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Dissociated neural basis of two behavioral hallmarks of holistic face processing: The whole-part effect and composite-face effect

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ABSTRACT

It has been long proposed that our extraordinary face recognition ability stems from holistic face processing. Two widely-used behavioral hallmarks of holistic face processing are the whole-part effect (WPE) and composite-face effect (CFE). However, it remains unknown whether these two effects reflect similar or different aspects of holistic face processing. Here we investigated this question by examining whether the WPE and CFE involved shared or distinct neural substrates in a large sample of participants (N = 200). We found that the WPE and CFE showed hemispheric dissociation in the fusiform face area (FFA), that is, the WPE was correlated with face selectivity in the left FFA, while the CFE was correlated with face selectivity in the right FFA. Further, the correlation between the WPE and face selectivity was largely driven by the FFA response to faces, whereas the association between the CFE and face selectivity resulted from suppressed response to objects in the right FFA. Finally, we also observed dissociated correlation patterns of the WPE and CFE in other face-selective regions and across the whole brain. These results suggest that the WPE and CFE may reflect different aspects of holistic face processing, which shed new light on the behavioral dissociations of these two effects demonstrated in literature.

1. Introduction

Humans have extraordinary face recognition ability. It has been long proposed that our extraordinary face recognition ability stems from holistic face processing: the tendency to percept the face as an inseparable whole (e.g., Jacques and Rossion, 2009; Tanaka and Simonyi, 2016; Young et al., 1987; Yovel, 2016; Yovel et al., 2014). Two traditional tasks have been widely used to probe holistic face processing, the whole-part task and the composite-face task. In the whole-part task, the recognition of a face part (e.g., eyes) is better when presented in a whole face compared to when presented in isolation, which is called the whole-part effect (WPE) (Tanaka and Farah, 1993). In the composite-face task, the recognition of the attended halves of composite faces is interfered by the unattended halves, which is called the composite-face effect (CFE) (Young et al., 1987). However, it remains unknown whether these two effects reflect similar or different aspects of holistic face processing.

If they reflect similar aspects of holistic face processing, the two effects would be expected to show similar patterns in studies of face recognition. Yet, the findings in literature are far from clear. A direct approach to investigate the role of holistic processing in face recognition is to examine the correlation between holistic face processing and face recognition ability. With the whole-part task, two studies have shown that the WPE is positively correlated with face recognition ability measured by the old/new face memory task (Wang et al., 2012) and the Cambridge Face Memory Test (CFMT) (DeGutis et al., 2013b). The results of the composite-face task are less consistent. While several studies have found correlation between the CFE and face recognition ability using either the partial or complete design of the composite task (DeGutis et al., 2013b; Richler et al., 2011; Wang et al., 2012), two other studies failed to found this link (Konar et al., 2010, 2013). It seems that the correlation between holistic processing and face recognition ability depends on multiple factors, including design factors of the composite task (partial vs. complete design, stimulus repetition, and image size, Richler et al., 2011, 2014, 2015), the tasks used to measure face recognition ability (memory vs. identification, Konar et al., 2010, 2013; Richler et al., 2011), and the measures used to calculate the WPE/CFE (regression vs. subtraction, DeGutis et al., 2013b) and face recognition ability (absolute vs. difference score, Wang et al., 2012).

Another approach to examine the role of holistic processing in face recognition is asking whether faces are processed less holistically when

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they are recognized less efficiently in some special groups (e.g., those with prosopagnosia or autism, and children) or during some suboptimal conditions (e.g., recognizing faces of other races). For example, some studies asked whether abnormal holistic processing of faces is a characteristic hallmark of prosopagnosia following brain damage (acquired prosopagnosia, AP) (e.g., Bodamer, 1947; Quaglino et al., 2003). Two studies found that AP patients showed no WPE, that is, their performances in the part condition were equal to those in the whole condition (Busigny et al., 2010; Ramon et al., 2010). However, the results of the composite-face task are mixed. While patient GG did not show the CFE (Busigny et al., 2010), patient PS showed some degree of the CFE (Ramon et al., 2010). Besides AP, developmental prosopagnosia (DP) also shows deficit in face recognition but without known brain injury (e.g., Behrmann and Avidan, 2005; Duchaine and Nakayama, 2006). Consistent with what have found in AP, DPs showed a lack of the WPE (DeGutis et al., 2011; Song et al., 2015). Further, one study (DeGutis et al., 2012) revealed the source of the impaired WPE in a large sample of DPs (N = 38). They found that DPs showed an absence of the WPE for eye region and an intact WPE for mouth region, and the WPE for mouth region was correlated with face recognition ability measured by CFMT (DeGutis et al., 2012). However, 3 of 4 studies using the composite-face task for DPs found normal CFE as the control group (Le Grand et al., 2006; Palermo et al., 2011; Susilo et al., 2010), whereas only one study found absence of the CFE in DPs, and the abnormality of the CFE was associated with the abnormality of face recognition measured by CFMT (Avidan et al., 2011). Taken together, the WPE and CFE show dissociation in prosopagnosia, that is, while the WPE is impaired in both types of prosopagnosia, most studies show a preserved CFE in prosopagnosia.

Individuals with autism often show impaired face recognition ability (e.g., Dawson et al., 2005; Sasson, 2006; Wang et al., 2015), and several studies have explored whether this impairment results from abnormal holistic face processing. Joseph and Tanaka (2003) conducted the first study focusing on holistic face processing in children with autism. They observed the WPE in children with autism, though this effect was present mainly for mouth recognition and was diminished for eye recognition. In another study, adolescents with autism showed the trend of better performance in the whole condition than the part condition for both eyes and mouth, though the trend did not reach significance (Lopez et al., 2004). A recent study confirmed the WPE for both eyes and mouth in children and adolescents with autism, but the WPE was only evident for mouth but not eyes in adults with autism (O'Hearn et al., 2014). Different pattern of results has been found for the CFE. That is, adults with autism demonstrated a normal CFE (Nishimura et al., 2008), while adolescents with autism did not show the CFE (Teunisse and de Gelder, 2003), and it was proposed that the absence of the CFE in adolescents with autism was caused by comparable interference in both alignment and misalignment composites (Gauthier et al., 2009). In short, it seems that while the WPE is more demolished for adults than children and adolescents with autism, the CFE is more impaired in adolescents than adults with autism.

Additionally, numerous studies have attempted to use these two tasks to investigate whether the development of holistic face processing underlies the development of face recognition ability. Early evidence demonstrated that 6-year-old children already showed a significant holistic effect indexed by both the WPE (Tanaka et al., 1998) and the CFE (Carey and Diamond, 1994; Mondloch et al., 2007). Studies found even preschool children (i.e., 4 years old) showed an adult-like WPE (Pellicano and Rhodes, 2003; Pellicano et al., 2006) and CFE (Cassia et al., 2009; de Heering et al., 2007). Taken together, using both the WPE and CFE, previous studies have found consistent results which suggest early maturation of holistic face processing. However, the results of the WPE and CFE are contradictory considering the aging effect of holistic face processing. One study found that older adults (70 years old) showed a significant WPE as younger adults (Boutet and Faubert, 2006). As for the CFE, while one study found a normal CFE in older adults with a perceptual composite-face task (Konar et al., 2013); Boutet and Faubert (2006) failed to find the CFE with a memory composite-face task in older adults. These results suggest a dissociation of the WPE and CFE in older adults.

Another long-standing controversy is whether the worse recognition of other-race than own-race faces (i.e., the other-race effect, ORE) results from the tendency that we process other-race faces less holistically. Studies using the whole-part task consistently found that Caucasians showed a larger WPE for same-race than other-race faces, while there was no difference between the WPE of other-race and same-race faces in Asians (Crookes et al., 2013; DeGutis et al., 2013a; Michel et al., 2006a; Mondloch et al., 2010; Tanaka et al., 2004). However, the results of the CFE showed a different pattern. Most studies found no race effect of the CFE for either Caucasians or Asians (Harrison et al., 2014; Hayward et al., 2013; Horry et al., 2015; Mondloch et al., 2010); though two studies found Caucasians exhibited a larger CFE for same-race than other-race faces (Michel et al., 2007, 2006b). Further, individual differences in the ORE are correlated with the race effect of the WPE (DeGutis et al., 2013a; but see Michel et al., 2006b), while the ORE cannot be explained by the races differences in the CFE (Horry et al., 2015; Michel et al., 2006a).

In short, the literature review indicated behavioral dissociations between the WPE and CFE, which may arise from multiple sources. For example, general cognitive factors such as attentional demands, response bias, and encoding-specificity effects on memory have been proposed to exert different influences on the two tasks (e.g., McKone et al., 2013). Critically, it is possible that these two effects may tap different mechanisms of holistic face processing. Neuroimaging studies on neural substrates of the two effects may provide new insights to understand the behavior dissociations in literature. Unfortunately, to our knowledge, there is no study that directly compares the neural basis of these two effects. There are several studies focusing on the neural correlates of the CFE. Two ERPs studies have shown the CFE reflected by the face-specific N170 component, which was more evident in the right hemisphere (Jacques and Rossion, 2009; Letourneau and Mitchell, 2008). Two fMRI adaptation studies found a release from adaptation effect for the composite faces with same top halves and different bottom halves. That is, even when the top halves of the two composite faces were the same, they looked different due to the interference of different bottom halves in the aligned condition, but not the misaligned condition (Schiltz et al., 2010; Schiltz and Rossion, 2006). This pattern of result was only found in the right fusiform face area (FFA) with an event-related design (Schiltz et al., 2010), but observed in both the FFA and occipital face area (OFA) with a block-design (Schiltz and Rossion, 2006). Additionally, transcranial direct-current stimulation (tDCS) on the OFA reduced the CFE in one study (Yang et al., 2014), but had no effect on the CFE in another study (Renzi et al., 2015). In short, neuroimaging studies have revealed the neural correlates of the CFE in face-selective regions, most reliably in the right FFA.

In the present study, we investigated whether the WPE and CFE involved shared or distinct neural substrates with individual differences approach, which identify brain response that contribute to individual differences in holistic face processing. One possibility is that the behavioral dissociations of the WPE and CFE arise from general cognitive factors and these two effects reflect similar mechanisms of holistic face processing. This hypothesis predicts that the two effects involve shared neural correlates in face-selective regions. Alternatively, it is possible that holistic face processing is not a unitary construct and the two measures tap different cognitive mechanisms of holistic face processing. This hypothesis predicts distinct neural correlates of the WPE and CFE in face-selective regions.

First, we used the whole-part task and the composite-face task to measure the WPE and CFE in a large sample of participants (N = 200). Then, we measured participants' face selectivity (i.e., response contrast of faces versus objects) when they viewed faces and non-face objects in fMRI scanner. Given that previous studies have demonstrated face