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The Many Faces of Neurocognitive Development:

Behavior and Neurocorrelates of Holistic Face Processing

A dissertation submitted in partial satisfaction of the

Requirements for the degree of Doctor of Philosophy

in

Cognitive Science

by

Silvia Paparello

Committee in charge:

Professor Joan Stiles, Chair
Professor Andrea Chiba
Professor Jeff Elman
Professor Frank Haist
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2007

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The Dissertation of Silvia Paparello is approved, and it is acceptable in quality and form for publication on microfilm:

Chair

University of California, San Diego

2007

To my grandfather and my grandmother, who had to drop out of school after third and fifth grade to work in the fields. To my mother who wanted to go to college, but decided instead to have a daughter. To my husband who believes that graduate school should end at a Master level.

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Organization for Human Brain Mapping
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Tethys Research Institute
Ocean Conservation Society

ABSTRACT OF THE DISSERTATION

The Many Faces of Neurocognitive Development:

Behavior and Neurocorrelates of Holistic Face Processing

by

Silvia Paparello

Doctor of Philosophy in Cognitive Science

University of California, San Diego, 2007

Professor Joan Stiles, Chair

Faces are central stimuli in our everyday life, hence, face processing is a sophisticated and highly specialized cognitive ability, at which adults are experts and children are proficient. Unlike other visuospatial abilities, face perception develops very slowly, becoming adult-like only well into adolescence. Some performance disparities between children and adults may reflect differences in general cognitive abilities, such as attention and memory. Alternatively, performance differences can be attributed to specific cognitive strategies implemented during face processing by different age groups; or to the interaction between the improvement of general abilities throughout development and the refinement of face specific cognitive strategies. The intent of the current studies was to further assess the development of and relationship between

cognitive strategies in face processing. Specifically, we investigated the behavior and neurocorrelates associated with holistic face processing in children (8- to 11-year-olds), adolescents, and adults, utilizing the composite face effect. The task requires participants to engage in both holistic and featural processing, but certain trials (aligned-same) elicit a visual illusion called the composite face effect (CFE, calculated as difference between misaligned-same and aligned-same trials), which is considered an index of holistic processing.

All age groups (adults, adolescents, 8- to 9-year-olds, 10- to 11-year-olds) showed a CFE, suggesting reliance on holistic processing. Notably, about half of the 8- to 11-year-old children displayed adult-like behavior and adult-like CFE, suggesting their reliance on holistic processing. However, the other half of the children performed below-chance on aligned-same trials, displayed an extremely large CFE, and a significant difference between different trials, suggesting reliance on a featural strategy. Thus child age groups were regrouped according to their accuracy performance on the hardest condition (aligned-same trials) into high performing and low performing children. We hypothesize that the aligned-same trials were too taxing for low-performing children, thus they fell back into relying on simpler strategies such as a difference-detection featural strategy.

In order to further investigate the CFE behavioral differences between age and performance groups, we completed an imaging study. For the fMRI study children were grouped by performance rather than age following the results of our behavioral study. Overall, our imaging results for the CFE, thus for holistic processing, resembled behavioral results in that adult and high performing child groups revealed a similar (but not identical) whole-brain pattern of activation, whereas the low performing child group showed a distinctive pattern of activation for the composite face effect. Adults and high

performing children showed a pattern of activation spanning frontal, parietal, temporal, and occipital lobes. In contrast, low performing children revealed a pattern of activation that spanned frontal, temporal, cingulate, and cerebellar regions. Brain areas typically associated with face processing, such as the right fusiform gyrus and right inferior temporal gyrus did not reach significance for the low performing child group. These differences may be attributable to the use of different cognitive strategies. However, the extent of frontal and cingulate cortex activation in low performing children may also suggest that because the task was especially difficult for them, working memory resources were particularly taxed, thus affecting the neural network engaged. Importantly, not only were performance differences associated with distinct neurocorrelates (i.e., differing profiles for low performing children vs. high performing children and adults), but age differences also had an appreciable effect. In fact, high performing children did not significantly differ from adults in the behavioral CFE, but did show differences in the neural CFE.

CHAPTER 1

GENERAL BACKGROUND

Distinctiveness of Faces and Definitions of Face/Object Cognitive Strategies

Faces are very important visual stimuli in our everyday life and their distinctiveness, compared to other visual complex stimuli, has motivated many research studies and theoretical debates. Notably, face processing is a sophisticated and highly specialized cognitive ability, with which typical adults are experts and children are proficient. Recently, imaging studies were able to map face sensitive brain areas, which were more active while participants viewed faces compared to objects (Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997). Moreover, newborn infants (tested shortly after birth) preferentially oriented and looked longer at face-like stimuli compared to non-face-like patterns (i.e., S. Johnson, Slaughter, & Carey, 1998; Simion, Valenza, Umilta', & Barba, 1998; Valentine, 1991). Some researchers interpreted these different lines of evidence as support for the hypothesis that faces constitute a special class of stimuli and that they are processed differently compared to other categories of complex visual stimuli (Spiridon, Fischl, & Kanwisher, 2006; J. W. Tanaka & Farah, 1993). Alternatively, other researchers have argued against faces being intrinsically special stimuli (Diamond & Carey, 1986; I. Gauthier, Skudlarski, Gore, & Anderson, 2000; Rhodes, 1993; Turati, 2004). Diamond and Carey (1986) were able to show inversion effect (described in next section) for non-face stimuli, specifically, pictures of dogs elicited inversion effect in dog experts, but not in participants whom were not dog experts (but see G. Yovel & Kanwisher, 2005). This experimental evidence, together with much more from the imaging literature, suggest that when encoding over-learned objects categories, like faces or dogs (for a dog expert), we predominantly rely on *configural cognitive strategies*, whereas we most often rely on featural cognitive strategies for general classes of objects. What is special is not the stimulus but the *cognitive strategies* used to process the stimulus itself (I. Gauthier, Skudlarski et al.,

2000; I. Gauthier & Tarr, 1997; Maurer, Grand, & Mondloch, 2002; C. A. Nelson, 2003). Although there is extensive literature on face processing in adults, which suggest that adults mostly rely on configural strategies during face processing, the terminology and the definitions used are not always consistent across the field. Moreover, some of the ongoing debates in the literature gave important contributions to our knowledge of cognitive strategies, but the main research questions of these studies did not directly investigated differences between configural and featural processing. One debate is often referred to as the Expertise Theory, for which faces appear to be special stimuli because the great expertise level we acquired in processing and most importantly identifying individual faces (e.g., Gauthier et al., 2000, Carey and Diamond, 1986). Alternatively, we usually do not need to discriminate, for example, among large number of daisies, thus we are not daisy experts and daisies are not special stimuli in to us. Another important debate is about the face specificity of the FFA (discussed later), an area of the fusiform gyrus which is activated with more intensity by faces compared to other objects (e.g., Kanwisher et al., 1997), but which does not seem to be affected by cognitive strategies (Kanwisher and Yovel, 2004; Maurer et al., 2007; but see Schiltz and Rossion, 2006). Thus for clarity sake, the next paragraph will briefly summarize the most accepted definitions in the field.

In general, there are two main cognitive strategies engaged during visual processing of faces and objects (for a review, see Maurer et al., 2002). Part processing also called *featural-processing* arises when we encode an object or a face and we do so by isolating its featural elements. Alternatively, whole processing, or *configural-processing* arises when we process the spatial relationships within an object/face. Most researchers agree that configural strategies are particularly important for face processing and some of the open debates in the field concern the specific nature of

configural processing. Furthermore, there are three different aspects or types of configural processing (a) *sensitivity to first-order relations*, which are basic topological relations such as above/below or left/right. First-order relations in faces refer to the arrangement of the eyes above and the mouth below the nose. They are also present in object stimuli. (b) *Holistic processing strategies*, which capture the indivisible whole, or gestalt, of a stimulus; (c) *sensitivity to second-order relations*, specify the particular relationships among features. For faces this involves processing the spatial distances and spatial relationships between face features (the eyes, nose, and mouth) and between features and face contours (Maurer et al., 2002; Peterson & Rhodes, 2003). It is critical to note that adults rely on all of above strategies to process faces, including featural strategies. However, configural strategies, and in particular on the sensitivity to second order relations, are most critical for face processing (Diamond & Carey, 1986; Freire, Lee, & Symons, 2000; Maurer et al., 2002; C. A. Nelson, 2003; Rhodes, 1993; Sergent, 1984; J. W. Tanaka & Sengco, 1997).

Face Processing in Adults

Most researchers acknowledge the coexistence of both featural and configural strategies during face processing, but the debate continues over the specific strategies used and on the degree at which they interact with each other. Among current theories of adult face processing, there is little support for a predominance of featural-based hypothesis which asserts that faces are perceived simply as the sum of their features, and thus construed as nothing but the joining of its isolated facial features (Garner, 1978; Penry, 1971, reviewed in Rakover, 2002). The few studies that support featural hypotheses usually utilize face reconstruction and identikit methodologies. Penry (1971), who invented the photo-fit identikit technology (commonly used by police and security services) defends the featural hypotheses, but also acknowledges that configural

processing plays some part in face processing. Alternatively, norm-based hypotheses state that facial information, both featural and configural, is represented and stored in the cognitive system as an abstract prototype. One difficulty with this hypothesis is that the prototype (or norm) can differ from an actual perceived face in both featural or configural information, which are essential for face encoding (Pullan & Rhodes, 1996; Rhodes, Carey, Byatt, & Proffitt, 1998; Valentine, 1991; Valentine & Ferrara, 1991). Finally, many lines of evidence support and highlight the configural hypothesis, which states that we process faces using both featural and configural information, but the whole face is more accessible in memory than its parts and configural information is overall more important than featural information (Farah, Tanaka, & Drain, 1995; J. W. Tanaka & Sengco, 1997).

According to Hole and colleagues (1999) perhaps the clearest demonstration in upright faces of configural processing, more specifically of holistic processing, is given by the *composite face effect*, which was first reported by Young and colleagues (1987). In a typical composite face task, participants are presented with pairs of face stimuli and asked whether the top halves of the faces matched; importantly, the bottom half of the faces in these tasks always differ. In a typical composite face task, two types of trials, composite face trials and "misaligned" face trials are presented. Composite face stimuli are created by conjoining the top and the bottom halves of the faces of different individuals, creating the illusion of a new face configuration (a new individual). The misaligned face stimuli are also composed of the top and bottom halves of two different faces, but the two halves are laterally offset, thus breaking up the strong configural cues of the composite face stimuli. Adults are slower and less accurate in judging the top halves of a composite faces compared to the misaligned faces (see Figure 2.1). This robust effect demonstrates that it is extremely challenging to ignore only part of the features within the configuration of faces, suggesting that spatial relational information,

and not featural information, are dominant during upright face processing (Carey & Diamond, 1994; Hole, 1994; Hole et al., 1999; A. W. Young et al., 1987). When composite faces are inverted the judgment of composite faces is faster and more accurate than in the upright condition. The illusion of a new configuration is reduced, reaffirming the hypothesis that spatial relational information are disrupted during inverted faces processing, and featural processing becomes the prevailing cognitive strategy (Carey & Diamond, 1994; Hole, 1994; Hole et al., 1999; A. W. Young et al., 1987).

Tanaka and Farah (1993) designed and ran another very clever task to investigate holistic processing, in which the holistic bias is measured by the so-called *part-whole effect*. Participants have to recognize a single feature (e.g., the nose) of a particular individual (e.g., Bob) and they are typically faster and more accurate in recognizing the specific nose within the context of the face (even just the face contour) compared to the same nose in isolation. Therefore, these results seem to suggest that we store in memory holistic representations of faces, that is, the whole face and not the individual features (J. W. Tanaka & Farah, 1993; J. W. Tanaka & Sengco, 1997).

Some of the most widely cited evidence in support of configural hypotheses of face processing derives from studies that use *whole face inversion* methodologies. The inversion effect refers to the well-documented advantage in encoding upright faces versus inverted ones (Leder, Candrian, Huber, & Bruce, 2001; for reviews, see Rakover, 1999; Rhodes, 1993; Searcy & Bartlett, 1996; Sergent, 1984; Valentine, 1988; Yin, 1969). Typically, adult participants are slower and less accurate processing inverted faces compared to upright faces. Other object categories are not affected by inversion (e.g., Michael J. Tarr & Pinker, 1989 but see Diamond, 1986 and Gauthier et al., 2000). In addition, face-specific effects are known to be biased by holistic processing. For example, the part-whole effect (J. W. Tanaka & Farah, 1993), and the composite face

effect (A. W. Young et al., 1987), do not occur if the stimuli are upside down. Therefore, the inversion effect is considered to be an important piece of evidence demonstrating that upright faces are primarily processed holistically, whereas inverted faces are primarily processed featurally, similar to objects (Leder et al., 2001; Sergent, 1984; Yin, 1969). It is interesting to note that until recently, the most widely accepted explanation of the inversion effect was that it differentially affected the encoding of featural versus second order relations. Inversion was thought to interfere with perception of both the face configuration and with the spatial relations among the features that constitute a face, without substantially altering the perception of single features (Freire et al., 2000; Catherine J. Mondloch, Le Grand, & Maurer, 2002; Catherine J. Mondloch et al., 1999; Rhodes, 1993; Sergent, 1984; Valentine, 1988). Most of the evidence came from studies that manipulated features and spatial relations among them, within the same individual face (e.g., Jane) in both upright and inverted presentation (Freire et al., 2000; Maurer, Mondloch, & Lewis, 2007; Catherine J. Mondloch et al., 2002; C. J. Mondloch, Leis, & Maurer, 2006). When the stimuli are inverted, a larger inversion effect is found for the configural compared to the featural set, corroborating the hypothesis that second order relation information is disrupted to a greater degree by inversion than featural information (Freire et al., 2000; Richard Le Grand, Mondloch, Maurer, & Brent, 2001; Catherine J. Mondloch, Dobson, Parsons, & Maurer, 2004; Catherine J. Mondloch et al., 2002). However, Yovel and Kanwisher (2004) equated the difficulty level of featural and configural upright sets, typically the configural set is more difficult to match than the featural set, and this manipulation removed the inversion effect disparity between the two sets of faces, showing that featural and second order relations are equally impacted by inversion (Malcolm, Leung, & Barton, 2004; Riesenhuber, Jarudi, Gilad, & Sinha, 2004; Galit Yovel & Duchaine, 2006; G. Yovel & Kanwisher, 2004)

Yovel and Kanwisher (2004) suggested that holistic information is probably responsible for the inversion effect, in line with results from the composite face effect and part-whole effect, however, their task did not directly manipulate holistic information.

Face Processing Models: Interest on Infancy

One of the main controversies in this field focuses around the nature-nurture debate, specifically over the possibility that we are born with a specific mechanism to process faces. As a result, studies of newborns, who have no or very limited experience with faces, have become crucial to explaining how the functional and anatomical specialization of face processing emerges (Turati, Valenza, Leo, & Simion, 2005). Currently, there are three main hypotheses on how face processing emerges: (1) with an *experience-independent* mechanism, (2) by an *experience-expectant* process and (3) with an *experience-dependent* mechanism. Farah and colleagues (2000) proposed that face processing is based on an *experience-independent* mechanism, thus it is an ability that does not require experience with the actual stimuli in order to emerge and for which the anatomical localization is "explicitly specified in the genome". These strong statements were mainly based on a case study of a child who suffered lesions bilaterally in the ventral occipito-temporal cortex at one-day old. The child behavior matched typical adult prosopagnosic profile. He was greatly impaired in recognizing faces, whereas his object processing was somewhat spared (Farah, 2000). Slater and Quinn (2001) also support a nativist point of view suggesting that infants already possess a face prototype at birth. Their conclusions were based on results that indicated that 3-day-old infants showed preferences for attractive faces, because these were more similar to infants' face prototypes than the unattractive faces (Slater et al., 2000; Slater et al., 1998).

A second approach views face-processing specialization as an *experience-expectant* process, for which we have an innate and specific neural substrate that if

exposed to face stimuli during a critical time window will, as expected, develop and specialize for efficient face processing (M. de Haan, Johnson, & Halit, 2003; Scania de Schonen & Mathivet, 1989; Mark H. Johnson & Morton, 1991). Johnson and Morton (1991) tested newborns within their first minutes of life and found that they oriented more often toward face-like stimuli compared to controls; their findings were corroborated by other research groups (Deruelle & de Schonen, 1998; Mark H. Johnson & Morton, 1991; Maurer, 1983; Valenza, Simion, Cassia, & Umilta`, 1996). Johnson and Morton (1991) hypothesized that at birth a subcortical network (superior colliculus and pulvinar) functions as a "primitive kick-start mechanism" which bias the system in order to orient to faces, thus making sure that the "developing cortical circuits are preferentially exposed to faces. In other words, it serves to guide subsequent learning" (Mark H. Johnson & Morton, 1991). After 6-8 weeks from birth and active interactions with the environment, pathways in the infant ventral occipito-temporal cortex replace the subcortical system and they start learning specifically about faces. With time and experience this broad cortical area becomes more specialized and localized, eventually primarily comprising the middle fusiform gyrus (specifically a functionally localized part of it, called fusiform face area, FFA, by Kanwisher et al., 1997); this transition reflects a starting point for a more adult-like behavior toward faces (Mark H. Johnson & Morton, 1991). De Schonen and Mathivet (1989) proposed a similar model, but they highlighted the important role of the right hemisphere in face processing. They suggested that during the first year of life two different systems in the two hemispheres develop almost concurrently. The right hemisphere specializes in processing configural information (as in adults) and the left hemisphere processes local (or featural) information (Deruelle & de Schonen, 1998).

As an alternative to theories that hypothesize an innate mechanism, a number of investigators have proposed an *experience-dependent* model of the development of face

processing. By this view, the daily extensive and prolonged experience that people have with human faces is sufficient to explain the degree of specialization of this process (Diamond & Carey, 1986; I. I. Gauthier, 2000; C. A. Nelson, 2003; Turati, 2004). Chiara Turati (2004) challenged Mark H. Johnson's model (2000) stating that "nonspecific constrains of visual processing might be sufficient to trigger the emergence of the functional specialization for faces observed later in development". A series of studies designed at the University of Padua, Italy, suggested that newborns show preference for domain-general structural properties that are prevalent in faces, but that can be also shared by non-face-like geometrical stimuli (Cassia, Simion, Milani, & Umilta` 2002; Simion, Valenza, Cassia, Turati, & Umilta`, 2002). Infants are mostly attracted by two perceptual properties, which are shared by most visual stimuli, including faces. First, infants attend more to patterning in the upper part of the configuration than in the lower part. Second, they are attracted to congruency in the spatial relations between the inner features and the outer contour (e.g., most features located in the widest portion of the configuration). Newborns tested at 3-days-old preferred to look at stimuli with more elements in the upper half (Simion et al., 2002). This finding did not depend on the type of stimuli and was observed for both face-like and non face patterns. By 3-months, they no longer showed this preference with non-face stimuli, but they did with face stimuli (Turati et al., 2005). These data suggest that newborns do not seem to have a face-specific bias, but with experience, infants begin to show a face-specific preference as evidence by the data from 3-month-olds (Turati et al., 2005).

Some of the most substantial evidence on how face processing develops during infancy comes from studies that measured scalp-recorded brain electrical potentials (event-related potentials, ERPs). Adult ERP studies have been instrumental in characterizing how we process faces. In particular, faces elicit a negative potential

(N170) over occipital-temporal areas, which peaks between 140 and 170 ms after stimulus onset. Importantly, the N170 has larger amplitude and shorter latency to faces compared to objects and other stimuli (Bentin, Allison, Puce, Perez, & et al., 1996). Moreover, N170 is associated with encoding the whole configuration of facial features. In fact, it is delayed and enhanced when viewing inverted faces and it has higher amplitude over the right hemisphere (Bentin et al., 1996; Rossion et al., 2000). Taylor and colleagues (2001) observed components that responded to faces similarly to the N170 across childhood; however, N170 proper does not fully develop until adulthood. During infancy, a positive component, called P400, is considered (together with N290) to be a precursor of the N170 component observed in adults (Bhatt, Bertin, Hayden, & Reed, 2005; M. de Haan et al., 2003). The P400's latency peaks approximately between 450 and 390 ms (decreasing with age) over posterior and lateral (more medial for 3-month-olds and more lateral for 12-month-olds) electrodes. Moreover, infants (by 3 month-olds) displayed a positive slow wave (beginning at about 800ms after stimulus onset) over the right hemisphere while viewing upright faces, whereas they displayed it bilaterally viewing toys (M. de Haan et al., 2003; Charles A. Nelson & Collins, 1991). Also similarly to adults, infants (3-12-month-olds) show sensitivity to face inversion. Their P400 peaked more quickly for upright compared to inverted faces (M. de Haan et al., 2003; Michelle de Haan, Pascalis, & Johnson, 2002). The inversion effect is considered by most as an indicator of configural processing during face encoding, together with another effect called the "Thatcher illusion", which elicits holistic processing in a very similar manner. The Thatcher illusion is a phenomenon for which eyes and mouth are inverted in an upright face, creating a grotesque look, but when the entire face is inverted, the viewer does not immediately perceive that the features are in a different orientation (L. A. Thompson, Madrid, Westbrook, & Johnston, 2001; P. Thompson,

1980). The effect seems not to affect featural and first-order-relational processing, but disrupts second-order-relational processing (Bartlett & Searcy, 1993; Carbon & Leder, 2005; Hayden, Bhatt, Reed, Corbly, & Joseph, 2007; Lewis & Johnston, 1997; L. A. Thompson et al., 2001). Bentin and Bhatt (2004) showed that, like adults, 6-month-old infants are sensitive to the Thatcher illusion.

Alternatively, ERP studies also brought to light important differences on how infants and adults process faces. For example, Bushnell and colleagues (1989) impressively showed that newborns as young as 3-day-old are able to discriminate their mother from a stranger, but (unlike adults) they mostly rely on the single feature of their mother's hairline (Olivier Pascalis, de Schonen, Morton, Deruelle, & et al., 1995). Pascalis and colleagues (1995) showed that, in this particular task, infants become more adult-like only after 6-month-old, when they are able to recognize their mother's face even if a scarf is covering the hairline. An interesting cross-species study showed that adults are much better in discriminating human than monkey faces, suggesting species-specific expertise in face processing (Olivier Pascalis, Petit, Kim, & Campbell, 1999). Even more remarkably, six-month-old infants are better than adults in discriminating monkey faces, and perform equally well on monkey and human face discrimination trials, suggesting that the young infants are not yet specialized in processing human faces. Only by 9-months, the performance of infants does not differ from adults (Oliver Pascalis, de Haan, & Nelson, 2002).

Not all investigators agree that the observed changes are specific to faces. For example, Leslie Cohen and Cara Cashon (2001) explained these developmental transitions as *common sequences* in development, not only for face processing, but also for any type of information processing (similar transitions reoccur in different forms and different domains throughout development). For example, in a task where infants were

processing line drawings of imaginary animals, 4-month-olds processed the animals as a collection of individual features, whereas 7-month-olds were able to process the relations among the features (Younger & Cohen, 1986). Interestingly, when the task was made more difficult (incrementing the number of features in each animal), 7-month-olds fell back at the performance level of the younger infants, whereas 10-month-olds could perform well even with an additional level of added difficulty (a categorization problem). In face processing, 7-months-old (depending on the specific task and on the measure used) infants go through one of their several developmental transitions. Specifically, they stop processing features independently and start integrating features into higher order units, thus processing the spatial relations among them (Cashon & Cohen, 2004). In situations in which the system becomes overloaded, for example when complexity is added to the stimuli, it is also common to fall back to a lower level of processing. In the case of faces, for example, infants might fall back to process independent features before being able to reorganize the new more complex information into a higher level of analysis (Cohen & Cashon, 2001).

The Development of Face Processing: Behavior during Childhood and Adolescence

The research focus on infant and adult face processing has left a gap in the literature. Specifically, there is paucity of studies on school-age-children and adolescents and, not surprisingly, this lack of data has led to a number of open debates. One of the main controversies in the field concerns the nature (qualitative or quantitative) and duration of the period of developmental change in face processing. It includes questions about both the actual timing of development and the specific cognitive strategies employed at different ages. In one early formulation, Carey and Diamond (1977) proposed a developmental shift in processing strategies, from reliance on featural information to greater and greater reliance on configural information

beginning at approximately 10 years of age. However, later research ruled out this strategy switch (Carey & Diamond, 1994; Freire & Lee, 2001; J. W. Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998). Freire and Lee (2001) showed that 4- to 7-year-olds performed poorly, although better than chance level, when asked to detect a target face presented among distractor stimuli, which differed only in the spacing among its features (second order relational information). By contrast, children accuracy was higher when the distractors differed from the target in the shape of the individual features only. These finding suggest that while preschool-age children are capable of configural processing, they rely more on featural processing when encoding faces (Freire & Lee, 2001). Mondloch and colleagues (2004) tested 8-year-olds on a similar task (called the Janes Task) in which, in order to isolate the different cognitive strategies without confounding among them; they manipulated the stimuli in six different conditions. In the main task manipulations, features, spacing and outer contour of a baseline face (referred to as “Jane”) were altered. Results showed that 8-year-old children were comparable to adults in the featural conditions, almost as good as adults in the contour conditions and much worse in the spacing (configural) conditions (Catherine J. Mondloch et al., 2004 but see Yovel G, and Kanwisher, N., 2004 for different results with adults). Hay and Cox (2000) reported slightly different results and cognitive shift in the early school years. They compared 6- and 9-year-old children during a recognition task of whole faces versus parts of them (e.g., eyes, chin, nose). Results showed that 9-year-olds were better at recognizing whole faces and were sensitive to the inversion effect, while 6-year-olds did not show any inversion effect and were better at recognize the eye regions than the older participants (Hay & Cox, 2000). Carey and Diamond’s (1994) later work, using the composite face task, suggested that there is clearly an interaction between featural and configural processing (specifically holistic) of faces throughout development. From a

very early age, children are capable of at least rudimentary featural and configural processing, but through the preschool and school age period, children's processing of relational information becomes more fully articulated and their face processing more expert, more adult-like (Carey & Diamond, 1994). More recently, Mondloch and colleagues (2007) replicated this finding using the composite face task with 6-year-old children (with unfamiliar faces). De Heering and colleagues (2007) also employed the composite face task to study holistic processing in children. They found that even 4-to 5-year-old children were sensitive to the CFE, thus sensitive to holistic information. However, their composite face task had to be modified from the traditional version in order to be reliably performed by younger children.

Alternatively, Gudrun Schwarzer (2000; Schwarzer & Roebers, 2002) tested young children on a face categorization task, in which participants had to decide if faces (and non face-like stimuli) were similar to each other holistically (in overall similarity) or analytically (by a single element). Adults processed most of the upright faces holistically and most of the inverted faces analytically (as all the children did), whereas children (2- to 10-year-olds) categorized upright faces analytically. The young children barely used holistic categorization at all. Only 10-year-old children started using holistic strategy, but still much less often than the analytic one when categorizing faces (Schwarzer, 2000; Schwarzer & Roebers, 2002). These data are particularly interesting because they highlight a big difference in performance and in the use of cognitive information between adults and children (as old as 10 years of age) in a face processing using categorization, which is a highly complex cognitive skill very difficult to master. In studies in which simpler tasks are used (i.e., difference matching, recognition) children as young as 4 years old are able to use some level of configural/holistic information. Thus it is likely that the 8-year-olds in Freire and Lee's (2001) would also engage in both configural and

featural processing on a simple matching task. Importantly they appear to fall back to reliance on featural information in a task with more difficult tasks or stimuli (Schwarzer, 2000; Schwarzer & Roebers, 2002).

This flourishing of developmental studies has improved our knowledge of how face processing and visual pattern processing emerge. However, no single account has yet been able to capture all of the extant data. The principle unanswered question centers on defining the degree to which face processing relies on configural and/or featural information at different points in development. Some researchers believe that while young children process visual patterns configurally, they are more reliant than adults on featural processing. This dependence on featural processing makes children less efficient processors of facial information than adults in that it is not until they begin to rely predominantly on configural strategies that their face processing skills change qualitatively, leading them to become face expert in early adulthood (Carey, 1996; Carey & Diamond, 1994; Freire & Lee, 2001; Richard Le Grand et al., 2001; J. W. Tanaka & Sengco, 1997). By contrast, some researchers suggest that both configural and featural strategies slowly develop from infancy into adolescence in a quantitative fashion, and that the degree of reliance on one or the other strategy depends on the specific task and on the methodology used to test it (Roxane J. Itier & Margot J. Taylor, 2004; Margot J. Taylor, McCarthy, Saliba, & Degiovanni, 1999). In addition, some researchers disagree about the importance given to configural and featural processes in face processing, and believe that face stimuli themselves are special, or in other cases that the type of representation stored in our memory determines how a face is processed. Unfortunately they usually do not consider or explain how these special skills develop, thus they cannot be active players in the developmental debates (McKone & Boyer, 2006; Valentine & Ferrara, 1991; G. Yovel & Kanwisher, 2004, 2005).

As Leslie Cohen very elegantly explained emerging infant skills using information-processing theory as a framework, we can explain child face processing using a general *visuospatial analysis model*. Visuospatial analysis is defined as the process through which we analyze spatial pattern information, which is a major function of the ventral visual pathway in the brain (Akshoomoff & Stiles, 1995). Visuospatial analysis involves: 1) identification of the constituent parts of a spatial pattern and, 2) integration of those parts into a coherent whole or configuration. A fundamental aspect of visuospatial analysis is that it is organized in different levels from a more local to a more global organization (Natacha A. Akshoomoff & Stiles, 1995; Delis, Robertson, & Efron, 1986; Stiles, 2001). For example, given a face, its whole configuration is also the face's most global level, which comprises all its parts including more local levels like the eyes or other features within the face. In order to successfully process our visual-spatial environment we need to be able to both segment a visual pattern into constituent parts and to integrate those parts into a coherent configuration.

Young babies and children are indeed capable of spatial analysis processing, but they systematically differ from adults depending on their age and on the complexity of the stimulus and task. Young children tend to parse out simpler and more spatially independent parts than older children, and they combine those parts using simpler sets of relations than older children (Stiles & Tada, 1996). Three-year-old children can reproduce in drawing a simple plus sign, but they do so drawing four independent lines that meet at a center point, only by about age four they start drawing two intersecting lines, as older children and adults do (Natacha A. Akshoomoff & Stiles, 1995). Furthermore, complexity of the spatial pattern affects spatial analysis ability. For example, an "X" sign is more difficult to reproduce than a plus sign because its oblique lines, thus a typical 4-year-old can correctly reproduce a plus sign, but cannot replicate

the “X” sign. Predictably, young children tend to draw 4 independent lines or to intersect two lines in the wrong orientation resembling a plus sign instead of reproducing an ”X” sign (Natacha A. Akshoomoff & Stiles, 1995).

Thus, it is not surprising that infants and children are able to perceive and identify faces (highly complex stimuli), but they do not process them as efficiently as adults until the end of adolescence. Applying the spatial analysis model, it is possible that young children are able to process featural changes similarly to adults, but they are not as efficient as adults in processing configural changes, especially in cases in which the task is particularly challenging. During difficult tasks, they rely more on simple feature matching strategies, which represents an earlier developmental stage compared to configural strategies. Thus, the development of face processing and its cognitive strategies do not follow a simple linear developmental curve. A child relies on featural or configural strategies differentially in different situations, depending on his/her individual developmental age and on the complexity and difficulty of the specific tasks. However, not everybody in the field agrees with this theoretical model and more evidences specific to faces needs to be collected in order to support the different hypotheses.

Neural Basis of Face Processing: Brain Pathways (Inferior Temporal Cortex Inputs and Outputs)

Charles Gross (1969; Gross, Rocha-Miranda, & Bender, 1972) first reported the existence of face neurons, which fired action potentials two to ten times more often to faces than to simple geometrical stimuli or three-dimensional objects (Caan, Perrett, & Rolls, 1984; Logothetis, 2000; Perrett, Hietanen, Oram, & Benson, 1992). Specific face neurons are often selective for a particular head or view orientation; however they also maintain strong invariance responding to faces with different positions, orientations, translation degrees, color, size and illumination (Caan et al., 1984; Perrett et al., 1992).

Their response is instead weakened by vertical inversion (Perrett et al., 1992). Predominantly in the inferior temporal cortex (IT), clusters of neurons respond to specific features or partial features of a face (or of an object). Interestingly, clusters that code for the same feature are organized in columns and neighboring columns respond to similar and partially overlapping features, creating a remarkable system in which face or object features are represented by multiple cells organized in columns with overlapping selectivity (J. W. Tanaka & Sengco, 1997). Furthermore, face neurons encode holistic information; in fact the whole face configuration is critical for the neuron to fire action potentials (Logothetis, 2000). Therefore, face neurons are remarkably sensitive to changes in facial configuration, they respond to combinations of distances between facial features such as eyes, mouth, eyebrows and hair (M. P. Young & Yamane, 1992). Their response diminishes significantly if facial features are reduced or if their spatial relationship is changed (M. Tanaka, Weber, & Creutzfeldt, 1986; M. P. Young & Yamane, 1992)

Face neurons were first found in the inferior temporal cortex (IT), but they are actually distributed in different brain areas, mostly along the ventral visual pathway, the brain pathway for object and face perception and recognition (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). The ventral visual pathway starts at the retina from which ganglion cells project to the lateral geniculate nucleus of the thalamus and reach primary visual cortex (V1). From V1 the visual input is transmitted to visual areas V2 and V4 and ventrally to the posterior and anterior regions of IT. There are also redundant projections that go directly from V2 to posterior IT and from V4 to anterior IT (J. W. Tanaka & Sengco, 1997). Not only lesions of IT disrupt object and face recognition, but so do complete lesions of the intermediate stages along this pathway (Yaginuma et al., 1993)

Even if conventionally IT is considered to be the end of the ventral visual pathway, the visual input is projected and further processed in other (higher-order) areas. Important projections go from IT to the perirhinal cortex (Brodmann's areas 35 and 36). There, a representation of the object is reconstructed from the visual input, integrating and associating images from similar objects stored in memory, and most likely seen before under different conditions (i.e., orientation, size, illumination etc.). In fact, different types of information about the object or face are recovered from different brain areas. Projections from IT to the amygdala elicit emotional information. Projections to the prefrontal cortex associate behavioral significance to the object or face, and projections from IT to (and from) the parietal cortex give important information to locate and manipulate the object in view (Logothetis, 2000).

In addition, the advent and increasing availability of functional magnetic resonance imaging (fMRI) techniques have made possible to closely map specific-stimulus responses in the human ventral pathway (e.g., I. Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Haxby, Hoffman et al., 2000; Kanwisher et al., 1997). Kanwisher and colleagues (1997) were among the first to consider a particular area of the ventral pathway to be specifically selective for faces. In fact, they named an area in the fusiform gyrus the "fusiform face area" (FFA), defined as the area in the mid-fusiform gyrus that was significantly more active for faces than objects (about twice as active). Similarly, they defined a region in the parahippocampal gyrus that was significantly more active for scenes than objects and named it the parahippocampal place area (PPA) (Kanwisher et al., 1997; Spiridon et al., 2006). In the past decade a large number of studies and laboratories have corroborated and extended these finding, interestingly, most researchers agree on the localization and the selectivity of the FFA, but do not agree on the nature of its function (face specific vs. category selective) (i.e., Haxby,

Hoffman et al., 2000; Kanwisher et al., 1997; Sergent & Signoret, 1992; Spiridon et al., 2006).

More recently, the debate has moved back into investigating the network (not just one single region) of areas particularly important for face processing (Haxby, Hoffman et al., 2000; Ishai, in press; Rossion, in press). The inferior occipital gyrus (also called the occipital face area, OFA) seems to provide an essential input to the FFA, in particular computing the more fine grained features of a face (Halgren et al., 1999; Haxby, Hoffman et al., 2000; Rossion et al., 2003). As reviewed by Ishai (in press), the face processing network expands beyond the FFA and OFA. In fact, few other areas seem to have direct and probably reciprocal connection with the FFA. Among them are the superior temporal sulcus (STS) associated with gaze direction and speech related movements (e.g., Pageler et al., 2003), the amygdala and insula associated with social and emotional cues (e.g., Ishai, in press), the inferior frontal gyrus associated with attention, working memory and semantic information (e.g., Haxby, Petit, Ungerleider, & Courtney, 2000), and the orbitofrontal cortex and nucleus accumbens and temporal pole (e.g., Rossion, in press).

Neural Basis of Face Processing in Adults

The debate over the cognitive quality and distinctiveness of face processing escalated when new brain imaging techniques brought clear evidence in support of the hypotheses that specific brain areas are selectively active during face processing (Haxby, Hoffman et al., 2000; Sergent & Signoret, 1992). Kanwisher and colleagues (1997) showed that the right fusiform gyrus is more active for faces than other objects, and they termed this region the Fusiform Face Area (FFA). However, Gauthier and colleagues challenged the face module hypothesis. In a series of category-level/expertise studies they showed that the so-called face area was engaged for a

range of non-face objects if the participant was an expert in processing these other classes of stimuli (I. Gauthier & Tarr, 1997; I. Gauthier, Tarr et al., 2000; M. J. Tarr & Gauthier, 2000). According to Gauthier and her colleagues, the FFA is the optimal neural substrate to process highly familiar and homogenous object categories, which are processed at the subordinate level of analysis in the in the fusiform gyrus (I. Gauthier & Tarr, 1997; I. Gauthier, Tarr et al., 2000). Gauthier's group tested this hypothesis investigating effects of basic category level (e.g., table) and subordinate category level (e.g., school-desk, which is a sub-category of table) on non-face object processing. Seven out of eight participants showed the strongest activation in the fusiform and inferior temporal gyri when matching picture and words at the subordinate-level (I. Gauthier & Tarr, 1997). Moreover, bilateral FFA and the so-called occipital face area (OFA) showed significant activation during recognition of homogeneous categories (e.g., cars, birds), but only when presented to expert in that specific category (I. Gauthier, Skudlarski et al., 2000). Other brain areas were also active during presentation of subordinate level category of non-face objects, faces, or during presentation of specific categories to expert-participants, including inferior temporal gyrus, lingual gyrus and occipital cortex (I. Gauthier, Curran, Curby, & Collins, 2003; I. Gauthier et al., 1999). Haxby and colleagues (2000) provided additional evidence against the face module, mapping the representation of many objects (faces and non-faces) in a topographic fashion, demonstrating the presence of distributed and overlapping representations in the cortex, along the ventral visual pathway, including both occipital and temporal regions. Recently, Grill-Spector and colleagues (2006) utilized high-resolution fMRI methodology to further demonstrate that the FFA is not specific to faces, but is also sensitive to many others object categories; however, limitations in current imaging

techniques most often fail to reveal the complex pattern of overlapping object representations in a very small region of the cortex, such the FFA.

Few studies have investigated the neural substrate of the specific cognitive strategies and/or different information types used to encode objects and faces. Yovel and Kanwisher (2004) designed a behavioral and fMRI task to replicate the Janes task (Richard Le Grand et al., 2001; Catherine J. Mondloch et al., 2004). They modified the original task equating difficulty for the upright spacing (configuration) set and for the upright featural (part) set of stimuli in order to compare these two sets in the inverted condition without difficulty confounds. Contrary to the original studies, they did not find a significant difference, in both accuracy and percentage change of brain activation, between inverted spacing and inverted featural sets in the FFA (considered a main evidence for the crucial role of configural processing in making faces special stimuli). Yovel and Kanwisher (2004) interpreted these results as evidence of the domain-specific sensitivity of neural system to faces and as a rationale to undermine the role of configural and featural information in face processing. As expected they found more activation for faces in the right FFA compared to the left FFA, but also no effect of stimulus set (configural versus featural). However, they only considered activation within FFA and PPA areas, without reporting any other brain areas, thus precluding the possibility of finding related areas to FFA that may be sensitive to configural and featural information and not just whole faces (G. Yovel & Kanwisher, 2004).

Recently, Maurer and colleagues (2007) reported whole brain activation for a comparison of featural and configural (second-order relations) processing using the Janes task. They replicated Yovel and Kanwisher (2004) finding in which featural and configural information did not modulate brain activity in the FFA. Interestingly, a different section of the fusiform gyrus, just adjacent to the FFA, was found more active during

configural condition compared to featural condition. Beyond the FFA, both conditions yielded brain activity mostly in frontal and temporal areas. Moreover, most areas that were more active during the configural condition were in the right hemisphere, whereas most areas that were more active during the featural condition were in the left hemisphere.

Schiltz and Rossion (Schiltz & Rossion, 2006) investigated the neural correlates of holistic processing, using a composite face task. They only reported results from face-selective areas in occipito-temporal regions comparable to FFA and OFA (specifically, the middle fusiform gyrus and the inferior occipital gyrus), in which they found more intense activation for whole faces compared to top-half of the faces and a larger composite effect in the right hemisphere. Interestingly, even though the composite face effect (CFE) was larger in the right hemisphere, they also found a significant CFE in left occipito-temporal areas (Schiltz & Rossion, 2006). This study is the first to explore the neural correlates of holistic processing. However, it is difficult to reconcile its results to the typical behavioral findings (consistently replicated in the literature) because an atypical task design was used. The CFE was calculated contrasting the performance on two intact faces instead of subtracting the performance (or activation) of one intact and of one misaligned face. Moreover, during the imaging session participants were not asked to perform the composite face task, but to press a button when the face-tops became of a reddish color. Therefore, it is difficult to directly relate typical CFE performance found in the literature with the neural activation described by Schiltz and Rossion (2006).

Neural Basis of Face Processing: Clues from Patient Populations

Prosopagnosia. Before the advent of brain imaging techniques, studies on the neurocorrelates of cognitive processes centered on clinical studies of brain injured

patients with specific deficits. The localization and extent of the lesions, which for example affected face and/or object processing, gave us clues about brain areas needed for these processes. Prosopagnosia, a term coined by Bodamer (1947), is historically considered to be a specific agnosia to faces of familiar or famous people, which spared the ability to recognize common objects. Patients typically show lesions in the fusiform and lingual gyri or their interconnections and the lesions are often caused by strokes of the right posterior or both cerebral arteries, which extend from the level of the splenium of the corpus callosum to occipital pole (Damasio, Damasio, & Van Hoesen, 1982; Landis, Regard, Bliestle, & Kleihues, 1988; Logothetis, 2000). In severe cases patients fail to recognize faces of close relatives, even if are often able to recognize their facial expressions and identify of the person by her/his voice or other clues. Prosopagnosic patients were considered to have intact object processing abilities, but recent research has demonstrated that they also have deficits in object recognition. In particular, patients have difficulties processing configural information of objects (Barton, Zhao, & Keenan, 2003).

Moreover, some recently reported prosopagnosic cases provide further support for a network of critical brain regions underlying face processing. For example, prosopagnosic patient D.F. was able to perform relatively normally on simple face categorization tasks (e.g., recognizing that a certain shape is a face) and showed normal FFA activity. Nonetheless, he was severely impaired on more complex face processing tasks and was not able to recognize facial identity, gender or emotional expression (Steeves et al., 2006). Similarly, patient P.S. had a structurally intact middle fusiform gyrus, which responded normally to a basic face categorization task (e.g., discriminating a face from a cup), but showed an abnormal response pattern to individual face discrimination (e.g., discriminating Jane from Mary) (Schiltz et al., 2006). In both cases,

occipital regions (i.e., occipital face area and inferior occipital gyrus) were damaged and their failed interaction with the FFA was considered crucial for face discrimination deficits (Schiltz et al., 2006; Steeves et al., 2006).

Complementary to prosopagnosia studies, work by Moscovitch and colleagues (1997) described patients whose deficits disproportionately affected object recognition, while sparing face recognition. However, when patients were tested on face recognition of parts of the faces (e.g., eye area, mouth area, etc.), they could not recognize them, leading the researchers to infer that patients were specifically impaired in processing featural information. Moreover, these results provided evidence that object processing relies mainly on encoding featural information, while face processing mostly relies on configural information.

Congenital Cataracts. In another very informative patient study, Le Grand and colleagues (2001) provided evidence of cortical predisposition for particular types of cognitive strategy, and demonstrated that visual input in the first months of life is critical to normal development of face processing later in life. They tested children between 6 and 10 years old as well as adults who were born with binocular cataracts that caused blindness up to 2 or 6 months of their early life, when the cataracts were removed, and normal vision was gained. These former patients were tested with a set of face stimuli (called Janes) that varied in the actual features, or in the spacing among the features or in the face contour (Richard Le Grand et al., 2001; Catherine J. Mondloch et al., 2004). Very interestingly all age groups performed normally in the features and contour conditions, but cataract patients did poorly in the configural condition, and only in that condition (Richard Le Grand et al., 2001). Even more impressively, binocular cataract patients performed better that controls in a composite face task, because contrary to

typical adults they did not show any composite face effect, which is considered an indicator of holistic processing (R. Le Grand, Mondloch, Maurer, & Brent, 2004).

Patients with Localized Unilateral Perinatal Lesions. Children with localized unilateral perinatal lesions (PL) are an extremely interesting clinical population to investigate the effects of early brain injury, and more importantly, the course of developmental changes (plasticity), which occur across the entire lifespan (Ballantyne & Trauner, 1999; S. de Schonen, Mancini, Camps, Maes, & Laurent, 2005; Delis, Kiefner, & Fridlund, 1988; Moses et al., 2000; Stiles, 1998; Stiles et al., 2003; Stiles, Reilly, Paul, & Moses, 2005). Traditionally, studies of adult patient populations have been focused on identifying associations between cognitive deficits and the corresponding damage to neural substrate. For example, prosopagnosia patients have been studied to map the face-processing pathway and to identify cognitive deficits associated with its damage. Alternatively, PL patient studies did not focus on their deficits, but on their spared functions, and particularly, on the alternative brain pathways that emerge after an early injury (Stiles et al., 2005). A wide range of longitudinal studies conducted in San Diego, which assessed PL children on both language and visual-spatial cognition, demonstrated that (1) PL children always showed early deficits, but generally the deficits were subtle and much milder than the impairments reported by adult stroke patients with similar but late-onset lesions; (2) although generally milder that those observed among adults, their patterns of visuospatial deficits and their association with the side of lesion mirrored that observed among adults (Stiles, 1998).

Specifically, on a wide range of visual-spatial processing tasks (using non-face stimuli), PL children with right hemisphere lesions (RPL) showed configural processing deficits, whereas PL children with left hemisphere lesions (LPL) showed featural processing deficits, similarly to adult patients, who nonetheless, displayed much

more severe impairments (Akshoomoff, Feroleto, Doyle, & Stiles, 2002; Stiles et al., 2003; Stiles & Thal, 1993). In a typical visual-spatial task, the hierarchical form task, children (5- to 10-year-olds) were asked to reproduce from memory hierarchical shapes made of a global level and a local level (e.g., a big square made of small crosses) (Akshoomoff & Stiles, 1995). Similar to adult stroke patients, RPL children showed configural deficits in that were able to reproduce the local level small shapes, but failed to organize them into an accurate global level shape (e.g., patient EM, 6-year-old, correctly drew many crosses, but arranged them in the shape of a large cross rather than a square). Alternatively, LPL children showed featural deficits, correctly drawing the global shape, but without drawing any small shapes (e.g., they drew a large square made up of four connected lines, rather than crosses) (Delis et al., 1986; Stiles et al., 2005; Stiles & Thal, 1993). Similarly, a combined behavioral and fMRI study showed an unusual pattern of brain activation in two in older PL patients (12- to 14-year-olds) during a perceptual version of the hierarchical form task (Stiles et al., 2003). Typical adults and adolescent displayed greater right occipito-temporal activation for global level processing and greater left occipito-temporal activation for local level processing, whereas the RPL adolescent showed activation only on the left in both tasks and the LPL adolescent showed only right activation for both global and local task. Both adolescents showed only subtle deficits during the behavioral testing, thus their unilateral systems used for both global and local processing seem to be sufficient, but not optimal, in supporting both levels of processing (Stiles et al., 2003; Stiles et al., 2005).

Children with both RPL and LPL also show subtle levels of deficit on face matching tasks. Specifically, Stiles and colleagues (2005) showed that RPL children were significantly less accurate and slower than controls on a face-matching task.

Accuracy of LPL children was marginally worse than controls and did not differ from the RPL group, and their reaction times were intermediate and did not differ significantly from either the RPL group or controls. These performance profiles suggest a marked deficit in face processing in the RPL group and a less pronounced deficit in the LH group (Stiles et al., 2005). Interestingly, brain imaging studies of children on the face matching task reveal a different profile of organization than observed in the hierarchical forms processing task. Like typically developing controls, children with both RPL and LPL lesions showed activation in the typical right hemisphere anterior fusiform area (the fusiform face area), and did not show the shift in lateralization observed in the hierarchical forms task. Further, unlike controls, both showed activation in a region of the left fusiform that has been associated with increases in task difficulty. These findings suggest that while the PL children recruited typical brain regions for face processing, both their diminished performance on the RT task and the activation of the LH brain region suggest that the task was challenging for them.

The data from the face processing and hierarchical form tasks suggest that the ventral-temporal system may begin to adopt its functional roles early in development. However, it is also a developing system and thus capable of considerable adaptation and compensation. Performance is affected, but not compromised. Moreover, the evidence from the face processing in PL patients suggest that this ability may be more resilient that other visual-spatial functions and may have an advantage over other visuospatial processes in recruiting available RH resources (Paparello et al., 2004; Stiles et al., 2003; Stiles et al., 2005).

Neural Basis of Face Processing in Childhood and Adolescence

Face-processing cognitive skills continue to improve during development into adulthood, and few recent developmental imaging studies corroborated evidence of a parallel timeline for specialization and localization of the neural correlates of face processing (Aylward et al., 2005; Gathers, Bhatt, Corbly, Farley, & Joseph, 2004; Roxane J. Itier & Margot J. Taylor, 2004; Margot J. Taylor et al., 1999). Taylor and colleagues (2004; 1999) recorded event-related potentials of children at different ages (4- to 5-year-olds, 6-year-olds, 7- to 8-year-olds, 9- to 11-year-olds and 12- to 14-year-olds) during presentations of faces, scrambled faces (where parts of the faces containing certain features were rearranged in a random order), cars, scrambled cars and butterflies. Participants showed larger amplitude for the N170 component to faces, compared to the other stimuli, in the right posterior temporal brain region. Older children displayed larger amplitudes and shorter latencies compared to younger children. Therefore, Taylor and colleagues (2004; 1999) suggested that face processing follows a gradual quantitative development throughout childhood. In addition, Itier and Taylor (2004) tested a large number of children ages 8- to 16-year-olds and found no significant increase of the inversion effect along this age span, but just improvement in face processing (larger N170 amplitude) as a function of age. The authors suggested that face-processing skills are not special, compared to other cognitive abilities and that there is no qualitative change in strategies during development (i.e., from featural to configural). Rather, they suggested that there is steady improvement in face processing abilities, which is the product of the general cognitive maturation of attention, memory, perception and other basic cognitive skills across childhood (Roxane J. Itier & Margot J. Taylor, 2004).

Alternatively, Passarotti and colleagues (A.M. Passarotti et al., 2003) tested children (10-to 12-year-olds), teenagers (13- to 15-year-olds) and young adults (college students) in a face-matching task, using functional magnetic resonance imaging (fMRI) techniques. The three age groups showed brain activity in the same general areas, but with different pattern of activations. Adults and teenagers were most similar, activating medial fusiform gyrus, with right hemisphere activation greater than the left hemisphere activation, adult activity was also more localized compared to teenagers brain activation. Children also showed greater right hemisphere than left hemisphere activation, but within each hemisphere activation was more widely distributed. Children showed more lateral as well as more anterior activation in addition to activation in the medial fusiform gyrus (A.M. Passarotti et al., 2003). Gathers and colleagues (2004) compared young children (5- to 8-year-olds), older children (9- to 11-year-olds) and adults in an fMRI study with a simple passive-viewing task (faces vs. objects). All groups showed face-preferential activation along the ventral pathway. Adults and older children displayed face-preferential activation near the classically defined FFA, whereas young children displayed activation along a more posterior ventral pathway. Moreover, the degree of category specific activation in other brain areas increased with age (Gathers et al., 2004). Aylward and colleagues (Aylward et al., 2005) tested children groups (8- to 10-year-olds and 12- to 14-year-olds) on memory tasks for faces, houses, inverted faces and inverted houses in order to dissociate between configural and featural processing for faces. Only older children showed activation for faces in the bilateral fusiform gyri. Age and psychophysical measures were correlated with brain activation and activation in the fusiform gyrus did correlate with age and configural face processing; thus the older the participants, the more activation in the fusiform gyrus and the more reliance on configural processing. Moreover, faces and houses elicited more

distinct patterns of activation in older children suggesting that processing of the two stimulus types become more differentiated with age (Aylward et al., 2005). Two recent studies suggested that category selectivity in occipito-temporal areas develops early (by 6- to 8-year-olds) for objects, places and scene categories, whereas faces follow a more protracted developmental trajectory for face processing (Golarai et al., 2007; Scherf, Behrmann, Humphreys, & Luna, 2007). These results corroborate behavioral and electrophysiological studies that have suggested a protracted development of face processing relative to other complex visual stimuli (Carey, Diamond, & Woods, 1980; Roxane J. Itier & Margot J. Taylor, 2004; Catherine J. Mondloch et al., 2002; Margot J. Taylor et al., 1999).

The only developmental imaging studies that have investigated the neurocorrelates of the development of face processing strategies have used face inversion paradigms (Joseph et al., 2006; A. M. Passarotti, Smith, DeLano, & Huang, 2007). Joseph and colleagues (2006) revealed that, in general in the contrast between upright and inverted faces, children (8- to 10-year-olds) showed similar whole-brain activity to adults, with the exception of posterolateral occipital visual processing areas, in which children showed almost no activation. In addition, young children (8-year-olds) did not show a behavioral inversion effect, in contrast with adults and older children (10-year-olds). Therefore, the authors suggested that differences in the activation may be associated with more reliance on featural processing by children. Interestingly, Passarotti and colleagues (2007) found no behavioral difference between children and adults in the inversion effect (R. J. Itier & M. J. Taylor, 2004; A. M. Passarotti et al., 2007), but still found a distinct pattern of brain activity in the two groups. Thus, similar behavioral performance does not necessarily imply similar neural underpinnings, and

differences in activity localization and intensity may reflect the cognitive strategy recruited.

Outside the specific field of face processing studies, interesting evidence of diverging pattern of activation elicited by different cognitive strategies comes from a developmental behavioral and fMRI study assessing performance and brain activation in 12- to 14-year-old children and adults attending at the global or local level of hierarchical stimuli (Moses et al., 2002). Results showed that children engaged the same general brain regions of adults for both global and local processing. However, there was a developmental shift from more distributed and undifferentiated bilateral activation in younger (immature) children to a more localized and lateralized activation in older (mature) children and adults (Moses et al., 2002). Adults and mature children showed bilateral activation with right greater than left hemisphere activation viewing global stimuli, and left greater than right hemisphere activation viewing local stimuli. Alternatively, immature children displayed almost opposite pattern with bilateral activation for global conditions and a trend of right greater than left activation during local conditions (Moses et al., 2002). These results also corroborated that more global processing is localized in the right hemisphere, whereas local processing is preferentially localized in the left hemisphere (Deruelle & de Schonen, 1998). In parallel, we can infer that configural face information is predominantly processed in the right hemisphere and featural face information predominantly in the left hemisphere.

Taken together, these evidences suggest a fine-tuning of the face-processing system based on age or, more appropriately, based on learning and experience and on the relation between the use of configural strategies and the specific localization of face-related activation in the FFA. Neurocognitive development is not simply the linear maturation of the neural substrate in parallel with the child cognitive development, it is a

much more complex interaction among the intrinsic biological cues of the system, experience, exposure to certain stimuli and interactions among different brain areas and pathways. Mark Johnson (2000) has proposed a model for functional brain development called “interactive specialization”, in which he highlighted the complex interaction between changes in specialization and changes in localization of neurocognitive functions. In the case of face processing, early in development multiple pathways are activated when viewing faces, but these pathways are broadly tuned and under-specialized thus they respond to a large range of stimuli (e.g., objects, face-like patterns, inverted faces). With increasing experience different pathways and structures became more and more specialized for different types of stimuli and many of them decrease their sensitivity to faces. In a typically developing system, neurons that migrate to particular areas of cortex are constrained in their development by the complex set of interactions that they encounter by virtue of their position in cortex. In the face processing system, neurons that are in the ventral pathway (in the area that eventually will become the so called FFA) and that are well connected to the hippocampus, receive a particular and well defined set of input that bias them to become face processing neurons (M. H. Johnson, 2000; M. H. Johnson & Munakata, 2005). The great technological advances of these recent years will make possible to acquire more solid neural functional data on the developing brain and corroborate or disprove Johnson’s interaction specialization framework.

Current Studies

The intent of the current studies was to assess the development of holistic face processing investigating both its behavior and its neurocorrelates. In order to determine how face processing strategies change during childhood we utilized a converging measures approach by tracking indices of performance (task accuracy and reaction

time) and brain function in typical participants of different ages (8- to 11-year-olds, 13- to 15-year-olds and young adults). A main cognitive task (composite face task) was designed to assess the degree to which face processing relies on holistic and/or featural information at different points in development, and to help determine whether or not the developmental trajectories for these two cognitive strategies are qualitatively different or relatively similar in children and adults. More specifically, in Chapter 2 a psychophysical study investigates the degree at which face processing relies on holistic and/or featural cognitive strategies at different points in development; and asses if children process faces in a qualitatively different way from adults. The same composite face task was reutilized in Chapter 3 in which functional magnetic resonance imaging (fMRI) techniques are used in order to define the neural underpinnings of holistic face processing in adults. In Chapter 4 the same techniques and task are used to define the development of the brain network associated with holistic face processing. Together the following studies intend to clarify our knowledge on face processing cognitive strategies, on their development and on their neural underpinnings.

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CHAPTER 2

THE DEVELOPMENT OF HOLISTIC FACE PROCESSING IN CHILDREN

There are ongoing controversies in the field concerning the development of face processing. Specifically, there are contradictory findings on when children are able to reliably engage particular cognitive strategies in order to process faces efficiently. Unlike other visual-spatial abilities (e.g., simple shape discrimination), face perception develops very slowly, becoming adult-like only well into adolescence (e.g., Carey & Diamond, 1994; Itier & Taylor, 2004; Catherine J. Mondloch, Le Grand, & Maurer, 2002; Margot J. Taylor, McCarthy, Saliba, & Degiovanni, 1999). This fact is somewhat surprising considering that newborns are biased toward looking at face-like stimuli even in the first minutes of life (Goren, Sarty, & Wu, 1975; Johnson & Morton, 1991). Some performance disparities between children and adults may reflect differences in general cognitive abilities, such as attention and memory, which have not yet fully developed in children. This account is referred to as quantitative development (e.g., de Heering, Houthuys, & Rossion, 2007; Catherine J. Mondloch, Pathman, Maurer, Le Grand, & de Schonen, 2007; M. J. Taylor, Batty, & Itier, 2004). However, some researchers attribute performance differences to cognitive strategies implemented specifically during face processing, rather than in differing general abilities; this phenomenon is referred to as qualitative development (Carey & Diamond, 1977; Freire & Lee, 2001; McKone & Boyer, 2006; Slater & Quinn, 2001).

Despite the wealth of data that have been collected in the past 30 years, no single theory has yet been able to capture all of the extant findings. Early studies supported a qualitative model for school-age children. Carey and Diamond (1977) proposed a developmental shift in cognitive strategies beginning at approximately 10 years of age, from reliance on featural information to increasingly greater reliance on configural information. However, subsequent research challenged out this late processing switch, demonstrating that younger children were able to successfully

encode configural information (Carey & Diamond, 1994; Freire & Lee, 2001; Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998). More recently, a quantitative model of face processing has gained support (de Heering et al., 2007; Catherine J. Mondloch et al., 2007; M. J. Taylor et al., 2004). Within the debate on the cognitive strategies used in face processing, it is important to note that featural and configural information are both necessary, even though one class of information may dominate. Featural processing arises when we encode an object or a face by isolating its featural elements. Alternatively, configural processing arises when we process the spatial relationships among the features of an object or face.

While, most researchers agree that configural strategies are particularly important for face processing (Gauthier & Bukach, 2007; Maurer, Grand, & Mondloch, 2002; C. J. Mondloch, Maurer, & Ahola, 2006; Yovel & Kanwisher, 2004), the field is complicated by the coexistence of at least three different types of configural processing (for a review, see Maurer et al., 2002). The first type entails sensitivity to first-order relations, which refer to the general spatial arrangement of facial features, for example, eyes above a mouth, and mouth below a nose (e.g., Baenninger, 1994). The second type of configural processing involves sensitivity to second-order relations, which refer to the spatial distances among facial features (eyes, nose, mouth, face contour). This type of processing is considered the most critical for effective face processing (Maurer et al., 2002; Maurer, Mondloch, & Lewis, 2007). The third type of configural processing is referred to as holistic processing, which captures the indivisible whole (or Gestalt) of a face, and is more easily represented as a whole than as the sum of its individual parts (Diamond & Carey, 1986; Maurer et al., 2002; Peterson & Rhodes, 2003; Tanaka & Farah, 1993). These types of processing are in part confounded with one another by their own definitions, imposing limitations even on the most carefully designed

paradigms. For example, changing the outline of a face may also modify its second-order relations. Nonetheless, a number of clever tasks have developed to assess the role of the different strategies.

Sensitivity to second-order relations is considered necessary for expert face processing, and consequently, is probably the most studied face processing strategy (Freire & Lee, 2001; McKone & Boyer, 2006; Catherine J. Mondloch, Dobson, Parsons, & Maurer, 2004; Catherine J. Mondloch et al., 2002; Yovel & Kanwisher, 2004). A number of studies have manipulated spacing among facial features, and have used a variety of paradigms, such as matching tasks and attractiveness rating tasks. There is some evidence that sensitivity to second-order relations may begin to emerge in the late preschool period. For example, McKone and Boyer (2006) reported sensitivity to second-order relations in children as young as 4 years old, on a task that required them to rate faces according to attractiveness. However, other studies suggest the facility in processing second-order relation in faces may be more protracted. In Freire and Lee's (2001) paraphernalia study, children up to 7 years of age seemed to prefer featural over configural strategies. In a typical paraphernalia paradigm, participants are instructed to recognize previously seen faces, which have been modified by adding or removing such items as hats or glasses. Young children (4- to 7-year-olds) performed poorly, although better than chance level, when asked to detect a target face presented among distractor faces that differed only in the spacing of their features. By contrast, accuracy was higher when the distractors differed from the target in the shape of the individual features. These finding suggest that while preschool-age children are capable of configural processing, they rely more on featural processing when encoding faces (Freire & Lee, 2001). Mondloch and colleagues (2004; 2002) tested 6- to 10-year-olds on a similar task in which they altered features, spacing and outer contour of a baseline face. Results

showed that children were comparable to adults in the featural conditions, almost as skilled as adults in the contour conditions, but much worse than adults in the spacing conditions (Catherine J. Mondloch et al., 2004; Catherine J. Mondloch et al., 2002 but see McKone E. and Boyer B., 2006). Other work by Mondloch and colleagues (2004; 2002) has suggested that sensitivity to second-order relations does not reach adult levels until 14 years of age or later (Catherine J. Mondloch et al., 2004; Catherine J. Mondloch et al., 2002). Together these data suggest that sensitivity to second-order relations begins to emerge in the late preschool period, but undergoes significant developmental change through the school years

The present study investigated another very important type of configural processing, holistic processing. We employed the composite face task, which is considered to be one of the most robust paradigms to assess holistic strategies (de Heering et al., 2007; Hole, 1994; Hole, George, & Dunsmore, 1999; Le Grand, Mondloch, Maurer, & Brent, 2004; Catherine J. Mondloch et al., 2007; Schiltz & Rossion, 2006; Young, Hellawell, & Hay, 1987). In typical composite face stimuli, the upper half of one face is conjoined with the lower half of a second face. Participants are asked to judge whether the upper halves of two faces are the same or different. Typically, the upper halves of the stimulus pair match 50% of the time, while the bottom halves always differ. Because the bottom halves of the composite faces always differ, a visual illusion is created in which the pairs with matching tops actually appear to be different. This illusion is driven by our bias to process faces as indivisible whole, which prevails even when we are instructed to ignore part of the face configuration. For example, when the stimuli are composed of famous faces, it is surprisingly hard to recognize the top half of very familiar faces such as President Bush or Angelina Jolie. This strong holistic bias disappears if tops and bottoms of the composite stimuli are laterally offset. Thus,

participants are slower and less accurate in matching same tops of aligned faces, relative to same tops of misaligned faces, in which the bottoms can be easily ignored. This specific phenomenon, referred to as Composite Face Effect (CFE), has been replicated with familiar and unfamiliar faces, with different parameters and designs, and with different age groups (de Heering et al., 2007; Hole, 1994; Hole et al., 1999; Le Grand et al., 2004; Catherine J. Mondloch et al., 2007; Schiltz & Rossion, 2006; Young et al., 1987).

Carey and Diamond (1994) were the first to use the composite face task to investigate holistic processing in children. They found that children as young as 6 years were sensitive to the “composite face effect illusion”, and thus to holistic information. This finding was inconsistent with their previous work that suggested that children rely principally on featural information for face processing (Carey & Diamond, 1994), but consistent with subsequent studies showing at least limited facility with different types of configural processing earlier in development. More recently, Mondloch and colleagues (2007) replicated this finding with 6-year-old children (with unfamiliar faces). De Heering and colleagues (de Heering et al., 2007) also employed the composite face task to study holistic processing in children. They found that even 4- to 5-year-old children were sensitive to the CFE, thus sensitive to holistic information. However, their composite face task had to be modified from the traditional version in order to be reliably performed by younger children.

Holistic processing has also been assessed with the part-whole advantage task. In this task, participants are asked to recognize either isolated facial features, or features presented within the context of an intact face. Adults more accurate in recognizing target facial features (eyes, mouth, nose) within a face configuration than in isolation (Tanaka & Farah, 1993). Tanaka and colleagues (1998) have also shown that 8- to 10-

year-old children performed similarly to adults. Pellicano and Rhodes (2003) replicated these findings with 4- to 5-year-old children. Together, these studies suggest that children begin to engage in holistic processing as early as 4- to 6-year-old (Carey & Diamond, 1994; de Heering et al., 2007; Catherine J. Mondloch et al., 2007; Pellicano & Rhodes, 2003), but mature holistic processing may emerge over a more protracted period of development.

Recently, a separate debate on whether face processing abilities are innate or experience-based has motivated a great flourishing of infant studies. Evidence from infant literature seems to somewhat contradict the school-age literature suggesting that newborns are able to employ the same face processing strategies that adults engage in, including sensitivity to second-order relations (Hayden, Bhatt, Reed, Corbly, & Joseph, 2007). Despite low visual acuity (e.g., Maurer & Barrera, 1981), newborns can process individual features of a face (Kestenbaum & Nelson, 1990; Quinn, Yahr, Kuhn, Slater, & Pascalils, 2002; Schwarzer & Zauner, 2003; Schwarzer, Zauner, & Jovanovic, 2007). For example, Schwarzer and colleagues (2007) showed that 4-month-old infants are sensitive to featural changes in a face to which they were previously habituated. Infants can also process configural information. Many studies have assessed sensitivity to first-order relations (Goren et al., 1975; Johnson & Morton, 1991; Catherine J. Mondloch et al., 1999; Simion, Valenza, Cassia, Turati, & Umilta`, 2002; Valenza, Simion, Cassia, & Umilta`, 1996). For example, Johnson and Morton (Johnson & Morton, 1991) showed that infants preferred a face-like configuration over a scrambled or a non face-like configuration. Only very recently, infants' ability to process second-order relations has been revealed by Hayden and colleagues (2007). Using the Thatcher paradigm (P. Thompson, 1980) they showed that 5- to 7-month-old infants are sensitive to the spatial distances and relations among facial features. Relatively few studies have assessed

holistic processing in infants (Cashon & Cohen, 2000; Cohen & Cashon, 2001; Slater et al., 2000). Cohen and Cashon (2001) habituated infants to familiar faces and then switched them with novel faces, which were composites of internal and external features from two of the familiar faces. Infants looked longer at the novel composite faces, thus showing sensitivity to holistic information. Unfortunately, the switch-design confounds infants' sensitivity to the new face context with the change in the outer contour, a feature to which infants are known to be sensitive (C. J. Mondloch et al., 2006).

Considering together infant and child literature and observing the different methodologies and age appropriate tasks used, it is then clear that infant data do not contradict child findings; alternatively, they provide important evidence on the early onset of rudimentary face processing abilities, which become adult-like only after protracted development into childhood and even into adolescence (Catherine J. Mondloch et al., 2004; Catherine J. Mondloch et al., 2002; M. J. Taylor et al., 2004; Margot J. Taylor et al., 1999). Data on pre-school and school-age children show that there is significant refinement and ongoing change for face processing abilities and that separate cognitive strategies may have different developmental trajectories. Infants have some early sensitivity to featural and configural information, but these abilities are not fully developed. Featural processing seems to reach adult-level relatively early in childhood by 2- to 4-years of age (Freire & Lee, 2001; Schwarzer, 2000). Configural processing, particularly sensitivity to second-order relations seem to reach adult level only into adolescence (Freire & Lee, 2001; Catherine J. Mondloch et al., 2004; Catherine J. Mondloch et al., 2002; Schwarzer, 2000). Holistic processing seems to be well developed between 4-to 6-years of age (Carey & Diamond, 1994; de Heering et al., 2007; Catherine J. Mondloch et al., 2007; Pellicano & Rhodes, 2003).

The current study assessed the development of holistic processing with a composite face task performed by school-age children, adolescents and adults. This study is part of a larger project designed to investigate the time points along development at which children utilize featural and/or holistic processing, and to characterize the quantitative and/or qualitative nature of this developmental change.

Methods

Participants

All participants were right-handed and had normal or corrected-to-normal vision. Prior to testing, the procedure was explained and informed written consent was obtained from adult participants, and parental and/or school permissions were obtained for child and adolescent participants.

Children. A total of 103 children (8- to 11-year-olds) were tested in the UCSD Developmental Cognitive Neuroscience Laboratory (DCNL) or at schools in the San Diego area. Twenty-eight individuals (mean age = 9.5; 11 males and 17 females) were excluded from the analysis because they did not meet the a priori criterion for accuracy level. In order to be included in the study, participants needed to perform at above chance level in the misaligned conditions of the composite face task[1] (68% average, binomial probability, $p<.05$, for 32 trials). Two additional children were excluded as outliers on the basis of their accuracy level. Specifically, individuals whose accuracy (for the composite effect value) was two standard deviations below the group mean were deemed outliers. The remaining 73 children were divided into two age groups, 40 children of 8- to 9-years of age (mean age 9, 5) and 33 children of 10- to 11-years of age (mean age 10, 5). Small toys were given to the children at the end of the session as prizes for their participation in the study.

Adolescents. Twenty-three adolescents were tested in the DCNL and at a school in the Los Angeles area. Two participants (1 female, 1 male; mean age 14, 2) were

[1] The accuracy inclusion criterion was based only on the misaligned conditions because the composite face task was designed to yield a large discrepancy in difficulty between intact and misaligned conditions. In some extreme cases, children performed between 75-100% on the misaligned-same condition and between 13-38% in the aligned-same condition. Therefore we based the inclusion criterion on the misaligned same and different conditions only, to assure that the participants were on task, but to avoid excluding participants who were both on task and showed large performance differences between aligned and misaligned conditions.

excluded because they did not meet the inclusion accuracy criterion, hence the data of 21 adolescents (mean age 14, 6) were analyzed. Adolescent participants received movie passes or $5 at the end of the session for participation in the study.

Adults. Thirty-two undergraduate students (17 males and 15 females, mean age: 20,2) from the University of California, San Diego received course credit for participating in the study. No adults had to be excluded.

Stimuli

The current study is part of a collaborative project with Daphne Maurer's Laboratory at McMaster University, and the experimental stimuli were provided by the Maurer's group. Composite face stimuli were produced from gray scale digitized images of adult Caucasian faces with neutral expressions. Models (equal number of females and males) wore no jewelry, glasses or makeup, and a surgical cap covered their hair and ears. Face images were edited using Adobe Photoshop. The images were split in half horizontally across the middle of the nose, and then recombined using the top and the bottom halves of different individuals. The same face composites were used in the two conditions tested: intact faces and misaligned faces. In the intact condition, the top and bottom face segments were properly aligned. In the misaligned condition, the top half of each face was misaligned by shifting it horizontally to the left so that the right-most edge of the top half was aligned with the middle of the nose in the bottom half of the image (see Figure 2.1). For every trial, the location of the top half of each face remained constant. Stimuli in the aligned condition were 9.8 cm wide and 14 cm high (5.6 x 8 visual degrees from the testing distance of 100 cm). Stimuli in the misaligned condition were 12.8 cm wide and 14 cm high (7.3 x 8 visual degrees from the testing distance of 100 cm). Although the misaligned stimuli occupied a wider horizontal visual angle, the face halves were of identical size in both conditions. Scrambled faces of the

same dimensions were also created in Adobe Photoshop for the control task. To create the scrambled faces, an 8X9 square grid was overlaid on four of the face stimuli. The squares within the grid were then randomly placed into a new grid to create the scrambled faces, such that major facial features (i.e., eyes, nose and mouth) were not distinguishable, while the same range of spectral frequencies as the experimental stimuli was represented.

Procedure and Design

Participants sat 100 cm from a laptop computer and were asked to judge as quickly and accurately as possible whether the top halves of the two faces, sequentially presented on the computer screen, were the same or different. On every trial the bottom halves of the faces were different. Participants responded by right-clicking on a computer mouse when the top halves of the two faces were the same, and left-clicking when the top halves were different. As shown in Figure 2.2, each trial began with a black fixation-cross displayed on a white background for 500 ms., immediately followed by a composite (or scrambled) face presented for 200 ms., 300 ms. inter-stimulus interval (ISI) occurred before a second composite face appeared for 200 ms. Between the second face and the start of the following trial a white background screen was displayed for 2300 ms. Participants gave a response during this inter-trail interval (ITI), if no response was given or if a button-press occurred after the 2300 ms ITI, the response was recorded as null. Three blocks (or runs) of trials were presented with each consisting of 80 trials presented in a quasi-random order, each block was composed of a different sequence of stimuli. During each run, 5 stimulus types were presented: 16 aligned same-top faces, 16 aligned different-top faces, 16 misaligned same-top faces, 16 misaligned different-top faces and 16 scrambled faces (see Figure 2.2). The three quasi-random trial runs were counterbalanced across participants. A short 6-trial practice

was always completed (and repeated if necessary) before participants performed two or three consecutive blocks. Percentage correct and reaction times (RT) were recorded.

Data analysis

Proportion of correct responses (accuracy) and mean reaction times of the correct responses (RT) were analyzed. Analyses on preliminary data assessed potential practice effects across multiple runs. Notably, reaction time and accuracy performance were poor during the first run but improved significantly by the second run [$F(51)=16.87$, $p< .001$, for RT] whereas runs 2, 3 and 4 were not significantly different from each other. Thus only run 2 was included in the analyses. In addition, analyses on preliminary data did not report any order or gender effects.

A mixed design three-way analysis of variance (ANOVA) was conducted for both accuracy and RT data in order to assess holistic bias during face processing in different age groups. Age (8- to 9-year-olds, 10- to 11-year-olds, adolescents and adults) was included as a between-subjects factor, whereas, Composite (aligned, misaligned) and Decision (same, different) were within-subjects factors. A series of simple effects analyses and 2-way ANOVAs were conducted separately on each age group in order to further investigate the significant higher order interactions. Specifically, a difference score for the composite face effect (CFE: misaligned-same – aligned-same) and one for the different-difference (DD: aligned-different – misaligned-different) were calculated and analyzed for each age group. Finally, post-hoc analyses (Tukey HSD) explored differences in the CFE and DD values across age groups in order to specifically assess age differences in holistic bias during face processing. It should be noted that RT data were primary analyzed in order to verify the reliability of the overall data, particularly to control for speed-accuracy trade-offs, to which younger participants are especially vulnerable.

Initial analyses were based on age groups, however, further inspection of the child data suggested that the magnitude of the composite face effect was not uniform across children. Specifically, in both child groups (8- to 9-year-olds and 10- to 11-year olds) some children appeared to perform as well as adolescents and adults, whereas others performed at or below chance in the hardest condition (i.e., aligned-same). Thus, behavior was not solely related to age, but accuracy level seemed to better capture group differences. Therefore, child groups were regrouped by performance (see later section for criterion used). Both age-based and performance-based analyses follow.

Results

Age-based Results

Accuracy. The 3-way ANOVA revealed significant main effects of Age, $F(3, 122) = 46.17$, $p > .001$, and Composite, $F(1, 122) = 50.34$, $p < .001$. These effects were further explained by the significant 2-way interaction between Composite and Decision, $F(1, 122) = 140.53$, $p > .001$, and by the 3-way interaction between Age, Composite and Decision, $F(3, 122) = 12.48$, $p < .001$. Thus, participants were more accurate on misaligned trials compared to aligned trials, and age groups seemed to differ in their use of holistic processing during face processing. In order to further investigate the components of the 3-way interaction, 2-way ANOVAs were conducted separately for each age group. As shown in Figure 2.3.a, all groups revealed a significant interaction between Composite and Decision, suggesting composite face effect, and consequently, holistic processing [$F(1, 39) = 85.23$, $p < 001$, for 8- to 9-year-olds; $F(1, 32) = 74, 92$, $p < .001$, for 10- to 11-year-olds; $F(1, 20) = 9.83$, $p < .005$, for adolescents; $F(1,31) = 16.78$, $p < .001$, for adults]. To fully characterize the components of the interactions, 1-way ANOVAs were calculated on the difference scores of the CFE and the DD [$F(3, 122) = 12.21$, $p < .001$, for CFE; $F(3, 122) = 3.23$, $p < .025$, for DD]. Finally, post-hoc analyses (Tukey HSD for unequal n) were conducted on the 1-way ANOVAs to distinctively demonstrate disparities in the magnitude of holistic bias among different age groups. In the CFE analyses, 8- to 9-year-old children displayed a trend of being significantly different from the 10- to 11-year-old children (Tukey HSD, $p < .08$); in addition, they were significantly different from adolescents (Tukey HSD, $p < .001$) and adults (Tukey HSD, $p < .001$). Children 10- to 11-years of age significantly differed from adults (Tukey HSD, $p < .021$). No differences in the DD scores were found among age groups. In summary, the magnitude of the holistic bias was largest in younger children and decreased as age

increased. In fact, as showed by the solid-colored bars of Figure 2.3.a, all groups displayed a robust CFE, but children showed the largest. Specifically, adult participants performed at a mean accuracy level of 98% on misaligned-same trials and 87% on aligned-same trials, 8- to 9-year-old children performed at a mean accuracy level of 88% on misaligned-same trials and only 58% on aligned-same. Consequently, CFE values (misaligned-same - aligned-same) were 0.11 for adults, 0.13 for adolescents, 0.22 for 10- to 11-year-old children and 0.31 for 8- to 9-year-old children.

Reaction Times. As shown in Figure 2.3.b, RT data broadly mirrored the accuracy data. Specifically, significant effects were found for Age, $F(3, 122) = 17.78$, $p > .001$, Composite, $F(1, 122) = 38.33$, $p < .001$, and Decision, $F(1, 122) = 10.47$, $p < .001$. In addition, a 2-way interaction between Age and Composite was found, $F(3, 122) = 3.10$, $p < .030$, and an interaction between Composite and Decision, $F(1, 122) = 36.60$, $p < .001$, was also found. In contrast to the accuracy results, there was no significant 3-way interaction. To further assess the age effect, post-hoc analyses (Tukey HSD for unequal n) were run on a series of simple effect analyses (1-way ANOVA). Age groups did not significantly differ from each other. However, all groups displayed a CFE (Tukey HDS, $p < .01$), thus suggesting the participants' bias towards holistic processing. No significant differences were found on the DD scores. As showed in Figure 2.3.b, all groups were faster in the misaligned trials (blue bars) than in the aligned trials (yellow bars), as well as in the different trials (striped bars) compared to the same trials (solid bars). As expected, adult participants displayed the fastest responses, matching the stimuli at a mean speed of 592 ms on misaligned-same trials, and at a mean speed of 658 ms on aligned-same trials (i.e., hardest condition). Whereas, 8- to 9-year-old children were slowest, responding with a mean speed of 842 ms on misaligned-same trials, and at a mean speed of 931 ms on aligned-same trials. Finally, the examination of

the reaction times confirmed that the error rate found in the accuracy data was not attributable to speed-accuracy trade-offs.

Age-based Analysis Discussion

The results of the age-based analyses replicated previous studies (Carey & Diamond, 1994; de Heering et al., 2007; Le Grand et al., 2004; Catherine J. Mondloch et al., 2007) indicating that both adults and children, as young as age 8, exhibited the composite face effect, in both accuracy and RT. The magnitude of the effect among young children was greater than among older groups, suggesting a decrease in the size of the composite face effect as a function of age. Overall, all participants seemed to show a similar behavioral pattern, suggesting an analogous underlying approach to face processing across the age range studied. In spite of this, further inspection of the child data suggested that the magnitude of the composite face effect was not uniform across children. Specifically, in both child groups some children appeared to perform as well as adolescents and adults, whereas others performed at or below chance in the hardest condition (i.e., aligned-same). Even though, on average child groups showed the typical discrepancy between misaligned and aligned faces on same judgments, many of the individual performances were below chance level on aligned-same trials (individual chance level = 63%, as calculated by binomial probability for the 16 trials of aligned-same condition). Thus, poorer performance was not solely related to age, but rather a subset of children at all ages appeared to have difficulty in the aligned-same condition. No adult participants showed this pattern of performance and only one out of 20 adolescents did. To formally examine this observation, the sample of children was regrouped on the basis of performance in the aligned-same condition, rather than by age. Two groups were created within the same age range, between 8 and 11 years of age. The low-performing child group included children who performed at or below

chance in the aligned-same trials (accuracy < 62%); and the high-performing child group included children who performed above chance in the aligned-same trials (accuracy > 63%). It is important to note that the so-called low-performing children performed above chance in the overall task (inclusion criterion: accuracy above 68% in the combined misaligned trials). However, their poor performance in the aligned-same trials makes the interpretation of their behavior in this particular condition unreliable, and suggests that they may have been doing something different while matching the hardest trials. Consequently, if the low-performing child group shows a CFE, which is calculated subtracting the accuracy and RT values of aligned-same trials from the ones of misaligned-same trials, we may not be able to reliably interpret this behavior as an index of holistic bias[2]. In summary, statistical analyses were calculated again after children were regrouped according to performance on aligned-same trials. Specifically, the low-performing child group included 32 children, 21 of which were 8- to 9-year-olds, and 11 were 10- to 11-year-olds (mean age = 9, 6); and the high-performing child group included 41 children, 19 of which were 8- to 9-year-olds, and 22 were 10- to 11-year-olds (mean age = 10, 4). Importantly, the regrouping resulted in a division of children that affected performance, rather than simply age.

Performance-based Results

Accuracy. The 3-way ANOVA revealed significant main effects of Groups (low-performing child, high-performing child, adolescent and adult), $F(3, 122) = 56.93$, $p < .001$, and Composite, $F(1, 122) = 63.43$, $p < .001$. The 3-way interaction between Group,

[2] It should be noted that a majority of the 30 children excluded from the study, showed an accuracy pattern very similar to the low performing child group, displaying a very large composite effect. Those children were not included in the analysis because their overall accuracy on the misaligned trials was at chance level or lower (62% or less), hence we could not accurately interpret their behavior, as we could not determine whether they were on task. Nevertheless, the excluded children showed an interesting trend, which could be interpreted as a behavioral stage which precedes that displayed by the low performing children.

Composite and Decision, F(3, 122) = 26.96, *p* < *.001*, and all its supporting 2-way interactions were also significant. In order to further investigate the components of the 3-way interaction, 2-way ANOVAs were conducted separately for each group. As shown in Figure 2.4.a, all groups revealed a significant interaction between Composite and Decision, suggesting composite face effect [F(1, 31) = 143.33, *p* < *001*, for low-performing children; F(1, 40) = 76, 94, *p* < *.001*, for high-performing children; adolescent and adult groups did not change from the age-based analyses]. To fully characterize the components of the interactions, 1-way ANOVAs were calculated on the difference scores the CFE and the DD [F(3, 122) = 35.80, *p* < *.001*, for CFE; F(3, 122) = 3.94, *p* < *.010*, for DD]. Finally, post-hoc analyses (Tukey HSD for unequal n) were conducted on the 1-way ANOVAs to distinctively demonstrate disparities in the magnitude of CFE and DD among different groups. In the CFE analyses, low-performing children significantly differed from all other groups, specifically, from the high-performance children (Tukey HSD, *p* < *.001*), from adolescents (Tukey HSD, *p* < *.001*) and adults (Tukey HSD, *p* < *.001*). Notably, high-performing children differed from low-performing children, but did not significantly differ from adolescents and adults. In the DD analyses low-performing children showed a trend to differ from adolescents (Tukey HSD, *p* < *.054*) and they were significantly different from adults (Tukey HSD, *p* < *.014*). As shown in Figure 2.4.a, all groups were more accurate in the misaligned trials than in the aligned trials. Across the four groups the discrepancy between the two conditions (aligned and misaligned) and the two decisions (same, different) was larger for the low-performing children group than the other three groups, thus low-performing children showed the largest composite effect. The CFE values were 0.40 for low-performing children, 0.16 for high-performing children and same as in the age-based analyses for adolescents and adults.

Reaction times. In the 3-way ANOVA significant main effects were found for Groups, $F(3, 122) = 18.13$, $p > .001$, Composite, $F(1, 122) = 38.06$, $p < .001$, and for Decision, $F(1, 122) = 9.37$, $p < .003$. The 2-way interaction between Composite and Decision was also significant, $F(1, 122) = 38.70$, $p < 001$. Alternatively from the accuracy results, there were no significant interaction among Age, Composite and Decision (Figure 2.4.b). To further assess the components of the 2-way interaction, post-hoc analyses (Tukey HSD) were run on a series of simple effect analyses within each performance group. All groups displayed a significant CFE (Tukey HSD, $p < .01$), but only low-performing children showed a different DD from adults (Tukey HSD, $p < .025$).

Performance-based Analysis Discussion

As in the age-based analysis all participant groups showed the typical composite face effect, in that participants' performance was less accurate and slower on the aligned-same trials than on the misaligned-same trials. However, low performing children showed a significantly larger composite face effect than high performing children, adolescents and adults. Moreover, these three latter groups did not differ from one another, indicating that some of the 8- to 11-year-old children performed at adult level, whereas others significantly differed from their age-peers. As shown in Figure 2.3.a (solid-color bars), according to the age-based analysis, the composite face effect appeared to linearly decrease as age increased. However, further examination of the individual data indicated that age alone did not effectively capture child behavior, thus children were regrouped on the basis of their performance on the hardest condition (i.e., aligned-same). As shown in Figure 2.4.a (solid-color bars), the performance-based analysis did not seem to show a linear decrease of CFE with increasing age, rather they highlighted two separate groups. On one side, adults, adolescents and high performing

children displayed a robust CFE. On the other side, low performing children displayed a much larger CFE.

However, it is unclear that the CFE measure captures the same information about the performance of this group of children as it does for the other groups. The CFE usually contrasts levels of above chance performance for two task conditions, aligned and misaligned stimuli. As such, it has been interpreted an index of the influence of holistic processing for the aligned, but not the misaligned, faces. However, for the low performing group, the computation contrasts a measure of above chance performance (misaligned condition) with a measure of chance performance (aligned condition). This results in a very large estimate of “CFE”, but that index is based upon a very different underlying metric. The implications of these finding will be taken up next in the discussion section.

Discussion

In the current study we further assessed the development of and relationship between holistic and featural face processing using the composite face paradigm (Carey & Diamond, 1994; de Heering et al., 2007; Hole et al., 1999; Le Grand et al., 2004; Catherine J. Mondloch et al., 2007; Young et al., 1987). The composite face task requires participants to engage in both holistic and featural processing. Specifically, the instruction to attend to only the top half of the faces requires the employment of featural strategies (or configural processing exclusively on the eye region). However, aligned stimuli are designed to bias towards holistic processing, in that participants are unable to ignore the bottom halves of the faces and a novel face configuration seems to appear. Thus, aligned trials should engage holistic processing significantly more than misaligned trials. School-age children, adolescents and young adults were tested in the current composite face study, and as expected all groups showed the typical CFE. Depicted in Figures 2.3.a and 2.4.b are the differences in performance (accuracy and response time) between misaligned-same trials (in which matching the top halves of the stimuli is relatively easy) and aligned-same trials (in which ignoring the configural interference from the bottom halves provides a more difficult task). The age-based analysis seemed to suggest a linear decrease of the CFE as a function of age. Specifically, younger children (8- to 9-year-olds) showed a larger CFE then older children (10- to 11-year-olds), adolescents and young adults.

However, the performance-based analysis on the same child participants revealed a different pattern of behavior for the two child groups (performance-based regrouping did not affect adolescent and adult groups). Specifically, 8- to 11-year-old children (N= 41) who performed above chance in the aligned-same condition (high-performing group) did not differ from adults and adolescents, whereas 8- to 11-year-old

children (N= 32) who performed below chance in the aligned-same condition (low-performing group) significantly differed from all other groups and displayed the largest CFE. This low performance on the hardest condition was likely caused by the inability to focus their attention on only the top halves of the intact faces, and ignore the distracting bottom halves. Although this behavior is interpreted as index of holistic processing for the other groups, we refrain from drawing the same conclusion for the lower performing children, because their below-chance behavior is likely unreliable. Moreover, a subgroup of low-performing children (N= 10 of 32, mean age = 9,5) showed extreme behavior, performing with an accuracy as high as 93% on misaligned-same and as low as 13% on aligned-same condition. These extreme scores on same-trials, coupled with the significant difference found between different-trials, paints a distinct behavioral profile for low-performing children, which clearly differentiated them from the other groups.

One possible interpretation proposes that low-performing 8- to 11-year-old children did not engage in holistic processing, but instead they implemented a simpler "difference-detection" strategy, matching all possible discrepancies, feature-by-feature in both tops and bottoms of the stimuli. They visually searched the whole stimulus in order to detect any featural difference between the two sequentially presented faces. Considering that 100% of the bottom halves of the faces mismatched, and that they were not able to ignore these distractors when the stimuli where aligned, they were biased to (correctly) press the "different" button for most of the aligned-different stimuli (87% correct responses). Similarly, they were biased to (incorrectly) press the "different" button for most of the aligned-same stimuli, thus showing a large CFE (misaligned-same – aligned-same), which in this case *was not* an index of holistic processing.

An alternative interpretation might suggest that low-performing children were extremely reliant on holistic information, significantly more than adults. Thus, because of

the strong biasing effects of the holistic cues present in the intact faces, the children were unable to limit their attention to the task relevant features. However, this last hypothesis seems unlikely, not only because the unreliability of their below-chance performance, but also in light of data from other face processing studies, as well as from visual-spatial research. Some studies provide evidence that children rely more heavily on featural processing compared to adults (Freire & Lee, 2001; Schwarzer & Roebers, 2002; Schwarzer & Zauner, 2003), others show that children are able to engage in holistic processing (Carey & Diamond, 1994; Le Grand et al., 2004; Catherine J. Mondloch et al., 2007; Tanaka et al., 1998), but to our knowledge no studies have shown children with stronger reliance on holistic or configural processing compared to featural processing. For example, Gudrun Schwarzer and colleagues (2002; 2003) tested young children using a face categorization task, in which participants could classify faces (and non-face stimuli) holistically (i.e., according to overall similarity) or analytically (i.e., by single attributes). In this study, adults classified most of the upright faces holistically and most of the inverted faces analytically, whereas children (2- to 10-year-olds) categorized both upright and inverted faces analytically. Young children hardly engaged in holistic categorization, and only 10-year-old children started to rely on holistic strategies, but still did so much less often than they utilized analytic processing when categorizing faces (Schwarzer & Roebers, 2002; Schwarzer & Zauner, 2003). These data are particularly interesting because they highlight a disparity in use of cognitive strategies between adults and children during face categorization, which is a complex cognitive skill. In studies in which relatively simple tasks are used (e.g., attractiveness rating, recognition of familiar faces), children as young as 4 years old, and even infants in habituation tasks, are able to process some level of configural/holistic information (Bartlett & Searcy, 1993; Carbon, Schweinberger, Kaufmann, & Leder, 2005;

Hayden et al., 2007; Lewis & Johnston, 1997; L. A. Thompson, Madrid, Westbrook, & Johnston, 2001). Thus, when making generalizations across tasks and inferring the developmental learning curve of a particular cognitive strategy, it is imperative to consider the particular task and parameters used, and even more importantly, the degree of difficulty for child participants.

Taking into consideration only studies using composite face tasks, in which all participant groups (children 4- to 11-year-olds, adolescents and adults) showed a composite face effect, seemingly small methodological changes did influence the size of the composite effect (and different-difference, aligned-different – misaligned-different) and possibly its meaning and interpretation (Carey & Diamond, 1994; de Heering et al., 2007; Catherine J. Mondloch et al., 2007). For example, the composite face task used by de Heering and colleagues (2007) was cleverly designed to be performed by young children. The stimuli to be matched were presented simultaneously on the screen, and more importantly, the face top-halves were lightly colored in red, making the task of focusing attention only on the top-halves of the faces much easier for young children, who in fact showed holistic processing. Alternatively, the current task is challenging for children. Among the contributing factors for the higher level of difficulty is the sequential presentation of the stimuli to be matched, and the short presentation times and response-window. Moreover, strict inclusion criteria were used in the current study, and 30 children on a total of 103 tested had to be excluded, also demonstrating that the current version of the composite face task was difficult for children. Thus, we do not consider de Heering and colleagues' (2007) results in contradiction with the current data, but as evidence of both the early presence of holistic processing and its protracted development. The two tasks use different methodological parameters and have differing levels of difficulty; consequently 4 year olds engaged in holistic processing and

performed well above-chance (69%) in the aligned-same trials in de Heering and colleagues' (2007) version of the composite face effect, in which the top halves of the faces were artificially colored. Alternatively, some of the 8- to 11-year-olds in the current study performed below-chance (44%) in the aligned-same trials, possibly suggesting that their proficiency in holistic processing is not yet robust and during a challenging task they may instead rely on simpler strategies, such as a difference-detection strategy.

The current study uncovered a transitional developmental stage for face processing using the classic composite face task. About half of the 8- to 11-year-old children displayed adult-like behavior, mostly relying on holistic processing, underscored by the CFE. Alternatively, the other half of the children may have used a featural strategy, suggested by the below-chance performance on aligned-same trials and on the significant difference between different trials. Previous studies on the development of face processing seemed to suggest that children gradually achieve holistic processing in a quantitative manner, since they are slowly improving in most cognitive skills, consequently also becoming more adult-like in face processing (Carey & Diamond, 1994; de Heering et al., 2007; Itier & Taylor, 2004; Catherine J. Mondloch et al., 2002; Catherine J. Mondloch et al., 2007). Other studies described a more sudden developmental transition in the use of cognitive strategies attribute, which has been interpreted has a qualitative switch from featural to configural strategies specific to face processing (Carey & Diamond, 1977; Freire & Lee, 2001; McKone & Boyer, 2006; Slater & Quinn, 2001). However, the current study showed that both quantitative and qualitative interpretations of the data can depend upon the criteria on which participants are grouped, and upon the specific data analyses used, and that (at least for the current task) development of face processing and its cognitive strategies do not seem to follow a simple linear developmental curve. A child likely relies on featural or holistic strategies

differentially in different situations, depending on his/her developmental age and on the complexity and difficulty of the specific tasks. Most likely, developmental transitions are not specific to face processing, but rather reflect a combination of general cognitive and neural development (e.g., visual-spatial analysis, attention, memory), which together with experience, makes children more efficient and flexible face processors.

Leslie Cohen and Cara Cashon (2001) discussed developmental transitions (e.g., transition from use of featural to configural processing in a specific face task) as common sequences in development, not only for face processing, but also for any type of information processing (similar transitions reoccur in different forms and different domains throughout development). For example, in a categorization task in which infants processed line drawings of imaginary animals, 4-month-olds processed the animals as a collection of individual features, whereas 7-month-olds were able to process second-order relations among features (Younger & Cohen, 1986). Interestingly, when the task was made more difficult (increasing the number of features in each animal), 7-month-olds fell back to the performance level of younger infants, whereas 10-month-olds could perform well even with a higher degree of difficulty (Cashon & Cohen, 2004; Cohen & Cashon, 2001). In face processing, 7-months-old infants stop processing features independently and start integrating features into higher order units, thus processing the spatial relations among them (Cashon & Cohen, 2004). This is just one of the many developmental transitions they will go through before becoming adult-like face experts. When, for example, complexity is added to the stimuli, the system may become overloaded, at which point it is common to fall back to lower levels of processing, which were mastered earlier in development. In the case of faces, infants might fall back to process independent features before they are able to manipulate more complex

information and organize them into more sophisticated levels of analysis (Cohen & Cashon, 2001).

Importantly, the broader visual-spatial analysis literature also suggests that cognitive development of visual processing begins with feature-based analysis and later specializes to integrate features into more complex configurations (e.g., Akshoomoff & Stiles, 1995; Stiles & Tada, 1996). This process is highlighted by several cognitive transitions, from simpler to more complex strategies during the course of development. Specifically, with age and experience infants and children (even adults) stop processing features independently and start integrating features into higher order units, thus processing the spatial relations among them. Interestingly, in situations in which the system becomes overloaded, for example when task difficulty is increased, it is common to fall back to simpler levels of processing, previously mastered (Akshoomoff & Stiles, 1995; Cashon & Cohen, 2004; Stiles & Tada, 1996). In our difficult task, some of the children performed at the adult-level using holistic processing, but for other children in the same age range, the task was too overwhelming and they may have fell back into using simpler cognitive strategy, such as featural matching. We suggest that low-performing children may have relied on a simple difference-detection strategy (for both tops and bottoms of the stimuli), which represents an earlier developmental stage compared to configural strategies (applied to face tops only). Configural processing is usually more efficient for face processing, but in a difficult task, it may be more advantageous to process simpler featural information, which children can more easily manage and manipulate. Therefore, children rely on different cognitive strategies not only depending on the specific task and context, but also depending on the difficulty level of a task.

Thus, it is not surprising that infants and children are able to perceive and identify faces (highly complex stimuli), but they do not process them as efficiently as adults until the end of adolescence (Catherine J. Mondloch et al., 2004; M. J. Taylor et al., 2004; Margot J. Taylor et al., 1999). On simple and age-appropriate tasks, even infants are able to process faces with the same types of cognitive strategies used by adults. However, in tasks too challenging for their level of proficiency, infants and children fall back to simpler strategies, which they consolidated in the previous developmental stages. In the specific context of our study we found a transitional stage between 8 and 11 years of age, during which some children performed at an adult-like accuracy level, whereas others were overwhelmed by the task and fell back into using simpler but less efficient strategies. We also highlighted that the debate on the quantitative or qualitative nature of the developmental curve of face processing could be misleading. Indeed, regrouping our participants on a performance-based criterion, instead that purely on an age-based criterion, seem to change the shape of the developmental curve from linear (quantitative) to step-shaped (qualitative). Perhaps the shape of the developmental curve of face processing is generally linear and gradual, but at times also undergoes sudden changes. The changes correspond to developmental transitions, during which proficiency on newly mastered processing styles is challenged with difficult tasks. Children (and even infants) utilize holistic face processing strategies, but their proficiency is not yet stable. When at different stage of development, they are challenged by a complex context, they temporarily fall back to simpler featural strategies consolidating them, a step that may be crucial to strengthen their competence in manipulating increasingly complex material such as holistic information.

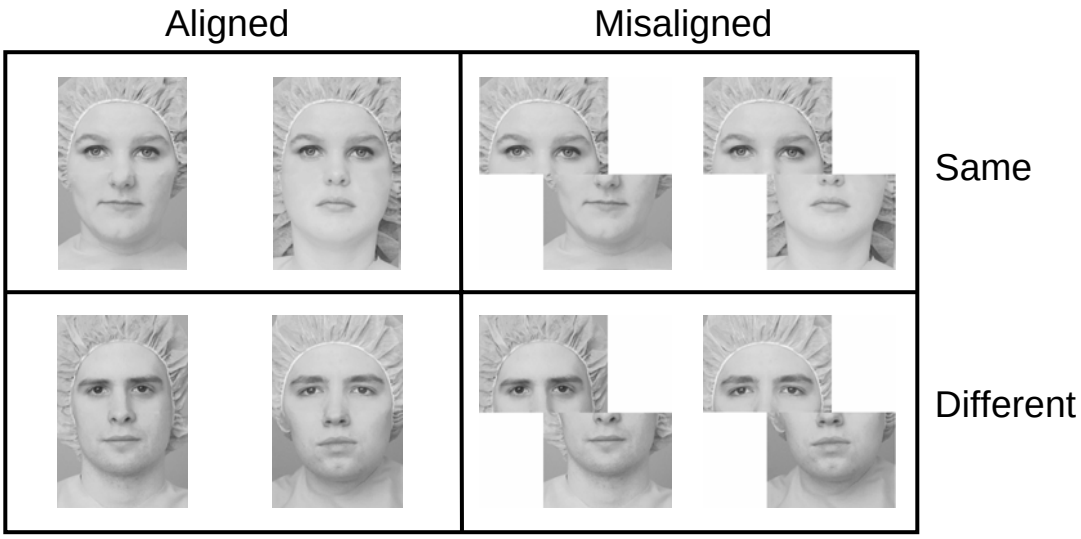


Figure 2.1 Composite face stimuli. Five stimulus types: aligned-same, misaligned-same, aligned-different, misaligned-different, and scrambled faces (not shown). Each run consisted of 80 trials presented in a quasi-random order.

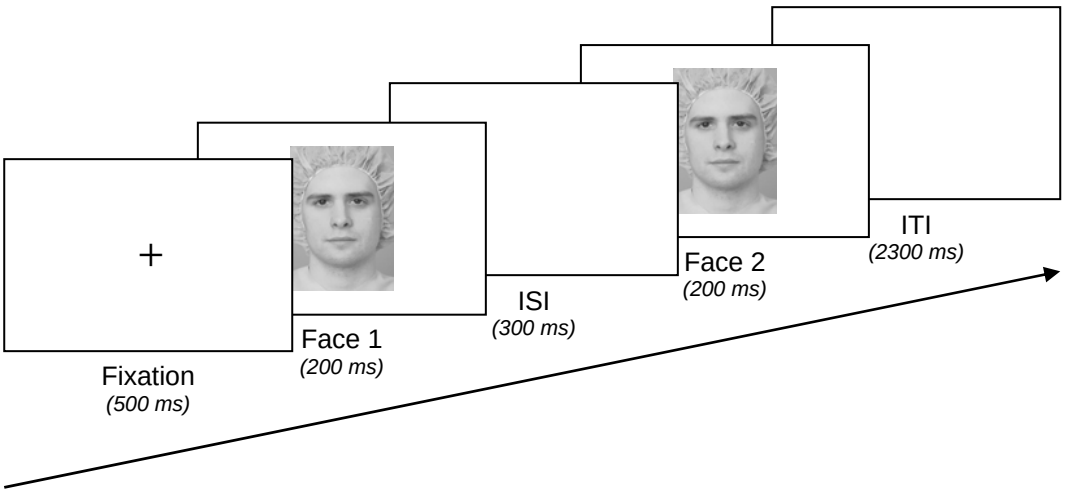


Figure 2.2 Task design. Each trial began with a black fixation cross on a white background for 500 ms, immediately followed by a composite (or scrambled) face presented for 200 ms. A 300 ms interstimulus interval (ISI) occurred before a second composite face appeared for 200 ms. The intertrial interval (ITI) was a white background screen for 2300 ms.

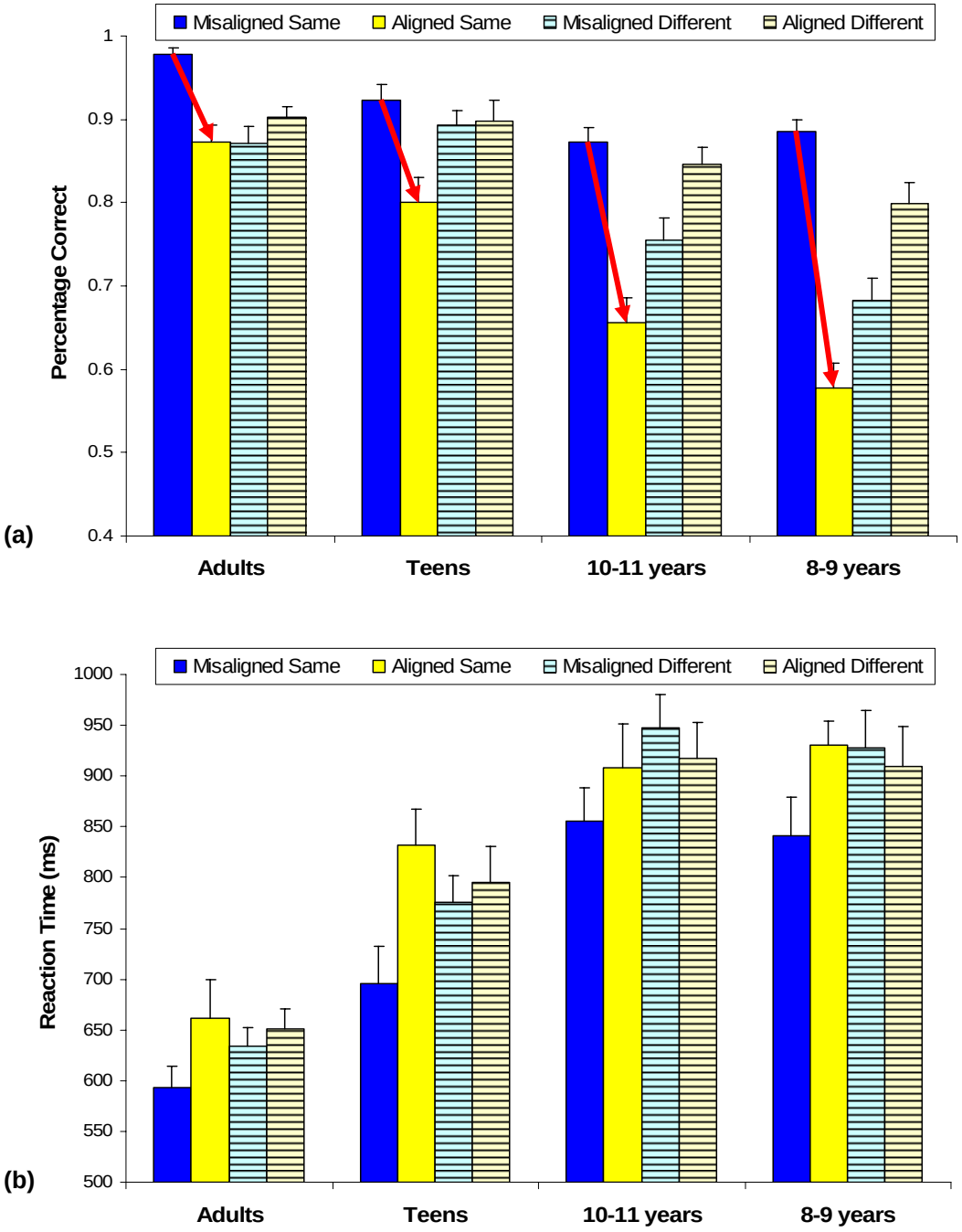


Figure 2.3 Age-based accuracy and reaction time. (a) Accuracy (percentage correct) as a function of four age groups (adults, teens, 10- to 11-year-old children, and 8- to 9-year-old children) and as a function of two conditions (misaligned, aligned) and two decisions (same, different); $F(3, 122) = 12.48$, $p \leq .001$. All CFEs are statistically significant (represented by red arrows). (b) Reaction Time (ms) as a function of four age groups (adults, teens, 10- to 11-year-old children, and 8- to 9-year-old children) and as a function of two conditions (misaligned, aligned) and two decisions (same, different); *not significant (shown for comparison purposes).

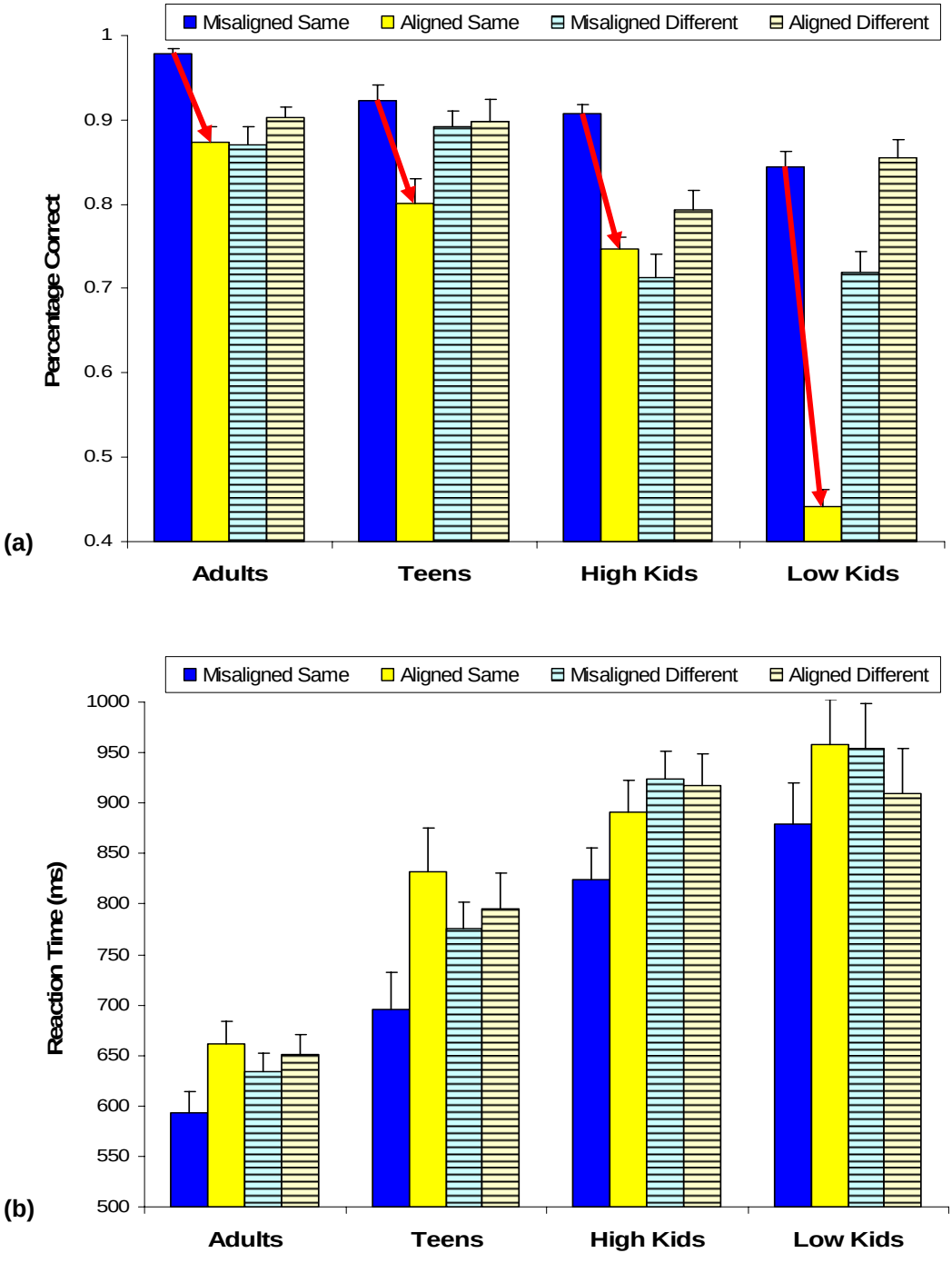


Figure 2.4 Performance-based accuracy and reaction time. (a) Accuracy (percentage correct) as a function of four performance groups (adults, teens, high performing children, and low performing children) and as a function of two conditions (misaligned, aligned) and two decisions (same, different); $F(3, 122) = 26.96$, $p \leq .001$. All CFEs are statistically significant (represented by red arrows). (b) Reaction Time (ms) as a function of four performance groups (adults, teens, high performing children, and low performing children) and as a function of two conditions (misaligned, aligned) and two decisions (same, different); *not significant (shown for comparison purposes).

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CHAPTER 3

LATERALIZED WHOLE-BRAIN NETWORKS SUSTAIN HOLISTIC PROCESSING OF COMPOSITE FACES

Faces are often considered a special class of stimuli in studies of visual-spatial processing and perception. Faces are central stimuli in our everyday live. Effective face-processing skills might have been selected through evolutionary adaptation (Parr, 2003). However, what is special might not be the face stimulus itself, but the cognitive strategies used to process faces (I. Gauthier, Skudlarski, Gore, & Anderson, 2000; Maurer, Grand, & Mondloch, 2002; Nelson, 2003). Faces appear to be processed differently from other types of visual objects. Specifically, faces are usually processed as a gestalt (a whole) (Bartlett, Searcy, & Abdi, 2003; Rhodes, 1993; Sergent, 1984; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987), whereas common objects are typically processed in a piecemeal fashion (Biederman, 1987; Donnelly & Davidoff, 1999; Driver & Baylis, 1995; Tanaka & Farah, 1993). However, both configural (whole) and featural (part) information are important in face and object processing, even if one type of information can be prominent over the other. Featural processing, arises when we encode an object or a face by isolating its featural elements. Alternatively, configural processing arises when we process the spatial relationships among the features of an object or face. Most researchers agree that configural strategies are particularly important for face processing and some of the ongoing debates in the field concern the specific nature of this strategy (I. Gauthier & Bukach, 2007; Maurer et al., 2002; Mondloch, Maurer, & Ahola, 2006; G. Yovel & Kanwisher, 2004). There are three different types of configural processing, specifically, sensitivity to first-order relations, which are basic topological relations such as above/below or left/right. First-order relations refer to the face arrangement of the eyes above a mouth and below a nose. The second type of configural processing involves sensitivity to second-order relations, which refers to the spatial distances among face features (eyes, nose, mouth, face

contour). The third type of configural processing is known as holistic processing, which capture the indivisible whole, or gestalt, of a face (Diamond & Carey, 1986; Maurer et al., 2002; Peterson & Rhodes, 2003). Most of the current debates in the literature focus on holistic and second-order information processing.

One of the key lines of evidence for the priority of configural processing for faces comes from studies of the “face inversion effect” or “FIE” (Freire, Lee, & Symons, 2000; Maurer et al., 2002; Nelson, 2003; Rhodes, 1993; Sergent, 1984). The FIE refers to the well-documented advantage in encoding upright versus inverted faces (Rakover, 2002; Searcy & Bartlett, 1996; Valentine, 1988; Yin, 1969). Typically, participants are slower and less accurate when processing inverted compared to upright faces. Notably inversion does not typically affect the speed or accuracy of object processing. The most widely accepted explanation of the inversion effect is that it differentially affects the encoding of featural versus configural information. Specifically, inversion is thought to interfere with perception of both the face configuration and with the spatial relations among the features that constitute a face, but it does not substantially alter perception of single features (Freire et al., 2000; Mondloch, Le Grand, & Maurer, 2002; Rhodes, 1993; Sergent, 1984; Valentine, 1988 but also see Yovel G. and Kanwisher N., 2004; Galit Yovel & Duchaine, 2006).

A second line of evidence for the predominance of configural, specifically holistic, processing of faces comes from studies of the “Composite Face Effect” or “CFE” (de Heering, Houthuys, & Rossion, 2007; Hole, 1994; Hole, George, & Dunsmore, 1999; R. Le Grand, Mondloch, Maurer, & Brent, 2004; Schiltz & Rossion, 2006; Young et al., 1987). In a composite face stimulus, the upper half of one face is conjoined with the lower half of a second face. The composite face task requires participants to judge

whether the upper halves of two composite face stimuli are the same or different. In the typical composite face task, the upper halves of the stimulus pair match 50% of the time, while the bottom halves always differ. Because the bottom halves of the composite faces always differ, a visual illusion is created in which the pairs with matching tops actually appear to be different. This illusion is driven by our bias to process faces as an indivisible whole, which prevails even when we are instructed to ignore part of the face configuration. This strong holistic bias disappears if tops and bottoms of the composite stimuli are laterally offset. Specifically, participants are slower and less accurate in matching same tops of aligned faces compared to tops of misaligned faces in which the bottoms can be easily ignored. Interestingly, inverting composite faces eliminates the CFE, thus it diminishes the holistic bias. This phenomenon supports the hypothesis that inversion disrupts holistic but not featural information (Carey & Diamond, 1994; Hole, George, & Dunsmore, 1999; Young et al., 1987).

Neuroimaging studies have enormously impacted the understanding of the brain basis for face and object processing. However, very few have assessed cognitive strategies and specific types of processing (Maurer et al., 2007; Bruno Rossion et al., 2000; Schiltz & Rossion, 2006; G. Yovel & Kanwisher, 2004). Most studies that have used imaging to investigate the neural correlates of face processing have done so with simple face categorization tasks and have focused on identifying brain regions that respond more intense to faces compared to other objects (I. Gauthier, Tarr et al., 2000; Haxby, Hoffman, & Gobbini, 2000; Haxby et al., 1996; Kanwisher, McDermott, & Chun, 1997; Maurer et al., 2007; Bruno Rossion et al., 2000; Sergent & Signoret, 1992). Kanwisher and colleagues (1997) named an area in the fusiform gyrus the “fusiform face area” (FFA), a region which they found to be significantly more responsive to faces than objects. Similarly, Gauthier and colleagues (2000) named another face-selective area (or

expertise-selective area) located in the inferior occipital region the “occipital face area” (OFA) (Fairhall & Ishai, 2007; Haxby, Hoffman, & Gobbini, 2000; Ishai, in press; G. Yovel & Kanwisher, 2005). A few other areas more selective for objects (e.g., scenes, body parts, words) than faces have been also identified (e.g., Grill-Spector et al., 1999; Malach et al., 1995).

Only recently, have studies began to investigate the neural correlates of specific cognitive strategies and/or different information types used to encode objects and faces (Maurer et al., 2007; Bruno Rossion et al., 2000; Schiltz & Rossion, 2006; G. Yovel & Kanwisher, 2004). Yovel and Kanwisher (2004) designed a behavioral and functional magnetic resonance imaging (fMRI) task to replicate a specific study (the so-called Janes task), which manipulated features and spatial relations among them within the same face (Richard Le Grand, Mondloch, Maurer, & Brent, 2001; Mondloch, Dobson, Parsons, & Maurer, 2004). Few studies utilized a similar design in which the same face stimulus is manipulated in order to assess both featural and configural (second-order relations) cognitive strategies (Freire et al., 2000; R. Le Grand, Mondloch, Maurer, & Brent, 2004; Maurer et al., 2007; Mondloch, Geldart, Maurer, & Le Grand, 2003; Mondloch et al., 2002; Mondloch, Leis, & Maurer, 2006; Mondloch et al., 1999; Mondloch, Maurer, & Ahola, 2006; Bruno Rossion et al., 2000). In the featural set, the face features are changed and the face contour and spatial position of the features is retained, whereas in the configural set features are retained, but the spacing among the features is altered. For example, eyes were moved few millimeters closer or farther away from each other. The resulting manipulated faces appear as different individuals from the original face, and participants engaged in a face matching task (Freire et al., 2000; Richard Le Grand et al., 2001; Mondloch et al., 2004; Mondloch et al., 2002; G. Yovel & Kanwisher, 2004). Typically, participants find the configural set more difficult to match

than the featural set. In addition, if the stimuli are inverted, a larger inversion effect is found for the configural set compared to the featural set (Freire et al., 2000; Richard Le Grand et al., 2001; Leder & Bruce, 2000; Mondloch et al., 2004; Mondloch et al., 2002). These results confirm the hypothesis that second-order relation information is disrupted to a greater degree by inversion than featural information. However, Yovel and Kanwisher (2004) created a new set of stimuli in which, unlike previous studies, difficulty was equated in both featural and configural upright sets (i.e., participants performed with same accuracy in both stimuli sets). Even more important is the fact that this manipulation reduced the inversion effect disparity between the two sets of faces in the behavioral task. In parallel, no effect of featural or configural manipulation was found in the FFA. Yovel and Kanwisher (2004) interpreted these results as evidence that processing second-order relation was not as central to face processing as had been previously thought (Freire et al., 2000; Mondloch et al., 2002). Therefore, they considered these results as evidence in support of their domain-specific sensitivity theory, for which FFA activity is not affected by cognitive strategies (Kanwisher & Yovel, 2006; G. Yovel & Kanwisher, 2004). However, slightly different task designs (blocked versus mixed trials) were used in the behavioral and imaging session of the study, making it difficult to relate behavior and brain activity in the FFA. Additionally, only activity within FFA and parahippocampal place area (PPA, a region selectively active for scenes) were considered, thus precluding the possibility of finding other brain regions sensitive to configural and featural information that might have themselves modulated FFA activity.

Recently, Maurer and colleagues (2007) reported whole brain activation for a comparison of featural and configural (second-order relations) processing using the Janes task. They replicated Yovel and Kanwisher (2004) finding in which featural and

configural information did not modulate brain activity in the FFA. Interestingly, a different section of the fusiform gyrus, adjacent to the FFA, was found more to be active during configural condition compared to featural condition. Beyond the FFA, both conditions yielded brain activity mostly in frontal and temporal areas. Moreover, most areas that were more active during the configural condition were in the right hemisphere, whereas most areas that were more active during the featural condition were in the left hemisphere.

Schiltz and Rossion (2006) investigated the neural correlates of holistic processing, using a composite face task. They only reported results from face-selective (occipito-temporal) areas comparable to FFA and OFA (specifically, the middle fusiform gyrus and the inferior occipital gyrus), in which they found more intense activation for whole faces compared to the top-half of the faces and a larger composite effect in the right hemisphere. Notably, even though the CFE was larger in the right hemisphere, they also found a significant CFE in the left occipito-temporal areas (Schiltz & Rossion, 2006). This study is the first to explore the neural correlates of holistic processing. However, it is difficult to reconcile its results to the typical behavioral findings (consistently replicated in the literature) because an atypical task design was used. The CFE was calculated contrasting the performance on two intact faces instead of subtracting the performance (or activation) of one intact face and of one misaligned face. Moreover, during the imaging session, participants were not asked to perform the composite face task, but to press a button when the face-tops had a reddish color. Therefore, it is difficult to directly relate typical CFE performance found in the literature with the neural activation described by Schiltz and Rossion (2006).

Investigating these occipito-temporal regions (FFA in particular), has certainly improved our knowledge and understanding of neural correlates of face and object

processing. Undeniably, the FFA plays a dominant role in face processing. However, it is also clear that the FFA does not perform this function in isolation. Evidence of the central role of the FFA and the importance of its connections to other brain areas originate from patient studies. Specifically, prosopagnosic patients who have severe face processing deficits, usually show bilateral lesions in the fusiform and lingual gyri (Damasio, Damasio, & Van Hoesen, 1982; Landis, Regard, Bliestle, & Kleihues, 1988). However, some prosopagnosic patients with posterior occipital lesions, but intact temporal fusiform gyri, are also severely impaired. This implicates a failure in communication between the FFA and more occipital areas and suggests an important role for this functional network in normal face discrimination (Schiltz et al., 2006; Steeves et al., 2006). Indeed, these areas are part of the so-called ventral visual stream, a fundamental cortical pathway for visual processing (Goodale & Milner, 1992; Mishkin & Ungerleider, 1982). In the cortex, visual input is first processed in primary visual areas and then projected to more anterior, higher-order areas in the extrastriate and frontal cortex. Important projections go from occipital and inferior temporal cortex to regions such as the perirhinal cortex, amygdala, parietal cortex and prefrontal cortex (e.g., Logothetis, 2000). Considering the many interconnected areas that subserve visual processing, whole brain analysis should be utilized in order to comprehensively investigate cognitive strategies of face processing.

Most researchers now agree on the localization and the selectivity of the FFA, even if there is no consensus on which cognitive processes modulate its response (I. Gauthier, Skudlarski et al., 2000; Kanwisher & Yovel, 2006; Maurer et al., 2007; Schiltz & Rossion, 2006; G. Yovel & Kanwisher, 2004). In order to understand the cognitive process and the neural correlates involved in perceiving and recognizing faces, it is important to consider more than one processing type and investigate how different cognitive strategies modulate different brain areas and brain networks. This task is

further complicated by the fact that all featural and configural strategies (including holistic) are intrinsically interconnected with each other and this interdependence can create confounds in research studies (Maurer et al., 2002). For example, making a featural change (e.g., wider mouth) can modify second-order relation as well (e.g., shorter distance from corner of the mouth to the face contour). Therefore, a combination of reliable behavioral and imaging studies is necessary to fully comprehend the complexity of face processing.

The current study is intended to establish the neural mechanisms supporting the classic behavioral CFE. If the CFE effectively elicits strong holistic processing, right-lateralized brain activation is expected in occipito-temporal areas and other regions such as frontal areas, which are implicated in working memory and attention (e.g., Corbetta, Kincade, & Shulman, 2002; Kastner & Ungerleider, 2000). Because participants were asked to pay attention only to top halves of the faces, featural processing is also expected, particularly when stimuli are offset or misaligned. Also, taking into account evidence from global-local hierarchical form studies, left-lateralized brain activity is expected for misaligned stimuli, in which only parts and features of the faces are salient. This study included two experiments. The first was a reaction time study that was designed to replicate the classic CFE finding and thus validate the primary task used in the imaging study. In the second experiment, functional neuroimaging was conducted while the participants performed the composite face task.

Methods

Participants

Two groups of participants, one group for the behavioral-only study and one group for the functional imaging study, were tested. All 32 participants in the behavioral session were undergraduate students (17 males and 14 females, mean age: 20.2) from the University of California, San Diego (UCSD); they were right-handed and had normal or corrected-to-normal vision. They received course credit for participating in the study. A different group of 16 UCSD students (7 males and 9 females, mean age: 23.6) participated in the imaging session; they also were right-handed, had normal or corrected-to-normal vision and reported no history of neurological or psychiatric disorder. At the end of the session they received a small monetary sum for participating in the study.

Stimuli

Composite face stimuli were the same as utilized in Le Grand and colleagues (2004). They were produced from gray scale digitized images of adult Caucasian faces with neutral expressions. Models (equal number of females and males) wore no jewelry, glasses or makeup, and a surgical cap covered their hair and ears. Using Adobe Photoshop, faces were horizontally split in half across the middle of the nose, and then recombined using the top and the bottom halves of different individuals. Each composite face was presented in two conditions: aligned faces and misaligned faces. In the aligned condition, the top and bottom face segments were properly aligned. In the misaligned condition, the top half of each face was offset horizontally to the left so that the right-most edge of the top half was aligned with the middle of the nose in the bottom half of the image (see Figure 3.1). The location of the top half of each face was the same for every trial. Stimuli in the aligned condition measured 9.8 cm wide and 14 cm high (5.6 x

8 visual degrees from the testing distance of 100 cm). Stimuli in the misaligned condition were 12.8 cm wide and 14 cm high (7.3 x 8 visual degrees from the testing distance of 100 cm). Although the misaligned stimuli occupied a wider horizontal visual angle, the face halves were of identical size in both conditions. Scrambled faces of the same dimensions were also created in Adobe Photoshop for the control task. To create the scrambled faces, an 8X9 square grid was overlaid on four of the face stimuli. The squares within the grid were then randomly placed into a new grid to create the scrambled faces, such that major facial features (e.g., eyes, nose and mouth) were not distinguishable, while the same range of spectral frequencies as the experimental stimuli were represented.

Procedure and Design: Behavioral Session

Participants were seated 100 cm from a laptop computer screen and were asked to judge, as quickly and as accurately as possible, whether the top halves of the two sequentially presented faces were the same or different. On every trial the bottom halves were different. Participants responded by right clicking on a computer mouse when the top halves of the two faces were the same, and left clicking when the top halves were different. As shown in Figure 3.2, each trial began with a black fixation cross displayed on a white background for 500 ms, immediately followed by a composite (or scrambled) face presented for 200 ms. A 300 ms interstimulus interval (ISI) occurred before a second composite face appeared for 200 ms. Between the second face and the start of the following trial a white background was displayed for 2300 ms. Participants gave a response during this intertrial interval (ITI). If no response was given or if a button-press occurred past the 2300 ms ITI, a null response was recorded. Each block consisted of 82 trials presented in a quasi-random order. During each run five stimulus types were presented: 16 aligned same-top faces, 16 aligned different-top faces, 16 misaligned

same-top faces, 16 misaligned different-top faces and 16 scrambled faces (see Figure 3.1). Three different quasi-random trial blocks were created and counterbalanced among participants. A short 6-trial practice was always completed (and repeated if necessary) before participants performed two consecutive runs. Accuracy (percentage correct) and reaction times (RT) were recorded. The first run for each participant was not included in the analyses; only results from second run were reported [1]

Procedure and Design: Imaging Session

Participants in the imaging study were first tested outside the magnet on the reaction time task. During the scanning session each participant completed two functional runs during which they performed the composite face task (as in the behavioral session) and one high resolution anatomical scan. The rapid event-related fMRI design used exactly the same design and parameters used in the behavioral session. RT and accuracy were obtained for performance while inside the scanner.

Image Acquisition. Imaging data were acquired at Thornton Hospital at the University of California, San Diego, using a 1.5 T Siemens Symphony MR scanner (Erlangen, Germany) equipped with a standard clinical head coil. Foam padding and a thermoplastic mask were used for head stabilization. Both earplugs and headphones with noise-cancellation capability were used to lessen scanner noise. Stimuli were rear-projected onto a screen located at the participants' feet. A small mirror was secured to the head coil above the participants' eyes in order to view the screen. Participants

[1] A preliminary study was run to assess potential practice effects. Notably, reaction time performance was poor during the first run but improved significantly by the second run [$F(51)=16.87$, $p< 5 \times 10^{-7}$], whereas runs 2, 3 (and 4) were not significantly different from each other. Similarly for accuracy data. Thus only run 2 was included in the analysis.

responded to the tasks with a hand-held mouse, connected to a laptop computer, which recorded responses. During each of functional runs, 82 whole-brain T2*-weighted axial images were acquired using a single-shot gradient-recalled echo-planar imaging pulse sequence (EPI) sensitive to blood oxygenation level-dependent (BOLD) contrast (TR =3.5 s, TE=40, FOV=220 mm, Flip Angle=90 degrees, 27 axial slices, 5 mm slice thickness, 64x64 matrix, 3.45 x 3.45 mm in-plane). The first two non-steady-state frames were discarded from each run. For anatomical localization, high-resolution T1-weighted structural images were obtained using an MP-RAGE sequence (FOV=256 mm, TR =10.7 ms, TE=5.2 ms, Flip Angle=10°, resolution = 1 mm^3; 180 sagittal slices).

Data Analysis

Preprocessing. FMRI analyses were conducted using the Analysis of Functional Neuroimages package (AFNI; version 2.5; http://afni.nimh.nih.gov/afni) (Cox & Hyde, 1997). Motion correction and three-dimensional registration were performed using 3dvolreg, an automated alignment program that co-registered each volume in the time series to the middle (39^{th}) volume acquired in that series (Cox & Jesmanowicz, 1999). All of the volumes in the two functional runs were then registered to the middle volume of the first run. The two runs were concatenated into a single time series file of 160 volumes, and then smoothed with an appropriate Gaussian filter. Individual MP-RAGE images were registered to an atlas representative target conforming to the atlas of Talairach & Tournoux (1988).

FMRI Analyses of Individual Participants. The FMRI data from individual participants were analyzed using a deconvolution approach (3Deconvolve program). Impulse response functions (IRFs) were estimated for the four TRs following stimulus presentation using a dirac delta function, providing a 14 second window for resolution of the hemodynamic response. IRFs for 12 motion parameters (three rotational and three

translational, both within and across runs) were estimated for the TR immediately proceeding stimulus presentation. A model including estimated stimulus parameters (four for each stimulus type), motion parameters, and four additional parameters to model the effects of global mean and linear trend for each run, was convolved with the input stimulus time series and submitted to multiple regression analysis. The linear contrast weights, computed by the regression analyses, estimated the BOLD signal change for each stimulus type relative to the control condition (scrambled faces) during the 2nd-3rd TR following stimulus presentation (i.e., 3.5-10.5 seconds). The resulting activation maps were converted to Z-score maps and resampled into Talairach space using the AFNI hand land-marking procedure (resampled voxel volumes = 3x3x3).

FMRI Group Analyses. A voxel-wise three-way repeated measures Analyses of Variance (ANOVA) was conducted using z-scores obtained from the multiple regression analyses. Factors included in the analysis were face aligment referred to as “Composite” (aligned and misaligned), correct responses referred to as “Decision” (same and different), and Paricipant as a random factor. In order to examine regions that display activity for the composite face effect (CFE and thus holistic processing across development), we constrained our analysis of the CFE (aligned-same - misaligned-same) contrast to examine only regions displaying a significant 2-way interaction. Thus, final contrast maps were masked to include only voxels above significance threshold (*p* ≤ *0.05* per voxel*) for* Composite by Decision interaction. After masking, the contrast maps were corrected for multiple comparisons using a voxel-cluster threshold technique (Forman et al., 1995) for an overall alpha level of 0.05, yielding a minimum cluster size of 32 contiguous voxels (864 µl) for interaction of Composite by Decision. Follow-up region of interest (ROI) analyses were also conducted, in order to further investigate face-sensitive occipito-temporal areas. However, more liberal statistical thresholds were

implemented. Specifically, ROIs were defined from the Composite by Decision interaction effect to include all voxels with intensity values above a threshold of $p \leq 0.05$.

Results

Behavioral Session Results

Separate, two-way within subjects ANOVAs were conducted on accuracy and RT data, with Composite (aligned, misaligned) and Decision (same, different) as factors. In addition, post-hoc analyses (Tukey HSD) were run to further assess composite and decision effects within the group. These analyses revealed the presence of a classically-defined composite face effect: participants' performance was less accurate and slower in the aligned-same condition compared to the misaligned-same condition. Specifically, significant main effect for the Composite factor [$F(1, 31) = 48.39$, $p < .000$] was found. However, it was moderated by a significant Composite X Decision interaction [$F(1, 31) = 7.82$, $p < .009$]. As showed in Figure 3.3, participants were faster when matching misaligned faces than aligned faces. Post-hoc analyses (Tukey HSD) revealed a significant difference ($p < .0002$) between the mean RT values for misaligned-same trials and the aligned-same trials (solid color bars in Figure 3.3, composite effect represented by a red arrow). Mean RT was 592 ms for misaligned-same trials, and 658 ms for aligned-same trials. Thus the composite effect value calculated as arithmetical difference between the mean RT for misaligned-same trials and aligned-same trials was 66 ms. No significant difference among different judgments (misaligned-different and aligned-different conditions, striped bars on Figure 3.3) was found. Misaligned-same trials were also found significantly different from misaligned-different ($p < .014$) and from aligned-different trials ($p < .0005$).

The ANOVAs for accuracy broadly mirrored the mean RT results revealing significant effects for the Composite factor [$F(1, 31) = 7.99$, $p < .008$]; and the Decision factor [$F(1, 31) = 8.16$, $p = .008$]. However, it was moderated by a significant Composite X Decision interaction [$F(1, 31) = 16.78$, $p < .0003$]. Post-hoc analyses (Tukey HSD)

revealed a significant difference ($p < .0007$) between mean accuracy scores for misaligned-same trials and the aligned-same trials. Mean accuracy level was 98% for misaligned-same trials and 87% for aligned-same trials, thus the composite effect value calculated as difference between misaligned-same and aligned-same trials was 0.11 (% correct). No significant difference among different judgments (misaligned-different and aligned-different conditions, striped bars on Figure 3.4) was found. Misaligned-same condition was also found significantly different from misaligned-different ($p < .0006$) and from aligned-different conditions ($p< .015$).

Imaging Results

In relating the fMRI analysis to the behavioral results, we focused on one contrast from the voxel-wise three-way ANOVA, the simple main effect referred to as the Composite Face Effect (CFE, aligned-same - misaligned-same). Ten areas showed a significant CFE (see Figure 3.5 and Table 3.1). In 8 cases there was a true CFE, in which brain areas showed more intense activity for aligned-same compared to misaligned-same faces. However, in left inferior parietal lobule and in right superior frontal gyrus there was a reverse CFE in which more intense activity was driven by misaligned-same than aligned-same faces. Overall, these findings highlight a group of brain areas involved in holistic face processing, which includes frontal areas such as the right medial frontal gyrus, parietal areas such as the right and the left precuneus and left inferior parietal lobule, and temporal areas such as the right fusiform gyrus and the right parahippocampal gyrus.

In order to further investigate some of the brain areas that have been associated with face processing (e.g., Haxby et al., 2000; Ishai, Schmidt, & Boesiger, 2005; Kanwisher et al., 1997), Regions Of Interest (ROIs) were drawn according to the ANOVA masks of the interaction Composite by Decision, with more liberal statistical thresholds

than accepted in the main analysis. Figure 3.6 shows brain activity associated with the four task conditions in the following regions (which served as foci for ROI placement): right and left fusiform gyrus, right parahippocampal gyrus, right inferior temporal gyrus, left middle temporal gyrus, and left middle occipital gyrus. Interestingly, all of the right hemisphere areas showed the same pattern, a significant CFE (marginally significant for the parahippocampal gyrus) and a non-significant difference between the different trials, as found in the behavioral results. Alternatively, in the left hemisphere no significant CFE was found and in the case of the middle temporal gyrus there was a significant CFE reversal, with misaligned-same trials yielding more activation than aligned-same trials.

Discussion

Faces are processed as indivisible wholes. Although, feature identification also plays an important role in recognizing a face, holistic processing is one of the main characteristics that differentiate object processing from face processing (Carey & Diamond, 1994; Hole, 1994; Lewis & Johnston, 1997; Tanaka & Farah, 1993; Young et al., 1987). Some of the more robust evidence of holistic dominance in face processing has been obtained with the composite face task (de Heering, Houthuys, & Rossion, 2007; Hole, 1994; R. Le Grand et al., 2004; Young et al., 1987), a face-matching paradigm that explicitly requires attending to the top halves of the face stimuli. Because the bottom halves are always from different individuals, a visual illusion is created for the pairs with same tops, which appear to be different from each other. In the present study, the classic composite face effect (CFE) was replicated, as participants were more accurate and faster when matching same-top from misaligned faces (which reduced the salience of the bottom halves) compared to same-top from aligned faces (with different bottom halves promoting the erroneous perception that the top halves were also different). Whole-brain fMRI analysis focused on the composite face effect (contrast between aligned-same and misaligned-same stimuli), which is considered an index of holistic processing (Carey & Diamond, 1994; Isabel Gauthier & Tarr, 2002; Hole, 1994; Kanwisher & Yovel, 2006; Young et al., 1987). The most intense brain activity was found in the frontal regions (including the right superior and medial frontal gyri), parietal regions (including the right precuneus and the left inferior parietal lobule) and ventral temporal regions (including the right inferior temporal gyrus and the right fusiform gyrus). Thus, performing the composite face task activated brain regions known to be involved in working memory (frontal areas), visual-spatial processing and attention (parietal areas) as well as object/face processing (occipito-temporal areas). Region of interest (ROI)

analyses focused on occipito-temporal areas, which are critically involved in face processing (I. Gauthier & Tarr, 1997; McIntosh et al., 1994; Puce, Allison, & McCarthy, 1999; Sergent & Signoret, 1992). Certain ROIs such as the right fusiform gyrus and the right inferior temporal gyrus exhibited a significant CFE, showing the most activity for aligned-same faces and the least activity for misaligned-same faces (see Figure 3.6). Interestingly, all the ROIs in the right hemisphere nicely mirrored the CFE behavioral results (tasks used for behavioral and imaging sessions were identical). In contrast, occipito-temporal regions of the left hemisphere including the left middle temporal gyrus and the left middle occipital gyrus showed a reverse CFE, exhibiting the most activity for misaligned-same faces and the least activity for aligned-same faces. Therefore, right occipito-temporal areas were strongly activated by intact faces, whereas left occipito-temporal areas were strongly activated by face parts, specifically by the top halves of the face stimuli, in which the eyes were most prominent. However, no single brain area was dedicated exclusively for processing intact faces or face parts. Although some regions showed preference for a particular stimulus type, it is important to note that all regions of interest were activated by all stimuli. Overall, these results are consistent with our predictions regarding the lateralization of brain activity and cognitive strategies, specifically, holistic stimuli (aligned faces) were preferentially processed in the right hemisphere and features (top halves, eyes) in the left hemisphere.

A pattern of right lateralization of holistic information and left lateralization of featural information in face-matching tasks was also found by Maurer and colleagues (2007), by Rossion and colleagues (2000) in a PET study, and by a number of ERPs studies (e.g., Allison, Puce, Spencer, & McCarthy, 1999; Itier & Taylor, 2004; Rossion, Joyce, Cottrell, & Tarr, 2003; Sagiv & Bentin, 2001). Maurer and colleagues (2007) reported whole brain activation on a face-matching task in which features and spacing

among features were manipulated in a blocked design, in order to compare featural and configural (second-order relations) processing. Consistent with whole-brain analyses in the current study, they found most areas more active during configural conditions to be right lateralized and most areas more active during featural conditions, to be left lateralized. Also similar to the current findings, both conditions yielded brain activity in frontal areas, including the right middle and inferior frontal gyri (configural condition) and the left middle and medial frontal gyri (featural condition). Interestingly, configural conditions activated typical face areas such as right and left fusiform gyrus, but not the region of the gyrus that included the FFA (functionally determined by a localizer task). An area adjacent to the FFA was found to be sensitive to the manipulation of featural and configural information. Similarly, Rossion and colleagues (2000) found more right-middle fusiform gyrus activation for whole faces compared to face parts and the reverse pattern in the homologous region in the left hemisphere, whereas control objects did not induce any change in activity in these areas.

Additional evidence for the hemispheric lateralization of holistic and featural information is found in visual-spatial analysis studies, in particular the so-called global-local-hierarchical-form tasks, which specifically assess processing of visual stimuli that can be simultaneously encoded at both holistic and featural level (Fink et al., 1997; Martinez et al., 1997; Moses et al., 2002). Even though, hierarchical-form tasks cannot be directly compared to face-matching tasks, they provide important clues on the nature of visual processing strategies and on how contextual and methodological changes influence them. Typical hierarchical-form stimuli are composed of small elements that are organized into a larger configuration, for example, many small letters such as ‘h’s, arranged to form one big letter such as a T. Participants are asked to attend and identify the global pattern, in this case the letter T, or the local pattern, in this case the letter H

(Navon, 1977). Many behavioral and imaging studies have shown that holistic (global) stimuli are preferentially processed in the right hemisphere and local (featural) stimuli in the left hemisphere (Marotta, Genovese, & Behrmann, 2001; Martinez et al., 1997; Moses et al., 2002; Rhodes, 1985, 1993; Bruno Rossion et al., 2000). However, Fink and colleagues (1999) showed that changing stimulus type produced a reversal in the typical hemispheric lateralization, specifically, when hierarchical-form stimuli were created using common objects (such as cups and anchors) instead of letters. Holistic stimuli were processed faster and more accurately in the left hemisphere, and featural stimuli in the right hemisphere (Fink et al., 1999). Thus, context modification reversed the degree of processing efficiency in the two hemispheres.

More direct evidence that context and processing bias can facilitate or impede face recognition comes from Weston and Perfect (2005) study in which participants performed a global or local hierarchical-form task before a composite face task. Participants who performed the local task immediately before engaging in the composite face task were faster in recognizing aligned composite faces than the participants who performed the global task (or the control task) just before the composite face task (Weston & Perfect, 2005). The effect dissipated after few trials of the face task, demonstrating that the processing bias induced by the previous task had a temporally limited effect and eventually participants began using the cognitive strategy driven by the current context. Attending to the small elements of a configuration in a previous task, temporarily helped participants to maintain their attention on the features of the top halves of the faces, thus ignoring the distracting bottom halves. The same mechanism is most likely applicable to the misaligned-face blocks in Schiltz and Rossion (2006) study, during which participants quickly learn to pay close attention to the top-half of the faces to overcome the composite face visual illusion. Specifically, within blocks of aligned

faces, participants expected to view only whole faces and consequently this context biased them towards holistic processing. Alternatively, within blocks of misaligned faces, they were biased towards featural strategies. In the current study, participants could not predict the nature of the face stimulus in the next mixed trial, thus both holistic and featural strategies were active in parallel across the two hemispheres. Nonetheless, the present study largely replicated the work of Schiltz and Rossion (2006), who reported more intense activation for whole versus misaligned faces and a larger composite effect in the right hemisphere (specifically, in the middle fusiform gyrus and inferior occipital gyrus). However, we did not find a significant CFE in the left hemisphere. The presence of a CFE in the right hemisphere only, found in the current study, is consistent with literature on holistic processing with face and non-face-like stimuli and suggests that both holistic and featural strategies are being implemented in parallel in the two hemispheres (Marotta et al., 2001; Martinez et al., 1997; Maurer et al., 2007; Moses et al., 2002; Rhodes, 1985, 1993; Bruno Rossion et al., 2000). Alternatively, Schiltz and Rossion (2006) showed dominance of holistic processing in both hemispheres, and extremely similar pattern of activation for the four stimulus types in all regions of interest. The nature of their stimuli, procedure and task (i.e., detecting a color change in the top-half of the stimuli) minimized the necessity for computing featural information, thus reducing left hemisphere contribution. Concurrently, the context strongly promoted holistic strategy, implementing neural substrate in both hemispheres, but in larger extent and intensity in the right hemisphere.

This contextual hypothesis is additionally supported by the differences found in accuracy and responses across two almost identical composite face tasks, which used a blocked and a mixed design. Specifically, the present study used exactly the same stimuli and parameters used by Le Grand and colleagues (2004), with the exception that

they used a blocked design. While the overall behavioral results are consistent in the two studies, this method variation yielded differences in the magnitude of the effects. In the Le Grand and colleagues (2004) study, participants performed at lower accuracy level compared to the current study, but showed a much larger CFE (23% compared to 11% in the present study). Similarly, the CFE value in mean response time was 194 ms, much larger then the CFE found in the present study, 66 ms. Additionally, in another study by Rossion and colleagues a mixed design (with simultaneous face presentation) yielded results similar to the present findings, such as very high accuracy in all conditions and a modest CFE of 7% (de Heering et al., 2007). Thus, seeing composite faces within the context of a blocked design (compared to a mixed design) resulted in a stronger holistic bias.

A limitation in the comparison of our study with others (Schiltz & Rossion, 2006; G. Yovel & Kanwisher, 2004) is that we did not include a localizer task so we cannot directly address issues related to the functionally defined FFA. The FFA proper seems to be modulated by holistic processing, but not by second-order relation processing and featural processing (Kanwisher & Yovel, 2006; Maurer et al., 2007; Schiltz & Rossion, 2006); whereas a different section of the right fusiform gyrus, adjacent to the FFA is modulated by configural and featural processing (Maurer et al., 2007). In this debate it is important to highlight that all featural and configural strategies (including holistic) are intrinsically interconnected with one other (Maurer et al., 2002). In order to understand how cognitive strategies modulate brain activation, we have to consider more than one processing type, and more important, more than one brain area. While the field has focused on the FFA and its properties, it is clear that FFA cannot act in isolation and that face processing is mediated by a network of brain regions, which includes occipito-temporal regions, parietal regions and frontal regions.

The current study and Maurer and colleagues (2007) study are the only two neuroimaging studies to consider whole-brain areas modulated by configural and featural cognitive strategies. While more studies are needed (in particular using functional connectivity techniques), reports of prosopagnosic cases provide further support for a network of critical brain regions underlying face processing. For example, prosopagnosic patient D.F. was able to perform relatively normally on simple face categorization tasks (e.g., recognizing that a certain shape is a face) and showed normal FFA activity. Nonetheless, he was severely impaired on more complex face processing tasks and was not able to recognize facial identity, gender or emotional expression (Steeves et al., 2006). Similarly, patient P.S. had a structurally intact middle fusiform gyrus, which responded normally to a basic face categorization task (e.g., discriminating a face from a cup), but showed an abnormal response pattern to individual face discrimination (e.g., discriminating Jane from Mary) (Schiltz et al., 2006). In both cases, occipital regions (i.e., occipital face area and inferior occipital gyrus) were damaged and their failed interaction with the FFA was considered crucial for face discrimination deficits (Schiltz et al., 2006; Steeves et al., 2006).

The current study found that temporo-occipital areas were not the most intensely activated areas by the CFE, but the most intense CFE was found in frontal and parietal areas, which are typically respectively associated with working memory and spatial attention tasks (e.g., Cavanna & Trimble, 2006; Corbetta et al., 2002; Kastner & Ungerleider, 2000; Rizzolatti & Matelli, 2003). Notably, these areas showed a lateralized preference for stimulus type; for example, the right precuneus and cuneus yielded more intense activity for aligned-same face, while the left inferior parietal lobule showed more intense activity for misaligned-same faces. These results suggest that the holistic-featural dichotomy in face processing is not limited to occipito-temporal areas, but

configurations and features are processed separately, at least within some parietal and frontal regions. In addition, parietal regions have been linked to feature binding of different types of information (Friedman-Hill, Robertson, & Treisman, 1995). In particular, Treisman and Gelade (1980) hypothesized that spatial attention is necessary to bind features (i.e., color, shape, lines, letters) of objects and parietal areas are pivotal in this process.

Overall, the current study replicated the classic behavioral composite face effect, which is considered to be an index of holistic processing. More importantly, the same task was used to investigate the neural correlates of the effect, finding that not only are occipito-temporal regions involved in holistic face processing, but that a fronto-parieto-temporal network is involved. Comparing our findings with others in similar tasks, we also found evidence that relatively small context changes can affect cognitive strategies. This consideration should caution us from generalizing results obtained in particular face processing tasks into general properties of face processing and its neural correlates. Face processing is not a unitary static ability; it is composed of a number of analytical skills which interact in different ways depending upon the particular context. Holistic processing is crucial, but featural, first-order relation and second-order relation processing also are important for perceiving, recognizing and memorizing a face (Diamond & Carey, 1986; Maurer et al., 2002). Many different factors can influence the context, and with the context, cognitive strategy dominance can shift in a paradigm. The complexity of face processing necessitate that imaging studies go beyond small regions of interest such as the FFA, and start investigating more consistently whole-brain networks, which would better capture this complexity and better characterize the role of cognitive strategies.

Table 3.1 Areas of Activation for the Composite Face Effect (CFE). Coordinates listed, according to Talairach and Tournoux (1988) atlas, correspond to foci of the maximum task difference. CFE activation based on the statistical mask on Composite by Decision interaction. The x, y, and z coordinates of Talairach space are defined with positive indicating the mm to the left, anterior, and superior of the anterior commissure, respectively.

	Talairach Coordinates			
Region	**X**	**Y**	**Z**	**z-score***
CFE (aligned > misaligned)				
L Precuneus	-7.5	-61.5	26.5	0.7986
L Anterior Cingulate / L Caudate	-4.5	19.5	17.5	0.7822
R Cuneus	-3	82	35	0.76
R Posterior Cingulate	-7	59	7	0.758
R Precuneus	-11	71	26	0.743
R Medial Frontal Gyrus	16.5	55.5	-3.5	0.6651
R Fusiform Gyrus	-28	35	-15	0.622
R Parahippocampal Gyrus	-28	35	-7	0.611
Reverse CFE (misaligned > aligned)				
L Inferior Parietal Lobule	26	-71	44	-0.8
R Superior Frontal Gyrus	13.5	49.5	29.5	-0.7371

L = Left, R = Right

* maximum intensity

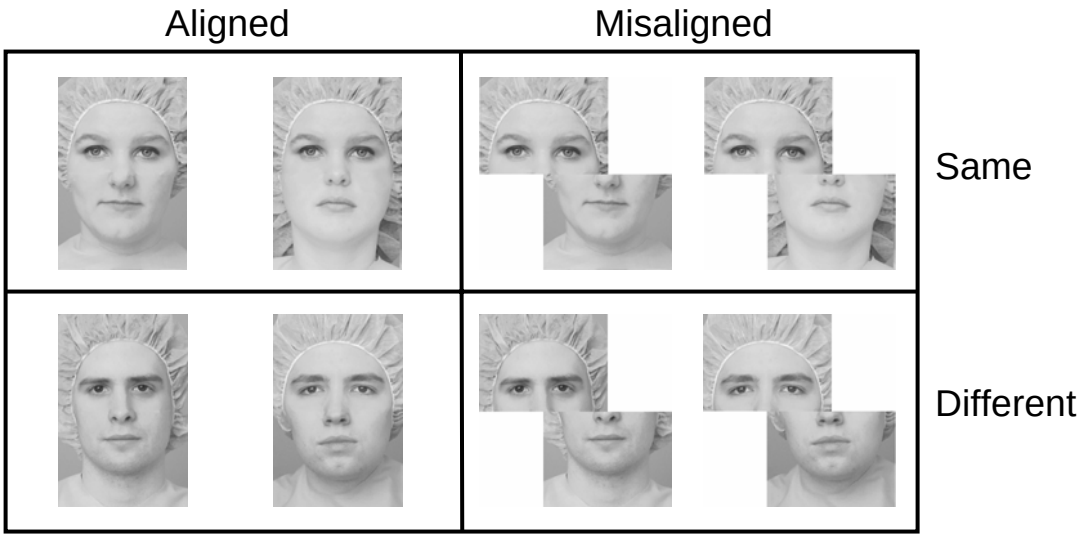


Figure 3.1 Composite face stimuli. Five stimulus types: aligned-same, misaligned-same, aligned-different, misaligned-different, and scrambled faces (not shown). Each run consisted of 80 trials presented in a quasi-random order.

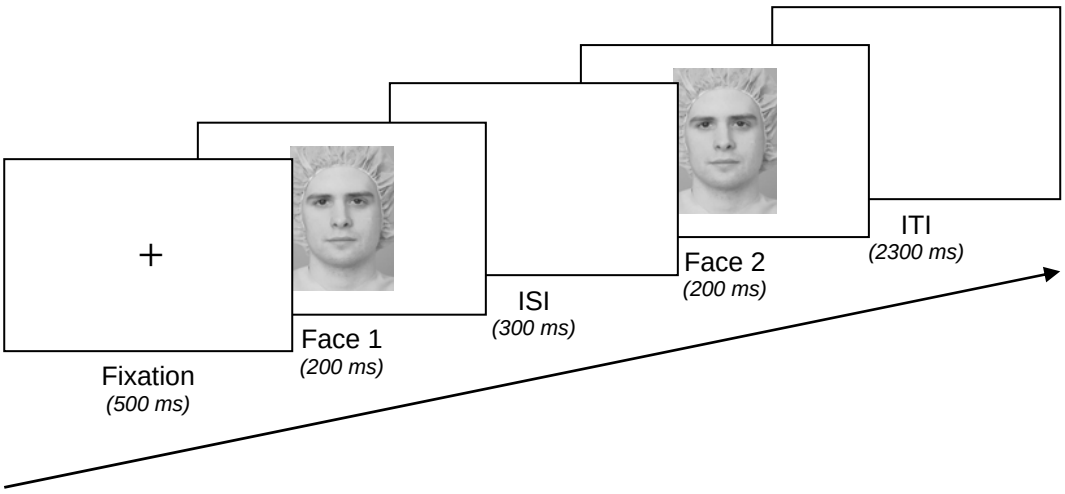


Figure 3.2 Task design. Each trial began with a black fixation cross on a white background for 500 ms, immediately followed by a composite (or scrambled) face presented for 200 ms. A 300 ms interstimulus interval (ISI) occurred before a second composite face appeared for 200 ms. The intertrial interval (ITI) was a white background screen for 2300 ms.

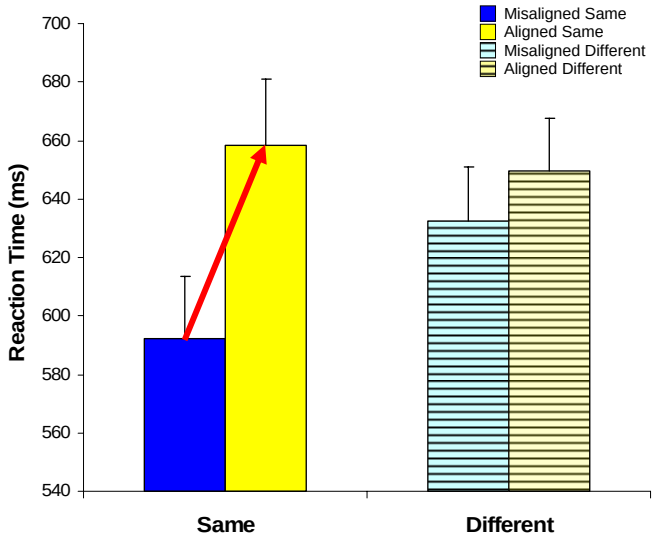


Figure 3.3 Reaction time (ms) as a function of composite (misaligned, aligned) and decisions (same, different); $F(1, 31) = 7.82$, $p \leq .009$. Post-hoc analyses (Tukey HSD) revealed a significant CFE (red arrow, $p \leq .0002$) between mean accuracy scores for aligned-same trials and misaligned-same trials.

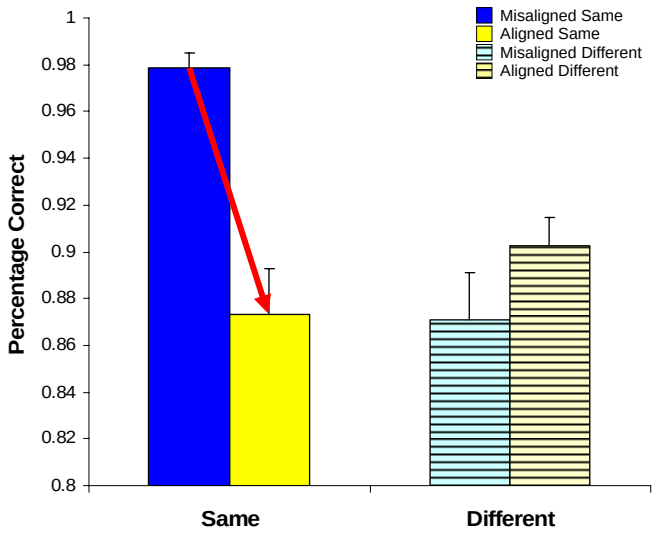


Figure 3.4 Accuracy (percentage correct) as a function of composite (misaligned, aligned) and decisions (same, different); $F(1, 31) = 16.78$, $p \leq .0003$. Post-hoc analyses (Tukey HSD) revealed a significant CFE (red arrow, $p \leq .0007$) between mean accuracy scores for aligned-same trials and misaligned-same trials.

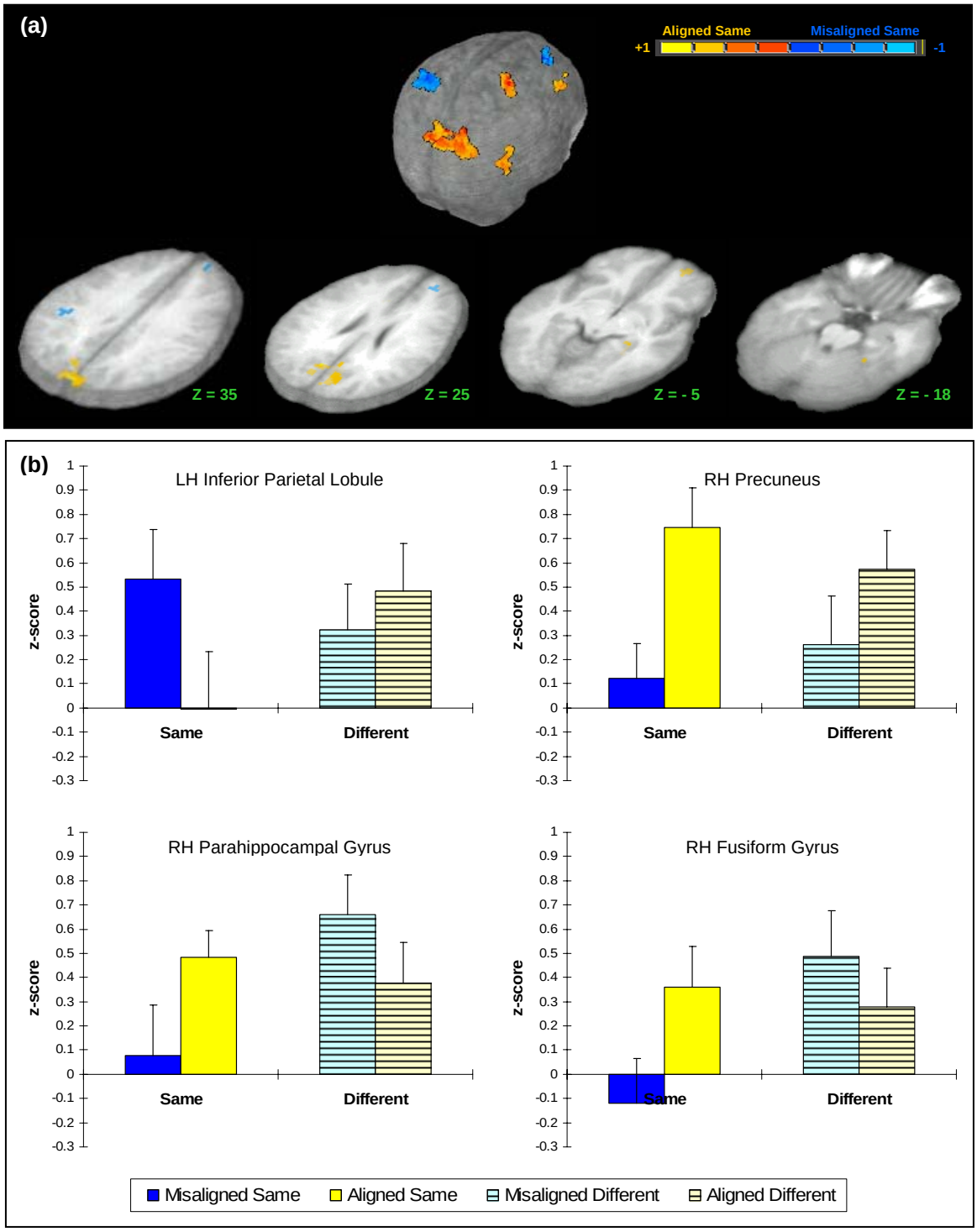


Figure 3.5 Whole-brain activation for the Composite Face Effect (CFE). (a) Areas with significant activity of CFE (aligned-same – misaligned-same) ($p \leq .05$, corrected). (b) Mean z-scores associated with each of the four stimulus conditions for the areas of interest. Right precuneus, right parahippocampal gyrus, and right fusiform gyrus displayed a significant "true" CFE; whereas, left inferior parietal lobule showed a reversed CFE with higher intensity for misaligned-same stimuli.

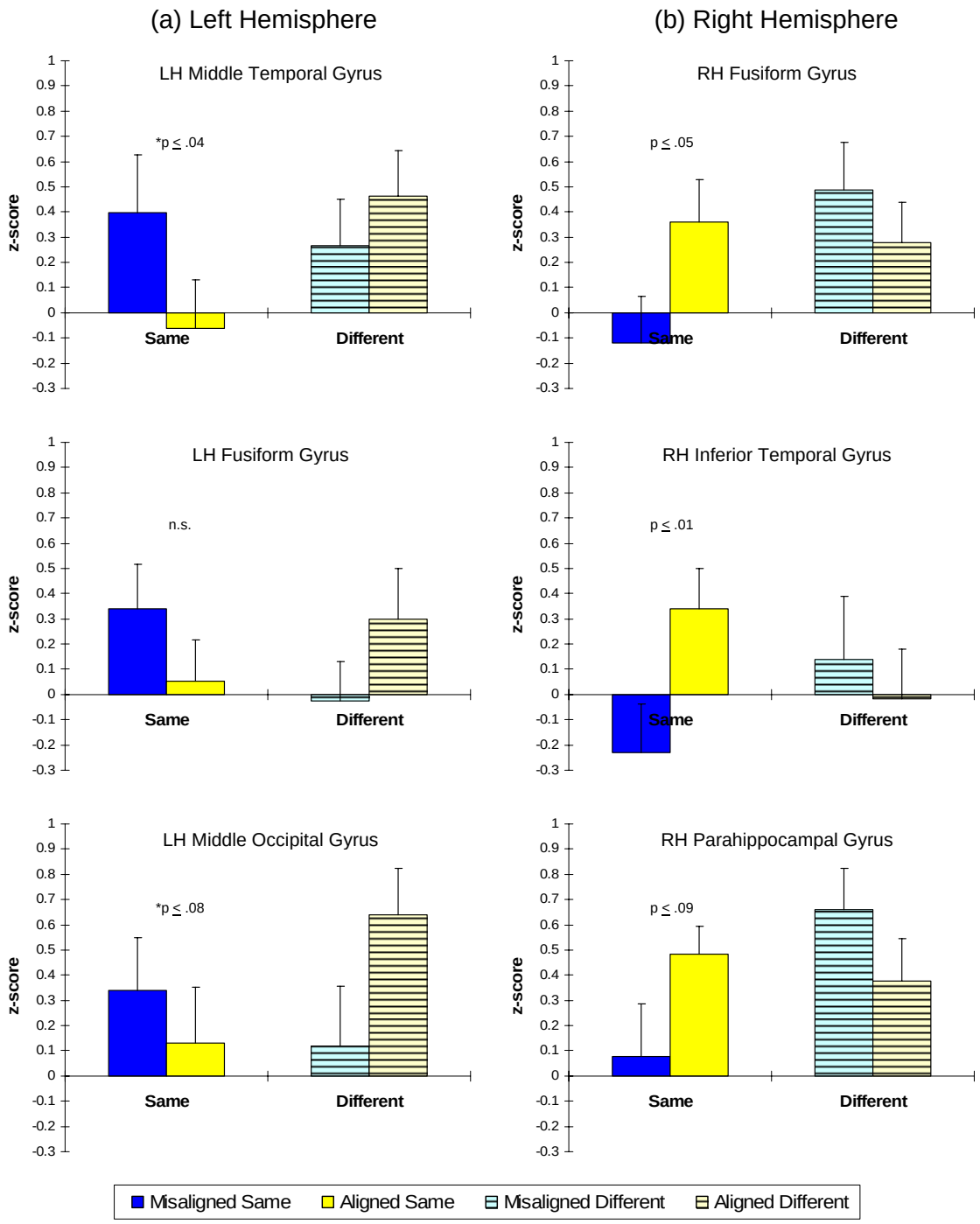


Figure 3.6 Right lateralized Composite Face Effect (CFE) in occipito-temporal areas. (a) Areas in the left occipito-temporal region with significant activity for the interaction of Composite by Decision ($p \leq .05$, uncorrected), but with no significant CFE. (b) Areas in the right occipito-temporal region with significant activity for the interaction of Composite by Decision (top and bottom graph: $p \leq .05$, corrected; middle graph: $p \leq .05$, uncorrected), and significant CFE. P-values for the CFE (solid color bars) are shown above graphs. *Indicates reversed CFE (misaligned-same > aligned-same).

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CHAPTER 4

DEVELOPMENT OF HOLISTIC FACE PROCESSING:

BEHAVIOR AND ITS NEUROCORRELATES

Adults are remarkably skilled in perceiving, recognizing and identifying faces (Bruce & Young, 1986; Carey, 1992; Haxby, Hoffman, & Gobbini, 2000; Rhodes, 1993; Sergent, 1984). Our visual attraction to faces and facility in processing them likely stems from a complex combination of evolutionary and social salience, extensive exposure to faces from birth, and the ongoing demands to recognize individual faces among a multitude of highly similar exemplars. Throughout development, the cognitive strategies recruited to perceive, recognize, identify, and remember faces are gradually refined (e.g., Carey, 1992; Margot J. Taylor, McCarthy, Saliba, & Degiovanni, 1999). Our attraction to faces starts at birth. Newborns are more attracted to face-like stimuli compared to other visual configurations from their very first minutes of life (Deruelle & de Schonen, 1998; Johnson & Morton, 1991; Maurer, 1983; Valenza, Simion, Cassia, & Umilta, 1996). However, across a wide range of face processing tasks, adult-like levels of performance are not achieved until adolescence (Carey, Diamond, & Woods, 1980; Golarai et al., 2007; Roxane J. Itier & Margot J. Taylor, 2004; Mondloch, Le Grand, & Maurer, 2002; Scherf, Behrmann, Humphreys, & Luna, 2007; Margot J. Taylor et al., 1999). Some performance disparities between children and adults may reflect differences in general cognitive abilities, such as attention and memory, which have not yet fully developed in children (e.g., de Heering, Houthuys, & Rossion, 2007; Mondloch, Pathman, Maurer, Le Grand, & de Schonen, 2007; M. J. Taylor, Batty, & Itier, 2004). Moreover, the developmental trajectory of face processing appears to be protracted relative to other equally complex visuospatial categories such as common objects and natural scenes (Golarai et al., 2007; Scherf et al., 2007). Therefore, some performance differences may be attributed to cognitive strategies implemented specifically during face processing, rather than differing general abilities (Carey & Diamond, 1977; Freire & Lee, 2001; McKone & Boyer, 2006; Slater & Quinn, 2001).

Behavioral studies of face processing in adults. In general, adults process objects in a piecemeal fashion, encoding them by isolating their constituent elements (Biederman, 1987; Donnelly & Davidoff, 1999; Driver & Baylis, 1995; Tanaka & Farah, 1993), whereas configural processing dominates the processing of faces (Carey & Diamond, 1994; Freire & Lee, 2001; Tanaka & Farah, 1993; Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998). The dominance of configural strategies in face processing is one of the main pieces of evidence used support the widely accepted proposal that faces constitute a special category of visuospatial stimuli (Gauthier & Bukach, 2007; Maurer, Grand, & Mondloch, 2002; Mondloch, Maurer, & Ahola, 2006; G. Yovel & Kanwisher, 2004). However, there is ongoing debate in the field concerning the specific nature of strategies employed during face processing. Notably, both configural (whole) and featural (part) information are important in face and object processing, even if one type of information predominates. The field is further complicated but the fact that there are three different types of configural processing (Maurer et al., 2002). The first type entails sensitivity to first order relations, which are basic topological relations such as above/below or left/right. First order relations refer to the basic face arrangement of a nose above a mouth and below the eyes. The second type of configural processing involves sensitivity to second order relations, or spatial distances among face features (eyes, nose, mouth, face contour). The third type of configural processing is known as holistic processing, which captures the indivisible whole, or gestalt, of a face (Maurer et al., 2002; Peterson & Rhodes, 2003).

One important index of the importance of configural information in face processing come from studies examining the effects in inverting face or object stimuli. The now well documented “face inversion effect” refers to the consistent finding that most adults are faster and more accurate in processing upright than inverted faces

(Rakover, 1999; Valentine, 1988; Yin, 1969). By contrast, other object categories are not affected by inversion (e.g., Tarr & Pinker, 1989). A number of behavioral studies have used face inversion in combination with manipulations of featural and second-order configural relations in face stimuli in order to test the hypothesis that face processing depends more on configural than featural information (Freire, Lee, & Symons, 2000; R. Le Grand, Mondloch, Maurer, & Brent, 2004; Maurer, O'Craven et al., 2007; Mondloch, Geldart, Maurer, & Le Grand, 2003; Mondloch et al., 2002; Mondloch, Leis, & Maurer, 2006; Mondloch et al., 1999). In these studies participants make same/different matching judgments of face pairs presented in both upright and inverted conditions. On mismatch trials, one of the faces in the pair is altered either configurally or featurally. In the inversion condition, performance with configurally altered stimuli drops relative to the upright condition, but no performance decrement is observed during inversion of stimuli that have been featurally altered (Freire et al., 2000; Richard Le Grand, Mondloch, Maurer, & Brent, 2001; Mondloch, Dobson, Parsons, & Maurer, 2004; Mondloch et al., 2002). Although the configuration specificity of inversion effect is well-documented and has been replicated many times, recent work has begun to challenge its generality. Several recent studies noted that most that the configurally and featurally altered sets of stimuli used in earlier work were not well matched for discriminability. Specifically, in the upright matching condition, performance with the featurally altered sets was significantly better (faster and more accurate) than performance with the configurally altered sets. The newer studies carefully matched performance with configurally and featurally altered stimuli during upright face processing and failed to replicate the configuration-selective decrements during in version. Rather, when discriminability of the configurally and featurally altered stimuli is well-matched, performance with both sets declines with inversion (Malcolm, Leung, & Barton, 2004; Riesenhuber, Jarudi, Gilad, & Sinha, 2004;

Galit Yovel & Duchaine, 2006; G. Yovel & Kanwisher, 2004). While the face inversion effect continues to be robust (i.e. inversion disrupts face processing), it does not appear to be specific to second order configural relations.

Another form of configural face processing, specifically holistic processing, has also been shown to be affected by inversion. Specifically, other face-specific effects known to be biased by holistic processing, the Part-Whole Effect and the Composite Effect, do not occur if the stimuli are upside down. In a whole-part task participants are typically faster and more accurate in recognizing a single feature (e.g., Bob's nose) within the context of a face (even just the face contour) compared to the same feature in isolation (Tanaka & Farah, 1993). Similar effects are not observed for scrambled faces or house stimuli. Further, the whole-advantage effect for faces is lost when the stimuli are inverted, suggesting that holistic processing is not dominant for inverted stimuli.

The composite face task is considered to be one of the most robust paradigms to assess holistic strategies in face processing (Hole, 1994; Young, Hellawell, & Hay, 1987). In typical composite face stimuli, the upper half of one face is conjoined with the lower half of a second face. Participants are asked to judge whether the upper halves of two faces are the same or different. Typically, the upper halves of the stimulus pair match 50% of the time, while the bottom halves always differ. Because the bottom halves of the composite faces always differ, a visual illusion is created in which the pairs with matching tops appear to be different. This illusion is driven by our bias to process faces as indivisible wholes, which prevails even when we are instructed to ignore part of the face configuration. This strong holistic bias disappears if tops and bottoms of the composite stimuli are laterally offset. Thus, participants are slower and less accurate in matching same tops of aligned faces than same tops of misaligned faces, in which the

bottoms can be easily ignored. This specific phenomenon, referred to as the Composite Face Effect (CFE), has been replicated with familiar and unfamiliar faces, with different parameters and designs, and with different age groups (de Heering et al., 2007; Hole, 1994; R. Le Grand et al., 2004; Mondloch et al., 2007; Schiltz & Rossion, 2006; Young et al., 1987). In addition, the difference between aligned and misaligned is lost under conditions of inversion. The illusion of a new configuration is reduced, reaffirming the hypothesis that holistic information is disrupted during inverted face processing, and featural processing becomes the prevailing cognitive strategy (Carey & Diamond, 1994; Hole, 1994; Hole, George, & Dunsmore, 1999; Young et al., 1987).

Behavioral studies of face processing in children. While it is generally agreed that adults rely primarily on configural information to process faces; however, data from children present a mixed picture. Early studies of face processing in children argued that very young children rely predominantly on featural information, and that the shift to reliance on configural information occurs over a protracted period with dominance emerging by about 10 years of age (Carey & Diamond, 1977). Subsequent research challenged this proposed late processing switch, demonstrating that children were able to successfully encode configural information at younger ages (4-6 years old) (Carey & Diamond, 1994; Freire & Lee, 2001; Tanaka et al., 1998). For example, Pellicano and Rhodes (2003) showed that children as young 4- to 5-year-old are sensitive to the part-whole advantage effect, in which they are more accurate in recognizing target facial features (eyes, mouth, nose) within a face configuration than in isolation (Tanaka & Farah, 1993). Infant studies have shown that infants are sensitive to first order relations (Goren, Sarty, & Wu, 1975; Johnson & Morton, 1991; Mondloch et al., 2002; Simion, Valenza, Cassia, Turati, & Umilta', 2002; Valenza et al., 1996), holistic (Cashon & Cohen, 2000; Cohen & Cashon, 2001; Slater, Quinn, Hayes, & Brown, 2000), and

complex facial information such as second order relations (Hayden, Bhatt, Reed, Corbly, & Joseph, 2007). While infants are able to process complex configural information in tasks specifically designed for them, their ability to perceive, manipulate and remember facial information are limited relative to adult skills (Carey, 1992; Cashon & Cohen, 2004). There is evidence that even though children are able to process configural information (Carey & Diamond, 1994; Richard Le Grand et al., 2001; Mondloch et al., 2007; Tanaka et al., 1998), they rely more heavily on featural processing than do adults (Freire & Lee, 2001; Mondloch et al., 2004; Mondloch et al., 2002; Schwarzer, 2000; Schwarzer & Roebers, 2002). Mondloch and colleagues (2004; 2002) tested 6- to 10-year-olds on a task in which they altered features, spacing and outer contour of a baseline face. Results showed that children were comparable to adults in the featural conditions, almost as skilled as adults in the contour conditions, but much worse than adults in the spacing conditions (Catherine J. Mondloch et al., 2004; Catherine J. Mondloch et al., 2002 but see McKone, 2006 #245). Other work by Mondloch and colleagues (2004; 2002) has suggested that sensitivity to second-order relations does not reach adult levels until 14 years of age or later (Mondloch et al., 2004; Mondloch et al., 2002).

Thus the central, and as yet unanswered, question concerning the development of face processing centers on defining the degree to which face processing relies on configural and/or featural information at different points in development. Some findings suggest that while young children process visual pattern configurally, they are more reliant than adults on featural processing. This dependence on featural processing makes children less efficient processors of facial information than adults in that it is not until they begin to rely predominantly on configural strategies that their face processing skills change qualitatively, leading them to become face expert in early adulthood

(Carey, 1996; Carey & Diamond, 1994; Freire & Lee, 2001; Richard Le Grand et al., 2001; Tanaka & Sengco, 1997). By contrast, other findings suggest that both configural and featural strategies slowly develop from infancy into adolescence in a quantitative fashion, and that the degree of reliance on one or the other strategy depends on the specific task and on the methodology used to test it (Taylor et al., 1999; Itier and Taylor 2004). Yet other studies question the importance of configural and featural processes in face processing, suggesting that it is the face stimuli themselves that are special. Unfortunately these study do not consider or explain how these special skills develop, thus they cannot be active players in the developmental debates (Valentine & Ferrara, 1991; G. Yovel & Kanwisher, 2004). In short, while the question of how face processing abilities develop has been an area of active debate for many years, the fundamental underlying developmental processes and trajectories have yet to be defined.

Neuroimaging studies of face processing. Behavioral data of the sort reviewed above highlight one of the major challenges to investigating a complex process such as face processing. Specifically, while one strategy may dominate processing, it usually occurs in the context of multiple, interacting strategies. When the question concerns development a wide range of additional factors, such as working memory load or differential experience, can affect task performance. Neuroimaging methodologies can help clarify behavioral findings, augmenting behavioral data by revealing the neurocorrelates of task performance. In the past decade, the number of published face processing studies using functional magnetic resonance imaging (fMRI) have grown exponentially, greatly increasing our knowledge of the brain basis of face and object processing. Unfortunately, very few studies have assessed cognitive strategies and specific types of processing (Maurer, Mondloch, & Lewis, 2007; Rossion et al., 2000; Schiltz & Rossion, 2006; G. Yovel & Kanwisher, 2004). Instead, most imaging studies

have investigated the neural correlates of face processing during simple face categorization tasks, and have focused on identifying brain regions that respond selectively to faces (e.g., Gauthier et al., 2000; Haxby et al., 1999; Ishai, Schmidt, & Boesiger, 2005; Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006; Sergent & Signoret, 1992; Spiridon, Fischl, & Kanwisher, 2006). There is now considerable data, and ongoing debate, concerning functions and characteristics of a small number brain areas that respond most strongly to faces compared to objects. Most prominent among these are the “fusiform face area” (FFA Kanwisher et al., 1997) and the “occipital face area” (OFA, e.g., Gauthier et al., 2000). There is still a need for more whole-brain studies in order to better understand neural processing networks that mediate the complex cognitive processes that underlie face processing (Bokde et al., 2005; Druzgal & D'Esposito, 2003; Gazzaley, Rissman, & Desposito, 2004; Grady, 1996; Haxby et al., 2000; Ishai, Haxby, & Ungerleider, 2002; Klopp, Marinkovic, Chauvel, Nenov, & Halgren, 2000; Maurer, O'Craven et al., 2007).

Only recently, have studies have begun to investigate the neural correlates of specific cognitive strategies and/or different information types used to process objects and faces (Maurer, O'Craven et al., 2007; Rossion et al., 2000; Schiltz & Rossion, 2006; G. Yovel & Kanwisher, 2004). A number of studies have compared fMRI activation (almost exclusively in the FFA) elicited by upright versus inverted faces (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Haxby et al., 1999; Kanwisher, Stanley, & Harris, 1999; G. Yovel & Kanwisher, 2004, 2005). These studies consistently reported a small reduction in activation intensity for inverted relative to upright faces in the FFA (Gauthier et al., 1999; Haxby et al., 1999; Kanwisher et al., 1999; G. Yovel & Kanwisher, 2004, 2005). Yovel and Kanwisher (2004) combined inversion with specific manipulations of either the features or the second order relational information in face stimuli in order to

investigate the effects of configural and featural processing demands on FFA activation. Interestingly, they found no effect of either the featural or configural manipulations within the FFA. They speculated that the higher activation elicited by upright faces might be associated with holistic processing, which unfortunately their task did not directly manipulate (Yovel and Kanwisher, 2004). Recently, Maurer and colleagues (2007) investigated whole-brain activation using a similar task in which both featural and configural (i.e., second order relations) information was manipulated (Freire et al., 2000; Leder & Bruce, 2000; Mondloch et al., 1999). They replicated the Yovel and Kanwisher (2004) finding in which featural and configural information did not modulate brain activity in the FFA. Interestingly, a different section of the fusiform gyrus adjacent to the FFA was found to be more active during the configural condition than featural condition. Beyond the FFA, both conditions yielded brain activity in frontal and temporal areas. Moreover, most areas that were more active during the configural condition were in the right hemisphere, whereas most areas that were more active during the featural condition were in the left hemisphere, corroborating the lateralization of featural versus configural information (Rossion et al., 2000; Sergent, 1984; G. Yovel & Kanwisher, 2004).

In order to address the question of what type of processing strategy directly affects FFA and OFA, Schiltz and Rossion (2006) implemented an unusual version of the Composite Face task to investigate neurocorrelates of holistic processing. Recall that the Composite Face Effect (CFE) refers to the finding that matching judgments for the upper half of two faces are better when the upper half faces are offset from the bottom half faces, than when the upper and lower halves are aligned to form a canonical face. The interpretation of this well-documented finding is that the dominance of holistic processing in the aligned face condition makes isolating the features in the upper part of

the face more difficult, and thus compromised performance relative to the misaligned condition. Schiltz and Rossion (2006) found more intense activation for intact relative to misaligned faces, thus for holistic processing. This finding was restricted to regions of interest localized in occipito-temporal face-selective areas corresponding to the FFA and OFA (specifically, the middle fusiform gyrus and the inferior occipital gyrus) in both hemispheres. The holistic bias was stronger in the right hemisphere, but also present in left occipito-temporal areas (Schiltz and Rossion, 2006). Unfortunately, it is difficult to reconcile these results with the typical behavioral findings because an atypical task design was used (see Ch. 3).

The current study. Holistic processing and its role in face processing have been increasingly investigated in the past decade and important studies have only recently been published (Carey & Diamond, 1994; de Heering et al., 2007; Hayden et al., 2007; Mondloch et al., 2007; Schiltz & Rossion, 2006). Carey and Diamond (1994) were first to use the composite face task to investigate holistic processing in children (6-year-old), and found that children showed a CFE for familiar faces. More recently, Mondloch and colleagues (2007) replicated this finding with 6-year-old children using unfamiliar faces. De Heering and colleagues (2007) found that 4-5-year-old children were sensitive to the CFE, thus sensitive to holistic information. However, their composite face task was modified from the traditional version in order to be performed by younger children.

The number of developmental fMRI projects of face processing remains small, even if recently their numbers are rapidly growing. The majority of developmental imaging studies did not directly investigate face processing strategies, but nonetheless found different patterns of brain activation between children and adults. For example, Passarotti and colleagues (2003) showed that children (10- to 12-year-olds) had a more bilateral and more diffuse pattern of activation than adults in the fusiform gyrus in a face

matching task. Gathers and colleagues (2004) also compared brain activity in occipito-temporal areas among young children (5- to 8-year-olds), older children (9- to 11-year-olds) and adults. The older child group selectively recruited parts of the right fusiform gyrus for faces, similar to adults; alternatively, young children recruited bilateral lateral occipital cortex (Gathers, Bhatt, Corbly, Farley, & Joseph, 2004). Similarly, Aylward and colleagues (2005) showed that older children (12- to 14-year-olds) activated the functionally defined FFA, whereas younger children (8- to 10-year-olds) recruited inferior occipital gyrus, an area that has been associated with processing individual face features (e.g., Haxby, et al., 2000). The authors suggested that younger children utilized a more feature-based strategy (Aylward et al., 2005; Gathers et al., 2004). Two recent studies suggested that category selectivity in occipito-temporal areas develops early (by 6- to 8-year-olds) for objects, places and scene categories, whereas faces follow a more protracted developmental trajectory for face processing (Golarai et al., 2007; Scherf et al., 2007). These results corroborate behavioral and electrophysiological studies that have suggested a protracted development of face processing relative to other complex visual stimuli (Carey et al., 1980; R. J. Itier & M. J. Taylor, 2004; Mondloch et al., 2002; Margot J. Taylor et al., 1999).

The only imaging studies that have investigated the neurocorrelates of the development of face processing strategies have used face inversion paradigms (Joseph et al., 2006; A. M. Passarotti, Smith, DeLano, & Huang, 2007). Joseph and colleagues (2006) revealed that children (8- to 10-year-olds) showed similar whole-brain activity to adults in the contrast between upright and inverted faces.. Nonetheless, in posterolateral occipital visual processing areas children showed almost no activation. In addition, young children (8-year-old) did not show a behavioral inversion effect, in contrast with adults and older children (10-year-old). The authors suggested that differences in the

activation may be associated with more reliance on featural processing by children. Interestingly, Passarotti and colleagues (2007) found no behavioral difference between children and adults in the inversion effect (Roxane J. Itier & Margot J. Taylor, 2004; A. M. Passarotti et al., 2007), but still found a distinct pattern of brain activity in the two groups. Thus, similar behavioral performance does not necessarily imply similar neural underpinnings, and differences in activity localization and intensity may reflect the cognitive strategy recruited.

Methods

Participants

All participants were right-handed, had normal or corrected-to-normal vision and reported to have no history of cognitive or neurological disorders. Prior to testing, the procedure was explained and informed written consent was obtained from adult participants, and parental permissions were obtained for child participants. At the end of the imaging session, all participants received a small monetary sum for participating in the study.

Children: 32 children[1] (8-11 years old) who had previously participated in the behavioral study (Chapter 2) agreed to take part in the imaging study. Children were selected according to their performance in the behavioral task. Specifically, children were divided in low performing and high performing groups according to their accuracy on aligned-same trials of the behavioral composite faces task. Thus, 16 children (mean age 9, 7; 7 males and 9 females) who had obtained an accuracy score between 31-56% on aligned-same trials were included in the low performing group; and 16 children (mean age 10, 7; 6 males and 10 females) who had obtained an accuracy score between 62-87% on aligned-same trials were included in the high performing group.

Adults: 16 young adults (mean age: 23,6, 7 males and 9 females) participated in the imaging study. All adults obtained an accuracy score superior to 63% on aligned-same trials in the behavioral session of the present study.

Procedure and Design

[1] Data from 5 additional children had to be discarded due to excessive movement, and data from 3 children had to be discarded due to technical problems during the scans.

Composite face stimuli were the same as those utilized by Le Grand and colleagues (2004), as well as in studies described in Ch. 2 and 3. Procedure and design were identical to the behavioral and imaging studies in Ch. 2 and 3.

Data Analysis

Preprocessing. FMRI analyses were conducted using the Analysis of Functional Neuroimages package (AFNI; version 2.5; http://afni.nimh.nih.gov/afni; (Cox & Hyde, 1997). Motion correction and three-dimensional registration were performed using 3dvolreg, an automated alignment program that co-registered each volume in the time series to the middle (39^{th}) volume acquired in that series. All of the volumes in the two functional runs were then registered to the middle volume of the first run. The two runs were concatenated into a single time series file of 160 volumes, and the smoothed with an 8 mm FWHM Gaussian filter. Individual MP-RAGE images were registered to an atlas representative target conforming to the atlas of Talairach & Tournoux (1988).

FMRI analyses of individual participants. The FMRI data from individual participants were analyzed using a deconvolution approach (3Deconvolve program). Impulse response functions (IRFs) were estimated for the four TRs following stimulus presentation using a dirac delta function, providing a 14 second window for resolution of the hemodynamic response. IRFs for 12 motion parameters (three rotational and three translational, both within and across runs) were estimated for the TR immediately proceeding stimulus presentation. A model including estimated stimulus parameters (four for each stimulus type), motion parameters, and four additional parameters to model the effects of global mean and linear trend for each run, was convolved with the input stimulus time series and submitted to multiple regression analysis. The linear contrast weights, computed by the regression analyses, estimated the BOLD signal

change for each stimulus type relative to the control condition (scrambled faces) during the 2nd-3rd TR following stimulus presentation (i.e., 3.5-10.5 seconds). The resulting activation maps were converted to Z-score maps and resampled into Talairach space using the AFNI hand land-marking procedure (resampled voxel volumes = 3x3x3).

FMRI group analyses. To directly compare CFE activation patterns across the 3 participant groups, a voxel-wise 4-way repeated measures ANOVA was conducted using z-scores obtained from the multiple regression analyses. Factors included in the analysis were: Group (adults, high performing children, low performing children), face alignment, referred to as “Composite” (aligned and misaligned), correct response, referred to as “Decision” (same and different), and Participant as a random factor nested under group. The CFE was examined in the context of the Group by Composite by Decision interaction by masking the contrast maps to include only those voxels surprassing an intensity threshold of $p \leq 0.05$ for the 3-way interaction. After masking, the contrast maps were corrected for multiple comparisons using a voxel-cluster thresholding technique (Forman, 1995) for an overall alpha level of 0.05.

A follow-up approach was then utilized to characterize each group’s unique profile of activation. In analyses conducted on the data from each group separately, the CFEs for each group were examined in the context of the individual group Composite x Decision interactions by masking the contrast maps to include only those voxels surprassing an intensity threshold of $p \leq 0.05$ for the within-group Composite by Decision interaction. After masking, the contrast maps were corrected for multiple comparisons for an overall alpha level of 0.05.

For the primary analysis the corrected alpha level corresponded to a cluster size of 30 voxels (810µl). For the secondary analyses these computations yielded a minimum cluster size of 32 contiguous voxels (864 µl) for the adult group, 35 contiguous voxels

(945 µl) for the high performing group, and 29 contiguous voxels (783 µl) for the low performing group. Follow-up region of interest (ROI) analyses were also conducted, in order to further investigate face-sensitive occipito-temporal areas. However, more liberal statistical thresholds were implemented. Specifically, ROIs were defined from the within-group Composite by Decision interaction effect to include all voxels with intensity values above a threshold of $p \leq 0.05$.

Results

Behavioral session results

Same as performance-based results in Ch. 2 (fig. 4.3.a and 4.3.b).

Imaging Results

Given that our primary objective was to examine holistic processing, as indexed by the composite face effect (CFE), the results described below focus largely on the contrast between aligned-same and misaligned-same trials. In interpreting these results, it should be noted that the CFE derives from the subtraction of two task conditions (aligned-same – misaligned-same), thus the direction of the intensity difference (i.e., positive or negative) informs whether the difference reflects a "true" CFE (positive difference), or a "reverse CFE" (in which response to misaligned-same trials is greater than that to aligned-same trials).

Primary Analysis

A CFE with intensity above the significance threshold was found in the right middle frontal gyrus. Figure 4.4 displays activity levels of the four task conditions for the 3 groups, only the low performing child group showed a significant CFE ($p \leq .002$). In the adult group the left inferior parietal lobule showed a response to misaligned-same trials greater than the response to aligned-same trials. In the high performing child group right middle to superior frontal gyrus and right middle temporal gyrus responded to aligned-same trials with higher intensity than to misaligned-same trials. In the low performing child group no regions showed differential response to these two conditions (Table 4.1). Contrary to predictions based on previous studies, the primary brain regions associated with CFE in the three groups were found in frontal and parietal areas, not in ventral-

occipito-temporal areas considered to be the principal centers of face processing. In order to investigate face-sensitive areas in each of the three groups follow up analysis were separately computed on each participant group.

Secondary Analysis

The goal of the secondary analysis was to characterize each group's individual profile of activation; however, it has to be noted that the following results do not allow direct comparison of the three groups.

Adult Group Results (same as in Ch. 3). In relating the fMRI analysis to the behavioral results, interest was focused on the simple main effect referred to as the Composite Face Effect (CFE, aligned-same - misaligned-same). Ten areas showed a significant CFE (see Figure 3.5 and Table 4.2). In 8 cases there was a true CFE, in which brain areas showed more intense activity for aligned-same compared to misaligned-same faces. However, in left inferior parietal lobule and in right superior frontal gyrus there was a reverse CFE in which more intense activity was driven by misaligned-same than aligned-same faces. Overall, these findings highlight a group of brain areas involved in holistic face processing (associated with the CFE) that includes frontal areas such as the right medial frontal gyrus, parietal areas such as the right and the left precuneus and left inferior parietal lobule, and temporal areas such as the right fusiform gyrus and the right parahippocampal gyrus (Figure 4.5)

In order to investigate brain areas that are not typically considered in studies of face processing (e.g., Haxby et al., 2000; Ishai, Schmidt, & Boesiger, 2005; Kanwisher et al., 1997), regions of interest (ROIs) were drawn according to the ANOVA masks of the Composite by Decision interaction, with more liberal statistical thresholds than accepted in the main analysis. Figure 4.6 shows brain activity associated with the four

task conditions in the following regions (which served as foci for ROI placement): right and left fusiform gyrus, right parahippocampal gyrus, right inferior temporal gyrus, left middle temporal gyrus, and left middle occipital gyrus. Interestingly, all of the right hemisphere areas showed the same pattern, a significant CFE (with the exception of the parahippocampal gyrus) and a non-significant difference between the different trials. These findings nicely parallel the behavioral results, in which adults showed a significant CFE but no difference between difference trials. Alternatively, in the left hemisphere no significant CFE was found and in the case of the middle temporal gyrus there was a significant CFE reversal, with misaligned-same trials yielding more activation than aligned-same trials.

High Performing Child Group Results. Fourteen areas showed a significant CFE, all showing more intense activity for aligned-same than misaligned-same faces. These regions included the right inferior and middle frontal gyri, parietal areas including the right precuneus and the right supramarginal gyrus, and temporal areas including the right fusiform gyrus and the right parahippocampal gyrus.

In order to further investigate specific occipito-temporal areas, ROIs were defined using a more liberal statistical threshold, specifically, in right fusiform gyrus, right cerebellum, left inferior temporal gyrus and left cerebellum. Across these areas, patterns of activation for the CFE (aligned-same – misaligned-same) were similar across both hemispheres, showing more intense activation for aligned-same stimuli (Figure 4.7).

Low Performing Child Group Results. The low performing child group failed to activate regions typically associated with face processing. As shown in Table 4.4 and Figure 4.5, brain regions that showed a CFE were: bilateral medial frontal gyri and

anterior cingulate, left nucleus accumbens, right middle and superior temporal gyrus, right supramarginal gyrus, left amygdala and left hippocampus.

The majority of the active areas revealed higher intensity for misaligned than for aligned faces. The whole-brain network of regions involved in holistic face processing for low performing children includes frontal areas such as right and left medial frontal gyrus, cingulate cortex areas such as right and left anterior cingulate gyrus, temporal areas such as left amygdala, left hippocampus and right middle and superior temporal gyrus. A small area of the right supramarginal gyrus was also active, but they showed very little activation in parietal areas. They showed no significant occipito-temporal activation, which is typical in face processing.

In order to further investigate occipito-temporal face-sensitive areas, ROIs were defined using a more liberal statistical threshold. Figure 4.8 shows brain activity associated with the four task conditions in the following regions: right and left fusiform gyrus, left parahippocampal gyrus and left amygdala and left hippocampus.

Summary of group results. It is important to note that the following observations are descriptive in nature and are not based on direct statistical comparisons among the groups. The low performing child group displayed a unique pattern of activation, whereas the high performing child group showed a pattern of activation similar to the adult group. For these latter groups brain areas associated with the CFE were found in frontal, parietal and temporal regions. Nonetheless, the active foci within the same general areas did not seem to share the same exact localization between high performing children and adults (i.e., active regions for the two groups did not seem to overlap). Furthermore, unlike the adult group, the high performing child group showed significant activation in the cerebellum. In the adult group two areas (right superior

frontal gyrus and left inferior parietal lobule) showed significantly more activation for misaligned-same stimuli, in the high performing child group all active brain areas, with the exception of the right medial frontal gyrus, responded more intensely for aligned-same face. In the low performing children almost no voxels were active for aligned-same trials in the right fusiform gyrus, which did not display a statistically significant CFE.

In the occipital-temporal ROIs, the adult group showed similarity across hemispheres revealing a lateralized pattern of higher activation for aligned-same stimuli in the right hemisphere, but higher activation for misaligned-same in the left hemisphere. Children showed similar pattern of activation bilaterally for the aligned-same and misaligned-same condition, with high performing children displaying higher intensity for aligned-same trials.

Discussion

The composite face task is considered one of the most robust paradigms to provide strong evidence in support of the predominance of holistic processing in face processing (Young et al., 1987; Le Grand et al., 2004; de Heering et al., 2007). Holistic processing and its role in face processing has been increasingly investigated in the past decade and the composite face effect (CFE) has been replicated with different age groups and with many different parameters and designs (Young et al., 1987; Hole 1994, 1999; Le Grand et al., 2004; Schiltz and Rossion, 2006; de Heering et al., 2007; Mondloch et al., 2007). However, very little is known about the neurocorrelates of the CFE and holistic face processing (Schiltz and Rossion, 2006). The intent of the present study was to assess and compare behavioral and neurocorrelates of holistic face processing across development. In order to do so, the same composite face task was implemented outside and inside the fMRI scanning environment for all participants. Following the results of the previous behavioral study (Ch. 2), child participants were grouped by performance instead of solely by age (Burgund, Schlaggar et al., 2006). In fact, children were recruited for the imaging study according to the accuracy score obtained in the most difficult condition of the behavioral task (i.e., aligned-same trials). In the behavioral task, all groups showed a significant CFE (aligned-same - misaligned-same), replicating past studies (Carey and Diamond, 1994; Le Grand et al., 2004; de Heering et al., 2007; Mondloch et al., 2007). Roughly half of the children (low performing child group) showed a larger CFE than the adults, whereas the other half of the children (high performing child group) did not significantly differ from adults.

Overall, imaging results for the CFE, thus for holistic processing, closely resembled behavioral results in that adult and high performing child groups revealed a

similar (but not identical) whole-brain pattern of activation, whereas the low performing child group showed a distinctive pattern of activation for the composite face effect. Similar to other reports of widespread activation during face processing, adults and high performing children showed a pattern of activation spanning frontal, parietal, temporal, and occipital lobes, including regions such as right inferior frontal gyrus, left precuneus, right inferior parietal lobule, right parahippocampal gyrus and right fusiform gyrus (Grady et al., 1996; Haxby et al., 2000; Druzgal and d'Esposito, 2000; Klopp et al., 2000; Ishai et al., 2002; Bernstein et al., 2002; Gazzaley et al., 2004; Bokde et al., 2005; Maurer et al., 2007). In contrast, low performing children revealed a pattern of activation that spanned frontal, cingulate and temporal regions, including right and left medial frontal gyri, subcortical areas such as the amygdala, hippocampus and putamen and bilateral cingulate cortex. Brain areas typically associated with face processing, such as the right fusiform gyrus and right inferior temporal gyrus (e.g., Kanwisher et al., 1997; Haxby et al., 1999; Rossion et al., 2000), did not reach significance for the low performing child group.

While these activation patterns very nicely map into the behavioral results, it is important to note that these results derive from within-group analyses, thus the nature of the comparison between groups is not quantitative but only descriptive. The between-group analysis yielded a parietal region for the adult group in which response intensity to misaligned-same trials was greater than to aligned-same trials, and yielded a frontal and a temporal region for the high performing child group, which displayed a true CFE. No regions in the whole brain showed differential response to the two conditions for the low performing child group. Thus, the quantitative difference among groups were found in areas not specifically associated with face processing, but in regions usually associated with attention and working memory (Corbetta et al., 2002; Treisman et al., 2006). The

lack of significant active regions for the CFE for low performing children and the minimal findings for the other two groups may highlight a few caveats of the current study. First, the CFE and thus holistic processing is measured as the difference between two conditions (aligned-same – misaligned-same), which need high-intensity brain activity in order to result in a significant difference. The CFE comprises only two of the four task conditions (excluding scrambled faces), thus the contrast analysis might be weakened by the presence of other contrasts in the data (e.g., aligned-different – misaligned-different, aligned-same – misaligned-different, etc.) which are not of interest in assessing holistic processing, but which may likely elicit certain effects in the brain. Lastly, the different pattern of activation for the low performing children may be related to their response to the constrained baseline condition (scrambled faces), to which adult and high performing child groups may be less responsive, thus, showing higher intensity of the main task stimuli. Unfortunately, we were unable to test this speculation for lack of an unconstrained baseline in our study (i.e., a null condition as baseline for the scrambled faces) so that we could have accounted for the differential response to scrambled faces among groups. Although the within-group analyses limit direct comparison of the three groups, it allows further characterization of each group's individual profile of activation, which well paralleled the behavioral results. A descriptive characterization of the activation profiles of the three groups in different brain regions follows.

Occipito-temporal areas. As explained in detail in Chapter 3, adults showed a limited extent of activation associated with the CFE in occipito-temporal face-sensitive areas (right fusiform gyrus and right parahippocampal gyrus), which was less robust than activation in parietal and frontal areas. The only other fMRI study to directly assess holistic face processing associated with the CFE focused solely on results in functionally

defined occipito-temporal face-sensitive areas (middle fusiform gyrus and inferior occipital gyrus), in which they found more intense activation for aligned compared to misaligned faces in both hemispheres, with the right hemisphere showing a larger difference between these conditions than the left hemisphere (Schiltz and Rossion, 2006). In the current CFE study, we found significant activation in the fusiform and inferior occipital gyrus in response to both misaligned-same and intact-same conditions separately, but not to their contrast (i.e., the CFE) (Paparello et al., 2004). Unfortunately, comparison of Schiltz and Rossion's (2006) study with the current one is complicated by the fact that they used an atypical composite face task so that the CFE was calculated as the difference between two intact faces, which could have strengthened the holistic bias (Schiltz and Rossion, 2006). Most other studies that have indirectly tested configural information effects in face-sensitive areas have contrasted the activation elicited by upright and inverted faces, and typically find an inversion effect for which face-sensitive areas respond more intensely to upright than inverted faces (Haxby et al., 1999; Kanwisher et al., 1999; Gauthier et al., 1999; Yovel and Kanwisher, 2004; 2005). Yovel and Kanwisher (2004) manipulated featural and second order information in both upright and inverted faces, and while they found the typical inversion effect in the FFA and OFA, they did not find an effect of cognitive strategy (i.e., featural vs. configural). Maurer and colleagues (2007) reported similar results; however, they reported whole-brain analyses and found an area adjacent to the FFA that appeared to be modulated by configural processing (second-order relations).

To our knowledge the current fMRI study is the first to directly investigate holistic face processing in children. The results in occipito-temporal areas are remarkably different for the two child groups. In fact, in the secondary analysis high performing children displayed more extensive activation than adults, whereas low performing

children showed no activation with the exception of more anterior regions such as the left temporal pole, left amygdala and left hippocampus. Thus, performance rather than age appears to affect holistic face processing in occipito-temporal areas. Certainly age (and experience) also has an important role in face processing development and its neurocorrelates. While adults and high performing children generally showed comparable patterns of activation, adults nonetheless displayed more localized and intense activity. Alternatively, high performing children displayed more widespread and less intense activity, particularly in occipito-temporal areas.

This general pattern of differences between children and adults has been found in many other face processing developmental studies (Gathers et al., 2004; Passarotti et al., 2003; Golarai, et al., 2007; Scherf et al., 2007). In fact, some studies found that young children did not recruit the classic fusiform gyrus region during face processing, but often engaged more bilateral and more occipital areas, which have been associated with processing individual face features (e.g., Haxby, et al., 2000). Therefore, it has been suggested that younger children utilize a more feature-based strategy (Gathers et al., 2004; Aylward et al., 2005). Other studies have revealed that face processing, compared to object and scene processing, has a more protracted developmental trajectory, continuing well into adolescence (Golarai et al., 2007; Scherf et al., 2007).

Among face processing developmental fMRI studies, the only two to investigate cognitive strategies assessed the neurocorrelates of the face inversion effect (Joseph et al., 2006; Passarotti et al., 2007). Joseph and colleagues (2006) revealed that children (8-10 years old) showed activation in frontal, parietal, temporal, and cerebellar regions, but little activation in posterolateral occipital visual processing areas compared to adults. In contrast to adults, children (8-year-olds) did not show a behavioral inversion effect, thus the authors suggested that the differences in activation in posterolateral occipital

areas may be associated with an increased reliance on featural processing for children. Notably, in other studies, differences in brain activity were found even when no behavioral difference was detected between children and adults in the inversion effect (Passarotti et al., 2007; Itier and Taylor, 2004b, ERP study); similar to the current findings for adult and high performing child groups in the composite face effect. In fact, Passarotti and colleagues (2007) did not find a behavioral difference in the inversion effect between adults and children. However, children showed significantly higher activity in the right lateral fusiform gyrus that showed a "reversed inversion effect" for which this areas responded more intensely to inverted compared to upright faces. In contrast with the pattern found in adult and adolescent participants. In addition, age differences were also found in the superior temporal sulcus (STS). While adult activation was limited to the right STS, children activated this area bilaterally (Passarotti et al., 2007).

Parietal Areas. Adults and high performing children both showed significant regions of activation for the CFE in the parietal lobe. Most of the adult activation was localized to the precuneus, while most of the activation for high performing children was localized to the right inferior parietal lobule. Interestingly, adults also displayed significant activation in the inferior parietal lobule, but in the left hemisphere, with higher response to misaligned-same faces, in contrast to the pattern of greater activation to aligned-same faces in the children. As with occipito-temporal areas, children who performed similarly to adults activated the same general brain areas, but with some differences between the two groups most likely attributable to age and differing levels of experience. Low performing children displayed only one very small parietal area of activation, specifically, part of the right supramarginal gyrus showed higher intensity of activation for misaligned-same stimuli. Parietal areas, as the main players in the so-called dorsal stream, are a

fundamental substrate for visual spatial processing (Ungerleider and Mishkin, 1982). Among their functions are abilities such as object awareness (e.g., Berti and Rizzolati, 1992), space perception (e.g., Rizzolati et al., 1997), reaching (Caminiti, 1996; Sabes, 2000) and visual spatial imagery (Selemon and Goldman-Rakic, 1988), as well as episodic memory (Fletcher et al., 1995; Krause et al., 1999) and self-processing (Kircher et al., 2000). Particularly relevant for the CFE, and for the nature of the composite face task, are functions such as eye movement control, visual search, active tracking (Shenoy et al., 1999; Culham et al., 1998), spatial attention and attention shifting (Le et al., 1998; Simon et al, 2002). Nagahama and colleagues (1999), in an fMRI card-sorting task, showed that the precuneus is not only important for spatial attention but might also underlay shifting attention between object features. Notably, Anne Treisman (2006, 1999) considers areas of the parietal lobe to be underpinnings of her Feature Integration Theory, in which she states that in order to perceive a complex object as a unit (unitary thought object), it is necessary to integrate its features. Spatial attention and allocation are fundamental processes for the correct binding of features (Wheeler and Treisman, 2002). The precuneus has also been associated with shifts in attention without eye movement (Gitelman et al., 1999; Beauchamp et al., 2001), which is consistent with a recent composite face study in which eye-tracking was used (de Heering et al., in press). Even more relevant for the CFE is a PET study by Fink and colleagues (1997) in which switching attention between local and global levels of complex visual stimuli (hierarchical forms, Navon, 1977) was associated with activation in medial parietal cortex. Similarly, in the composite face task, participants are instructed to pay attention to the top of the face (eyes, features), whereas during the aligned-same trials the holistic bias redirects their covert attention to the whole face. Considering these findings, it seems plausible that parietal areas are pivotal neurocorrelates of holistic face processing and of the CFE in

particular, even more important than occipito-temporal areas where most face processing studies are focused.

Frontal areas. The cognitive processes involved in Treisman's Featural Integration Theory (2006, 1999) seem relevant to holistic face processing. Holistic processing could be also defined as "automatic" or "covert" feature binding, thus if spatial attention and working memory are necessary for feature binding (Treisman and Gelade, 1980), they might also be essential for holistic face processing. Indeed, the pattern of brain activation for adults and high performing children for the CFE resembles the fronto-parietal network typically associated with attention and working memory, which share similar neural mechanisms (Desimone, 1998; Kastner and Ungerleider, 2000). Frontal areas associated with attention and working memory include brain regions such as the frontal and supplementary eye field, inferior and superior frontal gyri, dorsolateral prefrontal cortex, anterior cingulate cortex, and insula; most of these areas were found active for CFE in the current study (Corbetta et al., 1998; Kastner et al., 2000; Fink et al., 1997; Haxby et al., 2000; Ciesielski et al., 2006).

All three groups showed significant activity for the CFE in frontal areas, and as in occipito-temporal and parietal areas, brain activation patterns were most similar for adults and high performing children (Figure 4.5). Activity in working memory areas is positively correlated with difficulty level, thus it is not surprising that low performing children displayed more extensive and intense activity than the other groups in frontal areas, since their extreme behavioral CFE proved that the task was very difficult for them. Indeed, increased activity in DLPFC (dorsolateral prefrontal cortex) is associated with increased task demands and higher difficulty levels (Bokde et al., 2005; Cole, 2007; Gould et al., 2003; Barch et al., 2007). For example, Bokde and colleagues' (2005) study revealed right frontal activation for the baseline task, but bilateral frontal activation for the

more difficult task. In parallel, both adults and high performing children showed right frontal activation (more responsive for misaligned-same in adults and more responsive for aligned-same in children), whereas low performing children displayed bilateral frontal activation for the CFE, consistent with the task being more difficult for them. Moreover, increase in frontal activity has been associated with decrease in activity in visual cortex, also consistent with the finding that low performing children displayed the most frontal activation but showed no activation in visual cortex (Bokde et al., 2005; Grady et al., 1996; Holcomb et al., 1996 tone matching).

Studies on global and local hierarchical forms may also inform interpretation of the current results (Navon, 1977; Fink et al., 1997; Moses et al., 1999). Fink and colleagues (1997) showed that adults who had to switch between attending to global and local aspects of hierarchical forms activated not only parietal areas, but also ACC (anterior cingulate cortex) and prefrontal areas in the switching task, but not in the sustained task. In the ACC (which is associated with decision making, monitoring, and attention) our adults showed a significant CFE, whereas low performing children displayed higher intensity of activation for misaligned compared to aligned faces and showed a reversed CFE.

Cerebellum. Finally, it should briefly noted that in contrast with adults, high performing children showed extensive cerebellar activation in both hemispheres. Cerebellum activation has been found in many other whole-brain face processing studies; however, these results are rarely directly addressed or interpreted, most likely due to our limited knowledge of cognitive functions of the cerebellum (Katz and Steinmetz, 2002). Moreover, most of the limited data on cerebellar involvement in cognitive functions has come from patient studies, thus it is problematic to infer the extent of cerebellar involvement in typical development of cognitive functions (Steinlin,

2007). However, given evidence of cerebellar involvement in working memory and attentional switching (Akshoomoff and Courchesne, 1992; Le et al., 1998, Hayes et al., 1998), one hypothesis regarding our own cerebellar findings is that cerebellar input to working memory and attention networks might be more salient during learning and development and therefore constitutes part of the holistic face processing network only for the child group. However, further studies on the development of cerebellar functions are needed in order to better interpret the current findings.

Low performing children profile. Considering both behavioral and imaging evidence, it is clear that the low performing children are doing something quite different during task performance than the other two groups. One possible interpretation of their behavior suggests that they are more affected by the holistic bias than the other groups and were unable to selectively focus their attention to the task relevant features. However, this hypothesis seems unlikely for a few reasons. First, low performing children exhibited unreliable (i.e., below chance) behavioral performance on aligned-same trials. Second, their brain activation pattern differs considerably from adults, who are known to rely on holistic processing (Hole et al., 1994; Tanaka and Farah, 1993; Thompson, 1980). Third, developmental visual-spatial (Stiles and Tada, 1996; Stiles, 2001; Stiles et al., in press) and face processing studies do not support the hypothesis that children have stronger reliance on holistic/configural than featural processing. On the contrary, some studies provide evidence that children rely more heavily on featural processing compared to adults (Freire & Lee, 2001; Schwarzer et al., 2000; 2002).

An alternative interpretation of the low performing group behavior was first considered in order to explain the significant performance difference found in children between aligned-different and misaligned-different trials, a difference that is not typically reported in the literature and was not found in adults and teenagers. This hypothesis

suggests that low performing children did not engage in holistic processing during the difficult aligned-same trials, but instead they implemented a simpler “difference-detection” strategy, matching all possible discrepancies, feature-by-feature in both tops and bottoms of the stimuli. They visually searched the entire stimulus in order to detect any featural difference between the two sequentially presented faces. Considering that 100% of the bottom halves of the faces mismatched, and that they were unable to ignore these distractors when the stimuli where aligned, they were biased to (correctly) press the “different” button for most of the aligned-different stimuli (87% correct responses). Similarly, they were biased to (incorrectly) press the “different” button for most of the aligned-same stimuli, thus showing a large CFE (misaligned-same – aligned-same), which in this case *was not* an index of holistic processing. The imaging results reinforce this interpretation. In fact, low performing children were generally more responsive to misaligned faces, whereas adults and high performing children were generally more responsive to intact stimuli. Moreover, low performing children were the only group to show significant activation in the STS, which is associated with eye movements, possibly indicating that they were engaging in a visual search of the entire stimulus in order to detect featural differences. Interestingly, Fink and colleagues (1997) found a correlation between the number of attentional switches (per minute) between global and local levels and intensity of activation in the superior temporal gyrus. Thus, it is plausible that low performing children were “switching” or alternating more often between featural and holistic processing during the aligned-same trials, whereas the other groups were better able to sustain a holistic mode of processing. Notably, the STS is an area often associated with face processing and is considered to be part of a face processing network of occipito-temporal areas (Kanwisher et al., 1997; Puce et al., 1999; Haxby et al., 2000; Ishai et al., 2005; Pageler et al., 2003). In face processing tasks the STS has

been associated with perception of social signals such as gaze, head orientation, speech related lip movements, and facial expressions, all characteristics which should not have affected the present CFE. In general visual processing, the STS is associated with initiation and maintenance of eye movements (e.g., Newsome et al., 1985); thus, it is possible that low performing children moved their eyes more than the other two groups, scanning the visual field in search of differences within the aligned-same stimuli. Unfortunately this hypothesis cannot be directly assessed because we were not equipped with an eye-tracking system.

In conclusion, imaging results paralleled behavioral results in that adults and high performing children showed similar performance levels and similar brain activation patterns, whereas low performing children differed from the other groups in both performance and brain activation. Adults and high performing children showed a network of regions for holistic face processing that spanned frontal, parietal, temporal, and occipital lobes, whereas low performing children revealed a network which crossed mostly frontal, cingulated, and subcortical areas. These differences may be attributable to the use of different cognitive strategies. In particular, adults and high performing children seem to predominantly rely on holistic processing, whereas low performing children may rely more on featural processing (e.g., difference-detection strategy throughout the whole face stimulus). However, the extent of frontal and cingulate cortex activation in low performing children may also suggest that because the task was especially difficult for them, working memory resources were particularly taxed, thus affecting the neural network engaged. Importantly, not only were performance differences associated with distinct neurocorrelates (i.e., differing profiles for low performing children vs. high performing children and adults), but age differences also had an appreciable effect. In fact, high performing children did not significantly differ

from adults in the behavioral CFE, but did show differences in the neural CFE. Using the same task inside and outside of the fMRI scanning environment and matching participants of different ages by performance has been informative in the current investigation of the development of holistic face processing and its neurocorrelates. Future imaging studies should further explore the implementation of the composite face task. Particularly in developmental studies, we should aim to disentangle the neurocorrelates of the CFE from the possible effects of contrasts among the other task conditions.

Table 4.1 Areas of activation for the Composite Face Effect (CFE) for the three groups from the primary analysis. Coordinates listed, according to Talairach and Tournoux (1988) atlas, correspond to foci of the maximum task difference. CFE activation based on the statistical mask on Group by Composite by Decision interaction. The x, y, and z coordinates of Talairach space are defined with positive indicating the mm to the left, anterior, and superior of the anterior commissure, respectively.

	Talairach Coordinates			
Region	**X**	**Y**	**Z**	**z-score***
All Groups				
R Middle Frontal Gyrus (BA 9)	-31.5	34.5	35.5	0.5664
Adult Group				
L Postcentral gyrus / L inferior Parietal Lobule	52	-22	42	-0.845
High Performing Child Group				
Right Middle Frontal Gyrus / Right Superior Frontal Gyrus	-22	40	32	0.919
Right Middle Temporal Gyrus	-50	-50	12	0.853
*Low Performing Child Group^*				

L = Left, R = Right

* maximum intensity

^ no significant areas found

Table 4.2 Areas of activation for the Composite Face Effect (CFE) for the adult group. Coordinates listed, according to Talairach and Tournoux (1988) atlas, correspond to foci of the maximum task difference. CFE activation based on the within-group statistical mask on Composite by Decision interaction. The x, y, and z coordinates of Talairach space are defined with positive indicating the mm to the left, anterior, and superior of the anterior commissure, respectively.

	Talairach Coordinates			
Region	**X**	**Y**	**Z**	**z-score***
CFE (aligned > misaligned)				
L Precuneus	7.5	-61.5	26.5	0.7986
L Anterior Cingulate / L Caudate	4.5	19.5	17.5	0.7822
R Cuneus	-3	-82	35	0.76
R Posterior Cingulate	-7	-59	7	0.758
R Precuneus	-11	-71	26	0.743
R Medial Frontal Gyrus	-16.5	55.5	-3.5	0.6651
R Fusiform Gyrus	-28	-35	-15	0.622
R Parahippocampal Gyrus	-28	-35	-7	0.611
Reverse CFE (misaligned > aligned)				
L Inferior Parietal Lobule	26	-71	44	-0.8
R Superior Frontal Gyrus	-13.5	49.5	29.5	-0.7371

L = Left, R = Right

* maximum intensity

Table 4.3 Areas of activation for the Composite Face Effect (CFE) for the high performing child group. Coordinates listed, according to Talairach and Tournoux (1988) atlas, correspond to foci of the maximum task difference. CFE activation based on the within-group statistical mask on Composite by Decision interaction. The x, y, and z coordinates of Talairach space are defined with positive indicating the mm to the left, anterior, and superior of the anterior commissure, respectively.

	Talairach Coordinates			
Region	**X**	**Y**	**Z**	**z-score***
CFE (aligned > misaligned)				
R SupraMarginalGyrus / R Inferior Parietal Lobule	-46.5	-34.5	35.5	1.0287
R Cerebellum (IV-V)	-16.5	-40.5	-24.5	0.9859
R Fusiform Gyrus	-39	-61	-17	0.9719
R Middle Frontal Gyrus	-25.5	37.5	35.5	0.8851
R Fusiform Gyrus	-32	-61	-8	0.8436
R Inferior Frontal Gyrus (BA 47)	-40.5	16.5	-9.5	0.8261
R Inferior Frontal Gyrus / R Middle Orbital Gyrus	-37.5	34.5	2.5	0.7894
L Cerebellum (IV-V)	16.5	-49.5	-15.5	0.7442
L Cerebellum (VIII)	34.5	-58.5	-45.5	0.7284
R Middle Occipital Gyrus	-36	-60	10	0.7001
R Postcentral Gyrys	-39	-19	36	0.6673
R Parahippocampal Gyrus	-30	-35	-4	0.5921
R Insula	-35	21	6	0.5675
R Precuneus	-24	-55	19	0.5375

L = Left, R = Right * maximum intensity

Table 4.4 Areas of activation for the Composite Face Effect (CFE) for the low performing child group. Coordinates listed, according to Talairach and Tournoux (1988) atlas, correspond to foci of the maximum task difference. CFE activation based on the within-group statistical mask on Composite by Decision interaction. The x, y, and z coordinates of Talairach space are defined with positive indicating the mm to the left, anterior, and superior of the anterior commissure, respectively.

	Talairach Coordinates			
Region	**X**	**Y**	**Z**	**z-score***
Reverse CFE (misaligned > aligned)				
R & L Medial Frontal Gyrus (BA 10) / R & L Anterior Cingulate	-10.5	49.5	-3.5	-1.2271
L Nucleus Accumbens	13.5	10.5	-6.5	-0.8426
R Superior Temporal Gyrus	-52.5	-49.5	17.5	-0.7927
L Anterior Cingulate	8	35	-9	-0.746
R Supramarginal	-52	-50	27	-0.6987
R Middle Temporal Gyrus	-54	-47	10	-0.6897
L Inferior Frontal Gyrus	28	16	-12	-0.6494
CFE (aligned > misaligned)				
L Hippocampus / L Amygdala	19.5	-7.5	-24.5	0.9227
R Middle Frontal Gyrus	-25.5	40.5	11.5	0.826
R Superior Frontal Gyrus	-17	52	13	0.7271

L = Left, R = Right * maximum intensity

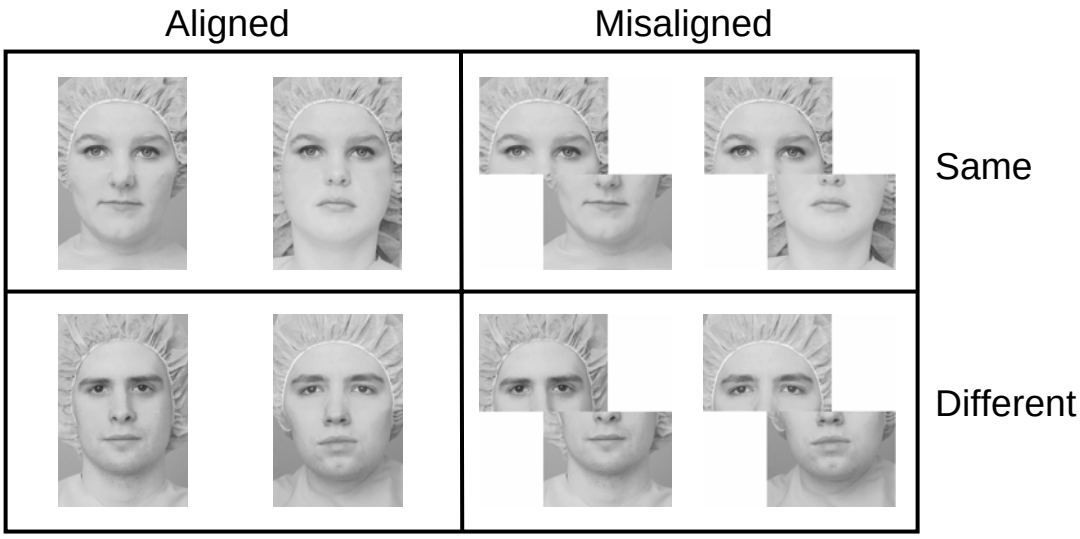


Figure 4.1 Composite face stimuli. Five stimulus types: aligned-same, misaligned-same, aligned-different, misaligned-different, and scrambled faces (not shown). Each run consisted of 80 trials presented in a quasi-random order.

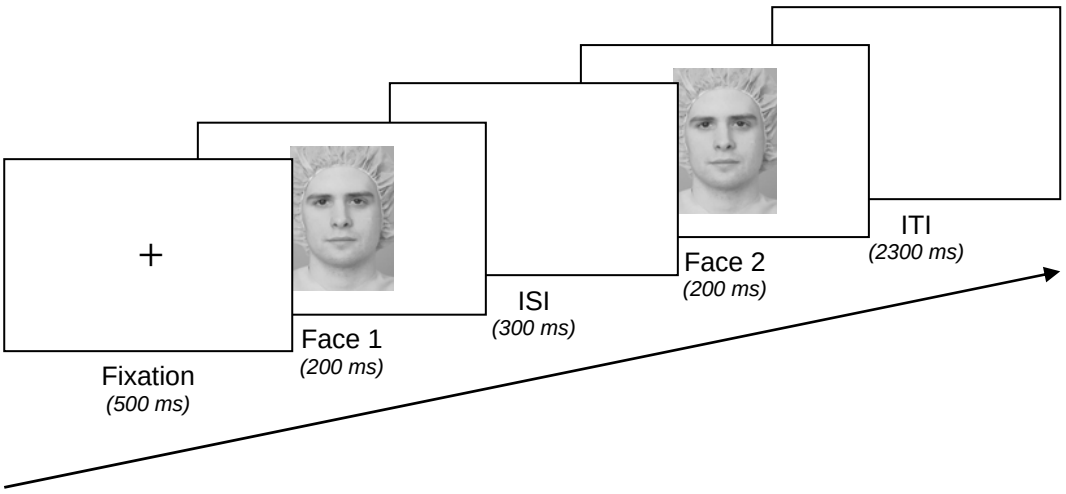


Figure 4.2 Task design. Each trial began with a black fixation cross on a white background for 500 ms, immediately followed by a composite (or scrambled) face presented for 200 ms. A 300 ms interstimulus interval (ISI) occurred before a second composite face appeared for 200 ms. The intertrial interval (ITI) was a white background screen for 2300 ms.

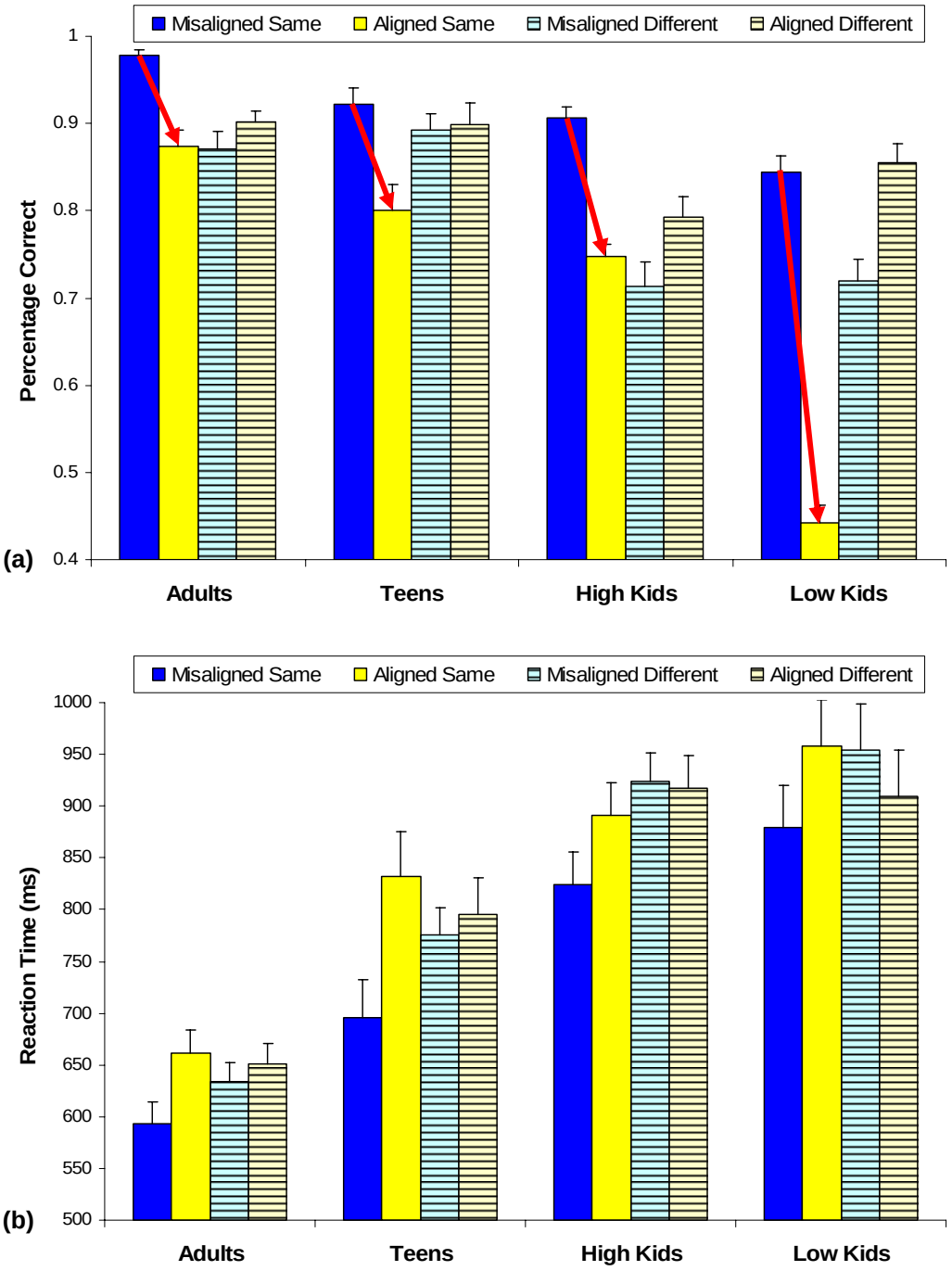
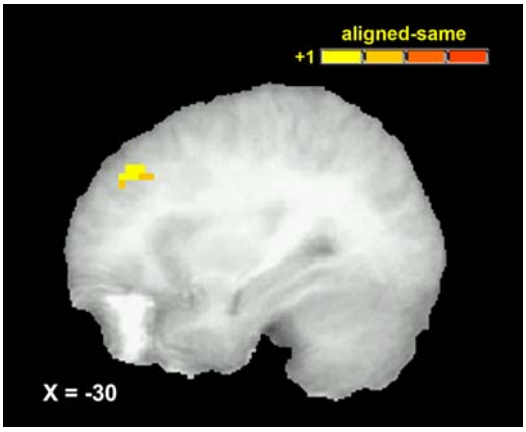


Figure 4.3 Behavioral Composite Face Effect (CFE). (a) Accuracy (percentage correct) as a function of four performance groups (adults, teens, high performing children, and low performing children) and as a function of two conditions (misaligned, aligned) and two decisions (same, different); $F(3, 122) = 26.96$, $p \leq .001$. All CFEs are statistically significant (represented by red arrows). (b) Reaction time (ms) as a function of four performance groups (adults, teens, high performing children, and low performing children) and as a function of two conditions (misaligned, aligned) and two decisions (same, different); *not significant (shown for comparison purposes). All CFEs are statistically significant.



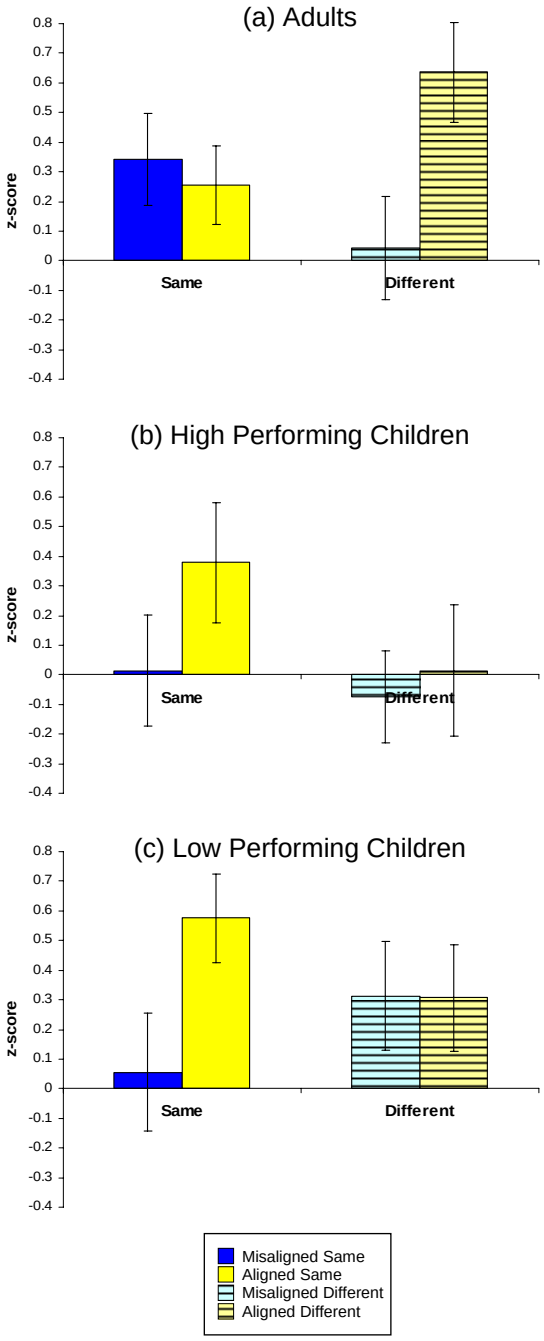


Figure 4.4 Area of activation for Composite Face Effect (CFE) for the three groups combined. Mean z-scores image is displayed, depicting the right middle frontal gyrus (-31.5, -34.5, 35.5; $p \leq 0.05$ corrected) active for CFE based on Group by Condition by Decision interaction. Graphs a, b, and c show the activity level for each of the four task conditions respectively for adults, high performing children, and low performing children. Only low performing children display a significant CFE (c.; $p \leq 0.002$).

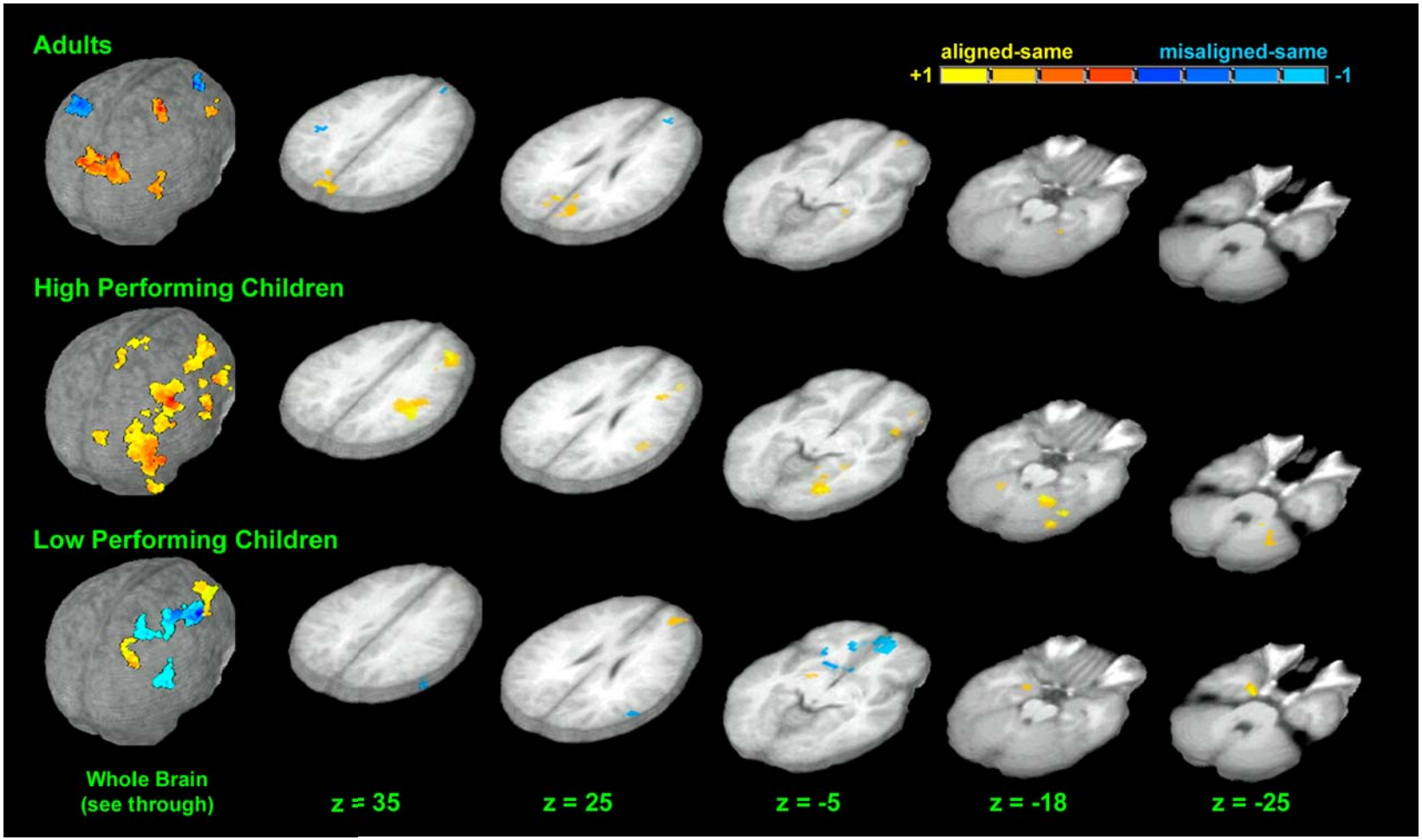


Figure 4.5 Areas of Activation for Composite Face Effect for each of the three separate groups. Mean z-score images ($p \leq 0.05$ corrected) are displayed for each of the three groups. The adult and high performing child groups revealed a similar whole-brain pattern of activation spanning the frontal, parietal, temporal, and occipital lobes. The low performing child group revealed a pattern of activation that spanned the frontal, temporal, cingulate, and cerebellar regions.

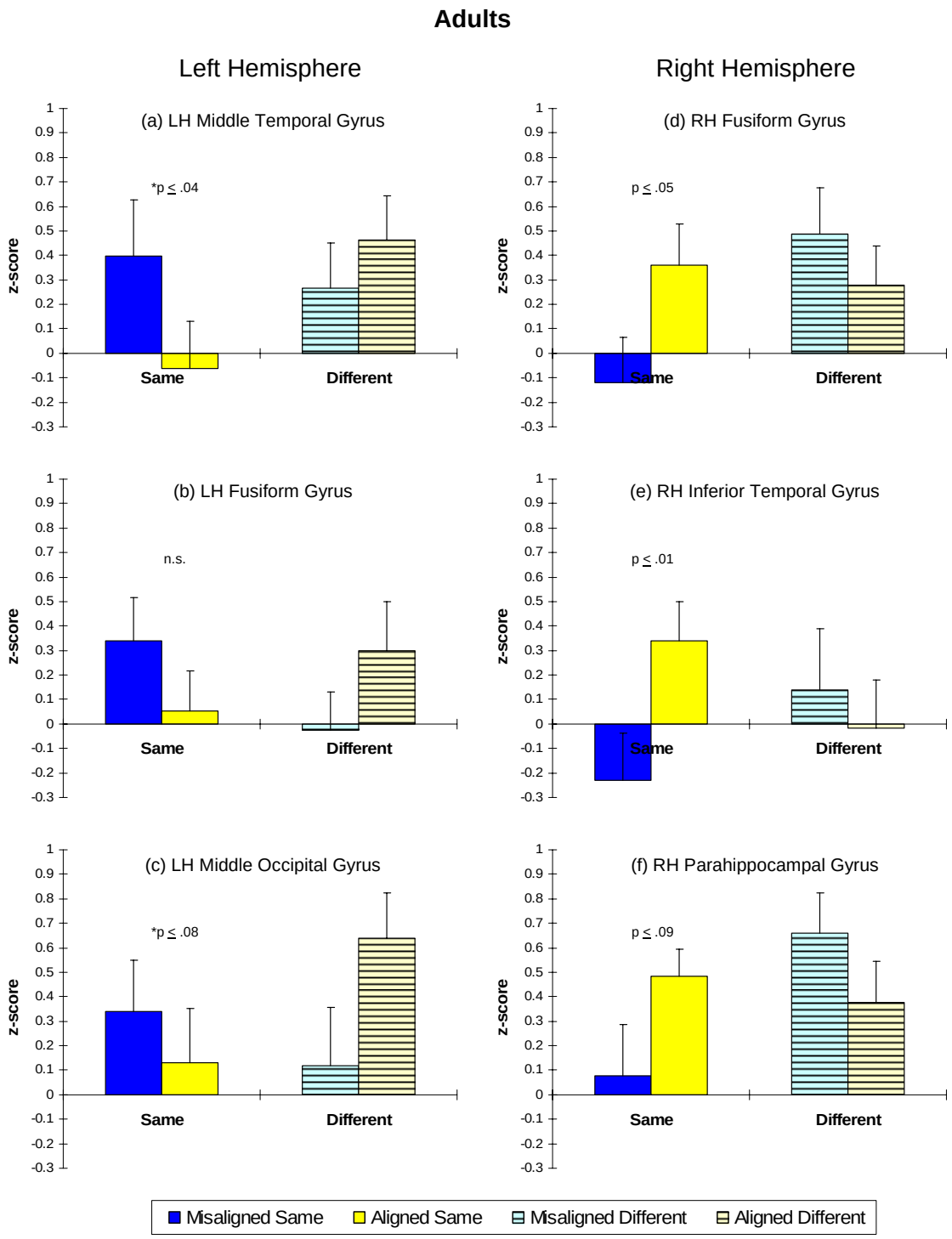


Figure 4.6 Right lateralized Composite Face Effect (CFE) in occipito-temporal areas. (a,b,c) Areas in the left occipito-temporal region with significant activity for the interaction of Composite by Decision ($p \leq .05$, uncorrected), but with no significant CFE. (d,e,f) Areas in the right occipito-temporal region with significant activity for the interaction of Composite by Decision (d and f: $p \leq .05$, corrected; e: $p \leq .05$, uncorrected), and significant CFE. P-values for the CFE (solid color bars) are shown above graphs. *Indicates reversed CFE (misaligned-same > aligned-same).

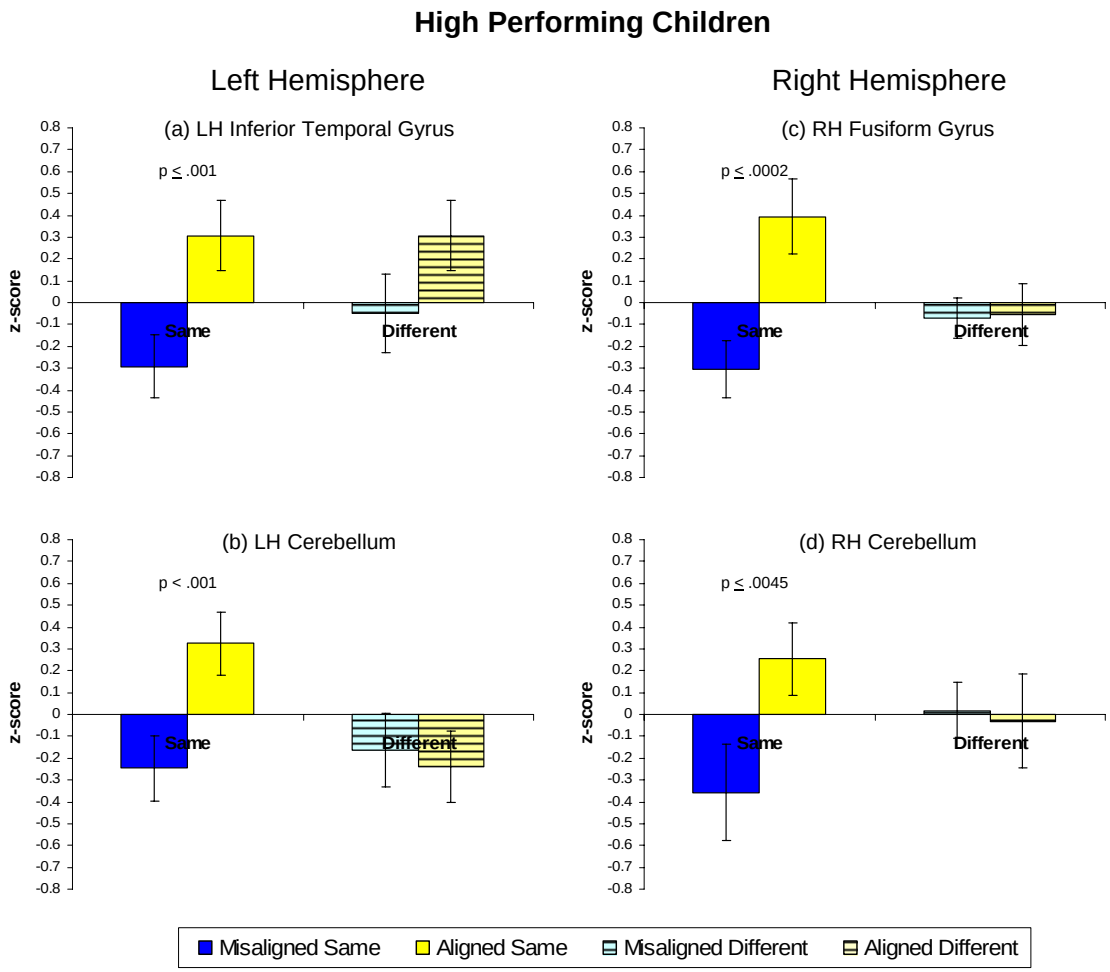


Figure 4.7 Activation for the four task conditions in some occipital, temporal, and cerebellar areas for high performing children. (a) Left inferior temporal gyrus. (b) Area in the left cerebellar region with few voxels overlapping with the left fusiform gyrus. (c) Right fusiform gyrus. (d) Right cerebellum. P-values for the composite face effect (solid color bars) are shown above graphs.

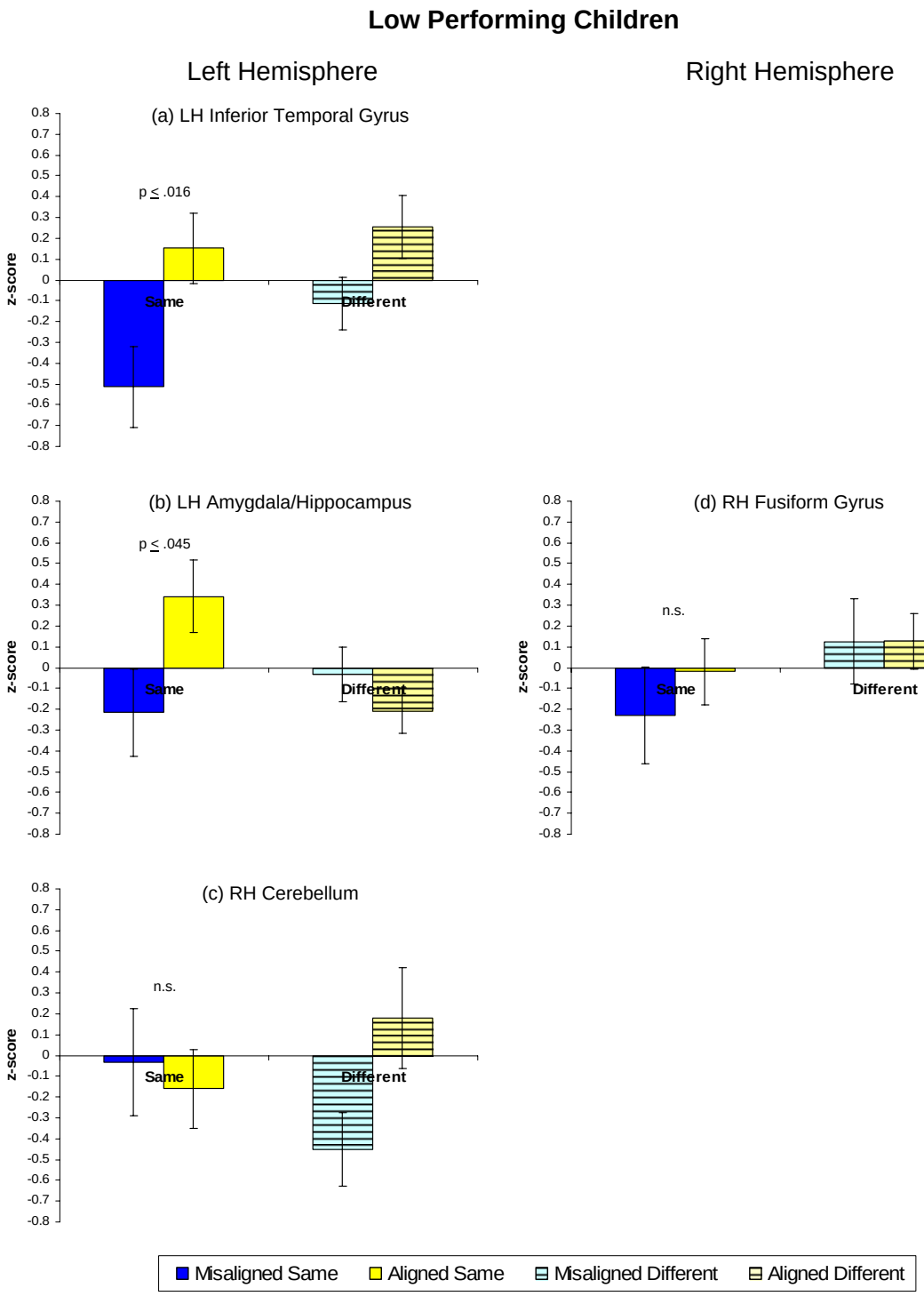


Figure 4.8 Activation for the four task conditions in some occipital, temporal, and cerebellar areas for low performing children. (a) Left inferior temporal gyrus. (b) Left hippocampus/amygdala. (c) Left cerebellum. (d) Right fusiform gyrus. P-values for the composite face effect (solid color bars) are shown above graphs.

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CHAPTER 5

GENERAL DISCUSSION

Faces are central stimuli in our everyday life, hence, face processing is a sophisticated and highly specialized cognitive ability, at which adults are experts and children are proficient. Unlike other visuospatial abilities (e.g., simple shape discrimination), face perception develops very slowly, becoming adult-like only well into adolescence (Carey et al., 1980; Taylor et al., 1999; Itier and Taylor, 2004, Mondloch et al., 2002). This fact is somewhat surprising considering that newborns prefer to look at face-like stimuli from their first minutes of life (Goren et al., 1975; Johnson et al., 1991). Some performance disparities between children and adults may reflect differences in general cognitive abilities, such as attention and memory, which have not yet fully developed in children. Alternatively, performance differences can be attributed to specific cognitive strategies implemented during face processing by different age groups (Carey and Diamond, 1977; Lee and Freire, 2001; McKone and Boyer, 2006, Slater and Quinn, 2001). Finally, the interaction between the improvement of general abilities throughout development and the refinement of face specific cognitive strategies maybe what leads children to become face experts.

In general, cognitive strategies for visuospatial analysis are organized in different levels from a more local to more global processing (Akshoomoff & Stiles, 1995; Delis, Robertson, & Efron, 1986; Stiles, 2001). For example, given a face, its whole configuration is also the face most global level, which comprises all its parts including more local levels such as the eyes or other features within the face. In order to successfully process our visuospatial environment we need to be able to both segment a visual pattern into constituent parts and to integrate those parts into a coherent configuration, hence to be able to implement both featural (local) and configural (global) cognitive strategies. Both these types of information are important in face and object processing, but one type of information can be prominent over the other. Faces, in

particular, appear to be processed differently from other categories of visual objects. Specifically, faces are usually processed as a gestalt (a whole) (Maurer, Grand, & Mondloch, 2002; Peterson & Rhodes, 2003), whereas common objects are typically processed in a piecemeal fashion (Biederman, 1987; Donnelly & Davidoff, 1999; Driver & Baylis, 1995; Tanaka & Farah, 1993). Featural processing, arises when we encode an object or a face by isolating its featural elements. Alternatively, configural processing arises when we process the spatial relationships among the features of an object or face. Most researchers agree that configural strategies are particularly important for face processing and some of the ongoing debates in the field concern the specific nature of this strategy (Gauthier & Bukach, 2007; Maurer et al., 2002; Mondloch, Maurer, & Ahola, 2006; Yovel & Kanwisher, 2004). There are three different types of configural processing, specifically, sensitivity to first-order relations, which are basic topological relations such as above/below or left/right. First-order relations refer to the shared spatial arrangement common to all faces, in which there are two eyes above a mouth, which is below a nose. The second type of configural processing involves sensitivity to second-order relations, which refers to the spatial distances among face features (eyes, nose, mouth, face contour). The third type of configural processing is known as holistic processing, which capture the indivisible whole, or gestalt, of a face (Maurer et al., 2002; Peterson & Rhodes, 2003). Most of the current debates in the literature focus on holistic and second-order information processing.

The intent of the current studies was to further assess the development of and relationship between cognitive strategies in face processing. Specifically, I investigated the behavior and neurocorrelates associated with holistic face processing in children (8- to 11-year-olds) and adults, utilizing the composite face effect (Young et al., 1987, Carey and Diamond, 1994; Hole et al, 1999; Le Grand et al., 2001, De Herring et al., 2006;

Mondloch et al., 2007). The composite face effect (CFE) is considered to be an index of holistic processing (Carey and Diamond, 1994; Schiltz and Rossion, 2006; Hayden et al., 2007; de Herring et al., 2007, Mondloch et al., 2007). The task requires participants to engage in both holistic and featural processing. The upper half of one face is conjoined with the lower half of a second face. Hence, the instruction to attend to only the top half of the faces requires the employment of featural strategies (or configural processing exclusively on the eye region). The upper halves of the stimulus pair match 50% of the time, while the bottom halves always differ. Because the bottom halves of the composite faces always differ, a visual illusion is created in which the pairs with matching tops actually appear to be different. This illusion is driven by our bias to process faces as indivisible whole, which prevails even when we are instructed to ignore part of the face configuration. This strong holistic bias disappears if tops and bottoms of the composite stimuli are laterally offset. Thus, participants are slower and less accurate in matching same tops of aligned faces, relative to same tops of misaligned faces, in which the bottoms can be easily ignored.

Carey and Diamond (1994) were first to use the composite face task to investigate holistic processing in children (6-year-old), and found that children showed a CFE for familiar faces. More recently, Mondloch and colleagues (2007) replicated this finding with 6-year-old children using unfamiliar faces. De Heering and colleagues (2007) found that even 4- to 5-year-old children were sensitive to the CFE, thus sensitive to holistic information. However, their composite face task had to be modified from the traditional version in order to be reliably performed by younger children.

Schiltz and Rossion (2006) were the first to investigate the neurocorrelates of the CFE. They found more intense activation for intact relative to misaligned faces, thus for holistic processing, in face-selective (occipito-temporal) areas corresponding to the FFA

and OFA (specifically, the middle fusiform gyrus and the inferior occipital gyrus) in both hemispheres. The holistic bias was stronger in the right hemisphere, but also present in left occipito-temporal areas (Schiltz and Rossion, 2006). Unfortunately, they did not report whole-brain data and it is difficult to reconcile these results with the typical behavioral findings, because an atypical task design was used; and participants did not perform the composite face task while being scanned (see Ch. 3).

Clearly, many questions about holistic face processing and its developmental trajectory are still unanswered. In order to carefully assess and compare the behavioral and neural CFE, thus behavioral and neural holistic processing in children (8- to 11-year-olds) and adults, the current studies measured the composite face effect using the same composite face task implemented in the behavioral developmental study (Ch. 2), in the fMRI studies (Ch. 3-4). In the behavioral study, about half of the 8-11-year-old children displayed an adult-like CFE, suggesting reliance on holistic processing. Alternatively, the other half of the children showed a very different profile from the other groups. They performed below-chance on aligned-same trials, they displayed an extremely large CFE and a significant difference between different trials (see Ch. 2). Their large composite face effect should suggest a strong reliance on holistic strategy. However, their below-change performance and their unique profile set them apart from the other two groups, which show the typical CFE profile. In addition, to my knowledge, there is no evidence in the literature suggesting that children rely more than adults on holistic processing. For these reasons, I do not believe that the CFE of the low performing children can be considered as a metric of holistic processing. One possible interpretation proposes that low performing children did not engage in holistic processing, but instead they implemented a simpler “difference-detection” strategy, matching all possible discrepancies, feature-by-feature in both tops and bottoms of the stimuli.

This interpretation suggests that low performing children may rely more of featural-based strategies. Thus, the current findings describe a more protracted development of holistic face processing compared to previous developmental CFE studies, in which children as young as 4-year-old showed a CFE and above-chance performance on aligned-same trials (Diamond and Carey, 1994; Le Grand et al, 2004; De Heering et al., 2007; Mondloch et al., 2007). One possible explanation for the different results compared to past studies, comprises the specific task design and the level of difficulty for the children. Recent studies have shown that even infants are able to process faces holistically (Hayden et al., 2007). However, it is clear that infant skills are still rudimentary compared to adult face processing skills. Similarly, 4-year-old children in de Heering and colleagues' (2007) version of the CFE, successfully engaged in holistic processing and performed well above-chance in the aligned-same trials (in which the top halves of the faces were artificially colored). In the current study, 8- to 11-year-old children engaged in a difficult task that challenged their ability to pay attention only to the top halves of the faces. Because their mastery of holistic processing may be not well developed as for other children in the same age range and for adolescents and young adults, they may fall back into relying on simpler strategies in which they are more proficient and skilled, such as a difference-detection featural strategy. In general, children likely rely on featural or holistic strategies differentially in different situations, depending on his/her developmental age and on the complexity and difficulty of the specific tasks (for related discussion see Stiles & Stern, 2001). Developmental transitions from simple to more complex cognitive strategies are not specific to face processing, but rather in many different domains reflect a combination of general cognitive and neural development (e.g., attention, working memory), which together with experience, makes children more efficient and flexible in complex tasks. Cohen and

Cashon (2001) discussed developmental transitions (e.g., transition from use of featural to configural processing in a specific face task) as common sequences in development, not only for face processing, but also for any type of information processing (similar transitions reoccur in different forms and different domains throughout development). Moreover, when the child's proficiency on newly mastered processing styles is challenged with difficult tasks or complex contexts, they temporarily fall back to simpler featural strategies in order to consolidate them, as a step that may be crucial to strengthen their competence in manipulating increasingly complex material such as holistic information (Akshoomoff & Stiles, 1995; Cashon & Cohen, 2004; Stiles & Stern, 2001; Stiles & Tada, 1996).

In order to investigate the CFE behavioral differences between age and performance groups, I completed an imaging study on the same groups (i.e., adult, high performing child, low performing child) utilizing the same task. For the fMRI study children were grouped by performance rather than age following the results of the behavioral study. Thus, the current imaging study not only investigated the neural correlates of holistic processing and its development based on age (i.e., adults versus children), but also compared groups of different age but similar behavior (i.e., adults and high performing children), who may rely on similar cognitive strategies during face processing. I also compared groups of similar age but whose performance differed (i.e., high and low performing children). Through this series of comparisons I attempted to disentangle the contributions of age and behavioral performance to brain activation patterns during holistic face processing.

Overall, the imaging results complemented the behavioral results in that adult and high performing child groups revealed a similar (but not identical) whole-brain pattern of activation, whereas the low performing child group showed a distinctive

pattern of activation for the composite face effect. Similar to other reports of widespread activation during face processing, adults and high performing children showed a pattern of activation spanning frontal, parietal, temporal, and occipital lobes, including regions such as right superior frontal gyrus, left precuneus, right inferior parietal lobule, right inferior temporal gyrus and right fusiform gyrus (Grady et al., 1996; Haxby et al., 2000; Druzgal and d'Esposito, 2000; Klopp et al., 2000; Ishai et al., 2002; Bernstein et al., 2002; Luebe et al., 2003; Gazzaley et al., 2004; Bokde et al., 2005; Maurer et al., 2007; Soto et al., 2007). In contrast, low performing children revealed a pattern of activation that spanned frontal, cingulate and temporal areas including right and left medial frontal gyri, bilateral cingulate cortex and subcortical areas such as the amygdala, hippocampus and putamen. Brain areas typically associated with face processing, such as the right fusiform gyrus and right inferior temporal gyrus (e.g., Kanwisher et al., 1997; Haxby et al., 1999; Rossion et al., 2000), did not reach significance for the low performing child group. Notably, for the CFE contrast (aligned-same - misaligned-same), these face sensitive areas did not significantly differ between the three groups upon direct comparison, which instead revealed activation differences in the right middle and superior frontal gyrus and left inferior parietal lobule. Interestingly, these regions subserve attention and working memory, not just face processing (Corbetta et al., 1998; Treisman, 1999). One interpretation of the current finding suggests that the differences in brain activation may be influenced by the use of different cognitive strategies across the three groups. Adults and high performing children seem to predominantly rely on holistic processing, showing a more pronounced right hemispheric lateralization associated with the CFE, and responding more intensely to intact faces compared to misaligned faces. Alternatively, low performing children who lacked a clear hemispheric lateralization and responded more intensely to misaligned faces may rely more on

featural processing (e.g., difference-detection strategy throughout the whole face stimulus). However, any interpretation of the low performing children pattern of activation is highly speculative. Given that their behavioral profile is also unique and hard to interpret, and that they were unable to perform above chance (in aligned-same trials), their activation pattern could be associated with any number of cognitive strategies or processes.

Previous developmental studies of the composite face effect documented sensitivity to configural aspects of face processing in very young children. However the data from those studies was obtained using greatly simplified tasks, task for which adult performance is at ceiling thus precluding direct comparison across age groups. The current study introduced a more challenging task, but one that could be used with both adults and school age children. Initial age-based analyses showed linear improvement in performance with age suggesting a gradual developmental shift that could be attributed to age-based improvement in either general cognitive abilities or in the specific holistic processing skills tapped by the task. Interestingly, closer inspection of the child data revealed two distinct subgroups distinguished by marked differences in level of performance. Reanalysis of the data using performance as a grouping variable for the children, proved to be a more sensitive measure of developmental change than simple assessment by age. The implementation of performance-based analysis and the synergic combination of behavioral and neural evidence proved to be instrumental in uncovering the protracted developmental trajectory of holistic face processing.

Finally, the key findings of this work concern the difference in brain activation between adults and high performing children. The comparison between these two groups is particularly interesting because while they show same behavioral profiles, they displayed similar but not identical neural profiles. Children who seem to have mastered

holistic processing at an adult-level based on behavioral results, still showed differences from adults in the pattern of brain activation associated with holistic face processing. These neural differences may highlight brain regions that undergo change across development, that is, given that the two groups employed the same cognitive strategies, differences may be associated with brain regions not fully developed. Some activation differences could also derive from age-related differences in BOLD response. An alternative interpretation may suggest that imaging data might have revealed differences in cognitive strategies, which were not detectable in the behavioral data. Notably, the combination of behavioral and imaging evidence uniquely describes the protracted trajectory of holistic face processing, which undergoes developmental changes quite late in development, later that previously thought on the base of only behavioral evidence (Carey and Diamond, 1994, Mondloch et al., 2007; de Heering et al., 2007).

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