Electrophysiological investigations of the timing of face processing

by

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Abstract

As important social stimuli, faces play a critical role in our lives. Much of our interaction with other people depends on our ability to recognize faces accurately. It has been proposed that face processing consists of different stages and interacts with other systems (Bruce & Young, 1986). At a perceptual level, the initial two stages, namely structural encoding and face recognition, are particularly relevant and are the focus of this dissertation.

Event-related potentials (ERPs) are averaged EEG signals time-locked to a particular event (such as the presentation of a face). With their excellent temporal resolution, ERPs can provide important timing information about neural processes. Previous research has identified several ERP components that are especially related to face processing, including the N170, the P2 and the N250. Their nature with respect to the stages of face processing is still unclear, and is examined in Studies 1 and 2.

In Study 1, participants made gender decisions on a large set of female faces interspersed with a few male faces. The ERP responses to facial characteristics of the female faces indicated that the N170 amplitude from each side of the head was affected by information from eye region and by facial layout: the right N170 was affected by eye color and by face width, while the left N170 was affected by eye size and by the relation between the sizes of the top and bottom parts of a face. In contrast, the P100 and the N250 components were largely unaffected by facial characteristics. These results thus provided direct evidence for the link between the N170 and structural encoding of faces.

In Study 2, focusing on the face recognition stage, we manipulated face identity strength by morphing individual faces to an "average" face. Participants performed a face identification task. The effect of face identity strength was found on the late P2 and the N250 components: as identity strength decreased from an individual face to the "average" face, the late P2 increased and the N250 decreased. In contrast, the P100, the N170 and the early P2 components were not affected by face identity strength. These results suggest that face recognition occurs after 200 ms, but not earlier.

Finally, because faces are often associated with social information, we investigated in Study 3 how group membership might affect ERP responses to faces. After participants learned in- and out-group memberships of the face stimuli based on arbitrarily assigned nationality and university affiliation, we found that the N170 latency differentiated in-group and out-group faces, taking longer to process the latter. In comparison, without group memberships, there was no difference in N170 latency among the faces.

This dissertation provides evidence that at a neural level, structural encoding of faces, indexed by the N170, occurs within 200 ms. Face recognition, indexed by the late P2 and the N250, occurs shortly afterwards between 200 and 300 ms. Social cognitive factors can also influence face processing. The effect is already evident as early as 130–200 ms at the structural encoding stage.

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I dedicate this work to my parents, my grandmas
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Chapter 1

General introduction

"*I never forget a face, but in your case I'll be glad to make an exception.*"

– Groucho Marx

Such witty lines have contributed to the great success that Groucho Marx enjoyed in popular culture. On a more serious note, however, it reveals the importance of faces that often seems too obvious for us to realize until we lose the ability to recognize them.

"I was getting off a bus and somebody got on it and grabbed me, and I pushed them out of the way, and it was only when they opened their mouth that I realized it was my own mother."

– A patient with prosopagnosia

Early research interest in understanding face perception can be found in Francis Galton's work (1879) in the late 19th century, when he attempted to find ways to measure physiognomic features so that they could be related to races or families for the purpose of studying heredity. Revolutionary at the time, the method invented by Galton (aligning pictures of faces on top of each other to create a composite face for either members of a family or members of a race) seems primitive by today's standards. Nevertheless, the central theme and the main research questions are still with us today. For example, what information do we use to decode and recognize a face? How are faces represented and organized in such a way that we can recognize them so effortlessly, despite the fact that they all share similar structures and that we have encountered thousands of them over our lifetime? With technologies today, we are better equipped to address these questions.

Behaviorally, the earliest experimental research on face recognition was reported by Yin (1969). In the study, participants were tested for their visual memory of faces and non-face stimuli (e.g., houses) that were presented in both upright and inverted orientations. While it is not surprising that inverting visual stimuli made it more difficult for participants to recognize them later, this inversion effect was much greater for faces than for non-face stimuli, suggesting something special about face processing. Subsequently, using a variety of experimental designs, many researchers have aimed to uncover these special mechanisms associated with face processing.

In one behavioral study considered classic today, Young, Hellawell, and Hay (1987) created "composite" faces, of which the top-half and the bottom-half were taken from two different famous individuals. When participants were asked to identify a face based on either its top or its bottom half, it was found that the "composite" faces took longer to be identified compared to the "non-composite" faces in which the two halves were misaligned. Similar results were also found for "composite" faces that consisted of internal and external features of different individuals. Because the longer time to identify a "composite" face from one part of a face is likely due to the interference from the other part of a face that contains a different face identity, these results are considered to have revealed the holistic nature of face processing: different parts of a face are integrated to form a whole rather than being processed in isolation. Interestingly, when faces were inverted, there was no longer a difference between “composite” and “non-composite” faces in face identification, suggesting that inverting a face may disrupt this holistic processing. This may also explain why people have a greater difficulty recognizing inverted faces than upright faces. As a robust phenomenon, the composite face effect was also reported with unfamiliar faces (Hole, 1994), and has been widely used to examine how holistic face processing may change developmentally (de Heering, Houthuys, & Rossion, 2007; Diamond & Carey, 1986; Mondloch, Pathman, Maurer, Le Grand, & Schonen, 2007; Turati, Giorgio, Bardi, & Simion, 2010) or differ in special populations (e.g., autistics) (Gauthier, Klaiman, & Schultz, 2009; Nishimura, Rutherford, & Maurer, 2008; Teunisse & Gelder, 2003). It has also been studied at a neural level (Harris & Aguirre, 2010; Jacques & Rossion, 2009, 2010; Letourneau & Mitchell, 2008; Schiltz & Rossion, 2006).

Further evidence to support the holistic processing of faces was also reported in another classic study by Tanaka and Farah (1993), when face parts (e.g., eyes, nose) were presented either alone or within the context of faces. They found that when presented within the context of faces, changes in face parts (e.g., eyes, nose) were much easier to detect than when they were presented alone, suggesting again that face parts are processed in relation to one another and together form a gestalt, holistic representation of a face. When faces were inverted, the advantage of intact faces for detecting changes in face parts was no longer found, supporting further that inversion disrupts the holistic processes. Like the composite face effects, the paradigm involving face parts presented either alone or within a face has been widely used to study face perception and recognition (Annaz, Karmiloff-Smith, Johnson, & Thomas, 2009; Jemel, George, Chaby, Fiori, & Renault, 1999; Joseph & Tanaka, 2002; Rossion, et al., 2000; Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998; Tanaka, Kiefer, & Bukach, 2004).

Compared to non-face stimuli, faces also share a common configuration in that the eyes are above the nose and the nose is above the mouth. This fixed order among facial features is termed first-order relations; in comparison, the spatial relations among facial features (e.g., the distance between eyes, and the distance between eyes and nose) are referred to as the second-order relations (Diamond & Carey, 1986). Related to holistic processing, previous research has shown that not only facial features (e.g., the shape of eyes) but also second-order relations are important for recognizing individual faces (Freire, Lee, & Symons, 2000; Leder & Bruce, 2000; Mondloch, Le Grand, & Maurer, 2002). The second-order relations can also affect the processing of facial features (Pellicano, Rhodes, & Peters, 2006; Tanaka & Sengco, 1997): altering the second-order relational information (e.g., spacing between eyes) of a face made it more difficult to recognize a previously learned face part (e.g., a nose). When faces are inverted, the second-order relations are disrupted to a much greater extent than the featural information (Freire, et al., 2000; Leder & Bruce, 2000; Leder & Carbon, 2006). Furthermore, developmental research has demonstrated that the use of second-order relational information for identifying a face may reach adult-like levels later than the use of featural information (Mondloch, Geldart, Maurer, & Le Grand, 2003; Mondloch, et al., 2002).

Integrating previous research on face perception and other factors (e.g., attention and memory), Bruce and Young (1986) proposed a face recognition model, which is still influential today and guides much of the contemporary research. In the model, face recognition is understood as being a result of several stages of processes, including structural encoding, face recognition units, person identity nodes, and name generation. The structural encoding stage involves the analysis of featural and configural information that occur not only at a view-centered level that is important for processing such dynamic information as facial expressions, but also at a more abstract, view-invariant level necessary for recognizing a face. The holistic processes and configural processes, so central to face perception, are thought to occur at this stage. After various facial cues are analyzed through structural encoding, they are sent to face recognition units for a comparison. The face recognition units are thought to hold representations of the faces previously seen. As a result of comparing incoming facial information with the ones stored in the face recognition units, a face is either recognized as an “old” face or regarded as a “new” face. If a person is recognized, semantic information and the person’s name are subsequently accessed respectively at person identity nodes and at the name generation module.

Despite Bruce and Young’s framework being powerful at explaining a range of face-related phenomena, such as the dissociation between familiar and unfamiliar faces in recognition as observed in prosopagnosics (Malone, Morris, Kay, & Levin, 1982) or the tip-of-the-tongue" phenomenon that we all experience in everyday life, the mechanistic details of each stage were not fully specified. For researchers who are interested in the perceptual mechanisms underlying face perception and recognition, the initial two stages of the model, namely the structural encoding and the face recognition units, are particularly relevant.

The norm-based coding mechanism (Rhodes, Brennan, & Carey, 1987) and face prototype hypothesis (Valentine & Bruce, 1986), developed independently at approximately the same time, probably represent the most comprehensive models to account for the perceptual mechanisms for face perception and recognition. Essentially, the two models are similar by proposing that faces are coded in relation to a face norm/prototype in a multidimensional "face space"; the dimensions of the "face space" correspond to a variety of physiognomic information that includes both featural (e.g., shape of eyes, eye color) and configural information (e.g., distance between eyes) (Nishimura, Robertson, & Maurer, 2010; Zheng, Mondloch, Nishimura, Vida, & Segalowitz, 2011). Every individual face, depending on where its physiognomic features fall along these dimensions, can be either closer or further away from the face norm. Faces further away from the norm are perceived as more distinctive and have greater identity strength, while faces closer to the norm are perceived as more typical and have less identity strength (Johnston, Milne, Williams, & Hosie, 1997; Lee, Byatt, & Rhodes, 2000). Furthermore, because each dimension follows approximately a normal distribution, it implies that the regions near the norm are occupied by a large number of faces and have a greater density than the regions far from the norm that are only occupied by relatively few faces. Consequently, the greater density of regions closer to the face norm explains why it is more difficult to recognize typical-looking faces than to recognize distinctive faces (Going & Read, 1974) or caricatures (Lee, Byatt, & Rhodes, 2000; Mauro & Kubovy, 1992; Rhodes, et al., 1987; Stevenage, 1995). In contrast, the higher density near the face norm provides typical-looking faces with an advantage in a face vs. non-face categorization task: it is faster to categorize a typical face than to categorize a distinctive face as a face (Stevenage, 1995; Valentine & Bruce, 1986). Strong support for the norm-based coding mechanism was further found in face identity post-adaptation effect (Leopold, O'Toole, Vetter, & Blanz, 2001). Specifically, after participants were adapted to an individual face that lies along the same identity trajectory but on the opposite side of a test face for a short period of time (e.g., 5 seconds), the subsequent identification of the test face was facilitated, indicated by the lower identification threshold. More importantly, Rhodes and Jeffery (2006) further reported that this face identity post-adaptation effect was only found when an adapting face and the test face were on the same identity trajectory that passed through the face norm; in contrast, when participants were adapted to an equally distant face that was not on the same identity trajectory as the target face, the face identity post-adaptation effect was not found. Together, these results provide strong behavioral support for the importance of face-norm and the norm-based coding mechanism for face perception and recognition.

In summary, based on a brief survey of behavioral research in the past, several conclusions can be drawn with regard to our understanding of face perception and recognition (see Maurer, Le Grand, & Mondloch, 2002, for a review). Face perception and recognition likely involve several stages of processing and interact with other cognitive systems (e.g., attention and memory). At a perceptual level, faces are processed holistically, and both facial featural (e.g., eyes, nose, mouth) and second-order relational information (i.e., spacing among facial features) are important for identifying individual faces; when faces are inverted, the holistic processes and the processing of relational information are particularly susceptible to disruption. Individual faces are likely represented in relation to a face prototype/norm, and their positions relative to the norm determine their identity strength and the likelihood they are recognized. Understood within the classic face recognition model (Bruce & Young, 1986), these processes correspond to the structural encoding and the face recognition units.

From a neuroscience perspective, these behavioral findings related to face perception and recognition can be further examined in terms of either space or time. First, as a functional network, we hope to know the neural structures that are important for perceiving and recognizing a face, i.e., the location(s) where structural encoding and face recognition occur in the brain. Second, we also hope to know the timing of neural events associated with those processes.

For the former “where in the brain” type of questions, imaging studies of functional MRI or positron emission tomography (PET) with their better spatial resolutions have identified a distributed neural network with several key brain regions that are particularly responsive to faces relative to non-face objects, including the middle fusiform gyrus, lateral occipital complex (LOC), superior temporal sulcus, and anterior temporal pole. Of these regions, the fusiform gyrus seems to be particularly important for face perception, a conclusion that has been confirmed by numerous imaging studies since its first report (Chen, Kao, & Tyler, 2007; Davidenko, Remus, & Grill-Spector, 2011; Haxby, et al., 1994; Kanwisher, McDermott, & Chun, 1997; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Maurer, et al., 2007; Puce, Allison, Gore, & McCarthy, 1995; Rhodes, Byatt, Michie, & Puce, 2004; Rhodes, Michie, Hughes, & Byatt, 2009; Rotshtein, Henson, Treves, Driver, & Dolan, 2005); it also converges with the results found in prosopagnosic patients (Barton, Press, Keenan, & O'Connor, 2002; Damasio, Damasio, & Hoesen, 1982; Sergent & Signoret, 1992) who have lost ability to recognize faces because of damage to this part of the brain. In consequence, the term, "fusiform face area" (FFA) (Kanwisher, et al., 1997) has been widely adopted to formally recognize its importance for face processing. In parallel to behavioral research, the facial features and configural information have also been studied with regard to their neural correlates (Goffaux, Rossion, Sorger, Schiltz, & Goebel, 2009; Liu, Harris, & Kanwisher, 2009; Maurer, et al., 2007; Rhodes, Michie, et al., 2009; Rotshtein, Geng, Driver, & Dolan, 2007); similarly, there have been imaging studies on the difference between external and internal features (Andrews, Davies-Thompson, Kingstone, & Young, 2010), on the effect of composite faces (Harris & Aguirre, 2010; Schiltz & Rossion, 2006) and on the effect of face inversion (Goffaux, et al., 2009; Yovel & Kanwisher, 2005) in terms of neural responses from face-sensitive regions (e.g., middle fusiform gyrus and occipital face area). The norm-based coding mechanism was also supported with imaging data (Loffler, et al., 2005): it was found that blood oxygen level-dependent (BOLD) responses from FFA increased systematically with increase in face identity strength, but only when face identity strength was defined as the distance from a prototypical face; in contrast, when the face identity strength was defined as the distance relative to a non-prototypical face, it no longer affected the BOLD responses from FFA.

Although the imaging studies have an excellent spatial resolution, they are rather limited in their ability to address the "when in the brain" type of questions, given that they rely on hemodynamic responses and that there is typically a lag of several seconds between the hemodynamic responses and the triggering neuronal events (Heeger & Ress, 2002). Electroencephalography (EEG) with a temporal resolution in the order of milliseconds is often used instead. EEG can be recorded either intracortically with electrodes inserted directly into the brain structures (e.g., fusiform gyri) or at the scalp. Among the first intracortical studies, Allison et al. (1994) found that the negative field potentials, peaking around 200 ms (N200) from the fusiform and inferior temporal gyri were elicited by faces but not by non-face stimuli (e.g., cars, butterflies). The locations of the recording sites are consistent with the ones reported from the imaging studies (Haxby, et al., 1994; Kanwisher, et al., 1997) and with the regions damaged in prosopagnosics (Damasio, et al., 1982; Sergent & Signoret, 1992). More importantly, the study had further provided the temporal information about the neural events associated with face processing (i.e., they occur within 200 ms after a person sees a face) that had not been possible previously with imaging methods. However, despite the advantage of intracortical recordings in both temporal and spatial domains, the drawback of intracortical recordings is its obvious invasive nature. It can only be performed occasionally with patients who undergo specific surgeries for medical reasons (e.g., as a treatment of epilepsy).

Fortunately, EEG signals can also be measured at the scalp, and the quantitative EEG and event-related potentials (ERPs) are the two ways in which EEG signals are often analyzed, and each approach has its own philosophy about the nature of EEG signals. With quantitative EEG, the psychological functions (e.g., memory, perception) are thought to be reflected in oscillations of different frequencies (e.g., delta, theta, alpha, beta, and gamma) (Başar, Başar-Eroglu, Karakaş, & Schürmann, 2001; Klimesch, 1999). In contrast, for ERPs, which are EEG segments time-locked to a particular event (e.g., the onset of a face) and averaged across many trials, it is the components (peaks and troughs) occurring at a particular time that provide indices to psychological functions (Rugg & Coles, 1995). The intracortically recorded N200 described earlier is a good example of ERP components.

Both quantitative EEG and ERPs have been used to study the neural mechanisms for face perception. A majority of research however has taken the ERP approach. For my dissertation, I also focus on the ERP components that have been associated with face processing. Because the exact functions of these face processing related components are still matters of debate, we were hoping to clarify this issue by addressing some methodological issues that were not considered in the past ERP research. By knowing the processes and the stages that these ERP components map onto, we will gain a better understanding about the timing of face perception in the brain to answer the "when" type of questions.

Scalp-recorded ERP research on face processing

Shortly after the report of the intracortical face-sensitive N200 (Allison, McCarthy, et al., 1994), Bentin et al. (1996) found a similar electrophysiological marker in the scalp-recorded ERP data that reliably differentiates faces from non-face objects. Because it was observed as the negativities peaking around 170 ms at bilateral temporal-occipital sites, particularly strong on the right, it was named the N170 component. Although there had been an earlier report of similar findings (Bötzel, Schulze, & Stodieck, 1995), the work by Bentin et al. represents the first systematic approach to investigate the scalp-recorded ERP correlates of face processing. In a series of experiments, they ruled out the alternative explanations and concluded that a larger N170 is specific to human faces, rather than due to faces in general or due to body parts, because neither animal faces nor human hands elicited an N170 that is comparable in amplitude.

Considered as classic now, the study nevertheless left many questions unanswered. For example, it was not clear why N170 was bigger for eyes alone than for whole faces; it was not clear why N170 became larger when a face was inverted. Furthermore, because the study only made cross-category comparisons between faces and non-face objects, it was not clear about the specific aspect of face processing that is reflected in the N170. Subsequently, many of these questions have been taken up by ERP researchers with related research continuing today (Bentin & Deouell, 2000; Bentin, Golland, Flevaris, Robertson, & Moscovitch, 2006; Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Carmela & Bentin, 2002; Eimer, 1998, 2000b; Eimer, Gosling, Nicholas, & Kiss, 2011; Eimer, Kiss, & Nicholas, 2010; Ganis, Smith, & Schendan, 2012; Itier, Alain, Sedore, & McIntosh, 2007; Itier, Latinus, & Taylor, 2006; Itier & Taylor, 2004; Jacques & Rossion, 2006, 2007; Jemel, Pisani, Rousselle, Crommelinck, & Bruyer, 2005; Jemel, et al., 2003; Kaufmann & Schweinberger, 2008; Rossion, et al., 2000; Sagiv & Bentin, 2001).

Noticeably, it was found in an early study (Eimer, 2000b) that the N170 became attenuated after the removal of either internal or external features, suggesting that the N170 might be related to the structural encoding of faces and that this process occurs approximately between 140 and 200 ms post stimulus onset. In addition, a robust face inversion effect was also observed with the N170 component (Jacques & Rossion, 2007; Rossion, et al., 2000; Sagiv & Bentin, 2001): when faces are inverted, the N170 becomes larger and delayed. Furthermore, the changes in the N170 amplitude were found to correlate with the behavioral performance when face orientation was systematically manipulated (Jacques & Rossion, 2007): as faces deviated from their canonical upright orientation, it became more difficult to recognize a face, and the greater the effec of face orientation on face recognition, the larger was the N170 amplitude. Some ERP studies have also shown that composite faces affected the N170 in a similar way as the inverted faces (Jacques & Rossion, 2009, 2010; Letourneau & Mitchell, 2008): misaligning two halves of a face delays and increases the N170. Considering that previous behavioral research has linked both face inversion and composite face effects to structural encoding, the results that the N170 is also sensitive to these manipulations suggest further that the N170 might be a neural marker for the structural encoding stage of face processing.

In the first study of this dissertation (Chapter 2), we tested the hypothesis that the N170 is associated with structural encoding more directly. Specifically, using a large set of individual faces of real people, we examined whether the N170 relates systematically to variations in a number of facial characteristics (e.g., eye color, eye size, and mouth shape) that occur naturally. In the past, a small number of studies (Halit, de Haan, & Johnson, 2000; Scott & Nelson, 2006) had demonstrated that the N170 was not affected by changes in either featural or configural information. However, there were several limitations to those studies. For example, the facial features and configuration were only altered artificially to a small set of face stimuli; the number of changes made to the stimuli was also small. Compared to those studies, with a large number of faces (36) that vary naturally in facial characteristics, our study might be better suited to investigate the relationship between the N170 and facial characteristics. If there was such a close correspondence, it would provide direct evidence for the linkage between the N170 and the structural encoding of faces; in turn, it will also provide the timing (i.e., between 140 and 200 ms after a person sees a face) of structural encoding at a neural level.

In addition to the N170, another component that has received much research attention in the ERP face literature is the N250, which occurs between 200 and 300 ms post stimulus onset. It was first reported by Schweinberger, Pfütze, and Sommer (1995) and was further investigated by other researchers (Schweinberger, Pickering, Burton, & Kaufmann, 2002; Tanaka, Curran, Porterfield, & Collins, 2006). Based on the past research on the N250, it appears that the component is sensitive to face identity and differentiates between familiar and unfamiliar faces (Herzmann, Schweinberger, Sommer, & Jentzsch, 2004; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002), between faces that are primed by either the same- or different-identity (Schweinberger, Huddy, & Burton, 2004), and correlates with learning new faces (Kaufmann, Schweinberger, & Burton, 2008; Tanaka, et al., 2006). Therefore, the N250 might be a neural maker for the face recognition stage. However, a number of recent ERP studies have challenged this view (Caharel, d'Arripe, et al., 2009; Caharel, Jiang, Blanz, & Rossion, 2009; Jacques & Rossion, 2006), with results that seem to suggest that individual face recognition may also occur earlier at the N170 level. For example, it was found that the N170 response to a probe face was reduced (i.e., an adaptation effect) when the probe was preceded by a face with the same identity; in contrast, when the probe was preceded by a face with a different identity, there was no N170 adaptation effect. However, one limitation to these studies is that they all used an immediate repetition paradigm (i.e., a probe face follows immediately after a prime face). Considering that the N170 might also be sensitive to facial characteristics, we suspected that the "face identity" priming effect on the N170 amplitude using an immediate repetition paradigm might actually be a “facial characteristic” priming effect.

To further clarify which ERP component (N170 or N250) is sensitive to face identity and therefore to learn the timing of neural events associated with face recognition, we conducted the second study (Chapter 3). We manipulated face identity strength by morphing individual faces to an “average” face in steps, in a similar way as it had been implemented previously in imaging (Loffler, et al., 2005) and animal (Leopold, Bondar, & Giese, 2006) studies. Based on the behavioral research described earlier, faces further away from the “average” face were thus considered as having greater identity strength compared to faces closer to the “average” face. If N170 is also linked to face recognition, we would expect it to be affected by face identity strength. On the other hand, if face recognition didn’t occur until after 200 ms, we would expect to see the effect of face identity strength on the N250 only. In addition, we also avoided the immediate repetition paradigm; instead, a large set of face stimuli were randomly presented, while participants were performing a face identification task (see Chapter 3 for more details).

Finally, while the first two studies of this dissertation were mainly focused on the nature of the ERP components that will inform us about the timing of structural encoding and face recognition at a neural level, we took a different approach in the third study (Chapter 4). Specifically, we used the ERPs as a tool to investigate whether and how social information might influence neural processes for face perception. As described earlier, faces are socially meaningful to us. Therefore, it is likely that the social information carried by a face may change the way in which we perceive it.

A good example of this is the other-race effect (ORE), which refers to the phenomenon that people tend to have a greater difficulty recognizing other-race faces than own-race faces (Brigham & Barkowitz, 1978; Malpass & Kravitz, 1969; Shepherd, Deregowski, & Ellis, 1974). Two prominent models have been proposed to account for the ORE, with one focusing on a perceptual explanation (Valentine, 1991) and the other emphasizing on social-cognitive factors (Levin, 1996, 2000) (e.g., the level of motivation for individualizing other-race faces). Evidence in support of each model has been found in behavioral data (see Chapter 4 for more detailed description). At a neural level, although difference between own- and other-race faces have been reported in both imaging (Cunningham, et al., 2004; Feng, et al., 2011; Golby, Gabrieli, Chiao, & Eberhardt, 2001; Lieberman, Hariri, Jarcho, Eisenberger, & Bookheimer, 2005; Natu, Raboy, & O'Toole, 2011; Phelps, et al., 2000; Ronquillo, et al., 2007; Wheeler & Fiske, 2005) and ERP studies (Balas & Nelson, 2010; Brebner, Krigolson, Handy, Quadflieg, & Turk, 2011; Caharel, et al., 2011; Gajewski, Schlegel, & Stoerig, 2008; Herrmann, et al., 2007; Ito & Urland, 2003; Stahl, Wiese, & Schweinberger, 2008, 2010; Tanaka & Pierce, 2009; Vizioli, Foreman, Rousselet, & Caldara, 2010; Vizioli, Rousselet, & Caldara, 2010; Walker, Silvert, Hewstone, & Nobre, 2008) (see Chapter 4 for more detailed description of these studies), the perceptual expertise and social-cognitive factors were often confounded in these studies. As a result, the neural mechanisms underlying ORE are still poorly understood. Recently, by manipulating group memberships, a small number of imaging studies (Van Bavel, Packer, & Cunningham, 2008, 2011) have found some neural evidence to support social cognitive models of ORE. Specifically, despite the arbitrary assignment of group memberships, the neural responses from fusiform face area were nevertheless enhanced for in-group faces compared to out-group faces, and this effect was similarly found without regard to whether participants' attention was explicitly directed towards in-group or out-group members. Because no ERP research has examined the face processing in relation to social-cognitive factors, we investigated this issue in the third study of my dissertation. Controlling for perceptual expertise by using Caucasian faces only, we randomly assigned face stimuli to four distinctive groups based on two social categories: nationality (Canadian/non-Canadian) and university affiliation (Brock/non-Brock). Considering that participants at testing were Canadian Brock University students. Canadian Brock face was considered as double in-group member; the non-Canadian non-Brock was considered as double out-group member, while Canadian non-Brock and non-Canadian Brock faces were considered as mixed in-/out-group members. Previous social psychological research has shown that people's attitudes towards double in-group, mixed group, and double out-group members fall on a continuum (Crisp, Hewstone, Richards, & Paolini, 2003). With a similar cross-category manipulation, we aimed to examine how social cognitive factors (e.g., group membership), while controlling for perceptual expertise, might affect face-related ERP responses. Particularly, given the excellent temporal resolution of ERPs, we were interested in the timing and the stages when social cognitive factors may exert their influence on face processing at a neural level.

Overall, considering the three studies together, the results of the first two studies will help clarify the functions of the N170 and the N250 components, providing the temporal information about the different stages, namely structural encoding and face recognition, involved in face processing. Furthermore, as social stimuli, we typically see faces within social contexts. The results from the third study, when we manipulated one such aspect of social information (i.e., group memberships) while controlling for perceptual factors, will provide us with an opportunity to examine how quickly and at what stage social-cognitive factors alone may influence neural responses to faces; these results will further contribute to our understanding about the mechanisms underlying the other-race effect, which is not only theoretically interesting in its own right, but also bears significant social implications.

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Chapter 2

Study 1. Telling one face from another: Electrocortical correlates of individual facial characteristics

2.1. Introduction

The ability to recognize faces accurately and rapidly plays an important role in a person's social life. Adults rapidly detect faces, even in the absence of veridical facial features (e.g., in Mooney stimuli; in Archimbaldo's paintings), and despite all human faces sharing a common structure, adults are nonetheless able to distinguish among thousands of faces quite easily. Behavioral studies have shown that adults process faces holistically (Tanaka & Farah, 1993; A. W. Young, et al., 1987) and are exquisitely sensitive to subtle differences among faces in the shape of facial features and the spacing among them (Freire, et al., 2000; Mondloch, et al., 2002).

Brain studies using functional magnetic resonance imaging (fMRI) and event-related potentials (ERPs) have identified neural correlates that distinguish the perception of faces from the perception of other stimulus categories such as houses and cars; the fusiform gyrus responds more robustly (Kanwisher, et al., 1997) and the scalp N170 and the intracortical N200 have a larger amplitude (Allison, Ginter, et al., 1994; Bentin, et al., 1996) when adults view faces compared to non-face stimuli. In contrast to the large number of studies comparing faces with non-face stimuli, much less is known about the neural mechanisms for recognizing individual faces within the face category. Recently, when the issue was examined in humans (Loffler, et al., 2005) and non-human primates (Leopold, et al., 2006), it was found that the BOLD signals to individual faces within the face-sensitive regions (fusiform face area in humans and anterior inferotemporal cortex in monkeys) varied as a function of identity strength: neural responses were minimal to an “average” face and became larger to more distinctive faces. These neural findings are consistent with a classic model of face processing (Valentine, 1991), which proposes that individual faces are represented in a multidimensional “face space” and at the center of the face space lies the prototypical (“average”) face; the recognition of individual faces is subsequently determined by how and how much they deviate from the prototypical face.

Critical for individual face processing are differences among faces in featural (e.g., the shape of an eye) and spacing (e.g., distance between eyes) information. Whereas previous studies have demonstrated how neural responses are affected by face distinctiveness, they have not yet addressed the question of what specific facial information drives the face sensitive neurons’ responses. To our knowledge, there is only one study that has examined the neural profiles to variations in facial characteristics and that study tested monkeys (Freiwald, Tsao, & Livingstone, 2009). Using cartoon faces, it was found that the face-specific neurons along the superior temporal sulcus (STS) as previously reported by Tsao, Freiwald, Tootell, and Livingstone (2006) are sensitive to a variety of facial characteristics, especially to the variation in facial layout (e.g., face aspect ratio) and details in the eye region (e.g., iris size, inter-eye distance). The majority of these neurons showed ramp-shaped tuning curves, responding maximally to one extreme and minimally to the other extreme of their associated facial characteristics, which may help enhance the probability of differentiating among individual faces, consistent with norm-based coding models. Importantly, the study also showed the dependency of these effects on the facial context: when facial characteristics are presented in isolation, their effects on neural responses were either reduced dramatically or completely gone.

A parallel study has not been conducted with human participants. Here we tested the hypothesis that the N170 in humans, an ERP component that is functionally linked to the structural encoding of faces (Eimer, 2000b) and is modulated by individual identities in an adaptation paradigm (Caharel, d'Arripe, et al., 2009; Jacques, d'Arripe, & Rossion, 2007; Jacques & Rossion, 2006), is modulated by variations in individual characteristics in a large set of female faces using digital photographs of real persons. We further hypothesized that the effects should be particularly strong for information about facial layout and eye region as was found in monkeys (Freiwald et al., 2009). Participants performed a gender decision task (see Fig. 2.1 and Methods), while the electroencephalogram (EEG) was recorded. The N170 component was identified bilaterally from lateral occipital-temporal scalp regions between 130 and 190 ms after stimulus onset.

To examine whether or not the hypothesized relationships are specific to the N170, we performed similar analyses for the visually evoked P100 component, which precedes the N170 by approximately 50 to 70 ms, and the N250 component, a negative-going waveform at temporal and occipital-temporal sites usually between 250 and 330 ms post stimulus known to be affected by individual identities (Kaufmann, et al., 2008; Schweinberger, et al., 2004; Schweinberger, Pfütze, & Sommer, 1995; Schweinberger, Pickering, Jentzsch, et al., 2002; Tanaka, et al., 2006). Because the P100 is related in general to the processing of low-level visual information such as spatial frequency, contrast, and luminance (Regan, 1989), we hypothesized that it should not be affected by facial characteristics that require high-level processing and are face-context dependent. Likewise, because no single facial characteristic alone can define a particular face identity and all face stimuli were equally unfamiliar to participants, we did not expect to see any effect of facial characteristics on N250 – a component that is associated with face recognition and face familiarity (Kaufmann, et al., 2008; Schweinberger, et al., 2004; Tanaka, et al., 2006). Considered together, the effects of individual facial characteristics would therefore be unique to the N170 and should not be found in either the P100 or the N250.

2.2. Materials and Methods

2.2.1. Participants

Fourteen Caucasian female undergraduate students at Brock University (mean age = 20.3 years) participated in the current ERP study for either a research credit or a $15 honorarium. All participants were right-handed native English speakers with normal or corrected-to-normal vision. Participants reported no neurological disorders, psychiatric history, or attentional problems. The experimental procedures were approved by Brock University Research Ethics Board.

2.2.2. Stimuli and task

The experimental stimuli consisted of colored digital photographs of 36 female and nine male Caucasian faces with a neutral emotion. The female face stimuli, all with the same hair template, were used previously in a behavioral study (Nishimura, Maurer, & Gao, 2009) to examine whether there are developmental changes in the structure of face space from childhood to adulthood. The nine male faces were selected from a pool of 32 male faces that were used previously in a behavioral study on facial cues to aggression (Carré, McCormick, & Mondloch, 2009) and were presented (but not scored) to ensure that participants remained attentive throughout the task. All stimuli were 10.5 x 15.3 cm (360 x 520 pixels) in size and subtended a visual angle of 6.0° (horizontally) by 8.7° (vertically) at a viewing distance of 100 cm.

Participants performed 4 blocks of a gender decision task. Within each block, each of the 36 female faces and nine male faces was seen four times and the order of presentation was randomized. The face stimuli were presented for 500 ms each, followed by a randomly selected interval (ISI) of 600, 700, or 800 ms (Fig. 2.1). Participants were instructed to make either a left or a right button press, counter-balanced across participants, whenever they saw a male face. The response could be made either during the face presentation or during the ISI. The average response accuracy for detecting male faces was 96.7%.

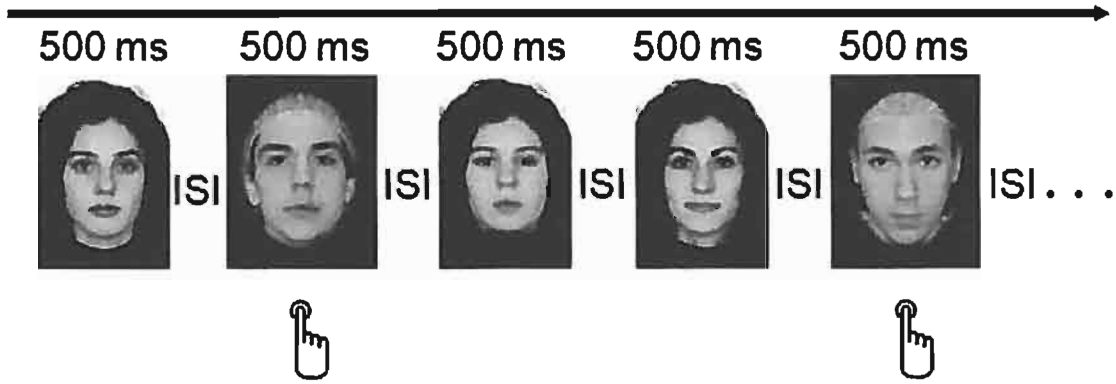

Figure 2.1. Experimental design. Each block consisted of trials of female and male faces that were presented in a random order for 500 ms, separated by an interstimulus interval (ISI) of 600, 700, or 800 ms. Participants were required to press either a left or a right button whenever they saw a male face.

2.2.3. Electrophysiological recording

The EEG was recorded from an elastic net (Electrical Geodesics, Inc.) containing 128 silver chloride plated electrodes embedded in sponges. Recorded EEG was referenced to the vertex (Cz) and amplified by Net Amps 200 (band-pass filter 0.01 – 100 Hz; digitized sampling rate 500 Hz; impedance below 50 kΩ). Eye movements and blinks were monitored by electrodes placed below and beside each eye. Raw EEG data were segmented into epochs starting 200 ms before and ending 800 ms after the stimulus onset. A band-pass filter of 1–30 Hz was applied off-line. Trials contaminated by movements were visually inspected and manually rejected. Trials containing eye artifacts were corrected using the artifact correction method provided by BESA 5.1 software (MEGIS Software GmbH). For each participant, we formed averages based on all 36 female faces and determined for each participant the scalp site where each component was maximal. The N170 component was defined in ERP data as local maximum negativities at the left and right lateral occipital-temporal sites within the region of P7 (P7, PO7, P9, PO9) and P8 (P8, PO8, P10, PO10) between 130 – 190 ms. The P100 component was defined as the local maximum positivities at the left and right occipital sites within the region of O1 (O1, PO3) and O2 (O2, PO4) between 90 – 130 ms. The N250 component was defined as the negative-going waveform between 270 and 320 ms post-stimulus at the lateral temporal-occipital regions, and was measured as the local maximum negativity of the mean amplitude over the 270-320 ms time-window, found around TP9 (P7, P9, PO9, TP9) and TP10 (P8, P10, PO10, TP10) (Fig. 2.2). We used the maximum values in each region in order to ensure maximal response for each participant despite minor variations across individuals in cortical morphology and generator orientation projecting to the scalp. Within each participant, the scalp locations where the maximum ERP responses were observed were consistent across face stimuli.

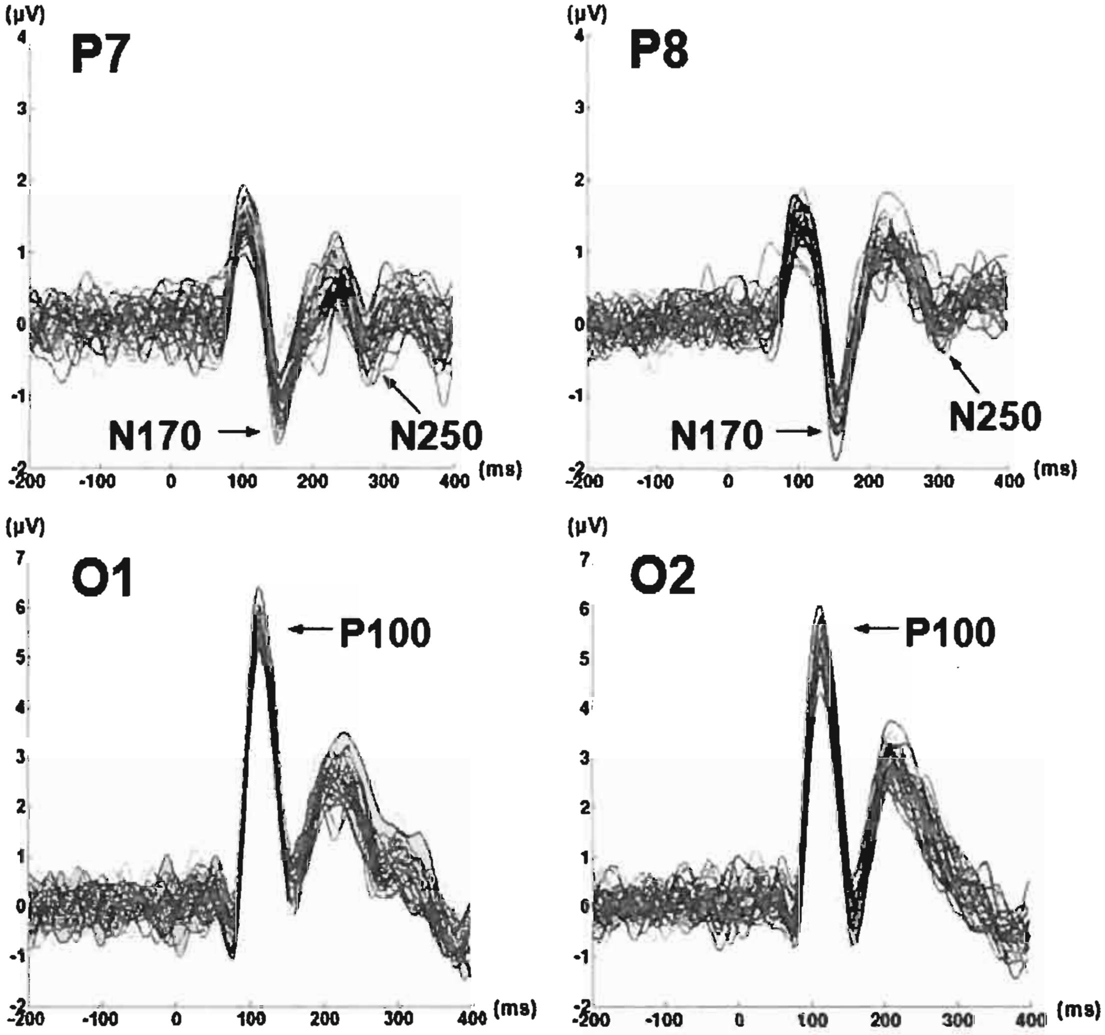

Figure 2.2. ERP waveforms elicited by individual faces. The P100, N170, and N250 waveforms at the contributing electrodes (see method) for the 36 face stimuli, averaged across 14 participants. For all faces, robust P100, N170, and N250 components were elicited at approximately 110 ms, 160 ms, and between 270 and 320 ms post-stimulus.

2.2.4. Measurements of physical facial characteristics

Our measurements of facial characteristics emphasized the eye region and facial layout, because these regions have been found to be particularly important for individual face processing by Freiwald et al. (2009) in their recent single-cell recording study with monkeys. Furthermore, previous ERP research has demonstrated that the N170 component is particularly sensitive to the presence or absence of eyes (Bentin, et al., 1996; Itier, et al., 2007).

For each of the 36 female face stimuli, the following measurements were made. For the facial layout, the specific measurements included top-of-face height (the distance from the top of the forehead to the mid-point between the eyebrows), bottom-of-face height (distance from mid-point between the eyebrows to the tip of the chin), and face width (distance between the cheekbones). For the eye region, the measurements included eye color (red, green, blue component in RGB units; three samples were taken from the iris region for each eye; averaged over the two eyes), eye width (distance between two corners of an eye; averaged over the two eyes), eye height (distance between upper and lower eyelid; averaged over the two eyes), and between-eye distance (distance between the centers of the eyes)[1]; the luminosity of the iris region was measured using a luminance meter (Konica Minolta LS-100) (three samples were taken from the iris

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[1] In a previous study (Nishimura et al., 2009), a different group of participants viewed these same faces in pairs. For each face pair, participants rated the similarity between the two faces. Applying multidimensional scaling to similarity ratings, a "face space" was constructed; each dimension of the "face space" represented presumably some facial information that participants used to make their similarity judgments. Relating the dimensional values obtained in that behavioral study to the facial characteristics measured for the present ERP study, strong correlations were found for eye color, face width, eye height and top-of-face height, suggesting that these facial characteristics are important for perceiving individual faces, at least in a behavioral task where participants were explicitly asked to make face similarity judgments.

region for each eye, and averaged over the two eyes). Additional measurements were also made for the nose and mouth region, including the nose height (distance between the center of the eyes and the tip of the nose), the nose-to-mouth distance (distance from the tip of the nose to the medial cleft of the upper lip) and the lip thickness (distance from the medial cleft of the upper lip to the bottom of the lower lip) (Fig. 2.3).

Because we were using real faces with no manipulation of any facial characteristics, some facial information (e.g., iris size, face direction), which was previously manipulated by Freiwald et al. (2009) with cartoon faces and found to be important at influencing neural responses, was not applicable to the current stimulus set and therefore was not measured for the current experiment.

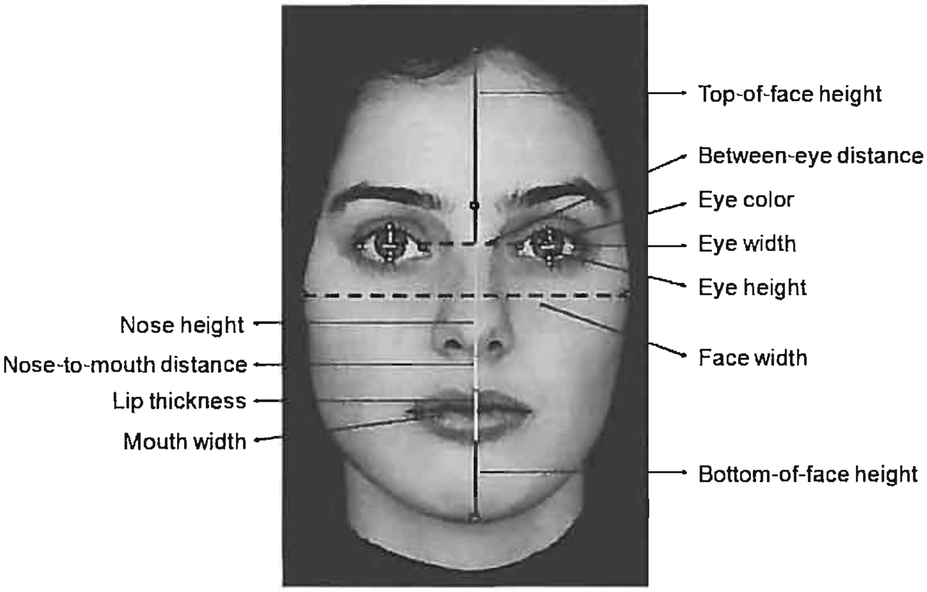


Figure 2.3. For each of the 36 female faces, a number of facial characteristics were measured that provided information about the eye region, the facial layout, the nose and the mouth region,

2.2.5. Data analyses

Using multiple regression analyses, we related these facial characteristics to the amplitude of the P100, the N170, and the N250 components to examine whether variation in individual facial characteristics is associated with differences in neural activity at each of these three time points. In addition, because of the holistic nature of face processing (Sergent, 1984; Tanaka & Farah, 1993; Yin, 1969), the effect of some characteristics may depend on other characteristics. Given the large number of possible ways that facial characteristics can be combined for interaction, it is thus necessary to choose a small set of interactions a priori to avoid potential type I errors. Based on previous findings with monkeys (Freiwald et al., 2009) and with humans in their face similarity judgments (see the footnote 1), we confined our analyses of interaction effects to eye region and to facial layout, including eye width by eye height (eye size), face width by bottom-of-face height, face width by top-of-face height, and top-of-face height by bottom-of-face height. Because of this selection, we acknowledge the possibility that other interactions (e.g., nose length by bottom-of-face), which were not examined in the current study, may also influence ERP responses. The same analyses were performed for the P100, N170, and N250 components, further separated by the left and right site, in order to examine their relationship with the facial characteristics first from the eye region, second about facial layout, and third from the nose and mouth region.

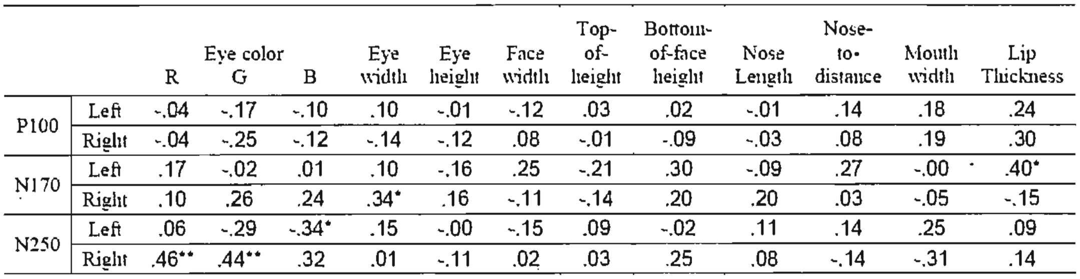
With the hierarchical multiple regression analyses, the simple effects of facial characteristics (e.g., eye width, eye height) on the ERP components were first considered and then followed by the analyses of the interactions (e.g., eye width by eye height). When significant predictors were found, the amount of variance accounted for in the ERP component was reported and summarized in Tables 2.2 – 2.4. When multiple factors affected an ERP component, they were considered together in one multiple regression model to examine whether their influences on the ERP component were unique when controlling for each other. Because we were interested in how variations among facial characteristics of female faces would influence brain responses in general, the main analyses and results presented were based on means for the individual face stimuli (non-target *female* faces) averaged over participants as scored at the maximum site for each person (as described earlier). When these results were examined subsequently for individual participants and tested using regression analyses with repeated measures (Lorch & Myers, 1990), similar patterns of results were found. Because there was almost no variation in the P100 and in the N170 latency across the face stimuli (Fig. 2.2), latency was not included in data analyses. Similarly, for the N250 component, only the mean amplitude over the period of 270-320 ms was considered for analyses, as it is typically performed in the literature because of the difficulty of finding a clear peak for the component.

2.3. Results

The simple correlations between measurements of facial characteristics and the amplitude of the P100, N170, and N250 component are presented in Table 2.1. Despite the lack of simple correlations between the N170 component and facial characteristics, when factors were considered together in multiple regression analyses with respect to eye region, facial layout, and mouth and nose region, we found that the N170 amplitude was sensitive to various facial characteristics involving the eye region and facial layout, consistent with findings of intracortical recordings in nonhuman primates (Freiwald et al., 2009). In contrast, the same multiple regression analyses demonstrated that the P100 and N250 component were largely not affected by these facial characteristics.

Table 2.1

Correlations between the measurements of facial characteristics and the amplitude of the P100, N170 and N250 component.



		Eye color			Eye width	Eye height	Face width	Top-of-height	Bottom-of-face height	Nose Length	Nose-to-distance	Mouth width	Lip Thickness
		R	G	B									
P100	Left	-.04	-.17	-.10	.10	-.01	-.12	.03	.02	-.01	.14	.18	.24
	Right	-.04	-.25	-.12	-.14	-.12	.08	-.01	-.09	-.03	.08	.19	.30
N170	Left	.17	-.02	.01	.10	-.16	.25	-.21	.30	-.09	.27	-.00	.40*
	Right	.10	.26	.24	.34*	.16	-.11	-.14	.20	.20	.03	-.05	-.15
N250	Left	.06	-.29	-.34*	.15	-.00	-.15	.09	-.02	.11	.14	.25	.09
	Right	.46**	.44**	.32	.01	-.11	.02	.03	.25	.08	-.14	-.31	.14

Note. $^*p < .05$, $^{**}p < .01$, uncorrected

2.3.1. N170 and facial characteristics

2.3.1.1. Right N170 and its relation to eye color and face width.

For eye color, although the right N170 did not correlate with red, green, or blue color component alone, a red-green interaction accounted for 35.8% of the variance in N170 amplitude ($p = .001$): for faces with greenish eyes (high in the green component), the N170 amplitude was greater with more red component, $r = .53$, $p = .024$, whereas faces with brownish eyes (low in the green component) showed the opposite relation, $r = -.59$, $p = .010$. Figure 2.4*a* shows this interaction effect, after we divided the face stimuli into two groups with a median-split based on the value of the green component. This effect is likely not due to luminosity differences, as we found no correlation between right N170 amplitude and overall luminosity of the iris region ($p = .789$).

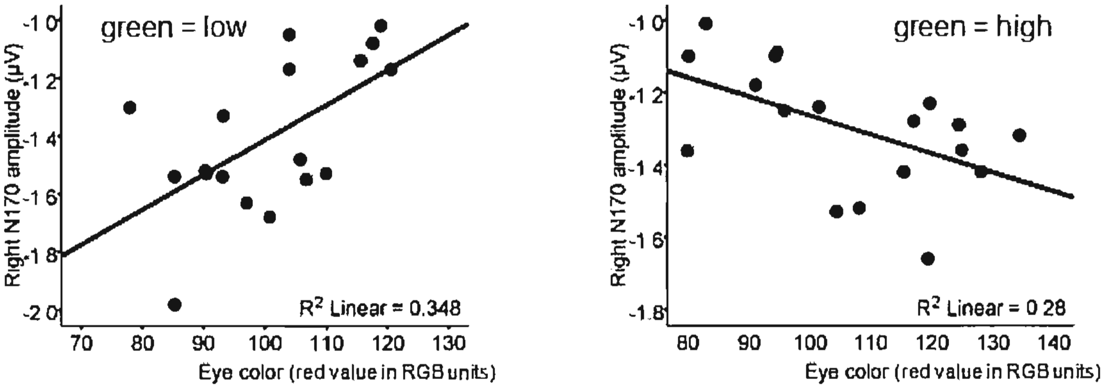


Figure 2.4a. The interacting effect between green and red component of eye color on right N170 amplitude. After dividing the 36 individual female faces equally into two groups based on the value of green component, either a positive or a negative relationship was observed between the red component of eye color and right N170 amplitude.

Of the eye-size factors, only eye width accounted for significant variance (11.5%) in the right N170 amplitude (*p* = .044); eye height and its interaction with eye width did not (*p*s > .30). The between-eye distance was not related to the right N170, either by itself or after controlling for effects due to other eye characteristics (i.e., eye color and eye width) (*p*s > .45). When both eye color and eye width were considered together in one regression model, only eye color was found to have unique contribution to the right N170 amplitude, accounting for 19.1% of the variance after controlling for eye width; in contrast, after controlling for eye color, eye width was no longer a significant predictor of the N170 amplitude.

No aspect of facial layout (i.e., face width, bottom-of-face height, and top-of-face height) related linearly to the N170, either separately, combined, or in their interactions (*p*s > .20). However, visual inspection of the scatter plot between face width and right N170 amplitude suggested a quadratic relationship (Fig. 2.4*b*). This was subsequently confirmed, and the quadratic term of face width accounted for 19.5% of the variance in N170 amplitude (*p* = .01). Such a quadratic relationship was not found for bottom-of-face height (*p* = .385) or for top-of-face height (*p* = .747). None of the nose and mouth region measures (nose height, nose-to-mouth distance, mouth width, lip thickness) was directly related to the right N170 amplitude (*p*s > .23).

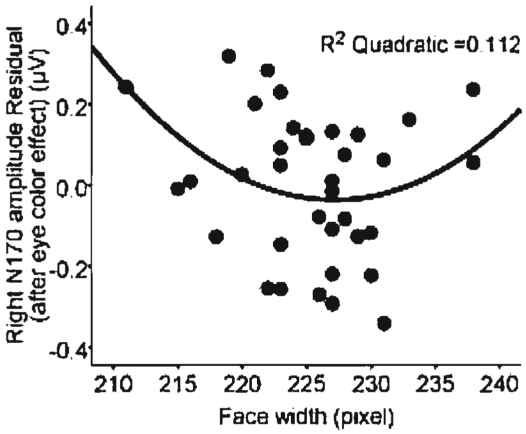


Figure 2.4b. The curvilinear relationship between right N170 amplitude and face width, after controlling for eye color.

In summary, the amplitude of the right N170 component was related to eye color, and the quadratic term of face width. When these two characteristics were considered together in a single regression analysis, the eye color effect was strong even after controlling for face width (*p* = .003), while face width also appeared to contribute uniquely to the N170 amplitude (*p* = .076). Together, these two facial characteristics accounted for 43.6% of the variance (*p* = .003) (see Table 2.2 for the complete analyses and results for the relationship between right N170 amplitude and various facial characteristics).

Table 2.2

Multiple regression analyses examining the relationship between the facial characteristics and the N170 amplitude.

			R	R^2 Change	*F* change	*p*
Right N170	Eye color	Step 1: eye color (red), eye color (green)	.257	.066	1.2	.324
		Step 2: eye color (red) x eye color (green)	.598	.292	14.5	**.001**
	Eye size	Step 1: eye width	.338	.115	4.4	**.044**
		Step 2: eye height	.357	.013	<1.0	.484
		Step 3: eye width x eye height	.394	.027	1.0	.318
	Facial layout	Step 1: face width	.106	.011	<1.0	.537
		Step 2: face width^2	.442	.184	7.5	**.010**
		Step 1: face width, top-of-face height	.190	.036	<1.0	.546
		Step 2: face width x top-of-face height	.284	.045	1.6	.222
		Step 1: face width, bottom-of-face height	.237	.056	<1.0	.386
		Step 2: face width x bottom-of-face height	.237	.000	<1.0	.957
		Step 1: top-of-face height, bottom-of-face height	.213	.045	<1.0	.465
		Step 2: top-of-face height x bottom-of-face height	.271	.028	<1.0	.332
		Step 1: eye color (red), eye color (green)	.257	.066	1.2	.324
		Step 2: eye color (red) x eye color (green)	.598	.292	14.5	**.001**
		Step 3: face width	.611	.015	<1.0	.394
		Step 4: face width^2	.661	.063	3.4	**.076**
		Step 1: face width	.106	.011	<1.0	.537
		Step 2: face width^2	.442	.184	7.5	**.010**
		Step 3: eye color (red), eye color (green)	.497	.052	1.1	.359
		Step 4: eye color (red) x eye color (green)	.661	.189	10.1	**.003**
Left N170	Eye color	Step 1: eye color (red), eye color (green)	.187	.035	.6	.554
		Step 2: eye color (red) x eye color (green)	.380	.110	2.0	.154
	Eye size	Step 1: eye width	.099	.010	.3	.565
		Step 2: eye height	.348	.112	4.2	**.049**
		Step 3: eye width x eye height	.352	.002	.1	.778
	Facial layout	Step 1: face width	.251	.063	2.3	.140
		Step 2: face width^2	.251	.000	<1.0	.956
		Step 1: face width, top-of-face height	.303	.092	1.7	.204
		Step 2: face width x top-of-face height	.332	.019	<1.0	.420
		Step 1: face width, bottom-of-face height	.378	.143	2.8	.078
		Step 2: face width x bottom-of-face height	.398	.015	<1.0	.459
		Step 1: top-of-face height, bottom-of-face height	.310	.096	1.8	.189
		Step 2: top-of-face height x bottom-of-face height	.488	.142	6.0	**.020**
		Step 1: eye width	.099	.010	.3	.565
		Step 2: eye height	.348	.112	4.2	**.049**
		Step 3: bottom-of-face height, top-of-face height	.395	.035	<1.0	.533
		Step 4: bottom-of-face height x top-of-face height	.577	.176	7.9	**.009**
		Step 1: bottom-of-face height, top-of-face height	.310	.096	1.8	.189
		Step 2: bottom-of-face height x top-of-face height	.488	.142	6.0	**.020**
		Step 3: eye width	.492	.005	<1.0	.669
		Step 4: eye height	.577	.090	4.054	**.053**

2.3.1.2. Left N170 and its relation to eye size and facial layout.

In contrast to the right N170, the left N170 amplitude was not related to eye color (*p* = .107). Instead, the left N170 was affected by eye-size factors: when controlling for each other, greater eye height and smaller eye width were associated with a larger left N170, accounting for 11.2% (*p* = .049) and 9.4% (*p* = .069) respectively of unique variance in N170 amplitude (see Fig. 2.4*c* and Table 2.2 for the relationship between left N170 and eye height, after controlling for eye width). The interaction between eye width and eye height was not significant (*p* = .318). As was the case for the right N170, the between-eye distance was not related to the left N170, even after controlling for eye height or width effect (*p*s > .30).

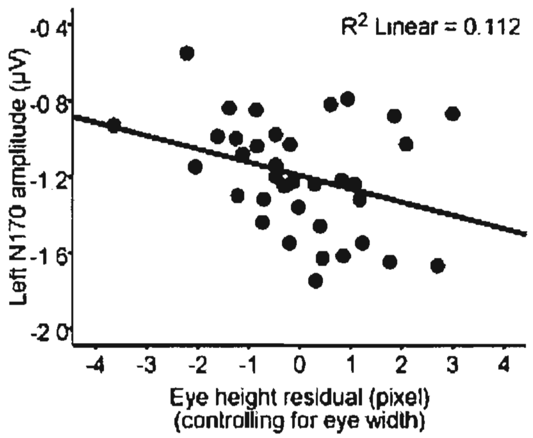


Figure 2.4c. The effect of eye height on left N170 amplitude, after controlling for eye width.

Of the facial layout factors, also different from the right N170, the left N170 amplitude was not related to face width either linearly or with its quadratic term (*p*s > .10). Neither was the left N170 amplitude related to the top- or the bottom-of-face height, when each factor was examined alone (*p* = .228; *p* = .079). However, the left N170 amplitude was sensitive to the top- by bottom-of-face height relationship (Table 2.2), as 23.8% of its variance was accounted for by this interaction (*p* = .02). For faces with a small bottom portion, top-of-face height correlated with N170 amplitude (*r* = .455, *p* = .058; see Fig. 2.4*d*, left panel), whereas for faces with a large bottom portion, the top-of-face height did not correlate with N170 amplitude (*p* = .669; see Fig. 2.4*d*, right panel). While top-of-face height and bottom-of-face height interact with each other, neither interacted with face width (*p*s > .40).

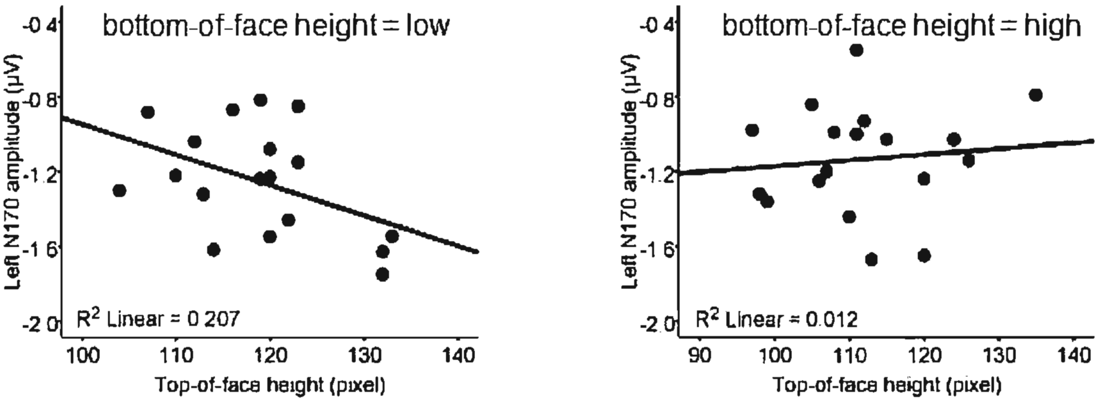


Figure 2.4d. The interacting effect between top-of-face height and bottom-of-face height on the left N170 amplitude: left N170 amplitude was related to top-of-face height only when bottom-of-face height was small.

With regard to the facial information from the nose and mouth regions, the left N170 amplitude correlated with lip thickness (*p* = .017), but not with nose length (*p* =. 588), mouth width (*p* = .982), or nose-to-mouth distance (*p* = .105). When we examined the effect of lip thickness further, we found that the lip thickness also correlated with bottom-of-face height (*p* = .003), which affected the left N170 amplitude by interacting with top-of-face height. After considering the interaction effect between bottom-of-face height and top-of-face height, lip thickness was no longer a significant predictor of the left N170 amplitude (*p* = .130).

In summary, the left N170 was sensitive to eye size and the top- by bottom-of-face height relationship, which did not affect the right N170. When both facial characteristics were considered together in one regression model, each contributed unique variance to the left N170 amplitude (*p* = .053; *p* = .009), and together accounted for 33.3% of the variance (*p* = .026) (see Table 2.2 for the complete analyses and results for the relationship between left N170 amplitude and various facial characteristics).

2.3.2. P100 and facial characteristics

When the same regression analyses were performed using measurements of facial characteristics to predict the amplitude of the P100 component averaged across participants, no relationships were found (see Table 2.3 for the complete analyses and results), except for eye color. Similar to the N170 results, the P100 amplitude was affected by a red-green interaction, which separately accounted for 33.5% of the variance in the right (*p* < .001) and 20.9% of the variance in the left (*p* = .011) P100 amplitude. Although neither of the two color components was significantly correlated with P100 individually, it appeared that for faces high in the green-color component (greenish eyes), there was a positive relationship between P100 amplitude and red-color component (for right P100, *r* = .316; left P100, *r* = .274); in contrast, for faces low in the green-color component (brownish eyes), the relationship between P100 amplitude and red-color component was reversed (for right P100, r = -.328; left P100, r = -.313). Despite this red-green interaction, the overall luminosity of iris region did not correlate with P100 amplitude on either left (*p* = .694) or right (*p* = .837) site.

Although both the P100 and N170 were affected by eye color, when they were tested together within one regression model, the red-green interactions on right P100 and on right N170 were found to be separable: controlling for the right P100 amplitude, there was still a red-green interaction affecting the right N170 amplitude, accounting for 18.4% of the variance (*p* = .009).

Table 2.3

Multiple regression analyses examining the relationship between the facial characteristics and the P100 amplitude.

			R	R^2 Change	*F* change	*p*
Right P100	Eye color	Step 1: eye color (red), eye color (green)	.251	.063	1.112	.341
		Step 2: eye color (red) x eye color (green)	.578	.271	13.056	**.001**
	Eye size	Step 1: eye width	.140	.020	<1.0	.416
		Step 2: eye height	.143	.001	<1.0	.874
		Step 3: eye width x eye height	.208	.023	<1.0	.389
	Facial layout	Step 1: face width	.083	.007	<1.0	.632
		Step 2: face width^2	.130	.010	<1.0	.564
		Step 1: face width, top-of-face height	.083	.007	<1.0	.893
		Step 2: face width x top-of-face height	.165	.020	<1.0	.421
		Step 1: face width, bottom-of-face height	.126	.016	<1.0	.766
		Step 2: face width x bottom-of-face height	.132	.001	<1.0	.830
		Step 1: top-of-face height, bottom-of-face height	.104	.011	<1.0	.836
		Step 2: top-of-face height x bottom-of-face height	.149	.012	<1.0	.543
Left P100	Eye color	Step 1: eye color (red), eye color (green)	.175	.031	<1.0	.599
		Step 2: eye color (red) x eye color (green)	.457	.178	7.199	**.011**
	Eye size	Step 1: eye width	.100	.010	<1.0	.562
		Step 2: eye height	.156	.014	<1.0	.491
		Step 3: eye width x eye height	.244	.035	1.2	.281
	Facial layout	Step 1: face width	.123	.015	<1.0	.475
		Step 2: face width^2	.137	.004	<1.0	.729
		Step 1: face width, top-of-face height	.124	.015	<1.0	.776
		Step 2: face width x top-of-face height	.160	.010	<1.0	.563
		Step 1: face width, bottom-of-face height	.126	.016	<1.0	.769
		Step 2: face width x bottom-of-face height	.236	.040	1.4	.252
		Step 1: top-of-face height, bottom-of-face height	.047	.002	<1.0	.964
		Step 2: top-of-face height x bottom-of-face height	.151	.020	<1.0	.419

2.3.3. N250 and facial characteristics

When the same analyses as with the P100 and the N170 components were conducted with regard to the N250 component, no significant relationships were found (see Table 2.4 for the complete analyses and results). However, in contrast to both the P100 and N170 results, the magnitude of N250 correlated with individual eye color components: the left N250 related inversely to the blue component ($r = -.34$, $p = .042$); the right N250 related directly to the green ($r = .435$, $p = .008$) and the red ($r = .462$, $p = .005$) components, with each color component contributing unique variance to the right N250 amplitude ($p = .032$ for red, controlling for green component; $p = .058$ for green, controlling for red component). Together, both eye color components accounted for 29.6% of variance in the right N250 amplitude ($p = .003$). In addition, the correlation between the right N250 amplitude and the overall luminosity of the iris region was highly reliable ($p < .001$).

Table 2.4

Multiple regression analyses examining the relationship between the facial characteristics and the N250 amplitude.

			R	R^2 Change	*F* change	*p*
Right N250	Eye color	Step 1: eye color (red), eye color (green)	.544	.296	6.9	**.003**
		Step 2: eye color (red) x eye color (green)	.566	.024	1.1	.297
	Eye size	Step 1: eye width	.012	.000	<1.0	.947
		Step 2: eye height	.174	.030	1.0	.319
		Step 3: eye width x eye height	.280	.048	1.7	.204
	Facial layout	Step 1: face width	.015	.000	<1.0	.932
		Step 2: face width^2	.088	.008	<1.0	.619
		Step 1: face width, top-of-face height	.033	.001	<1.0	.982
		Step 2: face width x top-of-face height	.094	.008	<1.0	.620
		Step 1: face width, bottom-of-face height	.252	.063	1.1	.340
		Step 2: face width x bottom-of-face height	.260	.004	<1.0	.706
		Step 1: top-of-face height, bottom-of-face height	.292	.085	1.5	.230
		Step 2: top-of-face height x bottom-of-face height	.296	.002	<1.0	.791
Left N250	Eye color	Step 1: eye color (red), eye color (green)	.341	.116	2.2	.130
		Step 2: eye color (red) x eye color (green)	.399	.043	1.6	.210
	Eye size	Step 1: eye width	.150	.022	<1.0	.383
		Step 2: eye height	.217	.025	<1.0	.361
		Step 3: eye width x eye height	.217	.000	<1.0	.982
	Facial layout	Step 1: face width	.151	.023	<1.0	.379
		Step 2: face width^2	.215	.021	<1.0	.373
		Step 1: face width, top-of-face height	.166	.027	<1.0	.632
		Step 2: face width x top-of-face height	.214	.018	<1.0	.439
		Step 1: face width, bottom-of-face height	.152	.023	<1.0	.681
		Step 2: face width x bottom-of-face height	.165	.004	<1.0	.716
		Step 1: top-of-face height, bottom-of-face height	.092	.009	<1.0	.868
		Step 2: top-of-face height x bottom-of-face height	.115	.005	<1.0	.700

2.4. Discussion

It is well known that adults can readily discriminate individual facial identities and that they are extremely sensitive to both featural and relational cues in faces (Freire, et al., 2000; Mondloch, et al., 2002). Previous studies investigating the neural mechanisms of face perception have emphasized differences in neural activity elicited by faces versus non-face stimuli (Allison, Ginter, et al., 1994; Bentin, et al., 1996; Haxby, et al., 2001; Kanwisher, et al., 1997). Here we provide, with human ERP data, the neural evidence for the processing of facial characteristics using a large number of female faces. The right and left N170 were differentially related to variations in multiple facial characteristics including eye color, eye height, face width, and top- by bottom-of-face height relationship. In contrast, as predicted on the basis of evidence that the P100 is linked to low-level visual processing and the N250 to face identity strength rather than structural encoding, the amplitudes of these two components were largely not affected by these facial characteristics (except for eye color, see below for further discussion).

Previous studies showed that neurons in particular regions (e.g., FFA or inferotemporal cortex in monkeys) increase in activity as the difference between individual faces and a face prototype increases (Leopold, et al., 2006; Loffler, et al., 2005). Furthermore, depending on whether adults are discriminating faces that differ in the appearance of individual features or in the spacing among them, frontal areas and face sensitive regions (e.g., FFA and occipital face area) are differentially activated (Maurer, et al., 2007; Pitcher, Walsh, Yovel, & Duchaine, 2007). Similarly, in ERP research, the N170 component is not only face-sensitive, but also sensitive to the presence of specific facial information (Eimer, 2000b): the amplitude of N170 is reduced bilaterally when either internal (e.g., eyes, nose, mouth) or external (e.g., face shape) facial cues are removed from a face, consistent with the single-neuron findings from early monkey studies (Desimone, Albright, Gross, & Bruce, 1984; Perrett, Rolls, & Caan, 1982).

Only one neurophysiological study to date (Freiwald, et al., 2009) has examined neural responses to variations in individual facial characteristics, but the participants in that study were non-human primates. Our study is the first to examine neural responses of human participants to natural variations in human facial characteristics using a large number of female faces. Like the results from non-human primates, N170 amplitude was especially sensitive to variations in the eyes and facial layout, and was not affected by information from the nose and mouth region. Our finding that the eyes are especially important for individual face perception is also consistent with the general conclusions in the ERP literature (Bentin, et al., 1996; Itier, et al., 2007). We further identified eye color and eye size as two distinct eye features that are important for the basic neural responses in individual face perception. To our knowledge, we are the first to demonstrate an eye color effect. Because many previous studies have used grayscale photographs of faces, eye color may have been missed as an important factor influencing face perception, a finding that seems to fit well with our personal experience. Indeed, when we informally asked participants what facial information stood out when they were viewing the individual female faces during the gender decision task, almost all participants reported eye color in their answers. Given that participants were not required to recognize individual face identities, the fact that people had nonetheless noticed differences in these facial characteristics (e.g., eye color and face width) across individual faces provides strong support for the automatic processing of these facial characteristics in perceiving individual faces. Our N170 results have further helped to temporally locate their corresponding neural correlates.

It is interesting to note that while our results showed that the N170 amplitude is sensitive to eye information (i.e., eye color, eye size), some ERP studies have found no change in the N170 amplitude after eyes were removed from a face (Eimer, 1998; Itier, et al., 2007; Itier, Van Roon, & Alain, 2011). To explain why the N170 amplitude is not affected by eye removal but is larger to eyes alone than to a face, Itier et al. (2007) have recently proposed an "inhibition" model with the suggestion that the eye-selective neurons are inhibited when eyes are present in a face. Therefore, there seems to be a discrepancy between our conclusion and the conclusion drawn by those studies. Several considerations might help to address this issue. First, the types of data analyses were very different between our study and the previous studies. The previous studies used group comparisons between the two conditions, i.e., faces with eyes and faces without eyes; in contrast, with multiple regression analyses, the eye information was treated as a continuous variable in the present study. This allowed us to take advantage of the subtle variations in eye information and to relate them to rather small changes in the N170 amplitude. As a result, the present study might be statistically more powerful than the previous studies in detecting any effect that eye information may have on the N170 amplitude. In fact, if we had used the group analyses to compare between faces with brownish eyes (see Fig. 2.4*a*, left panel) and faces with greenish eyes (see Fig. 2.4*a*, right panel), we would have concluded that eye color did not affect the N170 amplitude, because the average N170 amplitudes were very similar for the two groups of faces. However, it is clear that when we examined the N170 amplitude in relation to changes in eye color within each group, strong relationships were found for both groups.

Second, the question of whether and how the eyes may affect the N170 amplitude when they are present in a face cannot be adequately answered by examining the effect of their absence on the N170 amplitude. A face with the eyes removed may be perceived in a qualitatively different way than a normal face. Because of this, it may be difficult to generalize from brain responses to eyeless faces to brain responses to eye information within a normal face. Third, a recent study with monkeys (Freiwald et al., 2009) seems to suggest the opposite of the "inhibition" model with findings that neurons respond to, rather than being inhibited by, variations in eye information even when eyes are present with other facial characteristics. Thus, although somewhat surprising, our results provide novel insights about the influence of eye size and eye color on the N170, insights that are compatible with previous findings but enrich our understanding of the relationship between eyes and this well-studied ERP component.

The main focus of electrophysiological research on face perception in the past decade has been the N170, with debates about whether it is produced by unitary or multiple neural generators (Rossion & Jacques, 2008). Our finding that a variety of facial characteristics made unique contributions to the N170 component seems to support the multiple sources account, suggesting that the N170 component reflects a cumulative effect of several functionally separable processes. Whether these processes are mediated through the same or different brain structures needs to be addressed in future research. Possible regions of interest may include the lateral occipital complex, the mid-posterior fusiform gyrus, and the superior temporal sulcus—areas that are more active when people are viewing faces than non-face objects (Haxby, et al., 2001; Kanwisher, et al., 1997) and that may be involved in discriminating facial identities (Grill-Spector, Knouf, & Kanwisher, 2004; Rotshtein, et al., 2005). Among the neural studies that have examined the sensitivity of different brain structures to different types of facial information (e.g., featural or configural), the results are mixed. For example, while an early fMRI study (Yovel & Kanwisher, 2004) failed to find any difference in activation of either left or right FFA between configural and featural manipulations, a more recent study (Maurer, et al., 2007) found a region of right fusiform gyrus to be sensitive specifically to the spacing among facial features. Similarly, for the processing of local features (e.g., eyes and mouth), activation in lateral occipital cortex (Yovel & Kanwisher, 2004) or regions adjacent to it (e.g., occipital face area) (Pitcher, et al., 2007) has been reported. Despite such mixed results, these studies nonetheless support the possibility that the dissociable effects of face perception, as we observed in scalp-recorded ERPs in the present study, might be linked to specific neural responses of separate brain regions.

This prediction is further supported with more recent neuroimaging data that demonstrate that the FFA, OFA, and STS may respond selectively to different types of facial information (Liu, et al., 2009; Schiltz, Dricot, Goebel, & Rossion, 2010; but see Andrews, et al., 2010). Furthermore, it is also possible that within each of these regions, individual neurons may differ in the information to which they are sensitive, with some being "featural" and others being "configural" (see Freiwald et al., 2009, for this pattern in monkeys).

One novel finding in our data was the dissociation between the left and right N170 effects: eye color and face width affected the right N170 but not the left, whereas eye size and the top- by bottom-of-face height relationship affected the left N170 but not the right. Although many studies have emphasized that the right hemisphere is particularly tuned to face processing (Benton, 1980; Kanwisher, et al., 1997; McCarthy, Puce, Gore, & Allison, 1997; Yin, 1970), there are previous reports of bilateral activation (Halgren, et al., 1999; Haxby, et al., 1999). There are also reports that the left and right hemispheres play unique roles, with the right hemisphere being associated with tasks in which participants make holistic or spatial judgments, and the left hemisphere being associated with tasks that require attention to face parts (Maurer, et al., 2007; Rossion, et al., 2000). Therefore, it is likely that both hemispheres are involved in face processing, although the ways and the extent to which they contribute to face perception may differ. This is also consistent with the proposed distributed neural model of face and object representation in general (Haxby, et al., 2001; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999).

In addition, the results from the present study may further extend our knowledge about the differential processing by the left versus right hemisphere to natural variations in facial characteristics, the processing of which may also differ along the “part-based” vs. “whole-based” continuum. On the surface it is somewhat counterintuitive or surprising that top- by bottom-of face height relationship (a “configural” cue) affected only the left N170, whereas eye color (a “featural” cue) affected only the right N170. This pattern of results may indicate that what at first glance appears to be configural versus featural cues can be redefined in terms of the ways in which they are processed. For example, because the top- by bottom-of-face height relationship requires the computation and integration of its composite parts, the process involved may be similar to a “part-based” task, which might be the reason why it affected only the left N170. In contrast, eye color does not seem to require explicit analyses of its composite parts, but is rather processed more holistically and perceived, for example, as either more greenish or more brownish. The processing of eye color is thus similar to a “whole-based” task, and perhaps because of this, it affected the right N170. Our findings call attention to the difficulty of clearly separating configural vs. featural cues by whole vs. part processes, because the processing of facial features (e.g., eye color and eye size) can be either more holistic- or more part-based, and the same is also true for configural cues (e.g., face width and top- by bottom-of-face height). To test this hypothesis, future studies are needed to systematically examine the extent to which laterality effects for specific facial characteristics map onto the general task-related whole versus part processing that are associated with each hemisphere.

Our results show that the effects of eye color, eye height, face width, and the top- by bottom-of-face height relationship are mainly found in the N170 and not the P100 component, suggesting that these factors operate at a high-level of visual processing within the context of faces (as opposed to low-level processing of these physical characteristics in general). This interpretation is consistent with the general conclusion in the literature (see Rossion & Jacques, 2008, for a review) and seems to be further supported by the result that although both P100 and N170 were affected by eye color, the effects were separable. The P100 effect likely reflects the low-level processing of *color* in general, while the N170 effect may reflect high-level processing of *eye color* within the context of faces.

Collectively, the present study indicates a series of neural events that occur within the first 200 ms after a person sees individual faces. At about 100 ms, as seen in P100 responses, the brain processes visual information (e.g., spatial frequency, texture, color) at a low level, which may not be specific to faces but rather common to all visual objects. Approximately 50 ms after the P100 component, the visual information extracted from early stages is integrated and further analyzed, but now within the context of specific visual categories. When the system detects a face at some point between 100 and 150 ms, larger responses are subsequently elicited from specific brain regions (e.g., fusiform and occipital face areas) and greater electrophysiological responses (e.g., N170) are observed at the scalp. In the meantime, as suggested by our N170 results, various facial characteristics (e.g., eye color, face width, eye size and top- by bottom-of-face relationship) are now analyzed (structural encoding) in order to provide information that is necessary for the next stage (i.e., face recognition) to occur. Similarly, as suggested by both animal and human research (Schyns, Petro, & Smith, 2007; Smith, Fries, Gosselin, Goebel, & Schyns, 2009; Sugase, Yamane, Ueno, & Kawano, 1999), such a hierarchical sequence of neural events, from processing of low-level visual information in isolation to high-level integration, might also be involved in perceiving individual facial expressions.

Our findings of specific relationships between N170 and various facial characteristics are consistent with early ERP research suggesting the N170 as an index to the structural encoding of faces (Eimer, 2000b). Recent studies using adaptation paradigms have also reported that the N170 can be modulated by face identities: the amplitude of N170 was reduced to faces that were preceded by faces of the same identity versus a different identity (Jacques, et al., 2007; Jacques & Rossion, 2006), even when there were changes in viewpoint (Caharel, d'Arripe, et al., 2009; but see Kaufmann, et al., 2008). Although these findings may mean that face recognition could also occur during the N170 time-window, the modulation of N170 in these studies may be a result of adapted neural responses for processing facial characteristics (i.e., structural encoding) that were different across individual faces (Caharel, Jiang, et al., 2009), as would be suggested by the present study. In line with this interpretation, in studies where a target face and a prime face either do not share the same facial characteristics (e.g., Ronald Reagan – Nancy Reagan in associative priming) (Schweinberger, et al., 1995) or share them to a lesser degree (Schweinberger, Pickering, Jentzsch, et al., 2002), the priming effect only occurred between 200 and 300 ms, suggesting that face recognition occurs after the N170. In the present study, the N250 was not sensitive to the array of facial characteristics to which the N170 showed sensitivity. Considering that all the face stimuli were equally unfamiliar to participants and the strength of face identities may not be defined by a single facial characteristic, such null findings were expected and are compatible with the N250 being a marker for face identity processing that occurs after structural encoding. Interestingly, however, we did find a strong relationship between the N250 amplitude and eye color components. This raises a question with regard to the unique role that eye color may play in defining face identity strength. For example, people may perceive faces with either more greenish or more brownish eyes as more distinctive and having greater identity strength. However, because we did not have participants' ratings of distinctiveness for the current set of face stimuli, the present data cannot provide a definite answer for the relationship between eye color and face identity strength, an issue that should be examined by future ERP research.

We acknowledge the importance of being cautious in our interpretation given the novelty of our research approach and that other facial characteristics (e.g., face asymmetry) that we did not measure may also affect the N170. Nonetheless, several considerations appear to support the validity of our main finding that the N170 is modulated by the differences in facial characteristics among individual female faces. First and foremost, our findings are clearly consistent with previous ERP research with regard to the general function indexed by the N170 (i.e., structural encoding of faces), but we have taken it one step further by showing how the N170 changes with variations in specific structural information. Importantly, these effects were largely found in the N170 component, but not earlier in the P100 or later in the N250 component. Such dissociations also seem consistent with what would be predicted based on the functions associated with the P100, the N170, and the N250. Second, our ERP findings that the eye region and facial layout, in contrast to the nose and mouth region, are critical facial information that influence neural responses match well the recent report by Freiwald et al. (2009) with non-human primates. Their study had similarly demonstrated some complex patterns of neural responses in relation to various facial characteristics and interactions among them. Third, it is unlikely that our results are specific to our having used a gender decision task. The task was extremely easy (accuracy at 96.7%), and participants could have even used non-facial cues (e.g., the hair template for all female faces) to perform the task; nonetheless, the N170 was influenced by multiple facial characteristics, and similar effects were not found with other ERP components. These results together with participants' report of noticing differences in these facial characteristics suggest that the processing of these facial characteristic could occur automatically and may be relatively task-independent.

As the facial characteristics varied naturally across the face stimuli, some female faces might have more distinctive facial information (e.g., eye color, face width) than others. Because the distinctive faces might have attracted more attention during the experiment than non-distinctive faces, this raises another question that we need to consider, i.e., whether the relationships between the N170 amplitude and the facial characteristics might actually be explained by the difference in attention allocation. To address this issue, we need to consider whether attention alone would have any effect on the N170. In contrast to the well documented effects of selective attention on the P100 component, the relationship between attention and the N170 is however not clear. While some studies have reported attention modulation of the N170 component (e.g., Eimer, 2000b), others have not found such effects (e.g., Cauquil, Edmonds, & Taylor, 2000; Rutman, Clapp, Chadick, & Gazzaley, 2010) even when attention was explicitly manipulated. The mixed results for the attention effect on the N170 might be partly explained by the type of task used (e.g., a memory task or a repetition detection task) and by the ways in which attention was manipulated (e.g., through explicit instructions or by using a face-irrelevant task to drain the attentional resource). Several studies have also reported that attention affected the N170, but only when the condition for perceiving a face was less than optimal (e.g., Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003; Sreenivasan, Goldstein, Lustig, Rivas, & Jha, 2009). In the current study, we used a large number of faces, they were perceived under an optimal situation, there was no stimulus degradation, and the study did not involve any attention manipulation. With these considerations, it thus seems more reasonable for us to explain the current N170 results in terms of the processing of facial characteristics at a perceptual level, rather than by attention at a cognitive level. This explanation is also consistent with the view of N170 as an index to structural encoding and with the recent single-cell recordings from monkeys (i.e., Freiwald, et al., 2009). Nevertheless, the relationship between N170 and attention is important to consider. As an initial step, we demonstrated in the present study how the N170 was affected by changes in specific facial characteristics. For future research, the possibility of how these effects might be modified by attention should be examined.

One limitation in the present study is that we had only examined the relationships between the N170 amplitude and facial characteristics among female faces. It is an open question with regard to whether similar relationships will also be found among male faces that are overall different in such sexually dimorphic facial characteristics as face width. We would like to note, however, that in the previous monkey study by Freiwald et al. (2009), only cartoon faces were used. As a result, information such as gender and age was not available. Nevertheless, despite the simplicity of the cartoon faces, it was found in the study that information from eye region and facial layout affected neural responses, suggesting that the effects of these facial characteristics might be general. Therefore, although we could not examine in the present study the relationships between the N170 amplitude and the facial characteristics for male faces (nine male face stimuli only), we would expect similar findings, i.e., the N170 would also be affected by variations in eye color, eye size, face width, and face proportions. Despite these considerations, because of the limited research on individual face perception and even more limited research focusing on facial characteristics, future studies, preferably using a variety of face stimuli (e.g., males, females) with different experimental paradigms (e.g., passive viewing, adaptation), are needed in order to understand the neural mechanisms and the timing of each stage associated with individual face perception (Bruce & Young, 1986) in general. It is also important to examine the extent to which these effects are experience- and stimulus set-dependent. For example, East Asians, for whom eye color is relatively constant, may show different patterns of ERP sensitivity to various facial characteristics and the relative weighting of facial characteristics may be different when, for example, participants are viewing faces among which there is minimal variation in specific characteristics (e.g., in eye color when viewing Asian faces).

In summary, by relating early ERP components to various facial characteristics measured from faces of real people, we provided further evidence in support of the N170 as reflecting the structural encoding of faces. In addition, our results have demonstrated how the N170 systematically changes with variations in specific facial characteristics and that different characteristics modulate the N170 across the two hemispheres. Future studies may investigate whether other facial characteristics that we did not measure (e.g., face asymmetry) also affect the N170 and the time point at which the ERP is influenced by facial identity.

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Chapter 3

Study 2. The timing of individual face recognition in the brain

3.1. Introduction

Numerous behavioural and neuropsychological studies have provided evidence that adults' perception of faces is different from their processing of other visual stimuli. Adults rapidly detect that a stimulus is a face even when realistic features are not physically present, so long as the face-like configuration of two eyes above a nose above a mouth can be inferred. For example, they can see a face in paintings by Archimbaldo consisting of only fruits and vegetables and in two-tone Mooney stimuli in which black and white shadows lead to the perception of a face. Adults process faces holistically (Tanaka & Farah, 1993; A. W. Young, et al., 1987) and are sensitive to small differences among faces in the shape of individual features and the spacing among them (Freire, et al., 2000; Maurer, et al., 2002; Mondloch, et al., 2002). Collectively, these behavioral skills allow adults to extract a wealth of information each time they encounter a human face (e.g., age, race, gender, emotional expression). Most notably, adults are able to recognize the identity of hundreds of faces at a glance and they can do so under poor lighting conditions, from numerous viewpoints, and after a face has aged by several years, at least for the kinds of faces they encounter on a daily basis (e.g., upright same-race faces).

Although behavioural researchers have investigated each aspect of face perception quite thoroughly, neural research on face processing with both humans and non-human primates has primarily investigated the neural markers that distinguish faces from non-face objects (Allison, Ginter, et al., 1994; Bentin, et al., 1996; Bötzel, et al., 1995; Desimone, et al., 1984; Kanwisher, et al., 1997; McCarthy, et al., 1997; Perrett, et al., 1982; Puce, et al., 1995; Rolls & Baylis, 1986; Tsao, et al., 2006). As a result, several brain regions (e.g., middle fusiform gyrus, inferior occipital gyrus, and superior temporal sulcus) and electrophysiological signals (e.g., the intracortical N200 and the scalp-recorded N170) have been found to respond more strongly to faces than to non-face objects. In contrast to the face versus non-face distinction, however, much less is known about the neural mechanisms underlying the perception and recognition of individual faces within the face category.

To account for adults' expertise in face recognition, Valentine (1991) proposed a norm-based coding mechanism, a process by which individual faces are compared to a norm (prototype) that represents the average of all faces previously encountered. In his model, each face is represented as a point in a multi-dimensional face space; the origin of the face space corresponds to the prototypical face and the location of each face represents how and how much that face deviates from the average. Faces near the norm are rated as more typical/attractive than faces that are far from the norm and they are categorized more quickly in a face/non-face task. In contrast, faces far from the norm are recognized more quickly than typical faces, perhaps because they reside in a less populated area of face space (Valentine, 1991; but see Burton & Vokey, 1998, for evidence suggesting that distance from the norm and local densitity may be sufficient to produce differences in the recognition of typical versus distinctive faces).

Recently, two studies have tested Valentine's norm-based model at a neural level. Their results indicate that neural activity increases as a function of face identity strength (i.e., as a function of how much individual faces differ from an average face) (Leopold, et al., 2006; Loffler, et al., 2005). In each study, identity strength was manipulated by varying the relative weighting of an individual face versus the average face. Using synthetic faces of different identities, Loffler et al. (2005) reported greater BOLD responses from fusiform face area (FFA) as identity strength increased. Loffler et al. concluded that the BOLD response elicited by a face reflects the distance of the face from the average face because a) the BOLD response did not increase as a function of the distance from a non-average face, and b) adaptation to a single facial identity reduced the BOLD response to other faces along the same identity trajectory, but not to faces along different trajectories. Similarly, in a single-cell recording study with monkeys, Leopold et al. (2006) found that neural responses from anterior inferotemporal cortex became stronger as face identity strength increased. Although these studies indicate that the magnitude of neural activity may code for identity strength, which is consistent with Valentine's norm-based coding model, the temporal parameters of individual face perception remain unclear. The goal of the current study was to examine the timing of brain responses to face identity strength using scalp-recorded ERPs.

There is some evidence that the face-sensitive N170 component, traditionally interpreted as a neural marker for structural encoding of faces (Eimer, 2000b), may also be sensitive to visual face identities. When the same identity is presented on consecutive trials, the amplitude of the N170 is reduced relative to when two different identities are presented (Caharel, Jiang, et al., 2009; Campanella, et al., 2000; Jacques, et al., 2007; Jacques & Rossion, 2006; Schweinberger, et al., 2004; but see Schweinberger, Pickering, Jentzsch, et al., 2002), even when the viewpoints are different across presentations (Caharel, d'Arripe, et al., 2009). This adaptation effect on N170 may occur as early as 160 ms post face onset (Caharel, Jiang, et al., 2009; Jacques, et al., 2007). In addition, when a face discrimination task was made more difficult by rotating the faces away from their canonical upright orientation, N170 amplitude increased along with error rates and reaction times (Jacques & Rossion, 2007).

However, these immediate repetition effects on the N170 may not indicate that the N170 reflects individual face recognition; rather, the N170 may reflect the processing of individual facial characteristics (Eimer, 2000b; Zheng, et al., 2011), and adaptation to the face category (Eimer, et al., 2010). First, although N170 adaptation for upright faces is larger when the adaptor is a face than when the adaptor is a house, N170 adaptation occurs when the test face is preceded by an adaptor stimulus of a different facial identity and the magnitude of this effect is independent of whether the adaptor is an upright face, an inverted face, a face without eyes, or eyes only (Eimer, et al., 2010; Harris & Nakayama, 2008; see Harris & Nakayama, 2007, for similar results using MEG technology). Second, N170 is not influenced by face identity when faces are presented in a random order; under these conditions only later ERP components are influenced by identity (Bentin & Deouell, 2000; Eimer, 2000a; Gosling & Eimer, 2011; Kaufmann, et al., 2008; Bruno Rossion, et al., 1999; Tanaka, et al., 2006). Given that the priming effects on later ERP components are robust even when the prime (e.g., a picture of Nancy Reagan) shares no facial characteristics with the target (e.g., Ronald Reagan) (Schweinberger, et al., 1995), it is thus possible that modulation of the N170 reflects brain processes related to the encoding of facial characteristics (Eimer, 2000b; Zheng, et al., 2011) and that modulation of later components (e.g., N250) reflects brain processes related to the visual recognition of a face.

To further explore the temporal parameters of visual face recognition we adopted a method previously used to study the influence of face identity on the BOLD signal (Loffler et al., 2005) and single-cell activity (Leopold et al., 2006). Specifically, we investigated the influence of variation in identity strength relative to an average face on the magnitude of early ERP components (P1, N170, P2, N250). We manipulated face identity strength by first constructing an “average” face based on 32 individual female faces; each individual face was then morphed with this “average” face (Fig. 3.1*a*) to produce continua of face identity (Fig. 3.1*b*). The relative weighting of an original face in these morphed faces ranged from 100% to 0% in 10% decrements.

Participants performed a face identification task, in which they were instructed to press a button whenever they felt that they had detected a target face or a face that looked like a target face (see Fig. 3.1*c*). We predicted that the amplitude of one or more ERP components would increase with identity strength. Our primary question was whether this effect would be observed as early as in the N170 or only in later components.

3.2. Materials and Methods

3.2.1. Participants

Seventeen Caucasian female undergraduate students (mean age = 20.4 ± 1.5 years) at Brock University participated in the current ERP study for either a research credit or a $15 honorarium. All participants were right-handed native English speakers with normal or corrected-to-normal vision. No participants reported any neurological disorders, psychiatric history, or attentional problems. The experimental procedures were approved by Brock University Research Ethics Board, and written informed consent was obtained from all participants.

3.2.2. Stimuli

The experimental stimuli included 36 individual female faces (original) unknown to participants and their morphed versions that were created by gradually morphing each original face with an “average” of the 32 individual faces in steps of 10% using Norrkross MorphX® software. Four faces and their morphed versions served as targets in a face identification task, and the other 32 faces and their morphed versions served as non-targets. The “average” face was constructed using non-target original faces. For each original-average face pair, over 140 reference points were placed at various regions (e.g., eyes, eye brows, nose, mouth, cheeks, and face contour) on both faces (see Fig. 3.*1a* for the placement of reference points for an original-average face pair). Based on these reference points, the original faces (including both target and non-target faces) were morphed with the “average” face in steps of 10% to generate continua of morphed faces that vary in the amount of identity strength they carry, ranging from 100% (i.e., an original face) to 0% (i.e., the “average” face) (see Fig. 3.1*b* for an example).

Figure 3.1a. Based on over 140 reference points, an original face (left) were morphed with the “average” face (right) to produce a continua of faces varying in identity strength; the “average” face was constructed with 32 faces of different identities.

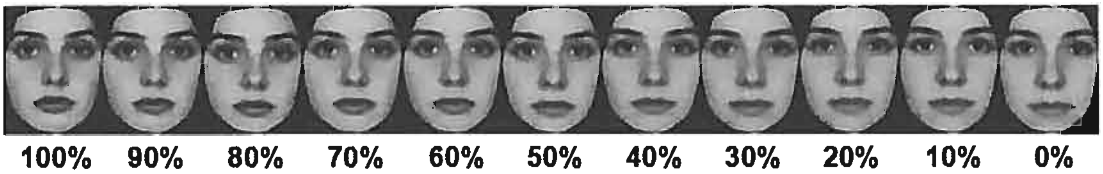

Figure 3.1b. Examples of the morphed faces along one identity trajectory, decreasing in identity strength in steps of 10%.

A black background with a diamond-shape cut out in the middle was placed on top of each face stimulus to exclude non-facial information (e.g., hair); the position of a face stimulus within the outline was vertically adjusted so that the eye region was at approximately the same level and did not differ systematically across faces that varied in face identity strength. In addition, because the overall average face was based on the averaging of 32 original faces, it appeared to be smooth and slightly blurry. As a result, the "smoothness" and "blurriness" of the morphed faces increased as facial identity decreased. To address this issue, we applied a Gaussian filter to each face stimulus using Adobe® Photoshop® software. The radius of filtering ranged from 0.1 to 1.0. The original faces were filtered to the maximum degree with less filtering applied as identity strength decreased. All face stimuli were approximately equal in size (7.4 – 8.1 cm for width; 9.2 – 10.8 cm for height) and viewed at a distance of 100 cm, subtending a visual angle of $2.4^\circ - 2.6^\circ$ (horizontally) by $2.9^\circ - 3.4^\circ$ (vertically); the faces along the same identity trajectory are equal in size.

3.2.3. Face identification task

Participants performed four blocks of a face identification task. At the beginning of each block, a target face (original) was presented, and participants were given as much time as needed to visually inspect and memorize the target face. On the following trials, a face stimulus was presented in the center of a computer screen for 500 ms, followed by a randomly selected interstimulus interval (ISI) of 600, 700, or 800 ms. Participants were instructed to press either a left or a right button, counter-balanced across participants, whenever they felt that they had detected a target face or a face that looked like the target (i.e., another face on that same identity trajectory). Responses could be made either during the presentation of a face stimulus or during the ISI. Both response speed and accuracy were emphasized (see Fig. 3.1*c* for the trial procedure).

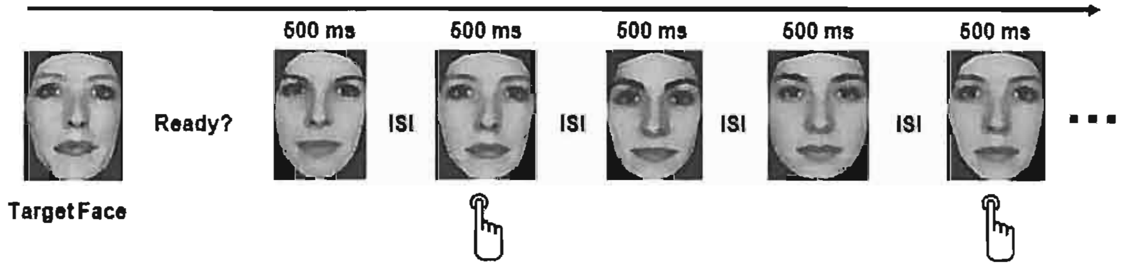

Figure 3.1c. The trial procedure for the face identification task. At the beginning of each block, a target face was shown for visual inspection; during the task, the face stimuli were presented sequentially, and participants were instructed to press a button whenever they felt that they had detected a target face or a face that looked like the target; both response time and accuracy were emphasized.

Each block consisted of 220 trials, including one target face and its morphed versions (including the "average" face) each presented four times, and 16 non-target faces and their morphed versions (including the "average" face) each presented only once. The order of presentation within each block was randomized. A different target face was used in each of four blocks. Each of the 32 non-target faces and their morphed versions appeared in two blocks (e.g., block 1 and 3 or block 2 and 4); the blocks in which a stimulus (including both target and non-target faces) appeared was counter-balanced across participants.

3.2.4. EEG recording and data analyses

The EEG was recorded from an elastic net (Electrical Geodesics, Inc.) containing 128 silver chloride-plated electrodes embedded in sponges. Recorded EEG was referenced to the vertex (Cz) and amplified by Net Amps 200 (band-pass filter 0.01 – 100 Hz; digitized sampling rate 500 Hz; impedance below 50 kΩ). Eye movements and blinks were monitored by electrodes placed below and beside each eye. Raw EEG data were segmented into epochs starting 200 ms before and ending 800 ms after stimulus onset. Trials were visually inspected for contamination by movements and were manually rejected. The number of trials rejected did not differ across conditions ($F(10, 160) < 1.0$, $p = .454$), and there were approximately 58 trials (i.e., 91.2% of the 64 non-target faces at each identity strength level, with a range of 89.7% - 92.2%) in each averaged ERP for each morphing condition. Trials containing eye artifacts were corrected using the artifact correction method provided by BESA 5.1 software (MEGIS Software GmbH). The 128-channel data were subsequently transformed through spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989) to the standard 81 electrode montage according to the expanded 10-10 system (Nuwer, et al., 1998).

The amplitudes of ERP components were measured as the positive or negative deflections relative to the pre-stimulus baseline of 200 ms. Specifically, the P100 was measured as the maximum peak positivity between 80 and 130 ms at occipital sites (PO3, O1, O9 for the left; PO4, O2, O10 for the right). The N170 component was measured as the maximum peak negativity between 140 and 190 ms at occipitotemporal sites (P7, P9, PO7, PO9 for the left sites; P8, P10, PO8, PO10 for the right sites). The P2 component was separated into an early (190 – 230 ms) and a late (230 – 270 ms) time window. The early P2 (dorsal P2) was measured as the mean amplitude between 190 and 230 ms at parietal-occipital sites (CP3, CP1, P1, P3, PO3 for the left; CP2, CP4, P2, P4, PO4 for the right); the late P2 (ventral P2) was measured as the mean amplitude between 230 and 270 ms but at more ventral sites (P5, P7, PO7, PO9 for the left and P6, P8, PO8, PO10 for the right). Following the ventral P2 component, the N250 was measured as the mean amplitude between 270 and 330 ms at occipitotemporal sites (P7, P9, TP9, PO9 for the left; P8, P10, TP10, PO10 for the right) (see Fig. 3.2 for the representative ERP waveforms of each component).

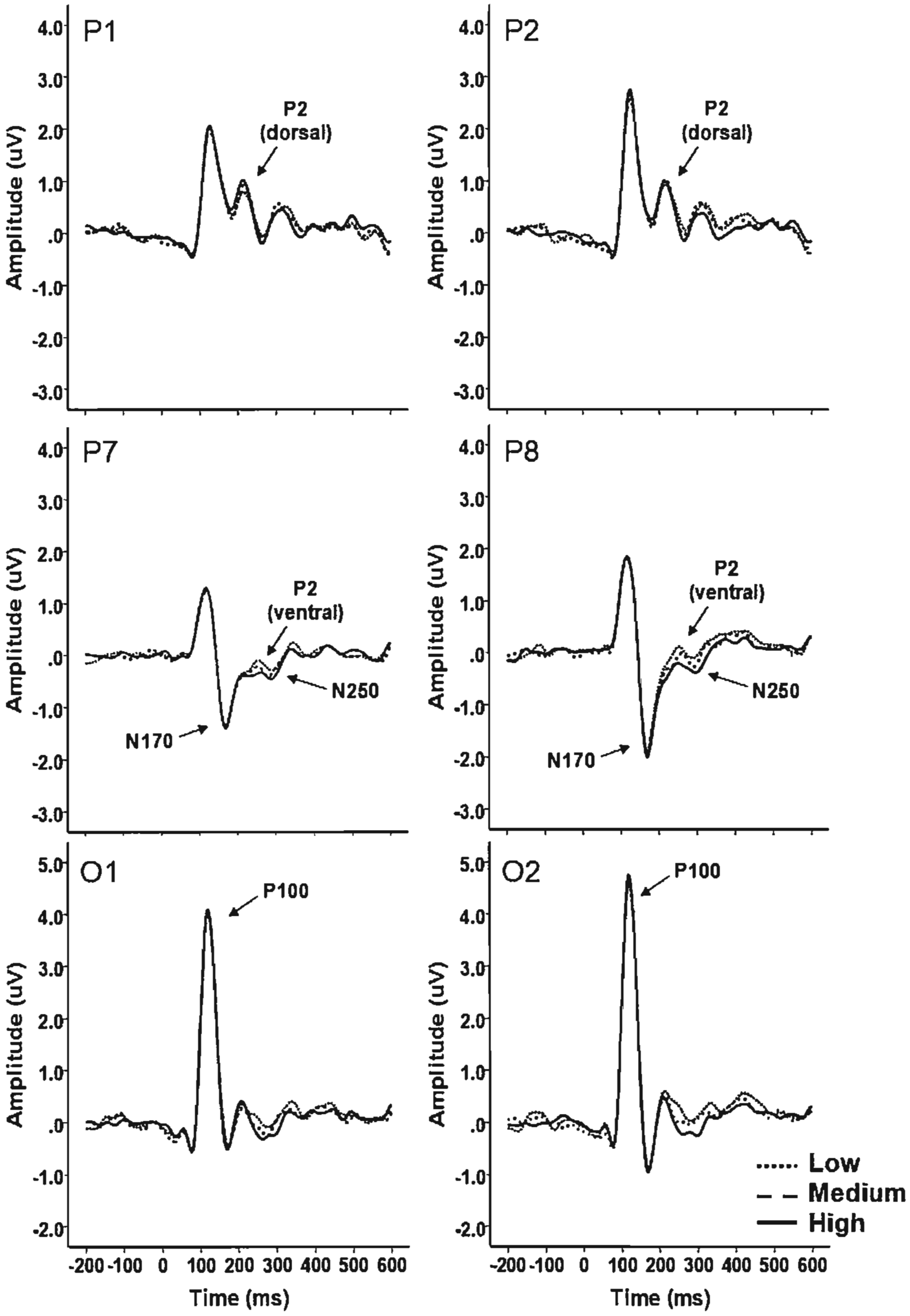

Figure 3.2. The representative ERP waveforms for the P100 (80 – 130 ms), N170 (140 – 190 ms), dorsal P2 (190 – 230 ms), ventral P2 (230 – 270 ms) and N250 (270 – 330 ms) components, averaged for non-target faces with either high-, medium-, or low-identity strength (see Methods)

All ERP components were first measured at individual electrode sites on both the left and the right sides; the most positive (P100, P2) and the most negative (N170, N250) values of those individual measurements for each side were then used to represent the components. Because all face stimuli elicited the P100 very close to 120 ms (sd ≈ 1 ms) and the N170 very close to 168 ms (sd ≈ 1.5 ms), the peak latencies of these two components were not further analyzed in relation to face identity strength. To investigate the timing of face identity strength affecting ERP responses, we correlated the amplitude of each ERP component (P100, N170, early and late P2, N250) with face identity strength (from 100% to 0% in decrements of 10%) for each participant. After Fisher transformation, the individual correlation coefficients were then analyzed with single sample t-tests to examine whether there was a significant relationship between face identity strength and ERP components across all participants as a group. For each participant, the ERPs used for these analyses were averages of 32 non-target faces and of their morphed versions. The same analyses were performed separately for the montages on the left and the right sides. The target faces and their morphed versions were excluded from the correlational analyses, because the number of trials for producing ERPs was rather small (16 trials at most) for each identity strength level, they were excluded from the correlational analyses.

When a significant relationship was found between face identity strength and ERP components across participants, we further assessed its consistency across individual faces. Because each non-target face stimulus and their morphed versions were presented only twice during the entire task, the number of trials for generating ERPs was small. Consequently, we randomly paired non-target faces and combined ERP responses to each pair and to their morphed versions accordingly. With single sample t-tests, the final face-based analyses were performed on the individual correlation coefficients (per face pair) between face identity strength and the amplitude of ERP components (averaged over all participants) of 16 combined non-target face pairs.

3.3. Results

3.3.1. Behavioral results

Averaged across all participants, accuracy in detecting target faces followed a cubic function with face identity strength (Fig. 3.3) (for target face 1, $p = .010$; for target face 2, $p = .014$; for target face 3, $p = .001$; for target face 4, $p = .001$; overall, for all target faces, $p < .001$)[2]. When examined individually for each participant (i.e., a cubic function was fitted for each participant to produce individual coefficients) and then tested with single sample t-tests based on individual coefficients, the relationship between accuracy and identity strength was significant for all target faces (for target face 1, $t(16) = -3.2$, $p = .006$; for target face 2, $t(16) = -3.3$, $p = .005$; for target face 3, $t(16) = -3.7$, $p = .002$; for target face 4, $t(16) = -12.6$, $p < .001$; overall for all target faces, $t(16) = -8.1$, $p < .001$). As shown in Fig. 3.3, participants performed poorly when identity strength was lower than 30%, performance increased gradually between 30%

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[2] The behavioral data similarly fitted sigmoid functions, which accounted for 94.8%, 97.0%, 97.1%, and 99.1% of the variance for the four target faces; averaging across all target faces, 99.6% of the variance was accounted for.

and 70% identity strength with no further increase after that. These observations were subsequently examined and confirmed by the ANOVA analyses with repeated measures. Dividing the target faces and their morphed versions into three groups, we found that for faces with strong identity strength (70%, 80%, 90%, 100%), there was no difference in success rate of identification ($F(3,48) < 1.0$, $p = .777$); for faces with low identity strength (0%, 10%, 20%, 30%), the success rate of identification differed among conditions ($F(3,48) < 10.5$, $p < .001$): post hoc comparisons with Bonferroni revealed that the success rates were lower for 0% and 10% condition than for 20% and 30% condition ($ps < .05$), while there was no difference in success rate between 0% and 10% ($p \approx 1.0$) or between 20% and 30% ($p = .535$); as the face identity strength increased from 30% to 70%, identification success rate increased ($F(4,64) = 70.2$, $p < .001$), with all conditions being different from each other (except for the comparison between 50% and 60%, $p = .078$).

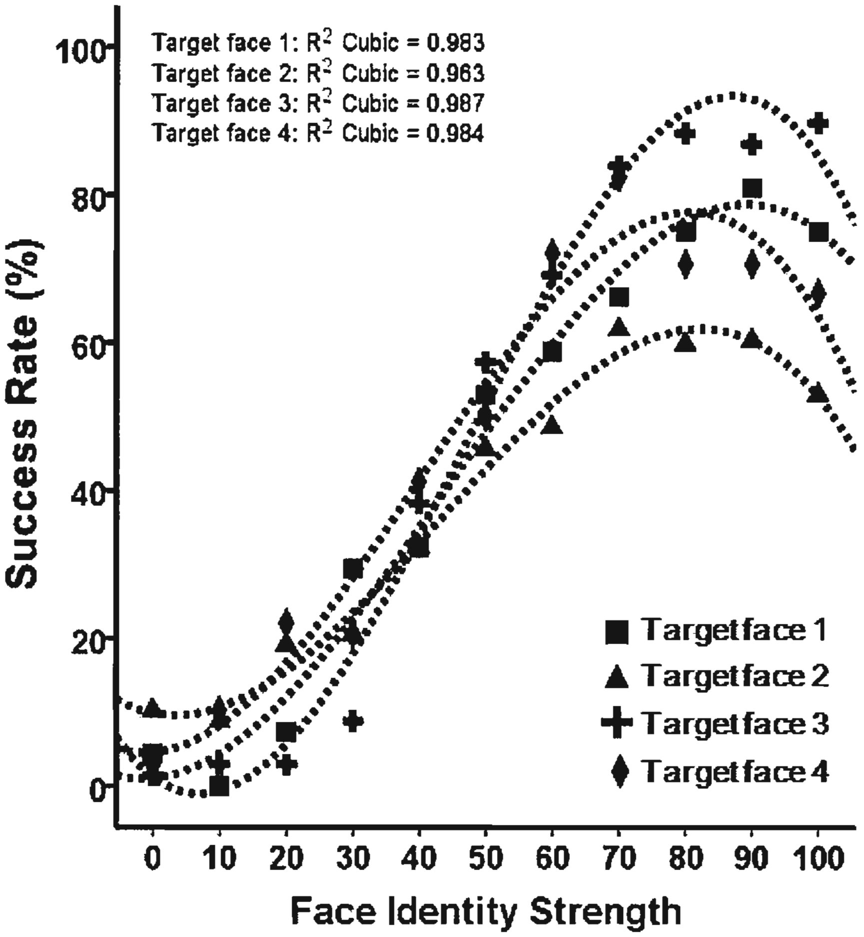


Figure 3.3. Success rate of identifying a target face as a function of face identity strength. The categorical boundary for face identification occurred at 30% and 70% of face identity strength.

3.3.2. Electrophysiological results

3.3.2.1. Participant-based analyses

When the amplitude of the ERP components (averaged over 32 non-target faces) was examined in relation to face identity strength for all participants as a group, a linear relationship between ERP amplitude and face identity strength was found after 230 ms post stimulus onset in the ventral P2 and the N250 components: as face identity strength increased, the ventral P2 became smaller and the N250 became larger. The relationship between face identity strength and the ventral P2 amplitude was found from both left and right sites (for the left ventral P2, $t(16) = -2.68$, $p = .016$; for the right ventral P2, $t(16) = -5.96$, $p < .001$) with a similar magnitude on the two sides ($t(16) = 1.28$, p = .218). For the N250, the effect of face identity strength was found on the right ($t(16) = -4.08$, $p = .001$), and there was also a similar trend on the left ($t(16) = -1.80$, $p = .090$). In contrast to the ventral P2 and the N250 component, such a linear relationship was not found during earlier time windows (i.e., prior to 230 ms post stimulus onset) with the P100, the N170 and the dorsal P2 component on either the left or the right (for left and right P100 and N170, and the right dorsal P2, $t(16) < 1.0$; for the left dorsal P2, $t(16) = 1.62$, $p = .124$). Separated by the different ERP components, Fig. 3.4 illustrates the individual correlation coefficients between the ERP amplitude and the face identity strength for each participant. A consistent relationship between the two was only seen after 230 ms, particularly on the right side. Unlike the behavioral data, there was no cubic relationship between ERP amplitudes and face identity strength (Table 3.1).

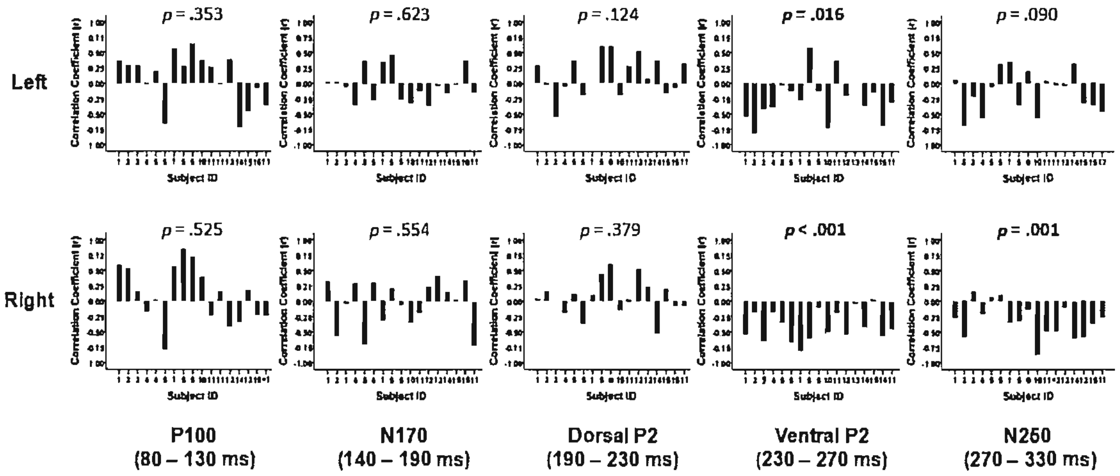


Figure 3.4. The correlation coefficients between face identity strength and the amplitude of ERP components for individual participants (over all non-target faces). Consistent relationships were found across participants shortly after 200 ms in the ventral P2 and the N250 component.

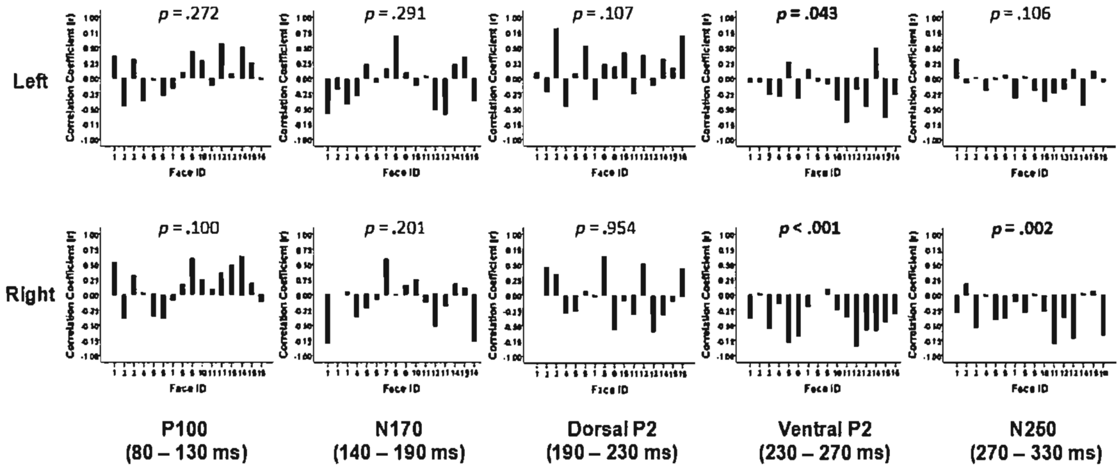
Table 3.1

The relationship between face identity strength and the ERP amplitudes for each component further separate by the left and right hemisphere.

		Face identity strength			Face identity strength		
		Linear	Quadratic	Cubic	Linear	Quadratic	Cubic
P1	Left	$p = .353$	$p = .136$	$p = .163$	$p = .272$	$p = .462$	$p = .270$
	Right	$p = .525$	$p = .335$	$p = .971$	$p = .100$	$p = .956$	$p = .705$
N170	Left	$p = .623$	$p = .478$	$p = .891$	$p = .291$	$p = .838$	$p = .122$
	Right	$p = .554$	$p = .147$	$p = .554$	$p = .201$	$p = .613$	$p = .501$
Dorsal P2	Left	$p = .124$	$p = .348$	$p = .574$	$p = .107$	$p = .341$	$p = .945$
	Right	$p = .379$	$p = .708$	$p = .474$	$p = .954$	$p = .765$	$p = .667$
Ventral P2	Left	**$p = .016$**	$p = .648$	$p = .560$	**$p = .043$**	$p = .334$	$p = .746$
	Right	**$p < .001$**	$p = .683$	$p = .507$	**$p < .001$**	$p = .859$	$p = .531$
N250	Left	**$p = .090$**	$p = .263$	$p = .956$	**$p = .106$**	$p = .296$	$p = .502$
	Right	**$p = .001$**	$p = .920$	$p = .689$	**$p = .002$**	$p = .460$	$p = .441$
		(based on individual participants)			(based on individual faces, with target faces excluded)		

3.3.2.2. Face-based analyses.

When the amplitude of ERP components was examined in relation to face identity strength for each face-pair stimulus (averaged over the 17 participants), the same results were found. A linear relationship between the two was found only for the ventral P2 and the N250 components: greater face identity strength was associated with a smaller ventral P2 and a larger N250. The relationship was found from both left and right sites for the ventral P2 component (for the left ventral P2, $t(15) = -2.22$, $p = .043$; for the right ventral P2, $t(15) = -4.64$, $p < .001$); it was mainly found from the right site for the N250 component (for the left N250, $t(15) = -1.72$, $p = .106$; for the right N250, $t(15) = -3.64$, $p = .002$). In contrast, the amplitudes of the P100, the N170 and the dorsal P2 did not relate to the face identity strength (for left P100, $t(15) = 1.14$, $p = .272$; for right P100, $t(15) = 1.76$, $p = .100$; for left N170, $t(15) = -1.10$, $p = .291$; for right N170, $t(15) = -1.34$, $p = .201$; for the left dorsal P2, $t(15) = 1.72$, $p = .107$; for the right dorsal P2, $t(15) < 1.0$, $p = .954$). The individual correlation coefficients between the ERP amplitude and the face identity strength for each pair of face stimuli are illustrated in Fig. 3.5. When we fitted cubic functions to predict the ERP amplitude using face identity strength, we found no significant effect for any ERP component on either left or right side, thus also consistent with findings from participant-based analyses (Table 3.1).



P100
(80 – 130 ms)

N170
(140 – 190 ms)

Dorsal P2
(190 – 230 ms)

Ventral P2
(230 – 270 ms)

N250
(270 – 330 ms)

Figure 3.5. The correlation coefficients between face identity strength and the amplitude of ERP components for individual non-target face-pairs (over all participants). The relationship between face identity strength and the amplitude of the ventral P2 and the N250 components was similarly found across non-target faces.

Together, these results suggested that neural responses to face identity strength did not occur within 200 ms, but rather occurred later, starting at approximately 230 ms after a face was presented. This conclusion was further supported when we divided the face stimuli into three groups based on their identity strength (0%, 10%, 20% for low strength; 40%, 50%, 60% for medium strength; 80%, 90%, 100% for high strength), and then compared their ERP amplitudes, using 2 (left/right) X 3 (low/medium/high identity strength) ANOVA with repeated measures.

3.3.2.3. *Group analyses comparing faces with low-, medium-, and high-identity strength.*

The average ERP amplitudes elicited by each face group for each component are illustrated in Fig. 3.6. The amplitudes of the three early ERP components were not affected by face identity strength: the P100 ($F(2,32) < 1.0$, *n.s.),* the N170 ($F(2,32) < 1.0$, *n.s.*), and the dorsal P2 component ($F(2,32) < 1.0$, *n.s.*). In contrast, significant differences in ERP amplitude were found for the ventral P2 ($F(2,32) = 17.14$, $p < .001$) and the N250 ($F(2,32) = 9.17$, $p = .001$) components. Post hoc comparisons revealed that higher identity strength was associated with a smaller ventral P2 and a larger N250, consistent with the findings from the correlational analyses. Although the effect of face identity strength on ERP amplitude appeared to be larger on the right than on the left for both the ventral P2 and the N250 components, the interaction between hemisphere and face identity strength did not reach significance for either component (for the ventral P2, *F*(2,32) = 1.03, *p* =.369; for the N250, *F*(2,32) = 2.16, *p* = .132).

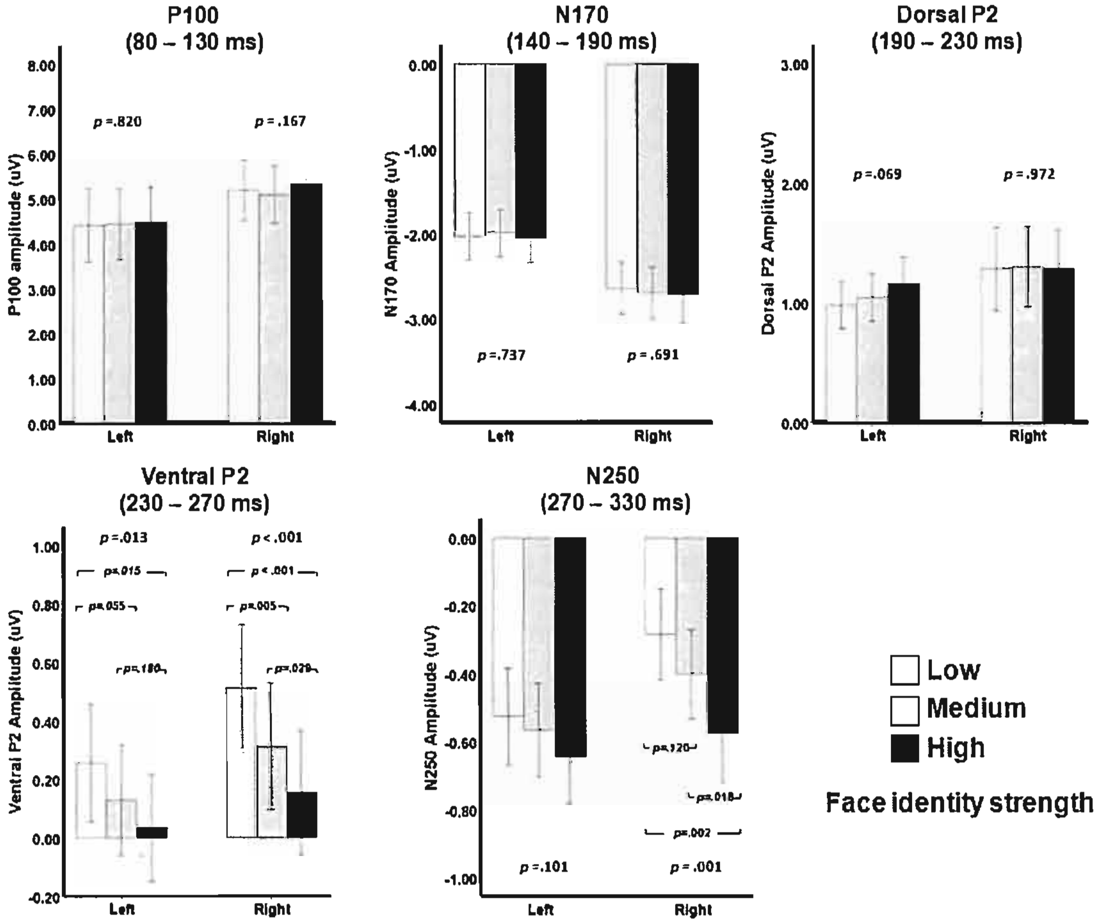


Figure 3.6. Comparing non-target faces with high (100%, 90%, 80%), medium (60%, 50%, 40%), and low (20%, 10%, 0%) identity strength, differences in ERP amplitude were found for the ventral P2 and the right N250 component, but not for the earlier components (P1, N170, dorsal P2). Error bars represent the s.e.m.

Grouping the target faces into low- (0%, 10%, 20%), medium- (40%, 50%, 60%) and high-identity (80%, 90%, 100%) strength conditions[2], similar results were obtained: The P100, the N170, and the dorsal P2 components were not affected by face identity strength (for P100, *F*(2,32) =1.9, *p* = .171; for N170, *F*(2,32) = 1.6, *p* = .226; for dorsal P2, *F*(2,32) < 1, *n.s.*). In contrast, a main effect of identity strength was found for the N250 (*F*(2,32) = 3.5, *p* = .043) and marginally for the ventral P2 (*F*(2,32) = 3.0, *p* = .066): greater identity strength was associated with a smaller ventral P2 and a larger N250 (Fig. 3.7). The effect of identity strength on the ventral P2 and on the N250 appeared to be much weaker for the target faces relative to non-targets. This however might be due to the smaller number of ERP trials used to produce the low-, medium-, and high-identity strength conditions for the target faces (48 trials) than for the non-target faces (192 trials).

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[2] Although we did not perform correlational analyses with the target faces due to the rather small number of trials (16 trials at most) obtainable for each identity strength level, grouping the target faces into low-, medium- and high-identity strength conditions increased the number of trials for each condition (48 trials at most). This allowed us to perform the same group analyses for the target faces as we did for the non-target faces.

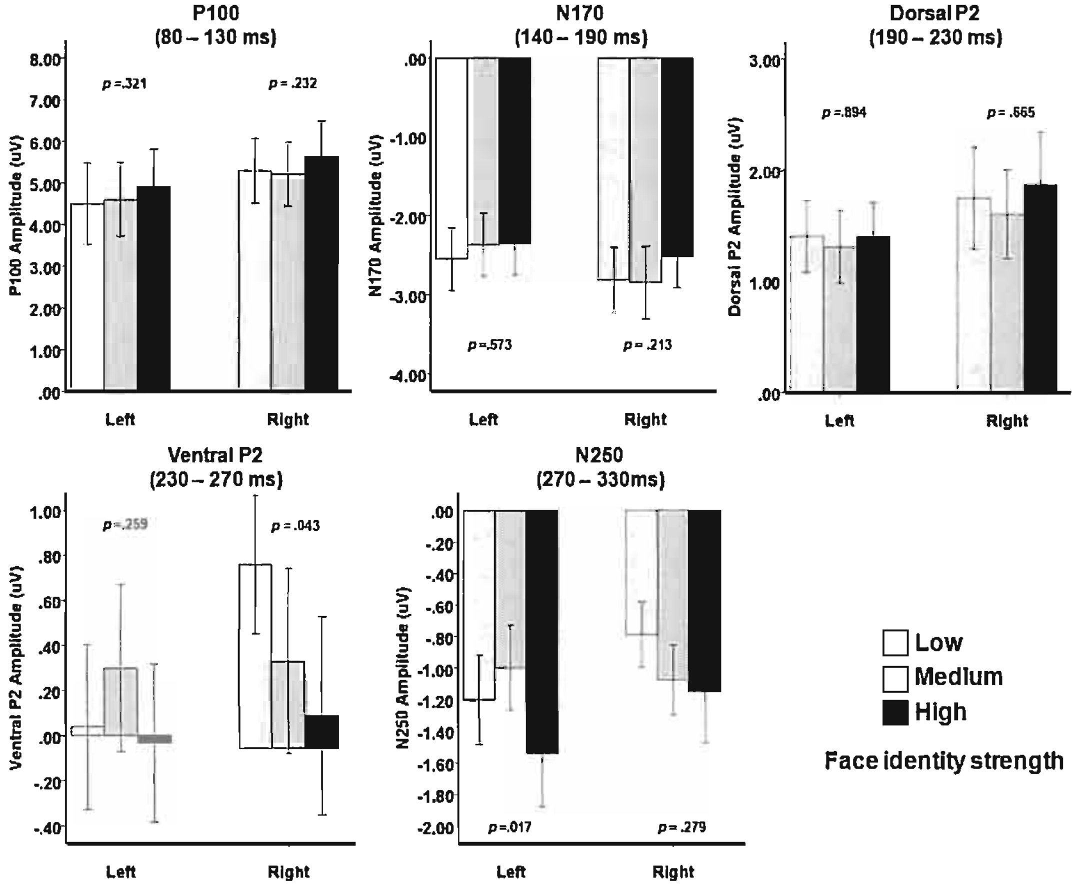

Figure 3.7. Despite the much smaller number of trials (see Methods), when the target faces were examined, similar patterns of results were found: differences in ERP amplitude among high (100%, 90%, 80%), medium (60%, 50%, 40%), and low (20%, 10%, 0%) identity strength was found for the N250 and marginally for the ventral P2 (see Results), but not for the earlier components (P1, N170, dorsal P2). Error bars represent the s.e.m.

3.4. Discussion

Recent studies with humans and non-human primates (Leopold, et al., 2006; Loffler, et al., 2005) have found that neural responses from face-sensitive regions are sensitive to the strength of face identities relative to an average face. In the present study we investigated the timing of these neural events (i.e., we investigated when the effect of face identity strength occurs in the brain). Face identity strength did not affect the amplitude of the P100 (80-130 ms) or the N170 (140-190 ms) or the dorsal P2 components (190-230 ms), but affected the two later components: the ventral part of the P2 (230-270 ms) and the N250 (270-330 ms). As face identity strength increased (i.e., when faces become more distinctive relative to the "average" face), the ventral P2 became smaller and the N250 became larger. This linear relationship between face identity strength and the amplitude of the ventral P2 and the N250 was found across individual participants and across face stimuli. Similarly, when we performed the group analyses to compare the amplitude of ERP components elicited by faces of high- (100%, 90%, 80%), medium- (60%, 50%, 40%) and low-identity strength (20%, 10%, 0%), the effect of identity strength was only found in the ventral P2 and the N250 components for both non-target and target faces. Our study is one of the first to investigate ERP responses in relation to systematic variations in face identity strength relative to an average face (see Kaufmann & Schweinberger, 2008, for a study using caricatures and anti-caricatures). Collectively, our results suggest that the brain does not respond to visual face identity until 230 ms after a person sees a face.

It is generally accepted in the literature that the P100 component reflects the cortical processing of low-level visual information (e.g., spatial frequency, contrast, luminosity) (see Regan, 1989) and is not associated with the processing of high-level information, such as a particular class of visual stimuli (e.g., faces, houses) (see Rossion & Jacques, 2008, for a review). Therefore, our result that the P100 amplitude was not affected by individual faces varying in identity strength is consistent with this established view.

Whether the N170 is influenced by face identity is more controversial. Our results are consistent with those of many studies suggesting that the N170 is not influenced by face identity (Bentin & Deouell, 2000; Eimer, 2000a; Gosling & Eimer, 2011; Kaufmann, et al., 2008; Rossion, et al., 1999; Schweinberger, Pickering, Jentzsch, et al., 2002; Tanaka, et al., 2006). For example, Gosling and Eimer (2011) reported that the N250, but not the N170, was modulated by whether participants were viewing famous faces that were explicitly recognized versus famous faces that were not recognized or non-famous faces. Likewise, the N170 was not modulated by face familiarity in a task in which different exemplars of learned faces were interspersed with novel faces; in contrast, the N250 was enhanced for learned faces (Kaufmann, et al., 2008).

We acknowledge that other studies have reported an influence of face identity on the N170. For example, Jacques and Rossion (2006) morphed two facial identities to create a continuum between face A and face B. The amplitude of the N170 response to a morphed face (e.g., with 65% of face A and 35% of face B) was smaller when that face was preceded by a face that was located on the same side of the perceptual identity boundary (e.g., with 95% of face A and 5% of face B) than when it was preceded by an equally-distant face that was located on the other side of the boundary and thus perceived as having a different identity (e.g., with 35% of face A and 65% of face B) (see Caharel, d'Arripe, et al., 2009; Jacques, et al., 2007, for other reports that the N170 adaptation is modulated by face identity).

One possible interpretation of these conflicting results is that the N170 is modulated by face characteristics rather than identity per se. The N170 is sensitive to a variety of face characteristics including the eyes, facial layout, and face outline (Bentin, et al., 1996; Eimer, 2000b; Itier, et al., 2007; Zheng, et al., 2011), so it is important for adaptation studies to control the potential influence of such facial information on the N170 component before a conclusion can be drawn on whether the perception of face identities occurs before 200 ms. Any time that the N170 is adapted when the same identity is presented on consecutive trials it is possible that adaptation is attributable to face characteristics rather than identity per se. In fact, even when it is not possible for N170 to have been modulated by identity, adaptation of this component can still be observed. For example, when the adaptor is a face of a different identity or even just a face part from a different identity (e.g., the eyes), the adaptation of N170 can still occur to the test face (Eimer, et al., 2010). Therefore, the adaptation of N170 in and of itself is not enough to support the claim that the N170 is a neural index of perceiving individual face identities. Furthermore, when the potential adaptation effect caused by facial characteristics was removed with associative priming (Schweinberger, et al., 1995) or reduced by using face stimuli from very different sources (Schweinberger, Pickering, Jentzsch, et al., 2002), the effect of face identity on ERPs is found later, and not earlier in the N170.

In the present study, instead of using an adaptation paradigm, we presented faces in a random order, with a large number of face identities appearing within each block (i.e., 16 non-target faces and one target face plus their morphed versions). As a result, the probability of one face immediately following another face along the same identity trajectory was relatively small (.06), minimizing any immediate adaptation effect attributable to either facial characteristics or face identities. Therefore, the effects of face identity strength on ERP responses likely reflected the underlying brain dynamics for processing visual face identities. Consistent with previous ERP studies (Kaufmann, et al., 2008; Schweinberger, et al., 2004; Schweinberger, et al., 1995; Schweinberger, Pickering, Jentzsch, et al., 2002; Tanaka, et al., 2006), we found the earliest evidence of face identity strength affecting brain responses after 230 ms (ventral P2 and N250) post stimulus onset, but not earlier (P100, N170, dorsal P2). The linear relationship between face identity strength and the amplitude of the ventral P2 and the N250 component, with the "average" face eliciting the largest ventral P2 and the smallest N250 compared to more distinctive faces, is in general consistent with the conclusion drawn from the imaging data in humans (Loffler, et al., 2005) and from the single-cell recordings in monkeys (Leopold, et al., 2006). It provides further support for the specific role played by an "average " face in a neural model underlying the perception of individual face identities.

Interestingly, in a recent paper, Davidenko, Remus, and Grill-Spector (2011) argued that the results of Loffler et al. (2005) and, by extension, our own results might be difficult to interpret because image variability across faces also varies as a function of the distance from the average face. In their study, the BOLD signal in FFA was measured, while participants viewed silhouettes that differed in face-likeness. When image variability was not controlled (i.e., was largest for the most distinctive, but least face-like silhouettes), the BOLD signal was largest for the least face-like stimuli. In contrast, when image variability was controlled, the pattern was reversed: the BOLD signal was largest for the most typical, face-like silhouettes. While their results seem to suggest that a larger image variability may account for the greater neural responses to distinctive silhouettes (or faces in general), a closer examination of their data suggests that their results might actually be driven by perceptual variability: while image variability was controlled in their second experiment, perceptual variability was not; it was largest for the most face-like silhouettes (see Supplementary Figure 7b in their paper), which may explain why the BOLD signal was enhanced for these stimuli. Therefore, their results can be viewed as consistent with the findings by Loffler et al. (2005) and our own results that the ventral P2 and the N250, but not the N170, are modulated by the perception of face identities relative to an average face; a similar conclusion that had also been reached from another recent ERP study in which participants viewed caricatures, veridical face images, and anti-caricatures (Kaufmann & Schweinberger, 2008). Indeed, perceptual variability/similarity and face identity strength are intrinsically linked in models of multi-dimensional face space (Valentine, 1991) and so the influences of these two variables are inherently confounded.

In addition to providing strong evidence that the effect of face identity strength in relation to an average face is evident only after 200ms, our results also provide new insights about when this effect occurs. Although previous ERP studies have reported the face identity effect on the N250 component, the time-window selected for measuring the N250 component was slightly different across studies. Some studies measured the N250 component as the averaged activity approximately between 260 ms and 320 ms (Kaufmann, et al., 2008; Schweinberger, et al., 2004); other studies have extended the time-window by including the early portion of the 200–300 ms period (Schweinberger, Pickering, Jentzsch, et al., 2002; Tanaka, et al., 2006). Thus, although these studies have provided converging evidence in support of a face identity effect after approximately 260 ms post stimulus onset, it was not clear whether the perception of individual face identities might start even earlier. Dividing the 230–330 ms period into two smaller time-windows, i.e., 230–270 ms for the ventral P2 and 270–330 ms for the N250, allowed us to demonstrate that the effect is present during both time windows and even stronger between 230- 270 ms. These results therefore help to further locate the timing of initial brain responses to individual face identities to as early as 230 ms post stimulus onset.

Although the P2 component has not been studied extensively in relation to individual face perception, there is some evidence in addition to our own results suggesting that the P2 is sensitive to face identities. For example, when faces were made more distinctive/atypical by enlarging the distance between eyes and nose and between nose and mouth, the P2 amplitude became smaller (Halit, et al., 2000), although the timing of this effect is unclear because of the very large time window (188–300 ms) used; in contrast, the N170 was not affected by the face typicality through this manipulation. In another study examining the ERP correlates of the other-race effect (ORE) in face recognition, Stahl et al. (2008) found that P2 amplitude is smaller for other-race faces than for own-race faces. Importantly, this effect was only found in individuals with minimal other-race experience, corresponding well with the face ethnicity by expertise interaction found in behavioral studies (Rhodes, Ewing, et al., 2009; Walker & Hewstone, 2006).

Identity strength influenced the N250 in addition to the ventral P2, raising an interesting question about the extent to which these two ERP components reflect the same processes involved in perceiving individual faces or separable processes associated with different aspects of individual face perception. For example, the ventral P2 might reflect the integration of structural information and the formation of a perceptual representation for the incoming face stimulus. In contrast, the N250 component might reflect the process by which that representation is compared to previously seen faces, and thus might be linked to face *recognition* more directly. The N250 might also be sensitive to other non-visual person information. This latter explanation, positing a functional dissociation between the ventral P2 and the N250 component that occur in sequence between 230 and 330 ms also seems to fit well with the classical stage model for face recognition (Bruce & Young, 1986), and with the lack of correlation we found between the right ventral P2 and the right N250 (r = .382, *p* = .130), despite each being strongly affected by face identity strength. Furthermore, when we statistically examined the right ventral P2 and the right N250 together, we found that their relationships with face identity strength were indeed dissociable: adjusting for the right ventral P2 in a regression model, the linear relationship between face identity strength and the right N250 amplitude was still significant, *t*(16) = -2.64, *p* = .018; similarly, the linear relationship between face identity strength and the right ventral P2 amplitude was also significant, *t*(16) = -3.40, *p* = .004, after adjusting for the N250.

Although these results are provocative, the current study was not designed to disentangle the relationship between the ventral P2 and the N250 component. To examine whether they reflect the same or different processes for individual face perception, future research is needed. For this purpose, using faces that differ at various perceptual and semantic levels might prove very useful. For example, Herzmann, Schweinberger, Sommer, and Jentzsch (2004) studied the effect of priming on ERP responses elicited by unfamiliar, famous, and personally familiar faces. After dividing the 230–330 ms period into two smaller time-windows as ours (i.e., 230–270 ms and 270–330 ms), they found that the priming effects on ERPs from the temporal region (similar to the locations where the ventral P2 and the N250 were measured in the present study), not only differed among the three types of face stimuli, but also changed slightly between the two time windows: while personally familiar faces showed a larger priming effect than did famous faces and unfamiliar faces for both time-windows, the larger priming effect for famous faces compared to unfamiliar faces only occurred later between 270 and 330 ms, raising again the possibility of dissociable neural processes underlying individual face perception during the 230–330 ms period. Similarly, in a recent study by Gosling and Eimer (2011), it was found that the occipital-temporal N250 differed between famous and unknown faces; however, this effect appeared to be driven primarily by famous faces that were explicitly recognized; in contrast, the N250 for famous faces that were not recognized but were only rated as familiar did not differ from the N250 for unknown faces. Their results and interpretations seemed to be consistent with our own suggestion that the N250 may be related to face recognition more directly and could be affected by semantic person information. However, because the N250 was measured with a large time window (i.e., 230–400 ms) in their study, it was not clear when this difference in N250 between recognition and familiarity initially occurred. If our hypothesis was correct, we think that this difference in N250 should happen close to 300 ms post stimulus onset, but not earlier.

Finally, for both the ventral P2 and the N250 component, the effect of face identity strength we found in the present study cannot be explained as a result of the morphing procedure or low-level visual information. Measures were taken to ensure that faces with different identity strength did not differ systematically in such irrelevant visual information as face outline and blurriness. In addition, if any low-level visual information might have accounted for the ventral P2 and the

N250 effect, we would expect it to affect the P100 component to at least some extent. However, we found no evidence of early effects due to face identity strength until 230 ms post stimulus onset. Therefore, the overall patterns of these results and their consistency with previous literature suggest that the effects of face identity strength on the ventral P2 and the N250 components are due to the processing of visual face identities only.

One limitation of our study is that all faces were unfamiliar to participants; it is plausible that a different pattern of results might be obtained for familiar/known faces. People have a remarkable ability to recognize familiar faces even under very challenging conditions (e.g., under poor lighting and for degraded images); in contrast, they perform quite poorly when asked to recognize or match identities for unfamiliar faces (see Hancock, Bruce, & Burton, 2000, for a review). Behavioral evidence suggests that the mechanisms for perceiving individual face identities might be different between these two types of faces (Ellis, Shepherd, & Davies, 1979; A. W. Young, Hay, McWeeny, Flude, & Ellis, 1985), and previous studies have shown different ERP effects for familiar versus unfamiliar faces (Eimer, 2000a; Rossion, et al., 1999; Schweinberger, Pickering, Jentzsch, et al., 2002) and for personally familiar versus famous faces (Herzmann, et al., 2004). Future studies should examine the effects of face identity strength on ERP responses for familiar faces.

A second limitation of our study is that every face along a particular identity trajectory was derived from the same original image. It would be very interesting to create new identity continua using multiple images, perhaps with some variation in head orientation and/or emotional expression. Doing so would not only enhance the ecological validity of this research by asking participants to recognize facial identities across images, but also contribute to the debate about the influence of image variability versus perceptual face distinctiveness per se on brain responses.

In summary, using scalp-recorded ERPs, we investigated the timing of brain responses to individual faces that varied in identity strength. Our results suggest that the initial brain responses to face identity information occur shortly after 200 ms, but not earlier. In light of previous ERP research and based on the classic face recognition model by Bruce and Young (1986), the results of the present study may allow us to temporally delineate the neural events that are associated with individual face recognition. Indexed by the P100 component at approximately 100 ms after a person sees a face, the brain processes low-level visual information (e.g., color, contrast, spatial frequency). At some point between 100 and 150 ms, the incoming stimulus is detected as a face; subsequently, between 150 and 200 ms, various facial information including both internal and external features are processed (i.e., structural encoding), and these processes are reflected in the N170 component. Shortly after 200 ms, following the structural encoding, the facial information is integrated to form a perceptual representation of the incoming face. This representation is then compared to face representations established previously, and the result of this comparison determines whether a face is visually recognized or not. By approximately 300 ms after a person sees a face, the neural processes involved in perceiving individual face identities should be completed. While Bruce and Young's model has provided a general account of the stages involved in face recognition, the exact timing for each stage to occur at a neural level has not been solved yet. Here, we tentatively provide such a timeline and hope it can serve as a working model for future testing.

Chapter 4

Study 3. Putting a face in its place: In- and out-group membership alters N170 responses

4.1. Introduction

As important social stimuli, faces provide information (e.g., identity, age, gender, emotional state, etc) that guides our behaviors. The ability to recognize faces however varies among individuals even within a normal population (Richler, Cheung, & Gauthie, 2011; Rotshtein, et al., 2007; Wang, Li, Fang, Tian, & Liu, 2012; Wilhelm, et al., 2010), and some of the individual differences in face recognition might be linked to a genetic basis (Wilmer, et al., 2010; Zhu, et al., 2010). In addition, faces differ in their ease of recognition. It should be no surprise that faces with more distinctive features are recognized more easily than typical looking faces (Going & Read, 1974; Light, Kayra-Stuart, & Hollande, 1979). Compared to faces of their own-race, people also have difficulty recognizing faces of another race, captured by the impression that "they all look alike". This "other-race effect" (ORE) in face recognition has been supported by numerous studies in the past (Brigham & Barkowitz, 1978; Malpass & Kravitz, 1969; Shepherd, et al., 1974), and is considered as one of the most reliable findings in the research literature on face recognition (see Meissner & Brigham, 2001, for a review).

To account for the mechanisms underlying the ORE, a number of theories have been proposed (see Sporer, 2001, for a review). Broadly, these theories fall under two umbrellas with one emphasizing perceptual explanations and the other focusing on social-cognitive factors. The "face-space" model (Valentine, 1991) might represent the best attempt of the former approach. In the model, faces are encoded as individual nodes in a multidimensional space and each dimension corresponds to certain physiognomic feature(s). Compared to own-race faces, other-race faces are overall in closer proximity to one another in a "face space", and are further away from the face norm that is primarily derived from past experience based on own-race faces. Because face recognition is presumably determined by the location of a face in relation to the face norm and to the faces in its vicinity, other-race faces, having a greater density and being further away from the norm, are disadvantaged for recognition. While the construction of a "face-space" is shaped through personal experience and social contact with both own- and other-race faces, the "face-space" model is essentially a perceptual account, suggesting that people are not as capable of perceiving other-race faces as they are own-race faces. The behavioral findings of a difference in configural processing (Michel, Rossion, Han, Chung, & Caldara, 2006; Rhodes, Brake, & Taylor, 1989) and also in processing features (Hayward, Rhodes, & Schwaninger, 2008; Rhodes, Hayward, & Winkler, 2006) between own- and other-race faces appear to provide some support for a perceptual explanation of ORE.

In contrast to the "face-space" model and perceptual expertise account, social-cognitive models do not assume that there is a difference between own- and other-race faces in perceptual processing. Rather, the difficulty of recognizing other-race faces is thought to be a result of reduced attention and lack of motivation to individuate other-race members, and is related to a person's social attitudes towards other races in general. In a series of experiments, Levin (1996, 2000) demonstrated that other-race faces were more attended to for race features. The selection of race-features for other-race members might in fact be beneficial and necessary for efficiently guiding social behaviors through the activation of social schemas. This is, however, at the expense of optimally differentiating other-race members; because of less individuation of other-race members, they are more difficult to recognize. Strong evidence in support of social-cognitive explanations for ORE is found in studies (Bernstein, Young, & Hugenberg, 2007; Short & Mondloch, 2010) in which in-group and out-group membership (e.g., based on personality type) was artificially created with own-race faces. Despite the same perceptual expertise participants had with in-group and out-group faces, face recognition was nonetheless better for in-group members than for out-group members, suggesting that perceptual expertise in itself is not a necessary condition in general for causing difference in face recognition, and that the social-cognitive processes should at least be taken into account when ORE is considered. When participants were informed about the ORE and were encouraged to individuate other-race faces, the ORE could be abolished (Hugenberg, Miller, & Claypool, 2007; Rhodes, Locke, Ewing, & Evangelist, 2009). The social categorization may also alter the perception of a face in a more subtle way. For example, studies have found that the extent to which a face is processed holistically (Michel, Corneille, & Rossion, 2007) or configurally (Cassidy, Quinn, & Humphreys, 2011) may depend on the social category to which the face belongs. Overall, based on the behavioral research in the past, it is likely that the phenomenon of ORE is due to both perceptual and social-cognitive influences and the interactions between the two, and needs to be understood with an integrative approach (see Hugenberg, Young, Bernstein, & Sacco, 2010; S. G. Young, Hugenberg, Bernstein, & Sacco, 2011, for a recent review).

Compared to the large number of behavioral studies, the amount of neural research on ORE is rather small. Among the first to investigate the neural correlates of ORE, Golby, Gabrieli, Chiao, and Eberhardt (2001) found in their fMRI study that the face-selective fusiform regions (Haxby, et al., 1994; Kanwisher, et al., 1997; Puce, Allison, Asgar, Gore, & McCarthy, 1996) showed greater responses to own-race than to other-race faces. In addition, the behavioral ORE was found to correlate with the changes in brain signals to own-versus other-race faces in the left fusiform and in the right parahippocampal and hippocampal areas: the greater the difference in neural activation, the larger the behavioral ORE. In a more recent study (Feng, et al., 2011), the greater FFA response to own-race than to other-race faces was also reported with Chinese participants when they were performing a race-categorization task. In addition to the overall response magnitude of FFA, Natu, Raboy, and O'Toole (2011) found that the own-race and other-race faces could also be differentiated reliably through the neural response patterns across the ventral temporal regions (including FFA). With these neuroimaging studies, a linkage between the ORE observed behaviorally and its underlying neural structures is tentatively established. Because these studies did not examine specific mechanisms, it was unclear whether their results were due to perceptual expertise or due to social cognitive factors (e.g., attention allocation). Furthermore, a number of studies have also shown that own- and other-race faces elicit different amygdala responses (Cunningham, et al., 2004; Lieberman, et al., 2005; Phelps, et al., 2000; Ronquillo, et al., 2007; Wheeler & Fiske, 2005). Considering the anatomical connections between amygdala and extrastriate visual cortices including the fusiform gyrus (Catani, Jones, Donato, & ffytche, 2003), it is likely that the difference seen in FFA responses to own- and other-race faces might be in part due to the feedback from amygdala.

To investigate how social cognition may play a role in influencing neural responses to faces, Van Bavel, Packer, and Cunningham (2008, 2011) manipulated the social group memberships by assigning faces to either an in-group or an out-group; through counter-balancing, the in-group and out-group faces were matched perceptually. Despite this arbitrary manipulation, they found that in-group faces, compared to out-group faces, elicited greater responses in FFA but also in amygdala and in orbitofrontal cortex. By demonstrating this group membership effect on face processing, the studies have provided some neural evidence in support of social-cognitive explanations for ORE. In the present study, using event-related potentials (ERPs) which provide a better temporal resolution of neural events than imaging methods and considering our findings from the previous two studies (i.e., different ERP components are associated with different stages of face processing), we investigated the timing and the stage when social category may affect face processing at a neural level.

Electrophysiological research on ORE

Event-related potentials (ERPs) can provide better temporal resolution for neural events than fMRI. Past ERP research has identified several components that are particularly relevant for face processing: the N170 (Bentin, et al., 1996), the P2 and the N250 (Schweinberger, Pickering, Jentzsch, et al., 2002). Functionally, these components may reflect different stages of face recognition (Bruce & Young, 1986; Zheng, et al., 2011; Zheng, Mondloch, & Segalowitz, 2012).

With regard to the ORE, while the effect of race on the N170 was not found initially (Caldara, Rossion, Bovet, & Hauert, 2004; Caldara, et al., 2003; but see Ito & Urland, 2005), a number of recent ERP studies have reported that the N170 was smaller (Balas & Nelson, 2010; Brebner, et al., 2011; Caharel, et al., 2011; Herrmann, et al., 2007; Stahl, et al., 2008, 2010; Walker, et al., 2008), and peaked earlier (Ofan, Rubin, & Amodio, 2011; Stahl, et al., 2008, 2010; Wiese, Stahl, & Schweinberger, 2009; but see Balas & Nelson, 2010;) for own-race faces than other-race faces. The face inversion effect on the N170 (Rossion, et al., 1999), a well-documented phenomenon, also seems to differ between own-race and other-race faces, although the specific results have not been entirely consistent across studies (Caharel, et al., 2011; Gajewski, et al., 2008; Vizioli, Foreman, et al., 2010). Using an adaptation paradigm and with single-trial analyses, Vizioli, Rousselet, and Caldara (2010) further found that the N170 was sensitive to face identity of own-race faces, but not with other-race faces. The effect of race on the N170 may also vary among individuals. It has been reported that the N170 amplitude difference between own- and other-race faces is related to the amount of social contact and individuating experience with other-race members (Walker, et al., 2008) and to a person's automatic racial attitude and controlled responses to prejudice-congruent information (Ofan, et al., 2011).

Although less studied than the N170, the P2 and the N250 component are also modulated by the race of a face stimulus. Stahl et al. (2008) found that the P2 was more positive for own-race faces than for other-race faces; this effect however was driven by participants who did not have much experience with other-race members. Consistent with these results, when task instructions were experimentally manipulated so that one group of participants were encouraged to individuate other-race members (judge for attractiveness) while the other group was asked to simply categorize based on race, the subsequent difference in P2 amplitude between own-race and other-race faces was only found with the latter group (Stahl, et al., 2010). The training to individuate other-race members also affected the N250 component: it was enhanced following individuation training, but did not change after training for face categorization (Tanaka & Pierce, 2009). There was also evidence suggesting that the N250 to a target face differed between own- and other-race faces, but only when the target face was not primed (Herrmann, et al., 2007).

Overall, these recent ERP studies suggest that the early face-related ERP components are sensitive to face race information, despite the fact that the specific neural mechanisms are not fully understood yet. In the present study, using only Caucasian faces to control for perceptual expertise, we randomly assigned face stimuli into four social categories based on university affiliation (Brock and non-Brock) and nationality (Canadian and non-Canadian). The research participants learned the social categories of the face stimuli through performing a social categorization task (see the Method for more details). Given that the participants were Canadians studying at Brock University, the Canadian Brock face represents a double in-group member; the non-Canadian non-Brock face represents a double out-group member, and the Canadian non-Brock (in/out-group) and the non-Canadian Brock (out/in-group) faces as in between. Previous social psychological research on cross-categorization has reported that a person's liking of a group and perception of the group's similarity to self decreased gradually from double in-group to double out-group, with mixed groups in the middle (Crisp, et al., 2003). By creating a similar change in group membership affiliation through this cross-category manipulation, we aimed to investigate whether the social-cognitive factors affects the early ERP components (P100, N170, P2, N250), and how soon the effect occurs. Furthermore, given the functions associated with these ERP components as they were suggested by our previous studies (Study 1 and 2), we may also infer the stage at which social-cognitive factors might influence face processing.

The EEG to the face stimuli of different social categories was recorded while participants were performing a target detection task (see Method for details). In addition, during the task, the faces were presented in both upright and inverted orientations. When faces are inverted, they are processed less configurally (Farah, Tanaka, & Drain, 1995; Freire, et al., 2000; Leder & Bruce, 2000; Leder & Carbon, 2006). This manipulation thus allowed us to determine whether social group membership is related to changes in configural processing, a factor not investigated in the previous imaging studies (Van Bavel, et al., 2008, 2011).

4.2. Method

4.2.1. Participants

Fifteen Caucasian female undergraduate students (mean age = 20.9 ± 2.0 years) participated in the current ERP study for either a research credit or monetary compensation. All participants were Canadians and were studying at Brock University at the time of testing. They were right-handed with normal or corrected-to-normal vision. There was no report of neurological disorders, psychiatric history, or attentional problems. The experimental procedures were approved by Brock University Research Ethics Board.

4.2.2. Stimuli

The stimuli were in black and white and consisted of four Caucasian male faces with a neutral expression selected from the NimStim face set (Tottenham, et al., 2009) and four houses used as non-face stimuli (Fig. 4.1*a*). A black background with an oval shape (8.7 cm in width x 14.4 cm in height) cut-out in the middle was placed on top of each stimulus. The positions of the face stimuli were adjusted so that their eyes were approximately at the same horizontal level.

There were two experimental conditions, a target detection task and a social categorization task, each performed multiple times. For the target detection task, the faces and the houses were presented in upright and inverted orientations. For the social categorization task, only upright faces were presented. For both tasks, participants viewed the visual stimuli from a distance of 100 cm, subtending a visual angle of 2.49° (horizontally) by 4.12° (vertically).

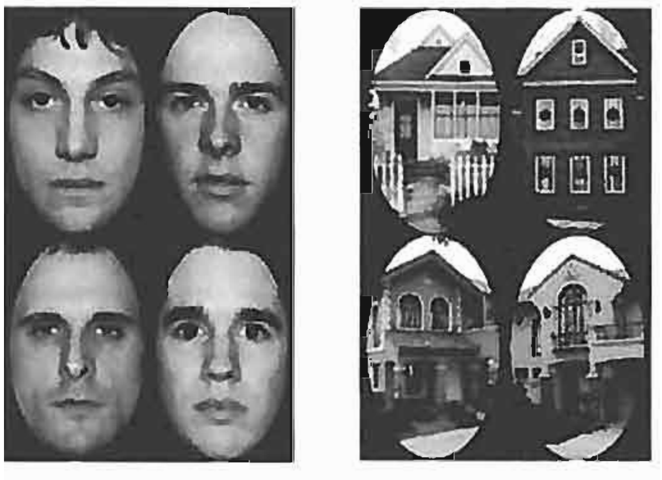

Figure 4.1a. Experimental stimuli in study 3

4.2.3. Procedure

Throughout the experiment, participants performed the target detection task three times interwoven with the social categorization task performed twice (Fig. 4.1*b*). This allowed us to investigate how the ERP responses to faces might change as participants gradually acquired social information associated with the faces.

The target detection task (Fig. 4.1*c*) had 400 trials in total. On each trial, a face or a house in either an upright or an inverted orientation was presented for 500 ms in the center of a computer screen, followed by a randomly selected interstimulus interval (ISI) of 450, 500, or 550 ms. There were 80 trials (40 upright; 40 inverted) for each face, and 20 trials (10 upright; 10 inverted) for each house model. The order of presentation was randomized. Participants were instructed to press a button whenever they saw a house without regard to its orientation.

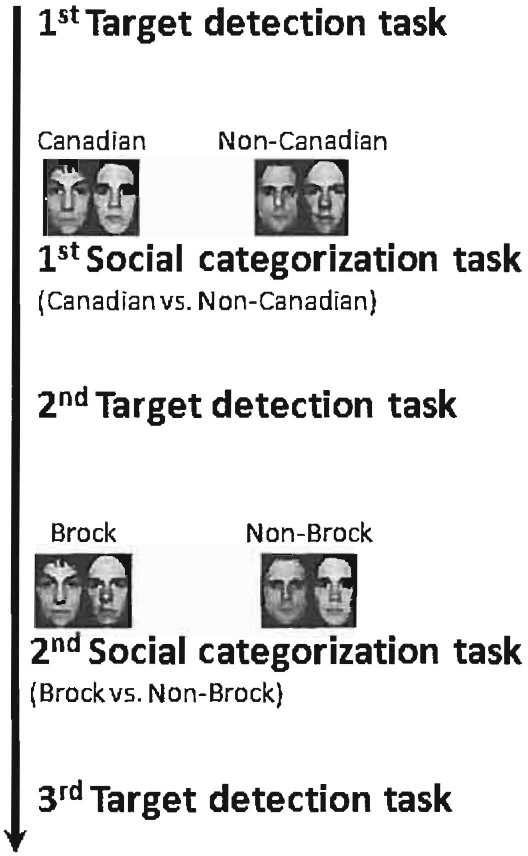

Figure 4.1b. Experimental design.

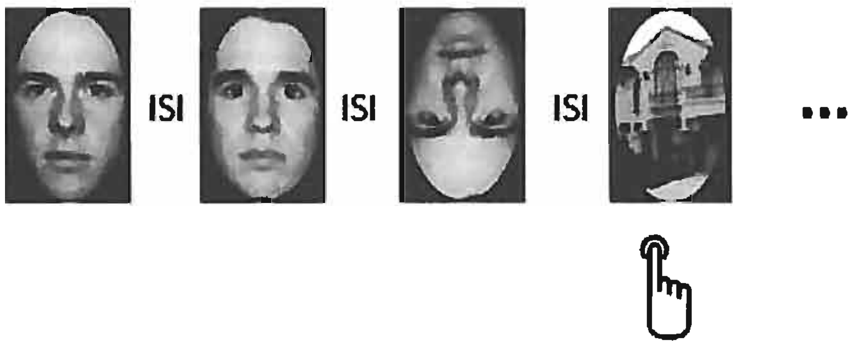

Figure 4.1c. Target detection task. Faces and houses were presented in both upright and inverted orientations. Participants were asked to press a button whenever they saw a house without regard to its orientation.

For the social categorization task, the four face stimuli were first shown simultaneously to participants, who were then informed that two faces were from one social category while the other two faces were not, indicated by the labels above the faces (Fig. 4.1*b*). After participants reported that they had memorized the group memberships, they started the social categorization task (Fig. 4.1*d*), in which an upright face was presented on each trial for 750 ms followed by a variable ISI of 450 ms, 500 ms, or 550 ms; there were 160 trials (40 trials for each face) presented randomly, and participants had to indicate the group membership for each face stimulus by pressing one of the two buttons (Fig. 4.1*d*). No feedback was given conceming their accuracy. The order in which the two social categorization tasks were performed based on either nationality or university affiliation was counter-balanced across participants. The assignment of nationality and university affiliation to the face stimuli was orthogonal so that each face was associated with a distinct group. Stimuli were rotated through social categories across participants.

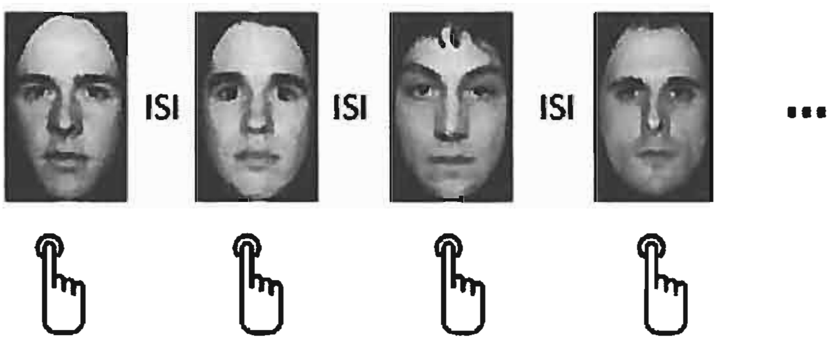

Figure 4.1d. Social categorization task. Only upright faces were presented. Based on the social category (either nationality or university affiliation) learned at the beginning of the task, participants on each trial categorized the face stimulus by pressing one of two buttons.

Finally, at the end of the study, to examine whether participants had learned the social categories successfully, we asked participants to identify the two social categories associated with each face.

4.2.4. ERP recording and analysis

The EEG was recorded from an elasticized net (Electrical Geodesics, Inc.) with 128 silver chloride-plated electrodes, referenced to the vertex (Cz), and amplified by Net Amps 200 (band-pass filter 0.01 – 100 Hz; digitized sampling rate 500 Hz; impedance below 50 kΩ). Eye movements and blinks were monitored by electrodes placed below and beside each eye. The EEG data were segmented into epochs of 1000 ms including a baseline of 200 ms prior to stimulus onset. After visual inspection, trials contaminated by movements were manually rejected, and approximately 38 trials (i.e., 95%; range: 94.9%-96.3%) remained for each stimulus type; trials with eye artifacts were corrected through the artifact correction method provided by BESA 5.1 software (MEGIS Software GmbH). The 128-channel data were then transformed through spherical spline interpolation to the standard 81 electrode montage according to the expanded 10-10 system.

The P100 component was measured as the maximum peak positivity between 80 and 130 ms post stimulus onset at occipital sites (PO9, PO7, PO3, O1, O9 for the left; PO10, PO8, PO4, O2, O10 for the right); the N170 component (Fig. 4.2) was measured as the maximum peak negativity between 130 and 220 ms post stimulus onset at occipital temporal sites (P5, P7, P9, PO7, PO9 for the left; P6, P8, P10, PO8, PO10 for the right); the P2 was measured as the mean amplitude between 190 and 230 ms at the parietal-temporal sites (P5, P3, P1, PO3, PO7 for the left; P6, P4, P2, PO4, PO8 for the right); the N250 was measured the mean amplitude between 250 and 300 ms at occipital-temporal sites (P7, P5, PO9, PO7 for the left; P8, P6, PO10, PO8 for the right). The use of maximum value from each region, rather than at a single site (e.g., P7 or P8), was to take into account individual differences in the topography of the ERP components.

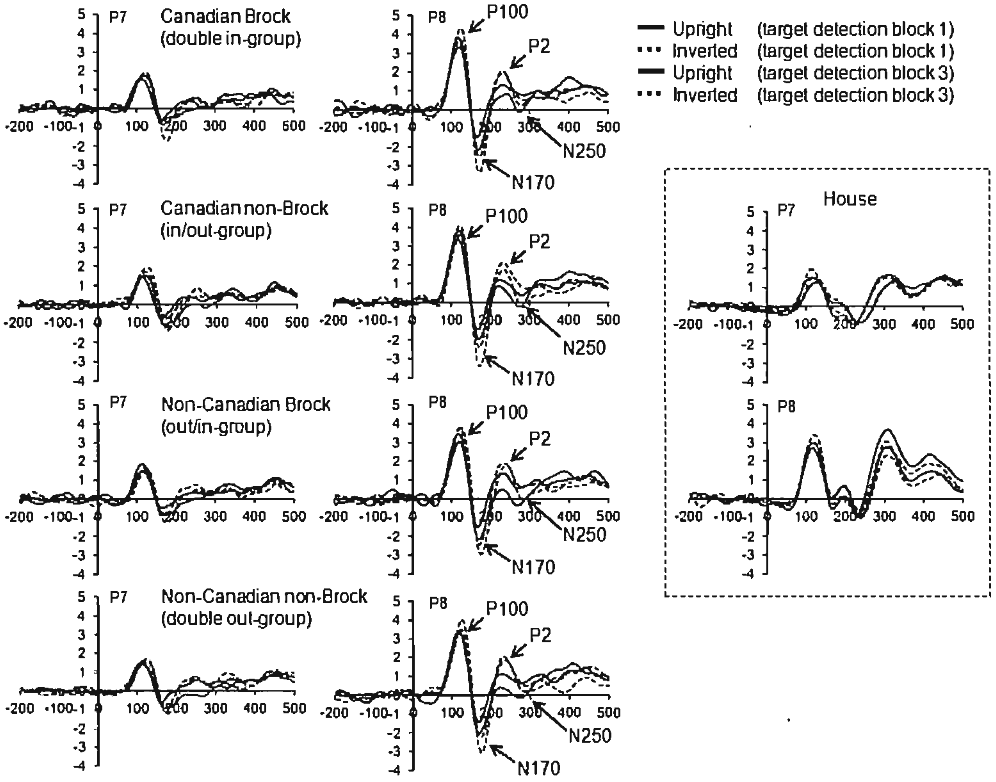

Figure 4.2. The ERP components to upright and inverted faces and houses at representative sites (P7, P8), in target detection block 1 (before social category learning) and in target detection block 3 (after social category learning).

Repeated measures ANOVAs were used to analyze ERP amplitudes for all components and ERP latencies for the P1 and the N170. Our analyses were focused on the comparison between the pre-learning (1st target detection task) and the post-learning (3rd target detection task) periods after participants had acquired the group memberships of the face stimuli through performing the social categorization task twice. Thus, with 2 (task block) x 2 (upright/inverted) x 4 (face type) x 2 (left/right) ANOVAs, we aimed to examine which ERP component might be influenced by the acquisition of social information. Post-hoc comparisons with a Bonferroni procedure were performed to follow up significant main effects. By comparing results across different ERP components, we may infer how early and at what stage social group membership might influence face processing at a neural level. Furthermore, comparing ERPs to upright and to inverted faces (e.g., as they are reflected in the face inversion effect on the N170 amplitude and latency), we aimed to seek the neural evidence for the effect of group membership on configural processing that has been demonstrated previously in behavioral data (Cassidy, et al., 2011; Michel, et al., 2007). Because the nationality and university affiliation were used solely to create changes in group membership affiliation, they were not considered as two separate factors; instead, the four face stimuli were considered together as one factor (group membership) in the ERP analyses.

Finally, we were primarily interested in the comparison between the 1st and the 3rd target detection task after participants learned both social categories, because previous social psychological research on cross-categorization has shown that people's attitudes towards double in-group, mixed group, and double out-group members fall on a continuum (Crisp, et al., 2003). Thus, with more levels of in- and out-group memberships, cross categorization might be more powerful than simple categorization to reveal any social-cognitive effect on neural responses. Nevertheless, it might still be interesting to examine whether simple categorization based on one social category might affect ERP responses. In the context of the current study, we addressed this question by examining ERP data from the 2nd target detection task after participants learned in-group and out-group memberships based on either university affiliation or nationality. ERP amplitudes and latencies were analyzed with 2 (in-group/out-group) x 2(upright/inverted) x 2 (left/right) ANOVAs.

4.3. Results

4.3.1. Behavioral data

Social categorization task. During the experiment, participants learned the social categories of the face stimuli successfully. The overall response accuracy was 90.1% for the 1st and 86.9% for the 2nd social categorization task (Fig. 4.3*a*). A 2 (1st/2nd social categorization) x 2 (in-/out-group) ANOVA with repeated measures was performed to examine how response accuracies might be affected by the two social categorization tasks and by in- and out-group membership. It was found that the overall response accuracy was greater for the 1st than for the 2nd social categorization task ($F(1,13) = 7.5$, $p = .017$), and was greater for in-group than for out-group faces ($F(1,13) = 5.4$, $p = .037$), without a task by group membership interaction (*F*(1,13) = 1.4, *p* = .265). When a similar analysis was performed on the response time, it was found that the response time was faster for the 1st than for the 2nd social categorization task (*F*(1,13) = 7.3, *p* = .018); it was not affected by group membership (*F*(1,13) < 1.0, *n.s.*) or the task by group membership interaction (*F*(1,13) < 1.0, *n.s.*) (Fig. 4.3*b*). At the end of the experiment, all participants were able to correctly identify the two social categories associated with each face.

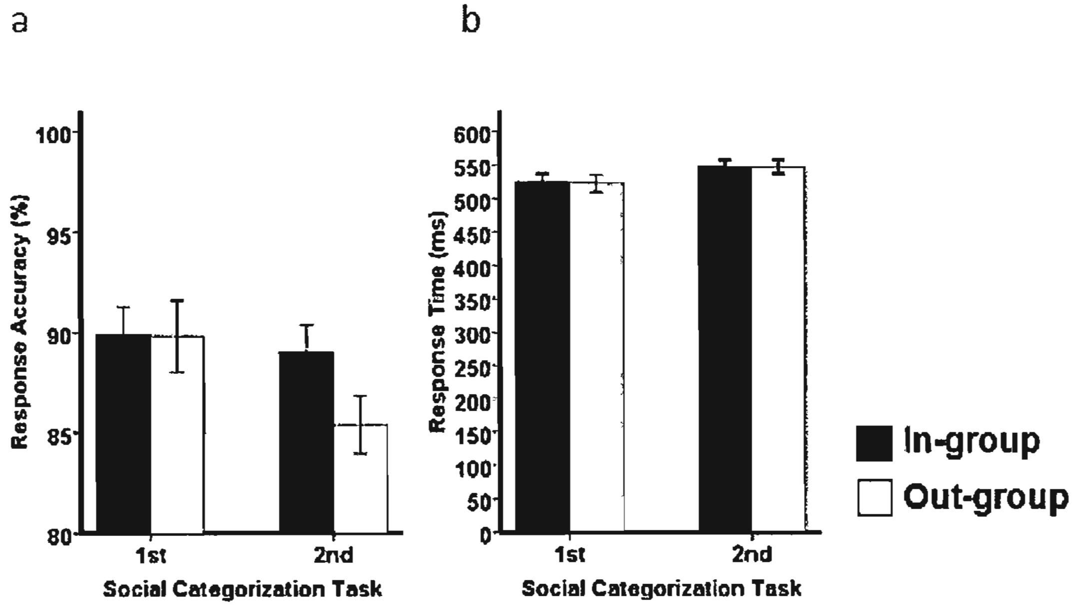

Figure 4.3. Behavioral results for the 1st and the 2nd social categorization task.

Target detection task. The average response accuracy for detecting the houses was 98.8% before (i.e., the 1st target detection task) and 95.4% after (i.e., the 3rd target detection task) participants learned the social categories of the faces (Fig. 4.4*a*). A 2 (task block) x 2 (upright/inverted) ANOVA with repeated measures was performed to examine whether response accuracies for detecting a house differed between the two task blocks and between upright and inverted houses. Overall, we found that the response accuracy was higher for the 1st than for the 3rd target detection task ($F(1,13) = 13.2$, $p = .003$); the orientation of the target stimuli did not affect response accuracy ($F(1,13) < 1.0$, *n.s.*), and there was no task block by orientation interaction ($F(1,13) < 1.0$, *n.s.*). When a similar analysis was performed on the response time, we found no main effects or interaction (for 1st vs. 3rd target detection task, $F(1,13) = 1.2$, $p = .299$; for face orientation, $F(1,13) < 1.0$, *n.s.*; for task block by face orientation interaction, $F(1,13) < 1.0$, *n.s.*) (Fig. 4.4*b*). One participant however performed poorly in both occasions, with response accuracies approximately three standard deviations below the group average, and so was excluded from subsequent ERP analyses[4].

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[4] When the participant was included in the ERP analyses, the results were similar to those reported.

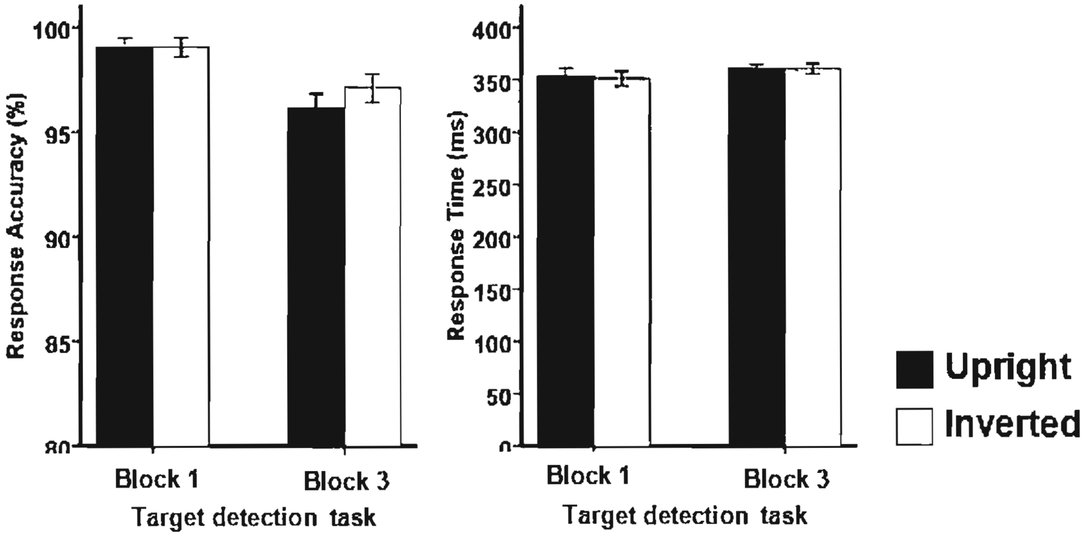

Figure 4.4. Behavioral results for the 1st and the 3rd target detection task

4.3.2. Electrophysiological results

Considering the 1st and the 3rd target detection tasks together, we analyzed the ERP data with 2 (task block) x 2 (upright/inverted) x 4 (face type) x 2 (left/right) ANOVAs to examine the possible interacting effects with task factor.

4.3.2.1. P100

Amplitude

The P100 was overall larger on the right than on the left (*F*(1,13) = 9.2, *p* = .010). It did not differ between the 1st and the 3rd target detection task (*F*(1,13) = 3.0, *p* = .108). There was a main effect for face orientation (*F*(1,13) = 10.2, *p* = .007): the P100 was larger for inverted faces than for upright face, and this face inversion effect was similarly found for both task blocks (1st target detection task, *F*(1,13) = 7.2, *p* = .019; 3rd target detection task, *F*(1,13) = 9.7, *p* = .008) (Fig. 4.5*a*). In addition, there was also a main effect for face type (*F*(3,39) = 5.4, *p* = .003). This face type effect appeared to be further affected by task block and by face orientation, indicated by a marginal three-way interaction (*F*(3,39) = 2.7, *p* = .058). Post hoc analyses suggested that while there was no main effect for face type during the 1st target detection task (*F*(3,42) = 2.2, *p* = .103), face type affected the P100 amplitude during the 3rd target detection task (*F*(3,39) = 5.2, *p* = .004): double in-group face (Canadian Brock) elicited a larger P100 than the other three types of faces (for in-out group face, *p* = .032; for out-in group face, *p* = .014; for double out-group face, *p* = .015), especially when the faces were inverted.

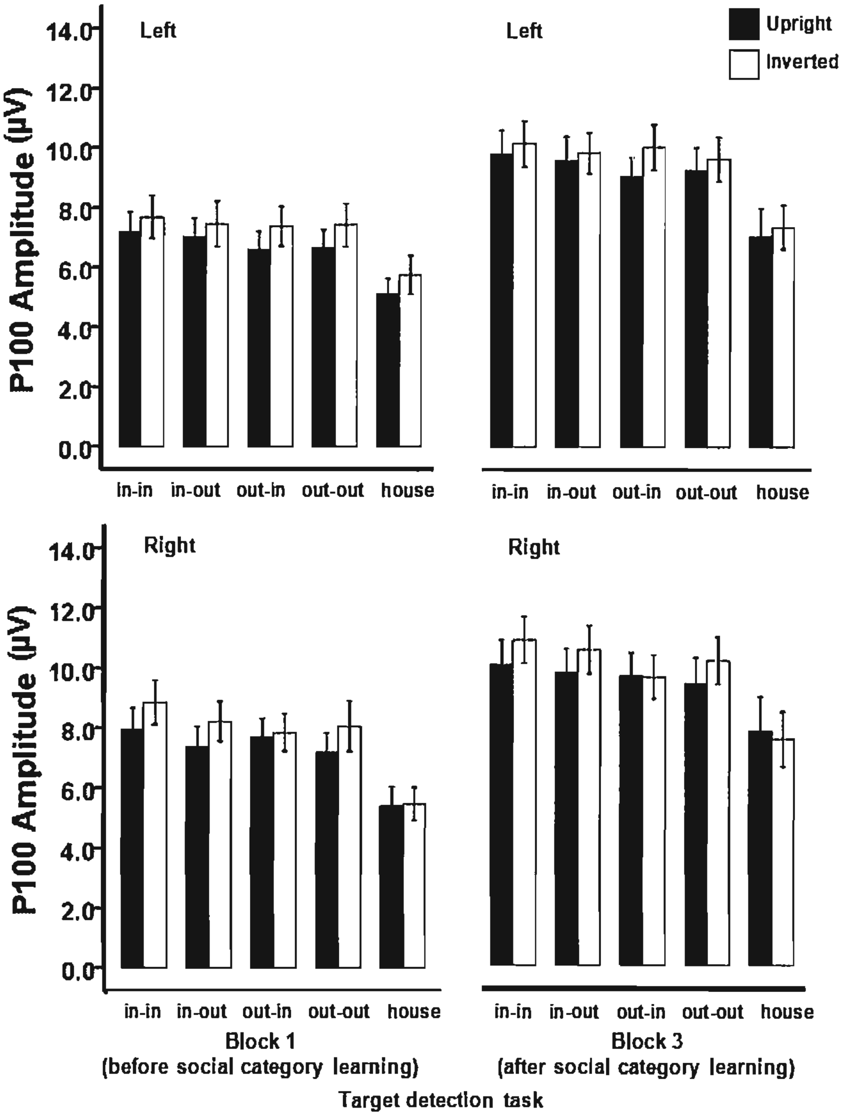

Figure 4.5a. The P100 amplitudes for each category of face in target detection block 1 (before social category learning), and in target detection block 3 (after social category learning), and for houses. Legend: in-in (double in-group; Canadian Brock); in-out (in/out-group; Canadian non-Brock); out-in (out/in-group; non-Canadian Brock); out-out (double out-group; non-Canadian non-Brock). Error bars represent the s.e.m.

Latency

The P100 latency was overall longer for the 3rd target detection task than for the 1st target detection task (*F*(1,13) = 5.1, *p* = .041. It was also delayed for inverted faces than for upright faces (*F*(1,13) = 5.6, *p* = .034), an effect that was similarly found in both task blocks (1st target detection task, *F*(1,13) = 3.8, *p* = .073; 3rd target detection task, *F*(1,13) = 3.6, *p* = .081) (Fig. 4.5*b*). There was no main effect for face type (*F*(3,39) = 1.1, *p* = .346); neither were there any interactions (*ps* > .269).

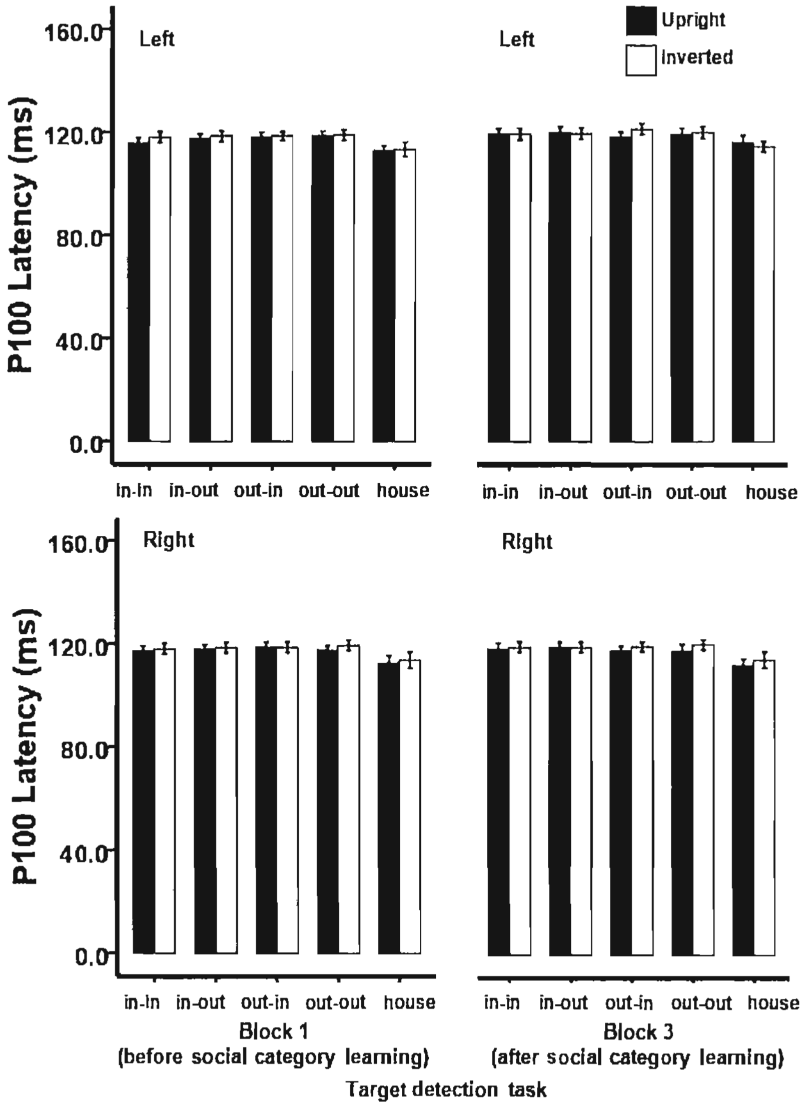

Figure 4.5b. The P100 latencies for each category of face in target detection block 1 (before social category learning), and in target detection block 3 (after social category learning), and for houses. Legend: in-in (double in-group; Canadian Brock); in-out (in/out-group; Canadian non-Brock); out-in (out/in-group; non-Canadian Brock); out-out (double out-group; non-Canadian non-Brock). Error bars represent the s.e.m.

4.3.2.2. N170

Amplitude

The N170, larger on the right than on the left ($F(1,13) = 8.8$, $p = .011$), was also larger for the 3rd target detection task than for the 1st target detection task ($F(1,13) = 21.3$, $p < .001$). A classic face inversion effect was found ($F(1,13) = 12.3$, $p = .004$) (Fig. 4.6*a*): the N170 was larger for inverted faces than for upright faces. This effect was mainly on the right (-1.045 µV) compared to the left (-.303 µV), indicated by an interaction between hemisphere and face orientation ($F(1,13) = 13.0$, $p = .003$). In addition, there was an interaction between task block and face orientation ($F(1,13) = 6.3$, $p = .026$). When the face inversion effect was examined separately for the two task blocks, it appeared to be larger for the 3rd target detection task ($F(1,13) = 13.0$, $p = .003$) than for the 1st target detection task ($F(1,13) = 9.7$, $p = .008$) (Fig. 4.6*b*). When the two task blocks were compared separately for the upright faces and for the inverted faces, the difference between the 1st and the 3rd task blocks was greater when the faces were inverted ($F(1,13) = 28.4$, $p < .001$) than the upright faces ($F(1,13) = 8.9$, $p = .010$) (Fig. 4.6*b*). Face type overall did not affect the N170 amplitude ($F(3,39) < 1.0$, $p = 717$). Neither did it interact with task block ($F(3,39) < 1.0$, $p = 987$), or with face orientation ($F(3,39) < 1.0$, $p = 486$), or with hemisphere ($F(3,39) = 1.2$, $p = .311$). Neither were there three-way interactions ($ps > .352$).

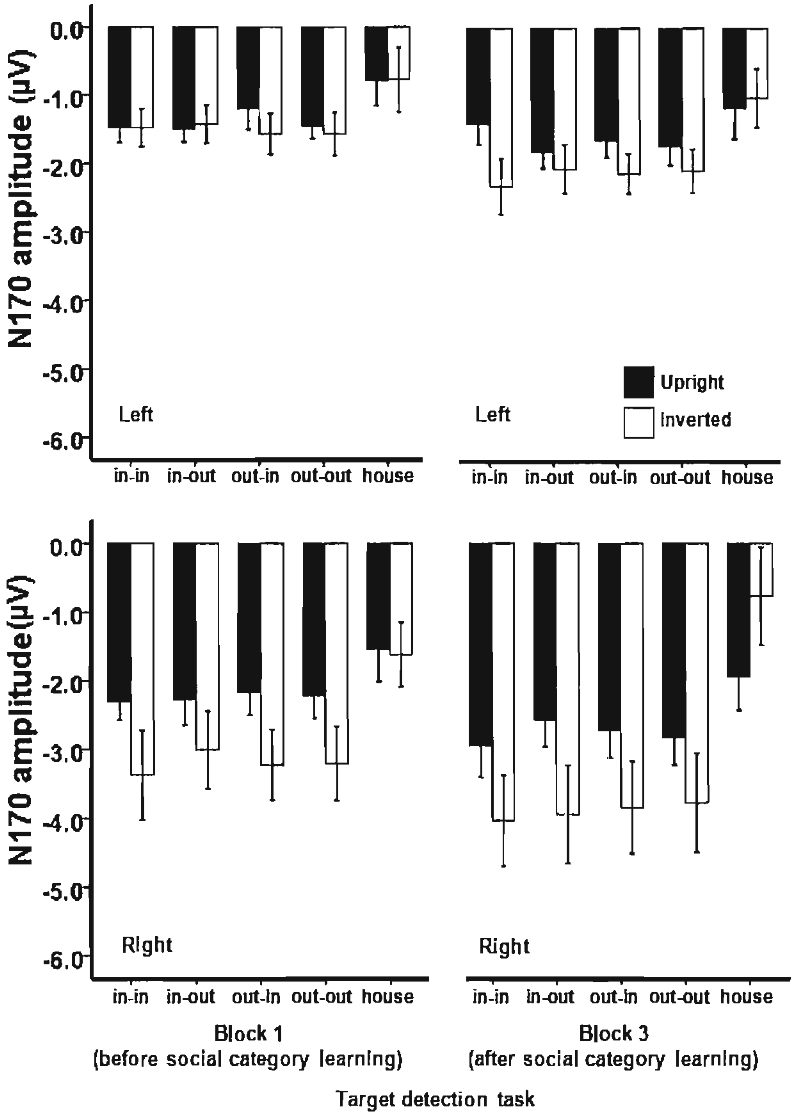

Figure 4.6a. The N170 amplitudes for each category of face in target detection block 1 (before social category learning), and in target detection block 3 (after social category learning), and for houses. Legend: in-in (double in-group; Canadian Brock); in-out (in/out-group; Canadian non-Brock); out-in (out/in-group; non-Canadian Brock); out-out (double out-group; non-Canadian non-Brock). Error bars represent the s.e.m.

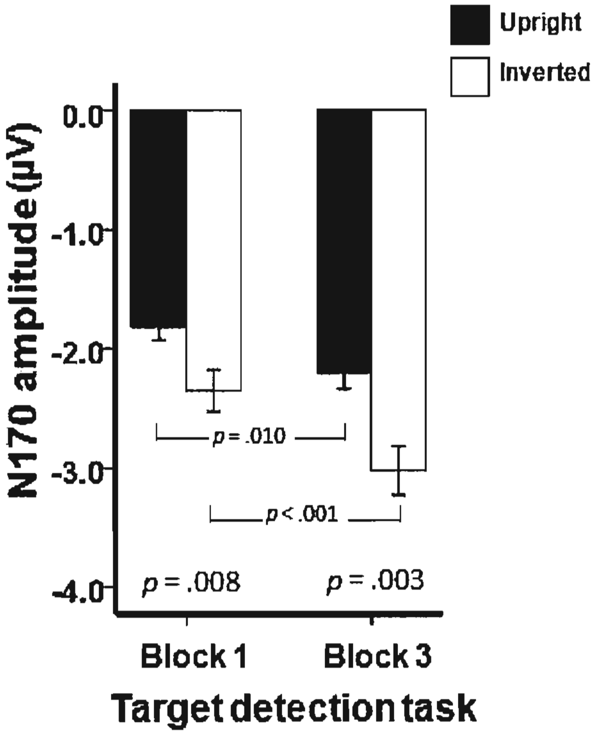

Figure 4.6b. The overall N170 amplitude increased from the 1st to the 3rd target detection block, as did the face inversion effect (the difference between inverted and upright faces). Error bars represent the s.e.m.

Latency

Compared to the 1st target detection task, the N170 latency was overall longer for the 3rd target detection task (*F*(1,13) = 17.7, *p* = .001). Furthermore, the N170 latency was delayed for inverted faces relative to upright faces (*F*(1,13) = 10.1, *p* = .007) (Fig. 4.7*a*). This face inversion effect on N170 latency was larger on the left (7.5 ms) than on the right (2.9 ms), indicated by an interaction between face orientation and hemisphere (*F*(1,13) = 5.2, *p* = .040). In addition, there was an interaction between task block and face type (*F*(3,39) = 5.4, *p* = .003): while face type did not affect N170 latency during the 1st target detection task (*F*(3,39) < 1.0, *p* = .836), the N170 latency differed among faces during the 3rd target detection task (*F*(3,39) =4.9, *p* = .005): the N170 latency was longer for the double out-group face (non-Canadian non-Brock) than for the double in-group face (Canadian Brock) (*p* = .029); the N170 latencies for the in-out group (Canadian non-Brock) and the out-in group (non-Canadian Brock) face were intermediate and did not differ statistically from the N170 latencies for either double in-group or double out-group faces (*p*s > .10) (Fig. 4.7*b*).

When the two task blocks were compared separately for each face type, it was found that for the double in-group face (Canadian Brock), there was no change in N170 latency between the 1st and the 3rd target detection task (.75 ms) (*F*(1,13) < 1.0, *p* = .539); in contrast, the N170 latency increased for the other three types of faces, particularly for the double out-group face (non-Canadian non-Brock): 3.6 ms for the in-out group face (Canadian non-Brock), *F*(1,13) = 12.2, *p* = .004; 4.5 ms for the out-in group face (non-Canadian Brock), *F*(1,13) =

16.6, *p* = .001; 5.1 ms for the double out-group face (non-Canadian non-Brock face) *F*(1,13) = 23.9, *p* < .001 (Fig. 4.7*b*).

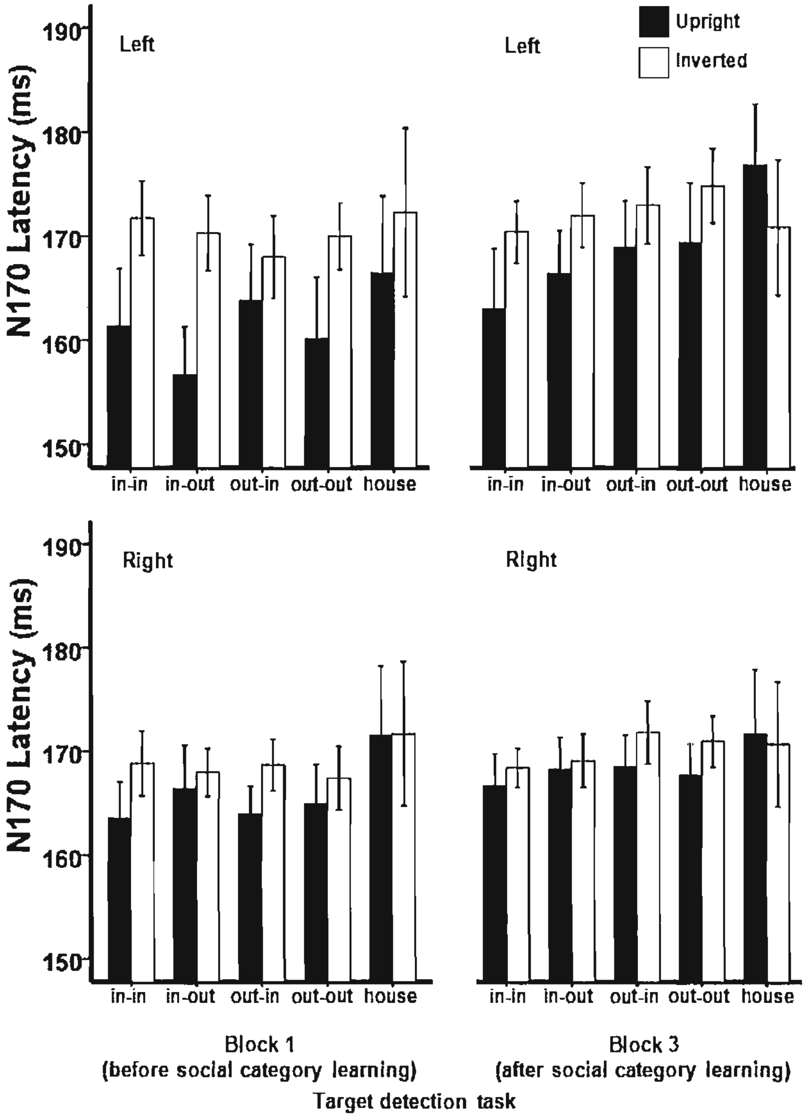

Figure 4.7a. The N170 latencies for each category of face in target detection block 1 (before social category learning), and in target detection block 3 (after social category learning), and for houses. Legend: in-in (double in-group; Canadian Brock); in-out (in/out-group; Canadian non-Brock); out-in (out/in-group; non-Canadian Brock); out-out (double out-group; non-Canadian non-Brock). Error bars represent the s.e.m.

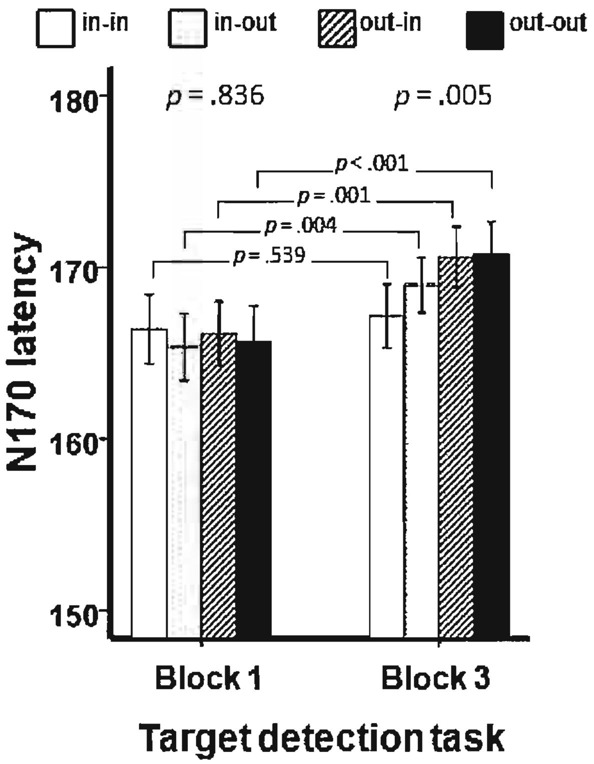

Figure 4.7b. From the first to the last target detection block, the overall N170 latency increased, driven by the out-group-related faces. In the final block, the N170 latency was shorter for the double in-group face and longer for the double out-group face; in contrast, in the first block, there were no differences in N170 latencies among the face stimuli. Legend: in-in (double in-group; Canadian Brock); in-out (in/out-group; Canadian non-Brock); out-in (out/in-group; non-Canadian Brock); out-out (double out-group; non-Canadian non-Brock). Error bars represent the s.e.m.

4.3.2.3. P2

A marginal effect for task block was found (*F*(1,13) = 4.6, *p* = .051): the P2 amplitude appeared to be larger for the 3rd than for the 1st target detection task. There was also a main effect for face orientation (*F*(1,13) = 4.9, *p* = .046) that was further affected by task block (*F*(1,13) = 5.0, *p* = .044) (Fig. 4.8). When the two task blocks were analyzed separately, it was found that the P2 was larger for inverted faces than for upright faces only during the 3rd (*F*(1,13) = 8.6, *p* = .012), but not during the 1st target detection task (*F*(1,13) < 1.0, *p* = .689). When separate analyses were performed for upright and for inverted faces, it was found that the larger P2 for the 3rd than for the 1st target detection task was only found when faces were inverted (*F*(1,13) = 7.3, *p* = .018), but not found with upright faces (*F*(1,13) = 1.4, *p* = .258). Face type did not affect the P2 (*F*(3,39) < 1.0, *p* = .791). Neither did it interact with other factors (*p*s > .194).

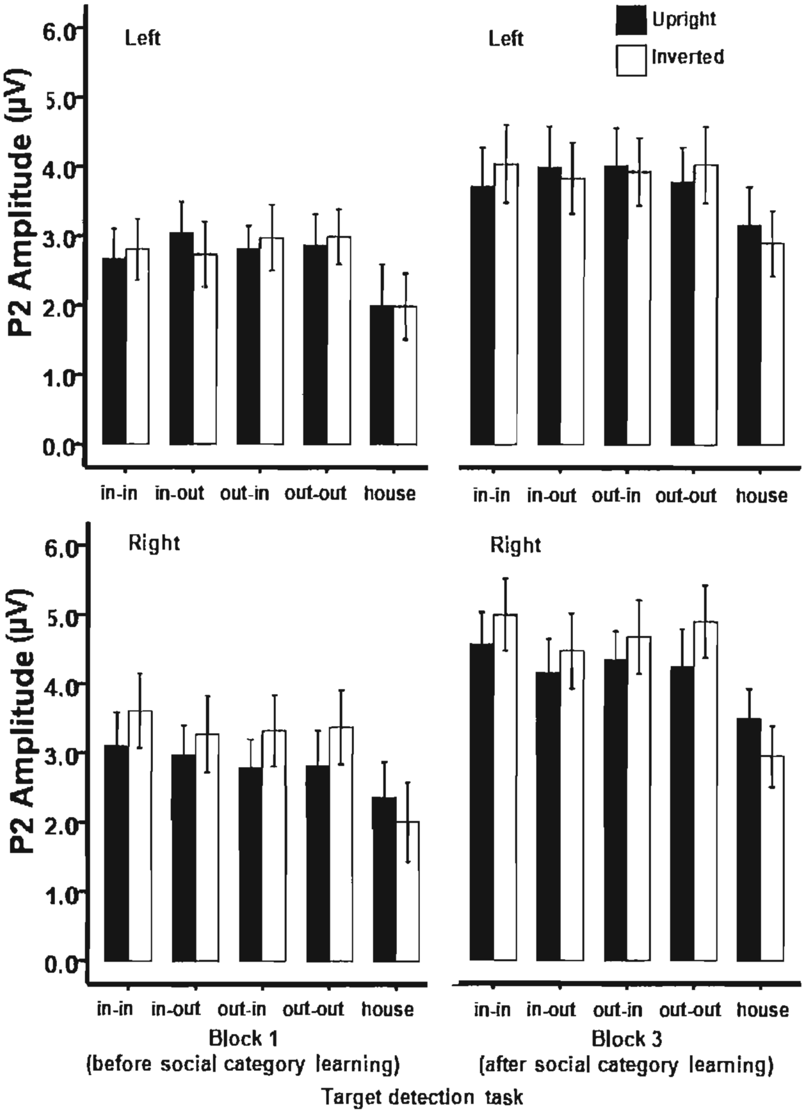

Figure 4.8. The P2 amplitudes for each category of face in target detection block 1 (before social category learning), and in target detection block 3 (after social category learning), and for houses. Legend: in-in (double in-group; Canadian Brock); in-out (in/out-group; Canadian non-Brock); out-in (out/in-group; non-Canadian Brock); out-out (double out-group; non-Canadian non-Brock). Error bars represent the s.e.m.

4.3.2.4. N250

The N250 amplitude was overall larger for the 3rd than for the 1st target detection task (*F*(1,13) = 11.7, p = .005). There was also a main effect for face orientation (*F*(1,13) = 6.7, p = .022) (Fig. 4.9): the N250 was larger for upright faces than for inverted faces. There were no other main effects or interactions (*p*s > .096).

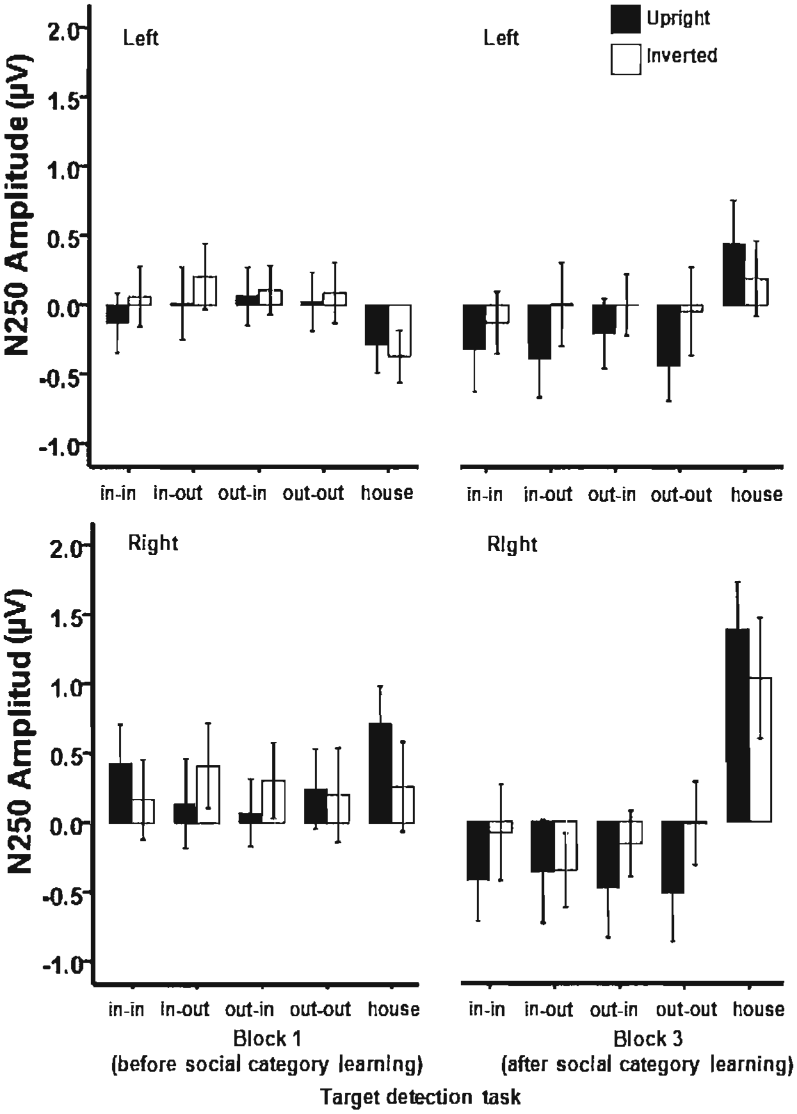

Figure 4.9. The N250 amplitudes for each category of face in target detection block 1 (before social category learning), and in target detection block 3 (after social category learning), and for houses. Legend: in-in (double in-group; Canadian Brock); in-out (in/out-group; Canadian non-Brock); out-in (out/in-group; non-Canadian Brock); out-out (double out-group; non-Canadian non-Brock). Error bars represent the s.e.m.

4.3.2.5. ERP responses after simple social categorization – results from the 2nd target detection task

After participants performed the first social categorization task and learned one social category (university affiliation or nationality) of the face stimuli, we found that in-group and out-group memberships did not affect any of the ERP responses from the 2nd target detection task, in terms of either amplitude or latency (P100 amplitude, $F(1,13) < 1.0$, $p = .648$; P100 latency, $F(1,13) < 1.0$, $p = .789$; N170 amplitude, $F(1,13) < 1.0$, $p = .931$; N170 latency, $F(1,13) < 1.0$, $p = .758$; P2, $F(1,13) < 1.0$, $p = .980$; N250, $F(1,13) = 1.4$, $p = .254$); neither did group membership interact with any other factors (*ps* >.170).

4.4. Discussion

Two prominent theories have been proposed to account for the mechanisms underlying people's difficulty in recognizing other-race faces, one with a perceptual explanation (Valentine, 1991) and the other focusing on social-cognitive factors (Levin, 2000). In most studies, the perceptual expertise and the social cognitive factors are confounded. In the present study using ERPs, we controlled for the perceptual expertise by testing Caucasian participants with Caucasian faces only, and demonstrated that the social cognitive factor of group membership can influence early neural correlates of face processing.

Specifically, we found that after participants learned group memberships of a face based on two social categories (i.e., nationality and university affiliation), the N170 latency differentiated between double in-group and double out-group faces, taking longer to process the latter. In contrast, prior to group membership assignment, there was no difference in the N170 latency among the face stimuli. To our knowledge, this is the first demonstration of a social-cognitive influence on face processing in the N170 component. Considering the previous findings of Study 1 and 2 and the discussion on the functions indexed by the N170, this result also suggests that the social-cognitive influence on face processing could occur early within 200 ms at the structural encoding stage. Our results also converge with ERP findings on the ORE that showed a delayed N170 for other-race faces than for own-race faces (Ofan, et al., 2011; Stahl, et al., 2008, 2010; Wiese, et al., 2009). A distinction however is that in the present study, we only manipulated the group membership information and controlled the perceptual expertise by using own-race faces only. The result that group membership alone can affect the N170 latency suggests that the N170 latency difference reported previously between own- and other-race faces might be in part, if not entirely, due to the social categorization processes, especially when we consider that the size of the effect found in the current study (5 ms between double in-group and double out-group faces) is almost identical to the ones reported previously between own- and other-race faces (approximately 3 ms in Stahl, et al., 2008; 4 ms in Stahl, et al., 2010; 3 ms in Wiese, et al., 2009).

In contrast to the N170 latency, the N170 amplitude and the amplitudes of the P2 and the N250 components did not differ among faces even after participants learned their group memberships. On the surface, these results may seem to suggest that the previously reported N170 amplitude (Balas & Nelson, 2010; Brebner, et al., 2011; Caharel, et al., 2011; Herrmann, et al., 2007; Walker, et al., 2008), the P2 (Stahl, et al., 2008, 2010) and the N250 (Tanaka & Pierce, 2009) race effects cannot be attributed to the social cognitive influence (i.e., race as a social category); in addition, considering that the P2 and the N250 are functionally related to face recognition and identification supported by our previous findings (Chapter 2 and 3), these results seem to further suggest that social cognitive factors in general do not affect the face recognition stage that occurs 200 ms after a person sees a face. Such conclusions however might not be accurate.

An important consideration of the current study is that compared to the large number of face stimuli used by other studies, we only used four individual faces and participants viewed them many times throughout the experiment. As a result, although the four faces were different in terms of in-group and out-group membership, it is possible that they were all well scrutinized at an individual level. In the behavioral studies, when participants were informed about the ORE and were encouraged to individuate other-race faces, the ORE could be abolished (Hugenberg, et al., 2007; Rhodes, Locke, et al., 2009). Similarly, while the P2 was more positive for own-race than other-race faces (Stahl, et al., 2008), when participants were encouraged to individuate other-race faces (Stahl, et al., 2010), the P2 race-effect was no longer found. Similar results were also reported with the N250 component (Tanaka & Pierce, 2009). Therefore, because the four faces used in the current study were likely processed at an individual level without regard to their group memberships, we did not see group membership effect on either the P2 or the N250. These “null” findings however should not be considered as evidence to negate the influence of social cognitive factors on face identification and recognition. In real life, out-group members are often perceived as more homogeneous and less individualized than in-group members (Ostrpm & Sedikides, 1992; Park & Rothbart, 1982). This is also the key feature of social-cognitive models to account for the ORE. Given the strong evidence for the social cognitive effect on face processing that occurs at an even earlier stage (i.e., indicted by the N170 latency results), we hypothesize that when a large number of in-group and out-group faces are used, group membership will also affect the P2 and the N250 components, and the effects will be in the same direction as the ones found previously between own-race and other-race faces. This hypothesis should be tested in future research.

In the past, there has also been behavioral evidence for increased holistic processing when racially ambiguous morphed faces are judged as the same-race (Michel, et al., 2007). Similarly, when the same-race faces are presented as in-group members, they are processed more configurally (Cassidy, et al., 2011). Based on these behavioral studies, it might be expected that we would find a further differentiation in the N170 face inversion effect between the in-group and the out-group faces. However, we did not find this result in our study: the N170 inversion effect was similar across faces during the 3rd target detection task after participants learned group memberships. Considering the previous discussion, because all faces were likely processed at an individual level, it might explain this lack of further differentiation in N170 face inversion effect between in-group and out-group faces.

An unexpected result in the study was that after participants learned group memberships of the face stimuli, the P100 amplitude was larger for the double in-group face than for other types of faces. Because the P100 is functionally related to the processing of low-level visual information and is not specific to faces, this group membership effect on P100 amplitude is rather puzzling. One possibility to explain this result might be that when participants learned group memberships, they might have picked up some low-level visual features that differ between double in-group face and other faces. Despite the fact that group memberships of the face stimuli were counter-balanced across participants through rotation, different features might nevertheless be picked up by different participants. Subsequently during the task, those features might have been selectively attended to. Because selective attention can modulate the P100 (Hillyard & Anllo-Vento, 1998), this might explain why we observed a P100 amplitude difference between double in-group face and other types of faces.

Comparing the 3rd target detection task (i.e., after participants learned group memberships) with the 1st target detection task (i.e., when the group memberships were not assigned to faces), we also found that the latencies of both the P100 and the N170 components became longer during the 3rd target detection task; in addition, the amplitudes also became larger for the N170, the N250, and marginal for the P2 components during the 3rd target detection task. While it might be tempting to explain these effects as a result of social category learning, they might also be interpreted as a general effect of increased attention or perceptual familiarity or practice, considering that participants viewed the same face stimuli after the learning phase. Similarly, although we found that the face inversion effect (e.g., as it was reflected in the N170 amplitude) became larger during the 3rd target detection task compared to the 1st target detection task, we cannot conclude definitely that social category learning had led to a greater degree of configural processing. Alternatively, the greater degree of configural processing might be simply due to perceptual familiarity.

Finally, two issues should be further noted with the current study. First, with regard to the behavioral data, we found that participants made more errors to categorize out-group faces than to categorize in-group faces, especially during the 2nd social categorization task. In contrast, the previous behavioral research has shown that in a race categorization task, other-race faces are typically categorized faster with a higher accuracy than own-race faces (Feng, et al., 2011; Levin, 1996; Valentine & Endo, 1992). This seemingly discrepancy between our results and others however can be resolved on the basis of two considerations. Firstly, in a race categorization task, the difference between other-race and own-race faces is due to that the former are more attended to for their race information and individuated less. In comparison, in our social categorization task, this could not occur, given that all faces are the same race; instead, to perform the task, participants had to process both in-group and out-group faces at an individual level. Because of this difference in mechanisms involved or strategies used by participants in the two tasks, the results might be different. Second, to help understand the results of the current study, it is important to note that we used cross-categorization to manipulate group memberships of the face stimuli. As a result, the group memberships of two faces changed during the 2nd social categorization task, making it more difficult to perform not only compared to a simple race categorization task, but also compared to the 1st social categorization task, which was indeed supported by the overall lower response accuracy and slower reaction time for the 2nd than for the 1st social categorization task. This difficulty due to switching group memberships might be greater when an in-group face switched to become an out-group member, compared to when an out-group face switched to become an in-group member. Consequently, this imbalance might lead to an overall lower response accuracy for out-group faces during the 2nd social categorization task.

The second issue worth noticing in the current study is that when we examined ERP responses in relation to simple social categorization during the 2nd target detection task, we found that in- and out-group memberships, when defined only by one social category, did not affect ERP responses. This is in contrast to the effects that we found during the 3rd target detection task, when group-memberships were defined by two social categories. A few possibilities might explain why simple social categorization did not affect ERP response. It might be that a single social category is simply not strong enough to alter ERP responses, or that the social categories (nationality and university affiliation) chosen in the study were not strong enough on their own, or that they may only work in a more face-related task, but not in a house detection task. In any case, these “null” findings have raised an interesting methodological issue that should be considered by researchers who decide to use only one social category in an ERP study.

Interestingly, even with cross-categorization, the types of categories and the nature of task are also important to consider. For example, in a recent ERP study (Wiese, 2012), young Caucasian participants were tested for their visual memory of young and old faces of either own- or another-race. The young Caucasian faces thus could be considered as the double “in-group”; the old other-race faces could be considered as the double “out-group”, and the old Caucasian faces and the young other-race faces could be considered as the “mixed groups”. Based on the measure of response sensitivity (d’), it was found that the visual memory was better for double “in-group” faces than for the other faces. Surprisingly, however, the visual memory was also better for double “out-group” faces than for “mixed-group” faces. As the author had acknowledged, the latter behavioral result was unexpected and did not seem to fit with any existing face recognition model (e.g., face space model). As for the ERP results, there were overall no interactions between the age and the ethnicity in the early ERP components (e.g., P1, N170, P2, N250), although the P1 latency was shorter for double “out-group” faces than other types of faces, a result that was not further discussed. Thus, it is not clear that double classification always produces effect on visual memory and face processing. This is in contrast to Crisp, et al. (2003), who created the in- and out-group memberships based on participants’ task performance. As a result, it is not surprising that participants would be able to identify more strongly with some groups than others, and therefore showed the gradual change across groups from double in- to double-out.

In summary, previous research has suggested that the phenomenon of other-race effect is likely a result of both perceptual and social-cognitive influences, and needs to be understood with an integrative approach (see S. G. Young, et al., 2011, for a recent review). Here, we provide neural evidence for the effect of group membership on face processing that could occur within 200 ms after a person sees a face: it slowed the processing of out-group faces indicated by a longer N170 latency. Considering the functions indexed by the N170 component reported in the previous two studies, this group membership effect likely occurs at the structural encoding stage. Our results are consistent with the general conclusion drawn from recent behavioral (Bernstein, et al., 2007) and imaging studies (Van Bavel, et al., 2008, 2011) when in-group and out-group memberships were similarly manipulated. Collectively, our results and these others suggest that perceptual expertise in itself is not necessary for differences in face recognition, and that social-cognitive processes should be taken into account when considering the ORE. Future research is needed to relate these ERP results to individual differences in social attitudes and in social contact with other-race/group members. The malleability of these neural findings should also be examined through a variety of task manipulations using a wide range of face stimuli (e.g., male and female faces of different age and ethnic groups) and participants (e.g., non-Caucasians), and the results should have implications in a broader societal context.

Chapter 5

General discussion

Among the large number of visual stimuli encountered in our life, faces are particularly important. Much of our social behaviors and interactions with other people depend on who they are. There is little doubt that the easiest way to learn a person's identity is to simply look at the person's face, and most of us seem capable of performing the task naturally without much difficulty. Nevertheless, in certain situations (e.g., when perceiving other-race members or unfamiliar faces in a poor lighting environment), we may fail, and when the ability to process faces is lost entirely, its consequences are dire, as we had heard from one prosopagnosic patient's own account at the beginning of this dissertation. In addition to its functional significance, face perception and recognition also pose a theoretical challenge. Considering how similar faces are to one another and the large number of faces we see throughout our life time, the fact that we nevertheless are able to differentiate them effortlessly is truly remarkable. How do we do it?

Since the initial report of the inversion effect on face recognition by Yin (1969), a large body of behavioral research has been conducted to investigate the mechanisms underlying face perception and recognition. As a result of this collective effort, it is known today that faces are processed holistically (Tanaka & Farah, 1993; A. W. Young, et al., 1987) in that different parts of a face are processed in relation to one another in a Gestalt manner. Not only are facial features (e.g., shape of eyes) important, the second-order relational information (i.e., spacing among facial features) (Diamond & Carey, 1986) also play a critical role in differentiating individual faces (Freire, et al., 2000; Leder & Bruce, 2000). The sensitivity to second-order relational information may develop more slowly than the sensitivity to featural information (Mondloch, et al., 2002). When faces are inverted, the processing of second-order relations are disrupted to a greater degree than feature processing (Freire, et al., 2000; Leder & Bruce, 2000). The norm-based coding mechanism (Rhodes, et al., 1987) and the prototype hypothesis (Valentine, 1991) were proposed with regard to face representation at a perceptual level in order to account for a range of phenomena associated with face perception and recognition (e.g., the advantage of distinctive faces over typical faces in a face recognition task). According to these models, faces are coded in relation to a face norm/prototype in a multidimensional space; the dimensions correspond to physiognomic features that include both featural and second-order relational information. Within this multidimensional "face space", the position of a face relative to the norm and to other faces determine the ease of its recognition. Strong evidence to support this norm-based coding mechanism has been found in the face identity post-adaptation effect (Leopold, et al., 2001; Rhodes & Jeffery, 2006). Situated within the classic face recognition model by Bruce and Young (1986), all of the behavioral research aforementioned has largely focused on the perceptual mechanisms and the initial two stages of face processing, namely the structural encoding (i.e., analysis of facial featural and second-order relational information) and the face recognition units (i.e., face representation).

In parallel to behavioral research, face perception and recognition can be further studied at a neural level in terms of "where" and "when" structural encoding and face recognition occur in the brain. With regard to the former "where" question, a distributed neural network, including middle fusiform gyrus, lateral occipital complex and superior temporal sulcus, has been found to be particularly involved in face processing (see Haxby & Gobbini, 2011, for a recent review). The neural responses from these brain structures have been investigated in relation to face inversion (Goffaux, et al., 2009; Yovel & Kanwisher, 2005), with composite faces (Harris & Aguirre, 2010; Schiltz & Rossion, 2006), or by manipulating facial featural and configural information (Goffaux, et al., 2009; Maurer, et al., 2007; Rhodes, Michie, et al., 2009; Rotshtein, et al., 2007). The neural support for the norm-based coding mechanism was also found in imaging data (Loffler, et al., 2005): the BOLD response from FFA increases with an increase in face identity strength defined as the distance from a face norm.

With regard to the timing of structural encoding and face recognition at a neural level, it is often studied by means of event-related potentials (ERPs), because of the excellent temporal resolution and non-invasive nature of the technique. Previous research has identified several ERP components (peaks or troughs that occur at a particular point in time) associated with face processing, including the N170 (Bentin, et al., 1996), the P2 (Halit, et al., 2000), and the N250 (Schweinberger, Pickering, Jentzsch, et al., 2002). Importantly, because these components occur at different time points after a person sees a face, understanding their functions in relation to the stages of face perception and recognition will help situate the timing of those stages at a neural level.

The N170 component is reliably larger to faces than to non-face stimuli, and it is further enhanced with a delayed latency when faces are inverted (Rossion, et al., 2000) or when face-top and face-bottom are misaligned (Jacques & Rossion, 2009). Removing external or internal features reduces the N170 amplitude (Eimer, 2000b). Although these findings support a link between the N170 and structural encoding (i.e., analysis of physiognomic information), the specific relationships between the N170 and natural variations in facial characteristics had not been examined. If the N170 was indeed functionally associated with structural encoding, such relationships would be expected.

In Study 1 (Chapter 2), using a large set of pictures of female faces, we examined this issue directly. For each picture, we measured a range of facial characteristics focusing on the eye region (eye color, eye width, eye height, between-eye distance) and facial layout (face width, top-of-face height, bottom-of-face height); some measures were also taken around the mouth-nose region (e.g., lip thickness, mouth width). Relating the natural variations in these facial characteristics to the N170 amplitude, we found that the right N170 was affected by eye color and by face width, while the left N170 was affected by eye size and by the face-top by face-bottom relationship; in contrast, facial information from the mouth-nose region did not affect the N170. Our results are consistent with the recent findings from monkey research (Freiwald, et al., 2009), when the response properties of face-selective neurons from the superior temporal sulcus were studied in relation to the similar facial characteristics encoded in cartoon faces. The strong influence of eye region on the N170 amplitude also converges with the general conclusion made recently about the importance of eye processing (Itier, et al., 2007; Itier, Van Roon, & Alain, 2011). The hemisphere difference in the N170 results was however somewhat surprising. Given that a hemisphere difference in the N170 was previously reported in some ERP studies between the processing of a whole face and the processing of face parts (Rossion, et al., 2000) and between the processing of configural information and the processing of featural information (Scott & Nelson, 2006), our results may suggest that the distinction between featural (analytical) and configural (holistic) processing in terms of hemisphere activation might also apply to the level of facial characteristics.

Furthermore, in contrast to the N170 effects, we found importantly that the P100 and the N250 components were largely unaffected by variations in facial characteristics. Considering that the P100 is associated with the neural processing of low-level visual information (e.g., spatial frequency) (Rugg & Coles, 1995) and that the N250 is associated with processing face identity (Schweinberger, Pickering, Jentzsch, et al., 2002) and that no single facial characteristic is adequate on its own to define face identities, these null findings were not unexpected. Together, the overall results of Study 1 have provided direct evidence to support a link between the N170 and structural encoding. Because the N170 occurs between 140 and 200 ms after a person sees a face, it suggests that the structural encoding stage also occurs during this period.

While the functional association between the N170 and structural encoding is supported in our own data and by others (Eimer, 2000b), some recent ERP studies (Caharel, d'Arripe, et al., 2009; Caharel, Jiang, et al., 2009; Jacques & Rossion, 2006) have suggested that the N170 might also be sensitive to face identities, implying that face recognition may also occur during the N170 time-window. Because these studies have mainly used an immediate repetition paradigm (i.e., a probe face follows immediately after a prime face), their results might be explained alternatively by the priming effect of either facial characteristics or a face in general (Eimer, et al., 2010). In contrast to the face identity effect on the N170, it has been found more reliably with the N250 component in a variety of tasks (Herzmann, et al., 2004; Kaufmann, et al., 2008; Schweinberger, et al., 2004; Schweinberger, Pickering, Burton, et al., 2002; Tanaka, et al., 2006), suggesting that face recognition occurs between 200 and 300 ms. To further clarify the issue and to better understand the timing associated with face recognition, we conducted Study 2.

Specifically, we manipulated face identity strength by morphing individual faces to an average face. In a norm-based coding model, the average face is considered as having the least identity strength; as faces move away from the average face, their identity strength increases. Correlating ERP amplitude to face identity strength, we found a linear relationship between the two for the ventral P2 (230 – 270 ms) and the N250 (270 – 330 ms) components: the average face elicited the largest ventral P2 and the smallest N250 compared to more distinctive faces. These results are generally consistent with the imagining data in humans (Loffler et al., 2005) and with the single-cell recordings in monkeys (Leopold et al., 2006). In contrast to the ventral P2 and the N250 components, the N170 was not affected by face identity strength. Dividing faces into low-, medium-, and high-identity strength groups, the same results were found in the group analyses for non-target faces and marginally for target faces: the ventral P2 and the N250 were affected by face identity strength in the same direction as it was found in the correlational analyses; the N170 was again not affected. These results are also consistent with the findings of ERP studies that compared veridical faces with their caricatured versions that were created using a similar morphing procedure (Kaufmann & Schweinberger, 2008, 2011). Given the timing of the P2 and the N250, our results thus support face recognition occurring after 200 ms, but not before.

In summary, in two studies with Study 1 focusing on the structural encoding and Study 2 focusing on face recognition, we examined the functions of ERP components in relation to face processing. We found that the N170, but not the N250, was affected by natural variations in facial characteristics; in contrast, face identity strength did not affect the N170, but affected the ventral P2 and the N250 components that appeared to further differentiate from each other; the P100 was neither affected by facial characteristics, nor affected by face identity strength. Collectively, based on these results, we may tentatively draw the following timeline, and thus provide an answer to the central question of this dissertation, namely when structural encoding and face recognition occur at a neural level: first, low-level visual information is processed at approximately 100 ms, indexed by the P100 component. After a face is detected at some point between 100 and 140 ms, its facial characteristics are then registered (i.e., structural encoding). This occurs between 150 and 200 ms and is reflected in the N170 component. After the physiognomic information is extracted through structural encoding, it is further integrated to form a face representation. This integration likely occurs during the first half of the 200 – 300 ms time window, observed in the P2. Finally, this newly formed face representation is compared to the representations of "old" faces established previously from a person's past experience. As a result of this comparison, an incoming face is either recognized as an "old" face when there is a match, or considered as a "new" face when there is a mismatch. This process likely occurs during the second half of the 200 – 300 ms time window, reflected in the N250. After a face is recognized at approximately 300 ms, retrieval process can begin as suggested by a study recording single-cells in patients who underwent surgery for epilepsy treatment (Quiroga, Reddy, Kreiman, Koch, & Fried, 2005). It was found that the neurons within the hippocampal regions showed invariant responses strongest between 300 and 600 ms to various pictures and naming of people in the stimuli.

Finally, taking a different approach in Study 3, we used ERPs as a tool to examine the relationship between face processing and social cognitive factors (e.g., in- and out-group membership), an issue that is particularly important for understanding the other-race effect (i.e., a greater difficulty recognizing other-race faces than own-race faces). While there have been behavioral (Bernstein, et al., 2007; Cassidy, et al., 2011; Short & Mondloch, 2010) and imaging studies

(Van Bavel, et al., 2008, 2011) demonstrating social cognitive influence on face processing, the timing and the stage when such influence occurs at a neural level is unclear. Given our findings from Study 1 and Study 2 that the N170 is associated with structural encoding and the N250 is associated with face recognition, we were able to address this question directly. Controlling for perceptual expertise, we tested Caucasian participants with four Caucasian faces. The group memberships of the face stimuli were manipulated based on two social categories (university affiliation and nationality). As a result of this manipulation, one face was considered as a double in-group member; one face was considered as a double out-group member; the other two faces were considered as having mixed group memberships.

Comparing ERPs before and after participants learned group memberships of the face stimuli, we found that prior to group membership assignment, there was no difference in N170 latency among the face stimuli; after group membership assignment, however, the N170 latency was delayed for the double out-group face compared to the double in-group face, and the difference between the two types of faces is comparable to the one found in the literature between other-race and own-race faces (Ofan, Rubin, & Amodio, 2011; Stahl, et al., 2008, 2010; Wiese, Stahl, & Schweinberger, 2009). These findings thus have provided strong ERP evidence for the social cognitive influence on face processing at a neural level. Furthermore, considering that the N170 is functionally related to structural encoding, it suggests that the effect of social cognitive factors (e.g., group membership) on face processing is already evident at this early stage within 200 ms. Our results also suggest that the race effect on the N170 latency reported previously (Ofan, Rubin, & Amodio, 2011; Stahl, et al., 2008, 2010; Wiese, Stahl, & Schweinberger, 2009) might be partly explained, if not entirely due to social category effect.

In contrast to the N170 latency effect, the group memberships did not affect the amplitudes of the N170, the P2, and the N250 components. On the surface, this result might seem strange. Because all faces were Caucasian, the identification of their group memberships must be based on their identities. Therefore, a group membership effect would also be expected at the face recognition stage and observed at the P2 and the N250 components. One possible explanation for why we did not find this expected effect might be the small number of face stimuli used in the current study. Because only four face stimuli were included in Study 3, they might have been well individualized without regard to their group memberships. Previous research has shown that individuation can abolish the behavioral ORE (Hugenberg, et al., 2007; Rhodes, Locke, et al., 2009) and reduce the difference between own- and other-race faces in the P2 (Stahl, et al., 2010) and in the N250 (Tanaka & Pierce, 2009) components. When a large number of in-group and out-group faces are used so that they may differ in individuation as is often the case in real life (Ostrpm & Sedikides, 1992; Park & Rothbart, 1982), we expect that their group memberships will also influence the P2 and the N250 components. This should be tested in future research. Despite this limitation, we have nevertheless found strong support for the social-cognitive influence in the N170 latency. While our results converge with the general conclusion from recent behavioral and imaging studies, we have provided extra temporal information, suggesting that a social-cognitive influence on face processing could occur as early as 140 – 200 ms at the structural encoding stage.

Overall, using ERPs with their excellent temporal resolution, the three studies together have allowed us to make some inference about the timing of face processing at a neural level. Compared to previous ERP research on these issues, the designs of our studies may have offered us some better opportunities to discover the effects reported in this dissertation. For example, compared to the previous studies (Halit, et al., 2000; Scott & Nelson, 2006) in which faces were manipulated artificially only to create a small number of changes in either facial featural and configural information, we used a large set of face stimuli in Study 1. By taking into account the large variations in facial characteristics among natural faces and by using regression analyses in contrast to group comparisons, Study 1 might be more powerful to detect the relationships between the N170 component and facial characteristics. These results also have a greater ecological validity. Furthermore, if we consider the complexity of some of these relationships (e.g., the relationship between N170 amplitude and eye color), the adoption of our design seems particularly necessary, because those relationships may not be easily found in group comparisons. Similarly in Study 2, we created morphed faces with more identity levels than previous studies (Jacques & Rossion, 2006; Kaufmann & Schweinberger, 2011). This had made correlational analyses possible, and the results converged with the ones found in group analyses, providing stronger evidence for the functional link between the N250 component and face recognition.

However, there is one limitation to all three studies. It is that only one type of face stimuli was used (i.e., only young Caucasian female faces were used in Study 1 and Study 2; only four young male Caucasian faces were used in Study 3) and that the participants in all three studies were Caucasian female students. While this might be necessary in respect to research design, future research should nonetheless use other types of faces (male/female; familiar/unfamiliar; faces of different age groups and of different races) and test them in different populations, so that we will learn how well the results reported in this dissertation can be generalized. In addition, faces are often seen in social situations. Although we had examined in Study 3 how two social categories, namely nationality and university affiliation, might affect face processing at a neural level, it might be ideal to use the social categories that participants are more strongly identified with personally. For this purpose, some questionnaire data might be helpful.

To conclude this Discussion, while “never forgetting a face” might be a bit of an exaggeration, faces are unique and play an extremely important role in our social life. In this dissertation, we have provided some preliminary evidence with ERPs about when and how face processing might occur at a neural level. Based on these findings, many directions can be taken for future research. Some have been described in the previous sections. For example, can the relationship between the N170 and facial characteristics (Study 1) be found with other-race faces? Will the effect of face identity strength on the N250 (Study 2) be the same or different between familiar and unfamiliar faces? How might the social category effect on the N170 latency (Study 3) relate to individual differences in social contact and in people's attitudes towards other-group members in general? Only by taking an integrative approach and considering faces within a broader context, shall we understand why Groucho Marx (or hardly anybody) ever forgets a face.

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