and blue arrows corresponds to the assigned weight of low-level neural responses by different facial parts in forming different dimensions of face perception; black solid arrows represent the effect of attentional resources on face adaptation, possibly through changing either the signal strength of the adapting face or the coding efficiency.

Limitations and Implications for Future Studies

First of all, in this research subjects were asked to judge facial expression or face identity, a high-level visual processing that is likely to be more subjective compared to low-level perception such as contrast differentiation. It may be questioned whether findings on such visual perception can be well generalized to other individuals, especially when the sample size is relatively small in the experiments ($n = 5$ to 11). Regarding this concern, first, before the formal experiment, subjects went through sufficient practice allowing them to establish a stable and relatively objective judgment standard for differentiating facial expressions or face identities in different conditions. Each subject was tested for all conditions in each of the experiments. Thus, comparisons of subjects' responses between different conditions were all within-subject analysis, which eliminated confounding effects of individual differences and extensively reduced vulnerability of the results to subjective interference. Meanwhile, unlike other methods such as questionnaire-based surveys where participants are usually tested once and thus provide only one data point per person for a particular condition, psychophysics experiments test subjects under the same condition for tens or hundreds of times and highly repetitive tests guarantee high stability and reliability of subjects' responses. In current experiments, each subject was tested for 140 to 180 times for each condition and each data point fitted by the psychometric curve was based on 20 repetitions of the test stimuli. Finally, all the results were tested with statistical analysis and thus robustness of the findings is also guaranteed by the power of statistical tests.

Second, in Study 1 and Study 2, we found a gestalt effect in face adaptation that a whole upright face could exert a significantly larger facial aftereffect than the linear summation of the aftereffects induced by its two facial parts. We believe this finding indicates that information of different local facial parts is projected via nonlinear functions from low-level vision regions to higher levels while forming the ultimate face representation, supporting a hierarchical multilevel model of face processing (Riesenhuber, et al., 2004; Riesenhuber & Poggio, 2002). However, due to the methodological limitation of psychophysical approach, we did not directly examine when and where the nonlinear interactions occurred in the neural network of the holistic face perception. Investigations integrating the face adaptation paradigm with other approaches (e.g., ERP and fMRI) would help to obtain a clearer picture of the holistic processing on its temporal and spatial properties.

Third, in this research, we addressed the question of how information from the same face image could be distinctively recruited in forming two different dimensions of face perception, i.e., facial expression and face identity. Results show that the top half part of a face is more important in face identity adaptation and the bottom-half face makes more contributions to facial expression adaptation. This finding may provide implications for a better understanding of some cognitive disorders related to face perception. For example, individuals with prosopagnosia (also referred to as face blindness) have difficulties in perception of face identity but their ability to differentiate facial expressions and infer other people's emotion remains intact (Duchaine, Parker, & Nakayama, 2003). Therefore, future studies may apply the current paradigms people with prosopagnosia to see how the results differ from the

current findings with normal individuals. It is possible that compared to healthy people, individuals with prosopagnosia may have employed a different strategy in recruiting facial information to form the two dimensions of face perception. Meanwhile, previous studies have found that compared to typically developing children, children with autism spectrum disorders who show difficulties in face processing have smaller face identity aftereffects (Pellicano, Jeffery, Burr, & Rhodes, 2007). With the current paradigms, future studies may further investigate whether the difference also exists in facial expression adaptation and which particular facial parts contribute to the different adaptation effects between children with autism and typically developing children. Findings from such studies may help researchers to better understand the neural coding mechanism underlying the occurrence of autism and provide practical insights for improving intervention programs for children with autism (Mundy & Crowson, 1997), e.g., training children to focus on certain face parts to perform better for a particular dimension of face perception just as normally developing children. Moreover, besides facial expression and face identity, face perception also contains a variety of other dimensions (see reviews in Sigala & Rainer, 2007), including objective properties (e.g., age, race, and gender) and subjective attributes (e.g., attractiveness and trustfulness). Investigations on more aspects of face perception through direct comparisons can provide a better understanding of the cognitive mechanism underneath face perception as a multidimensional network with dissociable and interactive subsections.

Fourth, in Study 3, while we showed that decreasing the amount of top-down attention deployed towards the adapting face could effectively reduce facial expression adaptation, we failed to drive more attention towards the

adapting face in the increasing-attention condition, which was evidently reflected by the microsaccades pattern. This might be because the adaptor with negative facial expression had captured sufficient attention (Pourtois & Vuilleumier, 2006; Vuilleumier & Schwartz, 2001) and therefore additional attention was not needed for observers to complete a simple cognitive task in the area where the sad face was presented. However, future studies are needed to test whether and how facial expression adaptation will be influenced while more top-down attention can be successfully directed towards the adapting face. Besides the orientation pattern of microsaccades, perceptual threshold (Bashinski & Bacharach, 1980) or manual reaction time (Posner, 1980) may also be used to measure attention in order to have a more reliable assessment of attentional manipulation. In addition, future studies may also investigate the attentional modulation on both face identity adaptation and facial expression adaptation to see whether and how top-down attention interacts with the dimension of face perception to affect face adaptation.

Finally, in this research subjects were all Chinese. Previous studies suggest that culture has prominent influence in face perception. East Asians and Western Caucasians use culture-specific cognitive strategies in both facial expression perception (Ito, Masuda, & Hioki, 2011; Ito, Masuda, & Li, 2013; Jack, Blais, Scheepers, Schyns, & Caldara, 2009) and face identity recognition (Blais, Jack, Scheepers, Fiset, & Caldara, 2008; Mielliet, Vizioli, He, Zhou, & Caldara, 2013). For example, Mielliet et al. (2013) found that in face recognition tasks Easterners tended to extract more information from the nose region, while Westerners were more likely to focus on the eye region. In another study by Jack et al. (2012), East Asians and Western Caucasians showed distinctive

internal representations even for the six basic facial expression previously considered the “universal language of emotion” (Ekman & Friesen, 1971). Therefore, it will be interesting and important for future studies to further investigate whether and how the gestalt effect found in this research with Chinese observers can be applied to population of other cultures. In addition, the real faces used in the current experiments all belonged to Western Caucasians. Previous research has reported robust other-race effects that people are better at recognizing faces of their own race than faces of other races in terms of higher accuracy and shorter reaction time (Furl, Phillips, & O’Toole, 2002). According to the holistic account, the other-race effect at least partially results from different processing strategies for own-race and other-race faces, namely that people use mainly configural processing for own-race face recognition and featural processing for recognition of other-race faces (Michel, Rossion, Han, Chung, & Caldara, 2006; Rhodes, Brake, Taylor, & Tan, 1989; Rhodes, Hayward, & Winkler, 2006; Tanaka, et al., 2004). Using the whole-part advantage paradigm, Tanaka et al. (2004) showed that for Caucasian participants, holistic processing was dominantly involved in recognition of Caucasian faces while featural processing was used in recognition of unfamiliar Asian faces. However, Asian participants showed holistic processing in the recognition of both Asian and Caucasian faces. In the current research, Chinese participants were asked to judge facial expression and face identity of unfamiliar Caucasian faces. Results revealed holistic processing in terms of the gestalt effect in face adaptation for both face tasks. This finding is consistent with Tanaka et al.’s study (2004), suggesting that East Asians shown holistic processing even for other-race faces. Moreover, previous research has

suggested that holistic processing is used for own-race face perception. Therefore, if Chinese or Caucasians participants are asked to recognize faces of their own races using the adaptation tasks in this research, the gestalt effect in face adaptation is likely to be observed. However, the effect may disappear if Caucasian participants are tested with unfamiliar East Asian faces in the adaptation tasks, given that Caucasians use featural processing in recognition of other races (Tanaka, et al., 2004). Future studies are needed to further investigate the possible interaction between the race of observers and the race of face stimuli regarding the holistic processing in face perception.

Summary and Conclusions

This research with three psychophysics studies carried out a systematic investigation on face-coding mechanisms from both bottom-up and top-down perspectives.

First, from a bottom-up perspective, we explored how individual facial parts are processed into a holistic representation of face perception. We found that a whole face produced a significantly larger aftereffect than the linear summation of the aftereffects induced by its two facial components, providing direct support for the holistic notion in the Gestalt theory (Koffka, 1935; Köhler, 1959) that “the whole is greater than the sum of its parts”. This finding suggests that the face-coding framework involves in a hierarchical multilevel model where higher-level visual areas recruit neural responses from lower levels via nonlinear functions (Riesenhuber, et al., 2004; Riesenhuber & Poggio, 2002). Second, also from a bottom-up perspective, we investigated how facial components contributed to two different dimensions of face perception (facial

expression and face identity). We found that the bottom-half face part contributed most to facial expression adaptation whereas the top-half face part made major contribution to face identity adaptation. This finding suggests that the face-coding framework is multidimensional with dissociable subsections that facial expression and face identity employ distinctive patterns of strategies in recruiting facial properties towards the holistic representation (Calder & Young, 2005). Third, from the perspective of top-down processing, we addressed the question of how attention plays a role in face adaptation. We found that when a brightness-change detection task failed to drive attention towards the adapting face, the facial expression aftereffect did not increase even when there was additional cognitive processing on the adaptor during adaptation. Meanwhile, when allocation of attention towards the adapting face was evidently decreased, reflected by reduced microsaccades towards the adaptor during adaptation, the facial expression aftereffect was significantly deteriorated. This finding demonstrates a close relationship between attention and facial expression adaptation, suggesting that the face-coding framework involves top-down mechanisms with adaptive plasticity modulated by attention deployment (Rhodes, et al., 2011).

Taken together, the current research sheds light on a more holistic and deeper understanding of the neural coding mechanism underlying face perception.

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