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Brain-behavior correlations during proposed transitions in the mother-child relationship : an examination of behavior and face-processing in six-month- olds and toddlers

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Brain-behavior correlations during proposed transitions in the mother-child relationship: An examination of behavior and face processing in six-month-olds and toddlers

A Dissertation submitted in partial satisfaction of the requirements for the degree
Doctor of Philosophy

in

Psychology

by

Margaret M. Swingler

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2008

The Dissertation of Margaret M. Swingler is approved, and it is acceptable in quality and form for publication on microfilm:

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2008

DEDICATION

I dedicate this dissertation to my parents, for their endless reminders to just keep going.

To Riley and Aaron, who made the long journey to California, and the even longer journey through graduate school, with me.

And to my sister, who is tired of all of the psychology talk.

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ABSTRACT OF THE DISSERTATION

Brain-behavior correlations during proposed transitions in the mother-child relationship: An examination of behavior and face processing in six-month-olds and toddlers

by

Margaret M. Swingler

Doctor of Philosophy in Psychology

University of California, San Diego, 2008

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The studies contained in this dissertation were conducted to examine potential connections between neurophysiological measures of face processing and behavioral responses to structured mother-child interactions in two ages that have been implicated as developmental transitions in both the face processing literature and the mother-child attachment literature. Chapter's I and II present data from a study that examined a relationship between 6-month-olds' responses to a series of separations and reunions with the mother and the same infant's event-related potential (ERP) responses to mother and stranger faces. In Chapter

I, a composite measure of infant behavior was used as a general index of amount of proximity and interaction seeking behaviors. Chapter II extended this investigation to examine three specific behaviors that have been implicated as highly influential in the development of the mother-child relationship during the first year. Taken together, the results of these two chapters suggest that a general measure of amount of proximity seeking exhibited by infants was associated with larger ERP responses to the stranger's face. However, the specific behaviors examined in Chapter II correlated with the identity of the two faces in unique and specific ways, although distress during separations seemed to be particularly related to neural responses to the mother's face.

Chapter III presents data from a study conducted with toddlers (28 to 40 months) using the same paradigm. Potential age-related changes in the neural correlates of processing the two faces were examined in this age range as well, as they have not been found in previous work. The findings presented in Chapter III indicated evidence of age-related change in processing faces in general, as well as the identity of the mother and stranger faces in this age range. In addition, related to the findings in Chapter III, toddler distress behaviors during separation were particularly related to neural responses to the mother's face. These results suggest an important relationship between the changing function of the mother-child relationship for the child and the child's neural responses to the mother.

Chapter I

Introduction

From birth, infants are predisposed to interact with social partners in a manner that leads to an understanding of another's thoughts, feelings and actions. This social 'understanding', often referred to as social cognition, is central to the human social experience and is necessary for normal functioning because it allows us to predict, explain and even manipulate other people's actions and behaviors (Hala, 1997). Throughout early childhood, and in the first two years of life especially, the majority of a child's cognitive and socio-cognitive development takes place in the context of interactions with the primary caregiver (e.g. Bornstein, 1985; Baldwin, 1993; Hsu & Fogel, 2003; Maccoby, 1992). These interactions provide the basis for the development of behaviors that will be important throughout the infant's life in many domains. It is difficult to imagine even the most basic of human interactions without social cognition, and indeed, it is often regarded as a unique feature of the human species. However, many of the early emerging and long enduring facets of social communication do not require language at all and are learned in the context of these early caregiver-child social interactions. Of particular concern for the work presented here, is the finding that even prelinguistic infants are able to communicate to and receive communication from others using a rapidly developed system for social cognition that is centered on the face (see de Haan, 2001 for a relevant review).

Faces convey critical social information and are a key channel for social communication (Happe, 2004); perhaps because of this, the ability and the inclination to use faces as sources of social communication is present early in infancy. A large body of work on the development of face processing has established that faces are among the most salient and significant stimuli for infants almost from birth (e.g., McGraw, 1943; Wolff, 1969; Fantz, 1961; Johnson, Dziurawiec, Ellis & Morton, 1991, de Haan, 2001). Indeed, faces are thought to be so important, that some researchers have suggested a dedicated neural system for processing them (Farah, Rabinowitz, Quinn & Liu, 2000; Kanwisher, McDermott & Chun, 1997). Evidence of an expertise for processing faces that emerges early in development and requires minimal visual experience to function has provided support for such a system. The early face preference has also led to a claim that faces are "special"; however support for this notion from the research is mixed. A number of studies have shown that infants are able to differentiate between face and non-face stimuli almost from birth and newborns as young as 9 minutes old display greater tracking and looking behaviors to a schematic face than to a face containing either scrambled features or a blank head shape (e.g. Goren, Sarty & Wu, 1975).

In addition, some work has demonstrated that a stimulus containing a face-like configuration of isolated features alone (Johnson, Dziurawiec, Ellis, & Morton, 1991; Maurer & Young, 1983) or face-like stimuli with features arranged unnaturally (Valenza, Simion, Macchi Cassia, & Umiltà, 1996) does not elicit the same degree of tracking or looking in infants as schematic face stimuli. However, more recent work has shown that the neonates' preference for faces extends to other face-like stimuli and even potentially non face-like stimuli (Simion, Macchi Cassia, Turati & Valenza, 2001; Turati, Simion, Milani, Umilta, 2002) that include anything with the spatial configuration typical of upright faces, with more features at the top of the stimulus than the bottom. While the debate over the reasons underlying the preference for faces remains, the existence of the preference is consistent across studies, and current theories of face-processing development suggest that the preference plays an important role in the later development of face processing systems (e.g. Nelson, 2001).

While it is clear that infants are able to distinguish face from non-face stimuli early in life, the pattern of processing that occurs quickly becomes sensitive to the social significance of the face and the emotional information it contains. For instance, from 3 to 7 months, the ability to distinguish the mother's face from a stranger's face becomes more robust and infants begin to show evidence of categorizing faces by familiarity, gender and facial expression (Nelson, 2001). Accumulated experience with a primary caregiver also appears to play a role in the development of infants' face processing. A behavioral study by Quinn, Yahr, Kuhn, Slater and Pascalis (2002) provided important new information that infants' responses to faces are affected by the gender of their primary caregiver. Prior work had suggested that infants preferred looking at female rather than male faces (e.g. Leinbach & Fagot, 1993; Quinn et al., 2002). Explanations provided in the prior work for this phenomenon suggested that there is something evolutionarily "special" about female faces. However, Quinn and colleagues (2002) demonstrated that infants with a male primary caregiver showed a spontaneous visual preference for male faces rather than female faces. This finding was interpreted as evidence that infant interactions with caregivers early in development shape how they process, represent and differentially respond to faces.

Evidence of developmental change in face processing that may be related to social experience is accumulating in another line of research in which event-related potentials (ERPs) are used to measure neural responses to mother and stranger faces in infants and toddlers (e.g. de Haan & Nelson, 1997, 1999; Carver et al., 2003). ERPs are measures of brain electrical activity in response to specified discrete events, such as the presentation of a face, and are advantageous for use with infants and young children because the method is a non-invasive and objective measure of neural response. The amplitude of the

ERP is thought to reflect the summation of neural activity in which greater absolute amplitude reflects greater neural activation in response to a stimulus. In addition, because ERPs require no behavioral response on the part of child participants it can provide valuable information where behavioral measures cannot. This fact was particularly evident in a study with infants that included both a visual preference test of recognition and an ERP response measure of face processing (de Haan & Nelson, 1997). Looking time proved to be a less sensitive measure of face processing than brain response; six-month-olds' looking time did not differ for the mother's face and a stranger's face, despite the fact that the amplitude of the ERP response was significantly different for the two.

Two primary ERP components have consistently been associated with face processing in infants and young children (see de Haan & Nelson, 1997, 1999; de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003). The first, the P400, has been used to index the development of face processing and has been suggested to be face sensitive, if not face specific (de Haan, Pascalis, & Johnson, 2002, Halit, de Haan, & Johnson, 2003). The P400 is so named because it is a middle latency positive component localized over occipital electrodes. This component is sensitive to differences between faces and objects (de Haan and Nelson, 1999; Dawson, Carver, et al., 2001), and between human and non-human faces in adults and older children, leading some researchers (de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003; de Haan, Johnson, & Halit, 2003) to suggest that it may be a developmental precursor to the N170, a face specific component seen in adults (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Although the P400 appears to be sensitive to faces and has shown variation with impairments in face processing in developmental disorders like autism, it also seems to be involved in more general aspects of object processing (Dawson et al, 2002). It may be that the P400 is a component that reflects aspects of visual attention and memory updating, and that this component is sensitive, but not specific, to face processing.

The second component, the Nc, is a middle-latency negative component that is maximal over central frontal electrodes and has been associated with increased attention, particularly to salient stimuli, (Courchesne, Ganz, & Norcia, 1981, Nelson, 1994) and with recognition memory (de Haan & Nelson, 1997, 1999; Nelson, 1994). de Haan and Nelson (1997) were the first to show that 6-month-olds' Nc component activity differentiated both a dissimilar and a similar looking strangers' face from their mothers', and that the pattern of neural activity elicited differed between these two conditions. However, the same component failed to distinguish between two strangers' faces, regardless of similarity between the two. This finding was robust even when the infants were first familiarized to one of the faces. This suggests that different higher-order cognitive processes beyond novelty detection are activated to process a familiar, socially significant face paired with an unfamiliar face versus two unfamiliar faces, and that the Nc component is a sensitive measure of these processes.

A number of studies now have found that the amplitude of the Nc component response to the mother and a stranger varies across early development. In the original work with six-month-olds by de Haan and Nelson (1997, 1999), the neural response to the mother's face was larger than the response to the stranger's face. Subsequent evidence from a longitudinal study using ERPs suggests that, in general, the pattern of processing the mother's face and a stranger's face reverses between 6 and 8 months and the neural response becomes larger to the stranger's face. This pattern stays stable at least through 12 months of age (Webb, Long, & Nelson, 2005) and is present in older (preschool age) children. There is further evidence that the pattern may reverse again during the third year of life. A study by Carver et al. (2003) found distinct, age-related changes in 18 to 54-month-olds brain responses to familiar and unfamiliar faces, but not to familiar and unfamiliar objects. The youngest children in their sample, between 18 and 24 months of age, showed greater ERP responses to the mother's face than to a stranger's face. However, the oldest children in their sample, between 45 and 54 months of age, showed the opposite pattern; they had larger Nc amplitude responses to the stranger's face than the mother's. Children in the middle age group (24 to 45 months) did not show differential brain activity to the mother and stranger faces. This led to a hypothesis by Carver and colleagues (2003) that the age-related changes they observed in the patterns of brain activity were related to changes in the mother-child relationship that might also occur across the age range tested. They suggested that perhaps due to changes in the mother-child relationship across this age range, the relative importance of the mother's and stranger's face may also change.

Despite the potential connections between maternal face recognition and the accumulating interactive experience that is known to shape the developing mother-child relationship (e.g. Hsu & Fogel, 2003; Maccoby, 1992; Sameroff & Chandler, 1975); no research to date has considered the association between these two areas of development. The reversal in Nc amplitude response to the mother and stranger faces that occurs between 6 and 8 months is of particular interest because it occurs precisely when the attachment literature proposes that the bond between caregiver and infant is being consolidated and when research has shown that a behavioral preference for the caregiver emerges. These findings and those in Carver and colleagues' (2003) study led to the hypothesis being explored in the work contained in this dissertation; namely, that significant transitions in the mother-child relationship, like those that are proposed to occur at six months (Bowlby, 1969/1982) and during the toddler years (Bowlby, 1969/1982; Marvin & Britner, 1999), result in both new behavioral responses to the mother *as well as* new neural responses. This purpose of the work contained in this dissertation is to investigate potential correlations between behavioral responses to the mother and neural responses to the mother and a stranger in infants at 6 months of age and in toddlers between 28 and 40 months of age.

While no work has looked specifically for potential brain-behavior correlations in the development of the mother-child relationship, evidence from work with a special population of children has demonstrated that interactions with caregivers early in development influence the neural patterns of face processing that develop. Parker and colleagues (Parker, Nelson, & The Bucharest Early Intervention Project Core Group, 2005) measured ERP correlates of face processing in a control group of non-institutionalized children and a group of children raised in Romanian orphanages. The Romanian orphanage environment has been established as a generally impoverished care-giving environment (Zeanah et al., 2003). These authors recorded ERP responses to the child's primary caregiver; this was a parent for the control group and a preferred caregiver for the institutionalized group. The results showed differences between the two groups for ERP components related to face processing, including the N170 and Nc. Although the children tested by Parker and colleagues covered a wide range of ages, the results showed a striking effect of early social experience on the face processing system. Institutionalized children had smaller and slower amplitude responses than non-institutionalized children, and although both groups differentiated familiar from unfamiliar stimuli, the developmental trajectory observed in ERP responses to faces differed between the groups. The results of Parker and colleagues' study suggest that early social interaction with a primary caregiver is important for how the brain systems involved in face processing develop and may even have implications for brain development in general.

Attachment theory and research on early mother-child interaction provide a possible explanation for how experience with past social interactions may influence the way brain systems for processing faces develops. Mary Ainsworth, a pioneer of attachment theory, noted in some of her later work that the attachment system includes not only its outward manifestations, but also an inner organization that is presumably rooted in neurophysiological processes. Further, she suggested that this inner organization is subject to developmental change because it is sensitive to environmental influences, and that this change manifests in outwardly observable behaviors (Ainsworth, 1989). These ideas led to an important avenue of research examining how interpersonal experiences may exert an influence on the social cognition that occurs during face-to-face interactions between mother and infant. Attachment theory posits that parents and infants construct mental representations or internal working models of one another and their relationship on the basis of repeated interactional experience (e.g. Pederson, Gleason, Moran & Bento, 1998; Slade, Belsky, Aber & Phelps, 1998; Hsu & Fogel, 2003). A separate line of work conceptualizing the development of close relationships in general has proposed that individuals develop cognitive structures based on regularities in interpersonal encounters, termed relational schemas (Baldwin, 1992, 1995). Importantly, a sensorimotor form of relational schemas may be available to infants before the formation of an attachment relationship during the second half of the first year of life (Hsu & Fogel, 2003). However, despite Ainsworth’s (1989) suggestions of their existence, no studies to date have looked for neural evidence of such an internal working model or relational schema in the context of the mother-child bond.

Evidence from behavioral studies of face processing suggests infants are predisposed to behaviors that may facilitate the development of such an internal working model. During the ages that comprise the proposed first phase of the formation of the mother-child attachment bond (i.e. Bowlby, 1969/1982), from birth to around 3 months of age, infants exhibit a preference for looking at the human face compared to other objects. In the proposed second phase, from approximately three months until six months, the infant begins assuming increasing responsibility for gaining and maintaining contact with the mother either by initiating more interaction or by exerting more control over the interaction. Infants do this through the use of increasingly complex behaviors, for example through increased visual attention to the mother’s face and the use and maintenance of direct eye gaze. An important feature of this phase is that the infant also increasingly begins to differentiate his or her primary caregiver from others and preferentially directs care-soliciting behaviors to the primary caregiver(s). The existence of these behaviors has been proposed to depend on the infant having an intact working model of the attachment figure (Bowlby, 1969).

The proposed third phase (the “consolidation phase”) begins between six and nine months and is when the infant is thought to consolidate attachment and specific distress and proximity-seeking behaviors to the primary caregiver exclusively (Marvin & Britner, 1999). Study one of this dissertation (Chapter II) aims to examine a potential link between amount of proximity and interaction seeking behaviors infants at this transitional age (six-month-olds) exhibited during interaction with their mother, and their neural responses to their mother’s face and a stranger’s face. As this was the first study to attempt to correlate infant behavior with brain responses, a general composite measure of infant behavior was used as an initial examination of a potential relationship. Multiple behavioral constructs were included in the behavioral composite score for each infant, but direction of measurement was kept constant so that higher scores indicated more behaviors that served to increase the infant's proximity and interaction with the mother. It was important in this first examination to use a more encompassing composite behavioral measure to provide initial evidence for a previously unexamined relationship between infant behaviors and brain responses to the mother.

Under Bowlby's (1969/1982) theories of attachment behavior, infants' early behaviors such as visual regard and visual search and distress during separation are all solicitous behaviors in the infant's behavioral repertoire that function to elicit and maintain close contact with the caregiver. In addition, work on eye gaze and eye contact has demonstrated the importance of these behaviors for the infant and the mother-infant relationship in the first year. Therefore, individual differences in the production of these behaviors may be uniquely related to ERP responses to the mother's face and a stranger's face. Study two (Chapter III) is focused specifically on these behaviors that are of particular theoretical importance for infants at six months in interactions with the mother. This chapter focuses on infant visual search and distress behavior when the mother is absent, and infant visual attention/eye gaze with the mother when she is present. These behaviors, in particular, are theorized to be very important for an infant at six months who has relatively limited behavioral resources available with which to signal and interact with the mother. Therefore, these behaviors are hypothesized to correlate specifically and distinctly with the neural responses to the faces.

By the toddler years, most children have a firmly established relationship with and representation of their caregiver and are beginning to become more interested in learning about new social partners. Research on the developmental progression of the mother-child relationship has demonstrated that between the ages of 6 and 24 months, infants and young toddlers are upset at separation from their mother (or primary caregiver) and seek to maintain close proximity with her, especially following a separation (Cassidy & Shaver, 1999). In contrast, by 36 months of age children are less distressed by brief separations, and are especially tolerant of separations from the mother in the presence of a friendly adult. By 48 months toddlers can separate easily from the mother, especially when they are prepared by a discussion with her before separation occurs (Marvin & Britner, 1999). Therefore, the mother-child relationship begins to serve a new purpose for toddlers between 24 and 48 months of age and other people become increasingly more interesting. It has been proposed that experience in social interactions and changes in social behaviors may be related to changes in brain areas involved in social development (e.g. Greenough, Black, & Wallace, 1987; Ainsworth, 1989; Carver et al., 2003). If social-emotional behavioral changes seen in the toddler years can be related to brain function, the changing role of the primary caregiver should be apparent in developmental changes in neural correlates of cognitive and social responses to her (Carver et al., 2003).

Study three (Chapter IV) of this dissertation presents a study aimed at investigating this hypothesis in a narrower age range of toddlers than have been examined before. The study by Carver and colleagues (2003) found that responses to mother and stranger faces varied as a function of age in a sample of 18- to 54-month-olds. While the younger and older children in their sample showed opposite patterns of neural responses to the two faces, of particular interest is the middle age group (24 to 45 months) in their sample, who showed no difference to the two faces. This suggested to Carver and colleagues (2003) that this may be a particularly transitional age range, not only in neural responses to the mother and stranger faces, but perhaps also in behavioral manifestations of the mother-child relationship. Therefore, study three (Chapter IV) of this dissertation was conducted with toddlers in the middle age range tested in the Carver and colleagues study. This age range was shortened to span one year (28 to 40 months of age) in order to examine more closely any potential age-related changes in face processing that might be present in this middle group. In addition, toddler behaviors during interactions with and separations from their mother were measured and a potential relationship between differences in behavioral responses and neural responses to faces was examined. Following the hypothesis that this age represents a more transitional age in the mother-child relationship and the face processing system, significant individual differences were expected. However, the relative importance of maintaining close proximity and interaction with the mother and interest in a new adult is hypothesized to be changing across this age range. While there is little doubt these changes will be reflected in the toddlers' behavioral responses, of particular interest is whether the change in behavioral responses will be related to changes in neural resources devoted to processing her face and a stranger's face.

The work contained in this dissertation addresses a void in the developmental literature that, until recently, has been relatively untouched. Although a great deal of developmental research has focused on neural development and behavioral development separately, little work has examined change and continuity at the interface of these two areas (Nelson, 1999). This task is an important and inherently challenging one. While inferring neural processes solely from behavior is problematic, it is also difficult to relate specific behaviors to the numerous changes occurring simultaneously in neurobiological systems (Nelson, 1999). Despite the challenges, this work is important to attempt because it will eventually provide us with a stronger theory of a brain-behavior relationship in development. Nelson (1999) suggests that given the numerous tools that exist in the neurosciences for examining brain function in the developing child (e.g. electroencephalogram, event-related potentials, fMRI), researchers are now in a position to be more precise than in describing the neural events that may underlie behavior. Therefore, he suggests a need to examine changes in the brain at the same time as we examine changes in behavior, and in so doing we may relate changes in underlying neurobiology to changes in behavior (Nelson, 1999). The studies presented in this dissertation make use of Nelson’s suggestions and measure changes in behavioral responses and changes in neural responses in infants and toddlers at transitional ages in the mother-child relationship. Work like this has the potential to provide evidence of continuity in behavioral and neural change in what is perhaps the most important relationship for an infant and young child.

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Chapter II

Relations Between Mother-Child Interactions and the Neural Correlates of Face Processing in 6-Month-Olds

Abstract

Developmental studies of face processing have revealed age-related changes in how infants' allocate neurophysiological resources to the face of a caregiver and an unfamiliar adult. We hypothesize that developmental changes in how infants interact with their caregiver are related to the changes in brain response. We studied six-month-olds because this age is frequently noted in the behavioral and neurophysiological literature as a time of transition in which infants begin to discriminate more readily between caregivers and unfamiliar adults. We used infants' behavioral responses to an original behavioral paradigm to predict event-related potential (ERP) responses to pictures of the mother's face and a stranger's face in the same group of participants. Our results suggest that individual differences in infants' proximity seeking behaviors during interactions with the mother correlate with their neurophysiological responses to the mother's face as opposed to an unfamiliar face for the Nc component of the ERP. These results have implications for understanding the role of the changing infant-caregiver relationship on the development of the face processing system in early infancy.

Relations between mother-child interactions and the neural correlates of face processing in 6-month-olds

Infants' face processing abilities appear to undergo significant developmental change during the first year of life. Infants' behavioral interactions with their primary caregiver(s) also change a great deal during this age range. In the current work, we investigated a possible relationship between the behaviors infants produce in response to the mother at six months and the neural correlates of processing familiar and unfamiliar faces in infancy.

Nature of early Face Processing

By 4 weeks of age, infants prefer looking at a schematic human face compared to other objects (McGraw, 1943; Wolff, 1969), colored shapes, or complex patterns (Fantz, 1961). Not only are infants able to differentiate between face and non-face stimuli early in life, but the face processing system requires little experience to discriminate between these two categories of stimuli. Newborns as young as 9 minutes old display greater tracking with head and eye movements to a schematic face than they do to a face containing either scrambled features or a blank head shape (Goren, Sarty, & Wu, 1975). Subsequent recent research demonstrated that a stimulus with a face-like configuration of isolated features alone was insufficient to elicit the same degree of eye tracking as schematic face stimuli (Johnson, Dziurawiec, Ellis & Morton, 1991; see also Cassia, Turati, & Simion, 2004).

Although it seems clear that infants are well equipped to respond preferentially to faces early in life, the developmental pattern of face processing becomes more complex with age and experience. From 3 to 7 months, the ability to distinguish mother from stranger becomes more robust and infants begin to categorize faces by gender and facial expression (Nelson, 2001). Experience-dependent face processing emerges during this time as well. Quinn, Yahr and Kuhn (2002) provided new evidence that infants' face processing skills are affected by the gender of their primary caregiver. Prior work suggested that, in general, infants appear to prefer looking at female faces over male faces (e.g. Leinbach & Fagot, 1993). Explanations for this phenomenon have suggested that there is something perceptually or evolutionarily special about the female face. However, Quinn and colleagues (2002) demonstrated that infants whose primary caregiver was male showed a spontaneous visual preference for male faces rather than female faces. This study provided evidence that infant's interactions with their caregivers early in development shape how they process and differentially respond to faces.

Neural Correlates of Early Face Processing

Event-related potentials (ERPs) have been used in a growing number of developmental studies as an index of the neural response to faces in infancy. ERPs are measures of brain electrical activity in response to pre-specified discrete events, such as the presentation of a face, and are advantageous for use with infants because the method is a non-invasive and objective measure of brain function. The amplitude of the ERP response is thought to reflect a summation of neural activity in which greater absolute amplitude reflects greater neural activation in response to a stimulus. In addition, because the ERP method requires no behavioral response on the part of infant participants, it can provide valuable information where behavioral measures cannot. For example, in a study that included both a visual preference test of recognition and an ERP response measure of face processing, looking time proved to be a less sensitive measure of face processing than brain response (de Haan & Nelson, 1997). Six-month-olds' looking time did not differ for the mother's face and a stranger's face, despite the fact that the amplitude of the ERP response was significantly different for the two.

An ERP component that has consistently been associated with face processing in infants and young children (see de Haan & Nelson, 1997, 1999, de Haan, Pascalis, & Johnson, 2002, Halit, de Haan, & Johnson, 2003) is the Nc component. The Nc component is a middle-latency negative component that is maximal over central frontal electrodes and has been associated with increased attention, particularly to salient (Nelson, 1994) or novel stimuli (Courchesne, Ganz, & Norcia, 1981, Reynolds & Richards, 2005), and with recognition memory (e.g. de Haan & Nelson, 1997, 1999; Nelson, 1994). De Haan and Nelson (1997) showed that 6-month-olds' Nc component activity differentiated both a dissimilar and similar looking stranger's face from their mother's, and that the neural activity exhibited in these two conditions differed in morphology. In contrast, the same component failed to distinguish between two stranger's faces, regardless of similarity between the two, and even when the infants' were first familiarized with one of the faces. This suggests that different higher-order cognitive processes beyond novelty detection are activated to process a familiar and unfamiliar face as opposed to two unfamiliar faces, and that the Nc component is a sensitive measure of these processes. From these results it is clear that perceptual similarity between two faces influences the morphology of the Nc component, but only if one of the faces is already meaningful for the infant (de Haan & Nelson, 1997).

Finally, the amplitude of the Nc component in response to the mother and a stranger has been shown to vary with age and developmental stage. Research with older children revealed age-related changes in brain activity to the mother's face versus a stranger's face (Carver, Dawson, Panagiotides, Meltzoff, McPartland, Gray & Munson, 2003). ERPs measured in a cross sectional sample of infants aged 18 to 54 months in response to pictures of the mother's face and a stranger's face revealed that the youngest group showed larger Nc activity when viewing pictures of the mother's face. The oldest group showed a larger Nc response to the stranger's face, while the middle group showed no significant difference between faces. The authors suggested that these developmental differences in the brain response to the faces might have occurred because infants' interactions with their caregiver were also changing dramatically across this age range.

The nature of the child-caregiver relationship may have an effect on the relative salience of the faces of the primary caregiver and an unfamiliar social partner. From a neuroscience perspective, this suggestion is plausible since it is expected that brain systems recruited to respond to social stimuli would change as children progress through social and cognitive developmental stages. New evidence from a recent ERP study provides further evidence that as the infant-caregiver relationship changes, so does the pattern of brain response infant's show to familiar and unfamiliar faces (Webb, Long & Nelson, 2005). This longitudinal study followed infants from 6 months through one year and showed that the pattern of processing the mother's face and an unfamiliar female's face reversed between 6 and 8 months and became larger to the stranger's face. This pattern of processing stays stable at least through 12 months (Webb et al., 2005). The reversal between 6 and 8 months is precisely when the behavioral literature proposes that the infant begins to show a strong behavioral preference for the caregiver.

The Infant-Caregiver Relationship and Neural Correlates of Face Processing

Most of the prominent current models of the development of face recognition (see de Schonen & Mathivet, 1989; Pascalis & de Schonen, 1994; Pascalis, de Schonen, Morton, Derulle & Fabre-Grenet, 1995; Morton & Johnson, 1991, Johnson et al., 1991, and Johnson & de Haan, 2001) suggest that the development of face processing after the first few months depends heavily on experience (Nelson, 2001). The experience of interacting in significant relationships, such as the infant's relationship(s) with primary caregiver(s), may be particularly important for the developing system, and is not included in the scope of these models. In the current study, we hypothesized that the experience-dependent developing relationship between the infant and the primary caregiver would concurrently influence the emergence of the infant's behavioral and visual preferences for the mother and would also be evidenced in the brain response to her face and a stranger's face during the ERP paradigm.

Literature on the development of the visual system during the first year lends support for the idea that visual experience with the caregiver could be a common component influencing the development of both the face processing and social behavior systems. Marvin and Britner (1999) note that at or very soon after birth, infants respond to stimuli in a manner that increases the likelihood of continued contact with others. Soon after birth, most infants are capable of visual orientation and tracking and are especially responsive to contour and pattern. This is perhaps why the visual system, more so than other sensory systems, is especially important in the development of the behavioral discrimination between the primary caregiver(s) and strangers that typically developing infants reliably show in the first year. Importantly, changes in the visual system co-occur with changes in infants' attention to and preference for faces that are thought to be an important foundation and indicator of the developing infant-caregiver relationship (Marvin & Britner, 1999).

One theory presented in the literature is that an innate interest in faces aids in the formation of a close infant-caregiver relationship by fostering a reciprocal relationship between mother and infant in the first year. The developing relationship may be facilitated by the infant's attention to the caregiver who in turn offers more security and nurturance (Ellis, 1992). Bowlby hypothesized in his theory of attachment that the mother must simply have stimulus characteristics that elicit proximity seeking behaviors from the infant (Bowlby, 1969). The logic of this theory is that it is adaptive for the infant to quickly and accurately recognize primary caretakers and, ultimately, any emotional signals communicated by the caregiver's face (Nelson, 2001). This model of the development of the infant-caregiver bond requires that the infant possess an internal working representation of the mother, established over the course of early experiences with her, as a prerequisite to establish this bond with her. During the early formation stages of the relationship, which coincide with the infant's extreme dependency on the caregiver, the infant would need to allocate more attentional resources to faces, and specifically to the mother's face, in an attempt to clearly identify and engage her every time she is in close proximity.

This model fits well with both the behavioral and neurophysiological evidence on infant response to familiar and unfamiliar faces early in the first year. At three months infants show differential behavior in response to their mother compared to an unfamiliar female stranger (Bronson, 1972; Turnure, 1971; Wahler, 1967). As early as two months of age infants show more distress behaviors in response to the departure of the mother than a stranger, yet this behavioral discrimination disappears if infants are first familiarized with the stranger for a ten-minute period (Fogel, 1980). By six months infants have built upon early distress and response behaviors and are able to produce more sophisticated behaviors likely to increase and maintain a close proximity and interaction with the mother. The question of interest here is how the behavioral changes in the first year that result in a marked behavioral preference for the primary caregiver correlate with the infant's neurophysiological discriminations between the primary caregiver and an unfamiliar adult before this bond is reliably present.

Current Study

Six-month-olds were chosen based on past research suggesting that this age marks the beginning of a behavioral preference for the child's primary caregiver(s) (e.g., Ainsworth, 1967; Bowlby, 1969/1982; Marvin & Britner, 1999). In the current research, we observed infants' interactions with their caregiver at six months during a series of short separations and reunions with her. We then measured infants' brain activity in response to pictures of their mother and a dissimilar-looking stranger.

Based on findings from the cross-sectional (Carver et al., 2003) and longitudinal (Webb et al., 2005) ERP work that found developmental change in the brain response to mother and stranger faces, we expected to find differences in the ERP response to faces that correlated with change in behaviors infants showed in response to the mother. The prior work has suggested the hypothesis that changes in the brain response to the mother and a stranger are related to developmental change in the nature of the mother-child relationship. Both studies found a reversal in the Nc response, i.e. a larger response to the stranger than to the mother, across ages that are hypothesized to be transitions in the developing infant-caregiver relationship. These results suggest that during times of transition in the infant-caregiver relationship, infants and toddlers allocate more attention to social stimuli that are outside of the infant-mother dyad.

Due to the nature of a developmental transition, infants in this process should show individual differences in the behaviors they produce during separations and reunions with the mother. We therefore expected to find that some infants would exhibit very few proximity and interaction seeking behaviors while other infants would exhibit very many, with the large majority falling somewhere in the middle. Individual differences in behaviors exhibited could then be correlated with the brain response to the two categories of faces, in order to directly test the hypothesis that changes in infant-mother dynamics of interaction are related to the developmental 'reversal' in the Nc response that becomes larger to the stranger than the mother, seen in previous work. We used individual differences in the infant's behaviors in response to the mother as an index of the changing nature of the mother-child relationship. Infant behaviors were correlated with infant neurophysiological responses to the mother and a stranger to investigate the influence that the mother-child relationship may have on the infant's developing neural system for responding to social stimuli. The aim of the current work is to provide new information about factors that may contribute to the neurological 'fine-tuning' of the face processing system that are often discussed in the face processing literature (e.g. Johnson & de Haan, 2001; Nelson, 2001).

Methods

Participants

The final sample of participants consisted of 30 full term, neurologically healthy six-month-olds ranging in age from 173 days to 191 days, with a mean age of 183.4 days (6.1 months). All of the infants were recruited from an existing list of parents who had volunteered to participate in research after being contacted by mail following the birth of their child. The majority of the children were Caucasian. Of the non-Caucasian participants, 3 were Hispanic, 2 were Asian, and 2 were African American. The children were primarily from middle-class homes and evenly split by gender, 16 were male and 14 were female. Families were given a small toy for the infant and a printout picture of the infant wearing the electrode cap as a thank-you for participating.

An additional 25 infants were tested but were not included in the final sample either because they did not provide interpretable ERP data, or because an error occurred during testing: 18 infants did not provide enough artifact free data for both conditions, 5 infants did not cooperate with the testing procedure, one mother talked throughout the ERP testing session, and one child's data was lost due to experimenter error. This attrition rate is the same as or lower than rates for other ERP studies conducted with a same or similar paradigm using this age group (e.g. de Haan & Nelson, 1997; de Haan et al., 2002).

Stimuli

Each child's mother was photographed with a color digital camera from the neck up against a light grey background. Mothers wore the same grey scarf in the picture to obscure the neck and clothing. Earrings and other jewelry were removed, but mothers that wore glasses were instructed to leave them on. Mothers assumed a neutral facial expression for the photograph. The image of the mother's face was matched with another mother based on a fixed set of rules. The experimenter selected the unfamiliar face stimulus so that paired faces were of the same ethnicity and faces of mothers who wore glasses were paired together. Otherwise, paired faces were chosen to be dissimilar in terms of hair color, face shape, eye color and facial features. Pictures of mothers were imported into Adobe Photoshop and standardized so that they all measured 18 (+/- 1) cm from the top of the head to the chin and 11 (+/-1) cm from ear to ear, and were of the same digital resolution and quality.

Behavioral Procedure

The behavioral portion of the study used an original paradigm designed to elicit and allow for observation of infant behaviors in response to the introduction of an unfamiliar adult, and two separations and reunions with the mother. The entire procedure was approximately 7 minutes long and was videotaped and later coded for behaviors exhibited by the infant. This behavioral paradigm was designed to illuminate infants' behavioral attempts to increase interaction and proximity with the mother both during and after separations from her. We structured the behavioral procedure to maximize the likelihood that it would elicit maternally focused proximity-seeking behaviors from the infant without stressing the infant unnecessarily. The behavioral assessment and coding were designed to emphasize the presence or absence of specific behaviors produced by the infant during separations and reunions with the mother that would result in increased interaction and proximity between mother and infant. Our goal was *not* to measure the quality of these behaviors.

Before the behavioral procedure began, the first experimenter acquired consent from the mother while the child sat on the mother's lap or played on the floor. The experimenter then took the mother's picture against the grey background and afterward signaled the experimenter in the adjacent camera room that the session was ready to begin. The first experimenter remained in the testing room until the first minute of the session was over. At commencement of the testing session the mother was instructed to sit wherever she was most comfortable, either on the floor or in a chair, and interact with her infant as she normally would. The entire session was videotaped with one camera focused on the infant and a second focused on the mother. See Table 1 for a detailed description of the behavioral procedure.

Behavioral Coding

Coders reviewed the recordings of the behavioral sessions and assessed infants' proximity-seeking behaviors toward their mothers. Two coders watched and coded behavioral session tapes for the infants. The first author trained coders until they reached 88% reliability with her. Both coders coded 25% of the subjects for the purposes of measuring reliability. Coding pairs achieved 87% reliability for the data on which they overlapped in this report. Coders were blind to the specific study hypotheses, and had no knowledge of the infants' ERP data or results.

Table 1 details the intervals of the behavioral procedure. To increase precision of coding, each of these intervals was further separated into 15-second segments. For each 15-second segment of intervals where the mother was not present (4 & 6), coders rated the following infant behaviors: overall affect, distress/attempts to locate mother, amount of looking for mother, and exploratory behaviors. Coders rated overall affect on a 1-5 Likert-type scale, where 1 indicated overall negative affect (e.g. clear indication of distress) and 5 indicated overall positive affect (e.g. laughing). Amount of looking for mother was also rated according to a 5-point scale, where 1 indicated that the infant did not look for mother at all, and 5 indicated that the infant looked for mother the entire 15 seconds. Distress/attempts to locate mother and exploratory behaviors were coded as they occurred as discrete yes/no decisions, and were summed within each 15 second segment. Distress/attempts to locate mother included crying, arm flailing or wiggling, looking for mother or head turning toward door, reaching for mother, and attempting to move toward mother's last location. Exploratory behaviors included reaching for toys, moving toward toys, holding toys, mouthing toys, manipulating toys with hands, and rolling, kicking, arm movement, crawling/scooting, or vocalizations relating to exploration.

For each 15-second segment of intervals where mother was present (1-3, 5, 7), coders assessed infants' overall affect, reaction to mother, distress/attempts to locate and interact with the mother, amount of looking at mother, proximity to mother, and exploratory behaviors. Overall affect and exploratory behaviors were coded in the same way as they were for separation intervals. Coding of distress/attempts to locate and interact with the mother during segments with mother present included additional behaviors of holding arms up, clinging to mother, burying face, calming, and smiling. Amount of looking at mother was coded on the same scale used for amount of looking for mother during separation episodes. Reaction to mother was coded on a 5-point scale, where 1 indicated withdrawal and 5 indicated responding to mother and initiating interaction with her. Proximity to mother was also coded on a 5-point scale, where 1 indicated mother holding the infant, and 5 indicated at least 4 ft of space between mother and child.

Behavioral Composite Measure

Coded information from only separation and reunion intervals (4 & 6, 5 & 7, respectively) was used to create a composite measure of mother-directed proximity-seeking behaviors, as it was hypothesized that the strongest and most reliable evidence of this construct would be apparent during separations from and reunions with mother.

As a first step toward composite creation, each measure was averaged across the 15-second segments in each interval, and measures were averaged across interval type. The result was a set of 4 separation measures and 6 reunion measures. Measures were reflected, if necessary, so that lower values would indicate lower levels of proximity-seeking behavior. The distress/attempts to locate mother and exploratory behaviors measures were also adjusted to fit a 5-point scale. These 10 measures were then averaged to create the overall mother-oriented proximity-seeking behavior composite, with higher values indicating more proximity-seeking behavior toward mother. Scores on this composite measure ranged from 2.31 to 3.30; the average score was 2.67 (SD= 0.19).

Event-related potential (ERP) testing

Upon completion of the behavioral session, the ERP testing began in another room where a third experimenter was present. The circumference of the child's head was measured and the vertex was marked. An appropriate size 32-channel electrode cap (Electro-Cap International) was placed on the child's head and fitted according to the manufacturer's specification. Event-related potentials were recorded from the 31 active channels placed according to the international 10/20 system of electrode placement. The following standard electrode sites were used: Pz, Fz, O1, O2, P3, P4, T5, T6, C3, C4, T7, T8, F3, F4, F7, F8CPz, FCz, CP5, CP6, CP1, CP2, FC1, FC2, FC5, FC6, FP7, FP8, AF7, and AF8 (See Figure 1 for a schematic of electrode positions on the scalp). Electrode gel was placed into each of the 32 electrodes and impedance measurements were recorded prior to testing. Scalp impedances were measured before and after testing and were always kept below 10 kilo-ohms. The mean scalp impedance before the testing procedure was 6.33 kilo-ohms, SD= 2.74 kilo-ohms. The mean of the post testing impedance measurements was 4.45 kilo-ohms, SD= 3.42. Upon entry to the ERP testing room four additional electrodes were manually placed around the infant's eyes for EOG measures of eye movements and blinking. Two electrodes were placed at the outer canthi of the eyes and two electrodes were placed above and below the right eye. Impedance measurements were also taken and recorded from these four electrodes prior to, and immediately following testing. EOG impedances were ideally kept below 30 kilo-ohms, however this goal was sacrificed if the infant was becoming fussy or impatient with the testing procedure. Average impedance measurements for the Horizontal eye electrodes were 57.05 kilo-ohms before testing and 39.90 kilo-ohms after testing. Average impedance measurements for the vertical eye electrodes were 60.88 kilo-ohms pre-test and 31.94 kilo-ohms post-test.

Testing for all children took place in the same sound attenuated and electrically shielded room. During the testing session the child sat on the mother's lap approximately 70 cm from the computer screen that delivered the stimulus. Mothers were instructed to remain as quiet as possible during the entire ERP testing session. A large, trifold grey partition obscured the back of the monitor and part of the room from view. Infants saw the pictures of their mother and a stranger displayed on the computer screen through a window in the partition. There were cracks between the panels of the partition through which an observer watched the infant and signaled the computer via button press if the infant was not attending to the stimuli. If needed, the observer shook a rattle or squeaked a toy behind the computer screen during the inter-trial interval to attract the infant's attention to the pictures. Each trial consisted of a 100-ms baseline and 500-ms presentation of the stimulus, followed by a 1200-ms post stimulus-recording period during which the computer screen was blank. Trials were separated by an inter-trial interval that varied in duration between 500 and 1000 milliseconds. The order in which the stimuli were presented was randomized across infants. Data collection was terminated when the child had seen all of the 100 trials (50 of the mother and 50 of the stranger) or when the child was no longer tolerant of the testing procedure. Trials on which the child did not attend to the stimuli or during which the experimenter was attempting to attract the child's attention were removed after data collection.

EEG Recording

EEG recording was conducted continuously from all thirty-two electrode channels. The signals were amplified and filtered through a .1 Hz high-pass filter and 100 Hz low-pass filter. The EEG signals were amplified with a gain of 20,000 and EOG signals were amplified with a gain of 5,000. Data were recorded continuously, with a sampling rate of 284 Hz, and saved to a file in the computer-assisted scoring program (Instep) on the data collection computer. A second computer generated the stimuli and the two computers were interfaced via serial port for precise synchronization. The timing of the stimulus onset and offset was registered together with the physiological recorder for off-line segmentation of the data. Each infant's EEG data was referenced to Cz and re-referenced off-line to an average reference using the computer-assisted program.

ERP Reduction

After testing, each infant's ERP data were edited off-line. Trials in which the child did not attend to the pictures were excluded from the data set. In addition, any channels in which the EEG signal amplitude exceeded 250 μV were excluded from the trial as artifact. Any trials in which EOG artifact occurred, i.e. eye blinks or large eye movement, were also excluded. Additional artifact was rejected when values exceeded A/D values, which results in clipping (flat-lining of the signal from the amplifier), and upon visual inspection. Data from any trials in which more than 4 channels met criteria for exclusion were not included in the final data set. Only subjects with more than 10 artifact free trials in each face condition were included in the final sample. The mean numbers of artifact free trials of each condition included in the final data set were not different from one another (Mother condition M = 23.48, SD = 9.15; Stranger condition M = 23.03, SD = 8.98). Grand averages of the ERP data were computed across subjects for visualization purposes.

ERP Measures

Grand mean ERP waveforms for all six-month-olds are displayed in Figure 2. Components of interest were identified based on previous research findings (e.g., de Haan & Nelson, 1997, 1999) and upon inspection of the grand-averaged data for each condition. The component analyzed for this study was a middle-latency negative component (Nc, see de Haan & Nelson, 1997, 1999) distributed over frontal electrode sites (other components were noted in the data, but did not show significant relations behavior and therefore are not reported here). The Nc component was defined as the maximum negative peak occurring between 230 and 1230 ms[1]. This time window was determined by examining the data for each individual participant and selecting a window that captured the peak of the component for each participant. A computer-assisted program calculated the peak amplitude and latency within this window for each subject. The electrodes over which we analyzed the components were determined by selecting those electrodes at which the waveform morphology was prominent, and by using electrode sites comparable to those used in previous research.

Results

Repeated-measures ANOVAs were conducted to determine if mother-oriented proximity-seeking infant behaviors, mother/stranger face processing, and electrode location (lead) had an impact on amplitude and latency of the Nc component. Effect size, as indexed by partial eta-squared (η_p^2), are reported for ANOVA effects where appropriate. Partial eta-squared is a commonly used estimate of strength of association because it is not dependent on number or magnitude of other effects in the model.

Two separate Nc analyses were conducted; one including only midline leads, and one including only lateral leads. Lateral leads were analyzed separately by hemisphere to enable detection of potential hemisphere effects on face processing. Nc midline leads included in analysis were Fz and FCz, while lateral leads included were fronto-central leads FC1/FC2 and FC5/FC6, and frontal leads F3/F4.

Amplitude and latency were analyzed separately. Analyses of latency effects yielded no significant results, and for that reason are not described further. For amplitude of the Nc component, more negative amplitudes are indicative of a larger brain response.

Midline Leads

A repeated-measures ANOVA was conducted to determine if FACE, LEAD (Fz vs. FCz), and mother-oriented proximity-seeking infant behaviors had an impact on amplitude of the Nc component. A significant LEAD effect indicated a more negative average amplitude for the FCz lead (M = -5.42, SE = .58) than for the Fz lead (M = -5.35, SE = .58), $F(1, 28) = 6.83$, $p = .01$, $\eta_p^2 = .20$. In addition, LEAD interacted significantly with infant behaviors, indicating that the relationship between amplitude and mother-oriented proximity-seeking behavior was different at FCz than at Fz, $F(1, 28) = 6.92$, $p = .01$, $\eta_p^2 = .20$. At the FCz lead, amplitudes of the Nc response were unrelated to infant behaviors ($b_1 = -0.72$, SE = 3.64). At the Fz lead, Nc amplitudes tended to become less negative as mother-oriented proximity-seeking behaviors increased ($B = 4.01$, SE = 4.26).

Lateral Leads

In this analysis, hemisphere was included as a potential effect; the FC1, F3, and FC5 leads provided data on Nc amplitudes in the left hemisphere, while FC2, F4, and FC6 provided data on Nc amplitudes in the right hemisphere. A repeated-measures ANOVA was conducted to determine if FACE, LEAD (FC1/FC2, F3/F4, FC5/FC6), HEMISPHERE (left vs. right), and mother-oriented proximity-seeking infant behaviors were related to amplitude of the Nc component.

Nc amplitudes resulting from viewing the stranger's face were significantly more negative (M = -5.11, SE = .43) than were amplitudes resulting from viewing Mother's face (M = -4.41, SE = .43), $F(1, 28) = 4.11$, $p = .05$, $\eta_p^2 = .13$. In addition, FACE interacted significantly with infant proximity-seeking behaviors, $F(1, 28) = 4.51$, $p = .04$, $\eta_p^2 = .14$. More mother-directed proximity-seeking behaviors were associated with larger Nc amplitudes when viewing the stranger's face, (B = -9.47, SE = 4.81), in comparison to viewing Mother's face, (B = 2.83, SE = 4.28).

A marginally significant interaction of FACE, LEAD, and HEMISPHERE emerged, $F(2, 56) = 2.63$, $p_{adj} = .08$, $\eta_p^2 = .09$, Huynh-Feldt $\varepsilon = .97$. Table 2 depicts means and standard errors for this interaction. In order to better determine the nature of this interaction, a series of post-hoc analyses were conducted, using Tukey-Kramer adjustments to preserve a family-wise $\alpha = .05$. First, Mother vs. Stranger face differences were examined within each lead and hemisphere. None of the Mother vs. Stranger comparisons achieved significance, $.24 \leq p \leq .99$. Next, reactions to Mother's face were compared with one another. At Lead 1 (FC1/FC2), average Nc amplitudes in response to Mother's face were significantly more negative in the left hemisphere than in the right hemisphere, $p < .001$. No significant hemisphere differences emerged at either Lead 2 (F3/F4) or Lead 3 (FC5/FC6), $ps \geq .45$. Within the left hemisphere, no significant differences between leads emerged, $ps \geq .23$. Within the right hemisphere, however, average Nc amplitude at F4 was significantly larger than the average Nc amplitude at FC2, $p = .002$. No other significant differences emerged within the right hemisphere, *ps* ≥ .27. Lastly, reactions to Stranger's face were compared with one another. No significant pair-wise differences emerged, either within lead, across hemisphere, or within hemisphere across lead, .30 ≤ *p* ≤ .99.

The relationship between infants' mother-directed proximity-seeking behaviors and Nc amplitude differed with marginal significance across FACE X LEAD X HEMISPHERE groups, $F(2, 56) = 2.95$, $p_{adj} = .06$, $\eta_p^2 = .10$, Huynh-Feldt $\varepsilon = .97$. Table 3 includes slope estimates and standard errors for each of these groups, as well as results of significance tests for each slope estimate. At F3, amplitudes in response to Mother's face tended to become less negative as mother-directed proximity-seeking behaviors increased, $\eta_p^2 = .27$. At F4, amplitudes in response to Stranger's face tended to become more negative as mother-directed proximity-seeking behaviors increased, $\eta_p^2 = .10$. Scatter plots for each of these relationships are depicted in Figures 3 and 4, respectively.

In order to determine which slope estimates differed significantly from each other, potential interactions between proximity-seeking behaviors and FACE were tested within each LEAD X HEMISPHERE group, and potential interactions between proximity-seeking behaviors and HEMISPHERE were tested within each FACE and LEAD. Note that a positive slope between amplitude and proximity-seeking behaviors indicates a tendency for amplitude to become less negative as infant proximity-seeking behaviors increase, while a negative slope indicates a tendency for amplitude to become more negative as proximity-seeking behaviors increase.

First, analyses were conducted to determine if the relationship between infant behaviors and Nc amplitude differed according to Mother vs. Stranger face presentation. No significant Mother vs. Stranger differences in slopes were found at FC1, FC2, F4, or FC5, *ps* $\geq$ .25. At F3, the slope estimate for amplitudes in response to Mother's face was significantly more positive than the slope estimate for amplitudes in response to Stranger's face, $F(1, 28) = 5.29$, $p = .03$, $\eta_p^2 = .16$. At FC6, the slope estimate for amplitudes in response to Stranger's face was marginally more negative than the slope estimate for amplitudes in response to Mother's face, $F(1, 28) = 3.40$, $p = .07$, $\eta_p^2 = .11$.

Next, the relationship between infant proximity-seeking behaviors, HEMISPHERE, and Nc amplitude was assessed separately within Mother face presentations only. The relationship between infant proximity-seeking behaviors and amplitude of the Nc response was significantly more positive at F3 than at F4, $F(1, 28) = 8.0$, $p = .009$, $\eta_p^2 = .22$; no significant differences emerged between FC1 and FC2 ($p = .14$), or between FC5 and FC6 ($p = .32$). Within the left hemisphere, the relationship between infant proximity-seeking behaviors and Nc amplitude was significantly more positive at F3 than at FC1 [$F(1, 28) = 9.56$, $p = .005$, $\eta_p^2 = .26$] or FC5 [$F(1, 28) = 9.64$, $p = .004$, $\eta_p^2 = .26$], but slopes did not differ between FC1 and FC5 ($p = .59$). No significant differences in relationships between infant proximity-seeking behaviors and Nc amplitude were found in the right hemisphere, $.16 \leq p \leq .53$.

Lastly, the relationship between infant mother-directed proximity-seeking behaviors and Nc amplitude was assessed separately within Stranger face presentations only, using the same method as the Mother-only analyses. No significant differences in relationships among infant behaviors, HEMISPHERE, and Nc amplitude were observed, $.19 \leq p \leq .91$.

Discussion

These results provide new evidence for the role of individual differences in behaviors infants produced during interactions with their mother on the neurophysiological processing of mother and stranger faces. We found that individual differences in the proximity and interaction seeking behaviors infants produced during a behavioral task correlated with their Nc response during a subsequent face-processing task in a number of ways. Six-month-olds in the current study who showed more proximity and interaction seeking behaviors with the mother also showed a larger Nc amplitude response to the stranger's face relative to the mother's face that was similar to the reversal of the Nc seen in the previous work with older children. However, six-month-olds who showed fewer proximity and interaction seeking behaviors with the mother did not show the larger response to the stranger's face than the mother's face. This suggests that individual differences in infant behaviors may be indicative of a transition in the infant-caregiver relationship that also has an effect on how the infant allocates neurophysiological resources for processing the mother and an unfamiliar female. Transitions in the infant-caregiver relationship may therefore underlie the reversal of the Nc response seen in the previous studies and again in the current work. These results provide preliminary support for the hypothesis of a possible role for the changing infant-caregiver relationship on the 'reversal' of the Nc component response to mother and stranger faces seen in previous studies with infants and toddlers older than 6 months.

At lateral electrode sites, Nc amplitudes for all infants tested here were significantly more negative to the pictures of the stranger's face than to the pictures of the mother's face. However, with regard to our specific hypotheses of interactions between the amount of infant proximity-seeking behavior directed to the mother and ERP responses to the two faces, the significant condition by behavior interaction at lateral electrode sites provides the strongest evidence for the hypothesized relationship. Infants who produced more proximity and interaction seeking behaviors towards the mother during separations and reunions with her also had significantly more negative amplitude responses of the Nc component when viewing the stranger's face compared to the mother's face. Therefore, infants who displayed more behaviors likely to increase proximity and interaction with the mother, behaviors that may be indicative of a transition in the nature of the mother-child relationship, also showed the Nc component 'reversal' seen in the previous studies with older infants and young toddlers. This brain-behavior relationship was only present for the infants who showed more behaviors likely to increase proximity and interaction with the mother during the separations and reunions with her. This finding provides some preliminary support for the hypothesis that the Nc component becomes larger to the stranger's face than the mother's face with development. At least in part, the present results suggest that this change is related to the developing nature of the child's interaction with the mother rather than simply a developmental shift in the pattern of face processing.

One interpretation for the perhaps counterintuitive relationship between more behavioral proximity and interaction seeking with the mother and a larger response to the picture of the stranger's face lies in the proposed complimentary relationship (Bowlby, 1969/1982) between the attachment system and the exploratory system during infancy and toddlerhood. It is possible that during the first year of life, when the early formation of the infant-caregiver bond is taking place, behaviors preferentially directed to the mother are fewer, but in addition, the infant is still allocating more attention to the mother's face in the service of a developing relationship. While this process is being carried out, infants may not spontaneously show as many initiations of proximity-seeking and interactive behaviors with the mother, as they are still in the process of specifying to whom these behaviors should be directed and consolidating a bond with the primary caregiver. Yet, allocating more neurophysiological 'attention' to the mother's face may be one way that infants begin to learn to whom these behaviors should be directed to produce the desired response.

After the infant-caregiver relationship is established, the competing exploratory system (Bowlby, 1969) may become more active and infants may now be able to allocate more attentional resources outside of this relationship towards more exploration of their social world. This would account for the reversal in the Nc amplitude response to the mother and stranger faces between 6 and 8 months that continued to the end of the first year (Webb et al., 2005) and emerged again in older toddlers (Carver et al., 2003) and is consistent with our findings here. Infants who have entered the consolidation phase of the infant-caregiver bond may have a freedom to 'explore' other individuals of interest outside of this primary relationship, and therefore show a neurophysiological novelty preference for unfamiliar faces while showing more proximity-seeking and interaction-seeking behavior in response to the primary caregiver. Once a primary caregiver has been identified infant behaviors have a specific target likely to produce the desired response (e.g. increasing proximity, physical contact and attention to the infant) and meet the infant's needs. Therefore, fewer attentional and neurophysiological resources need to be allocated to the caregiver and the infant can now begin to allocate more attention outside of the infant-caregiver relationship and activate more of the exploratory system necessary for social and cognitive development.

A second facet of having identified the primary caregiver is that presumably this figure is now a very familiar stimulus that can be identified quickly and easily. This effect of familiarity may be what is reflected by less negative Nc response to the mother's face as mother-directed proximity-seeking behaviors increase in our sample of infants. The pattern of behavioral and neurophysiological responses seen in infants who produced more mother-directed proximity and interaction seeking behaviors, but showed a larger neurophysiological response to the stranger, can be seen as social exploration of the unfamiliar within the safe context of an established behavioral interaction with the primary caregiver. Infants who direct more behaviors to the mother presumably have also identified her quickly and easily before they produce behaviors that are likely to increase proximity and interaction with her.

Further examination of the relationship between behavior and ERP response revealed an even more specific pattern of interaction. A first interesting point to note is that the brain-behavior relationship occurred at different locations on the scalp depending on which face was presented. In follow-up analyses, at the left frontal site F3 the slope of the relationship between infant behaviors and infant brain response to the pictures was significantly more positive for the pictures of the mother's face than the stranger's face. This result indicated that as the number of proximity and interaction-seeking behaviors exhibited by the infants increased, the amplitude of the Nc response to the mother's face became smaller. In contrast at the analogous right hemisphere electrode site, F4, brain responses to the stranger's face became larger as the number of mother-directed proximity-seeking behaviors increased.

Follow-up tests considering the relationship between proximity-seeking behaviors and the ERP response to each face separately revealed a specific pattern for the mother's face only. Again, the relationship between proximity-seeking behaviors the infants produced and the brain response to the mother's face was significantly more positive at the left frontal electrode site F3 than at any other electrode site location within the left hemisphere, or across hemispheres. This relationship at the left frontal electrode site F3 was present in the mother condition *only*. There were no significant slope differences over the right hemisphere electrode sites for the response to the mother, and there were no significant differences in the relationships between infant behaviors and Nc amplitude responses to the stranger. In addition, in the analysis of ERP response to the two face conditions regardless of infant behavior, response to the mother's face was largest over the left frontal-central site FC1, compared to its right hemisphere analog, FC2. No such hemisphere or lead differences occurred for the response to the stranger's face. This finding is consistent with that of Carver et al. (2003), who found age related changes in toddlers in response to the mother's, but not a stranger's face. Taken together, these results suggest a possible preferential processing by the left hemisphere of the mother's face in general, but also for interactions between behaviors infants produced in response to the mother and their brain responses to pictures of her.

These results are reminiscent of previous work that has suggested a possible left frontal bias for brain and behavior interactions with regard to positive emotionality and response to positive interactions between mother and infant (Fox & Davidson, 1987; Dawson, Frey, Self, Panagiotides, Hessl, Yamada & Rinaldi, 1999; Dawson, Frey, Panagiotides, Yamada, Hessl, Osterling, 1999). Previous work using both EEG and neuroimaging methods in adults and infants has led to the conclusion that left frontal activity is related to processing positive emotion and right frontal activity is related to processing negative emotion (Davidson, 1984a, 1984b; Davidson & Fox, 1982; Fox & Davidson, 1986). More importantly, the relationship between the caregiver and infant has been shown to mediate this effect (Dawson, Klinger, Panagiotides & Hill, 1992; Dawson, Klinger, Panagiotides & Spieker, 1992) as well as infant brain response to faces depicting emotion (de Haan, Belsky, Reid, Volein, & Johnson, 2004). Comparison between the results of these studies and the current work is difficult because of differences in design and age of participants. However, because the mother's face is likely a positive stimulus for the infant, the results of the current study seem to fit with previous evidence for a possible left hemisphere bias for processing positive stimuli. In addition, the results suggest that behavioral responses to the mother may mediate infant brain responses when processing mother's and stranger's faces.

Six-month-olds produce relatively subtle behavioral responses and have few motor and behavioral resources at their disposal. The use of a composite score of infant mother-directed proximity-seeking behaviors allowed us to combine these subtle behaviors into a stronger index of behavior. In future work, we intend to separate the components of the infant behaviors to provide a clearer picture of the relationship between the emergence of behaviors hypothesized to be precursors to the developing attachment relationship and neurophysiological processing of faces. In addition, examining relations between specific behaviors and face processing may allow us to better understand exactly which of the many changes that occur in the first year in the infant's behaviors toward their primary caregiver most index changes in the infant's developing brain system for processing faces.

The present study has demonstrated a possible interaction between behaviors infants produce at 6 months that are associated with transitions in the ways that they interact with their mother, and the neural correlates of face processing. Future research is necessary to examine subsequent stages of the child-caregiver relationship, when the attachment bond is universally agreed within the field of attachment research to have been established. Of particular interest are children between the ages of 28 and 40 months who are moving out of the most conservative stage of the attachment relationship, in which the primary caregiver(s) alone is the target of the attachment behaviors, and into a broader social existence. In this stage children begin to take more extended trips away from the primary caregiver(s) and show more social interest in other adults and peers. The relationship between behaviors directed towards the mother as well as a new unfamiliar female during separations and reunions with the mother could be used in combination with measures of face processing of the mother and a stranger face during an ERP session. Studies like this may help elucidate changes in brain development moderated by changes in the attachment system, both of which coincide with age-related changes in behavior. We are currently conducting such a study in our lab with 28- to 40-month olds and their mothers.

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Footnotes

[1] This interval reflected baseline to baseline activity for each infant. Note that the actual peak of the Nc did not vary this broadly across infants. The average latency of the Nc component across infants was 688.23 msec. The latency ranged from 555.31 to 800.29 msec. This range suggests that the Nc likely reflected a similar physiological response across infants.

Chapter II, Table 1

Behavioral procedure

INTERVAL	TIME (Minutes)	ACTIVITY
1	0:00-1:00	Experimenter 1 (Familiar), Mother & Infant interact.
1	1:00	Experimenter 1 exits to the video room.
2	1:00-2:00	Mother & Infant play in the testing room.
3	2:00-2:15	Experimenter 2 (Stranger) enters testing room from the video room and stands by the door.
3	2:15-3:15	Experimenter 2 approaches infant & initiates play.
3	3:15*	As cued by Experimenter 1, Mother exits to the video room.
4	3:15-4:15	Stranger continues to interact with the infant, comforts if infant distressed.
5	4:15-5:15	Mother returns to the room and resumes interaction. Stranger exits to the video room.
6	5:15-5:45*	Mother exits again to video room, infant alone in the testing room for 30 seconds or until the infant becomes upset.
7	5:45-6:45	Mother returns to testing room and resumes interaction with infant for final minute.

* Experimenter 1 cues Mother from the video room over the headphones.

Chapter II, Table 2

Descriptive Statistics for FACE X LEAD X HEMISPHERE Groups

	Face			
	Mother		Stranger	
	M	*SD*	*M*	*SD*
Left Hemisphere				
FC1	-6.61	5.01	-6.00	4.38
F3	-3.66	5.12	-3.91	5.00
FC5	-3.76	4.17	-3.73	5.15
Right Hemisphere				
FC2	-1.63	4.64	-4.67	4.08
F4	-6.27	3.91	-5.76	4.06
FC6	-4.51	3.34	-6.61	6.09

Chapter II, Table 3

Estimates of the Relationship between Proximity-Seeking Behaviors and Nc Amplitude

	Face			
	Mother		Stranger	
	B	*SE*	*B*	*SE*
Left Hemisphere				
FC1	-4.54	5.01	0.59	4.44
F3	14.20**	4.44	-2.97	5.04
FC5	-2.23	4.21	-3.54	5.18
Right Hemisphere				
FC2	6.41	4.54	-1.31	4.12
F4	-3.57	3.90	-7.02*	3.89
FC6	2.83	3.34	-9.47†	5.91

**$p < .01$; *$p < .10$; †$p = .12$

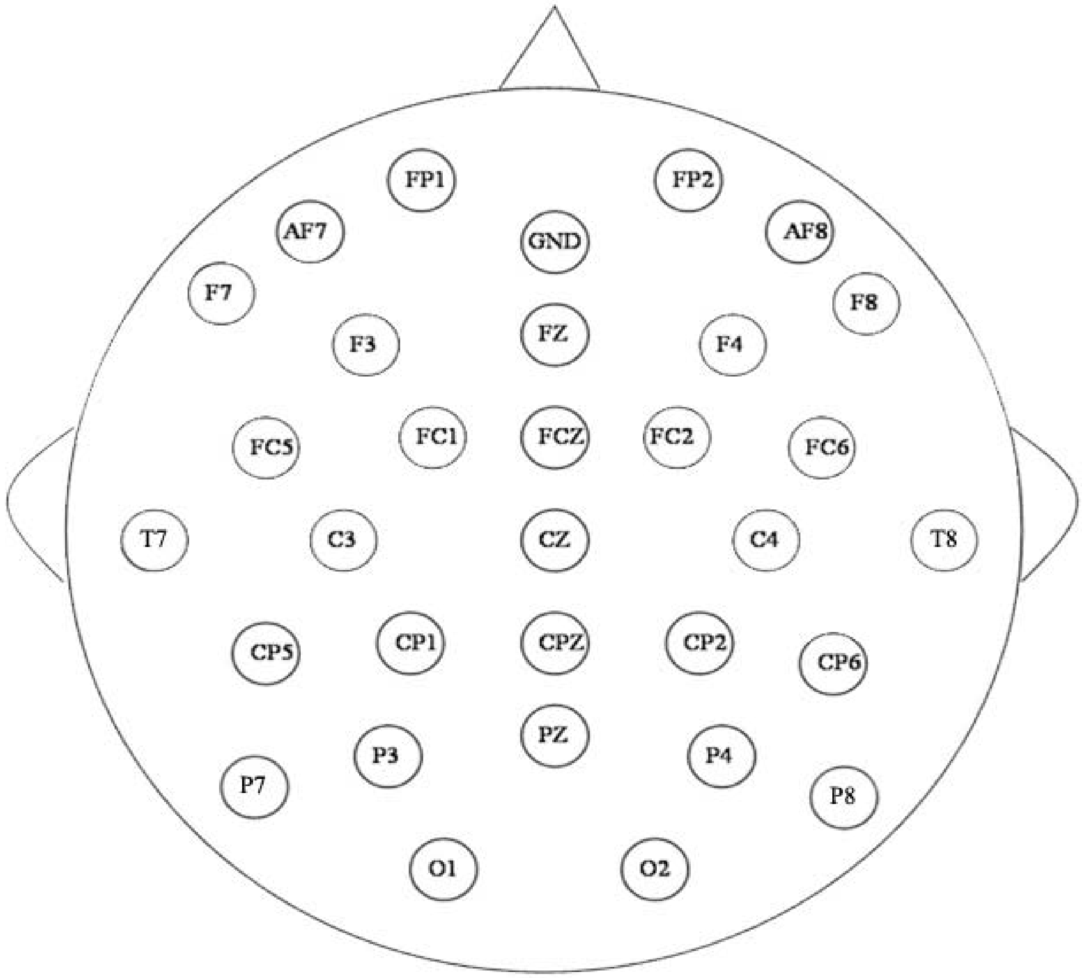
Figure Captions

Chapter II, Figure 1. Schematic of electrode locations on the scalp.

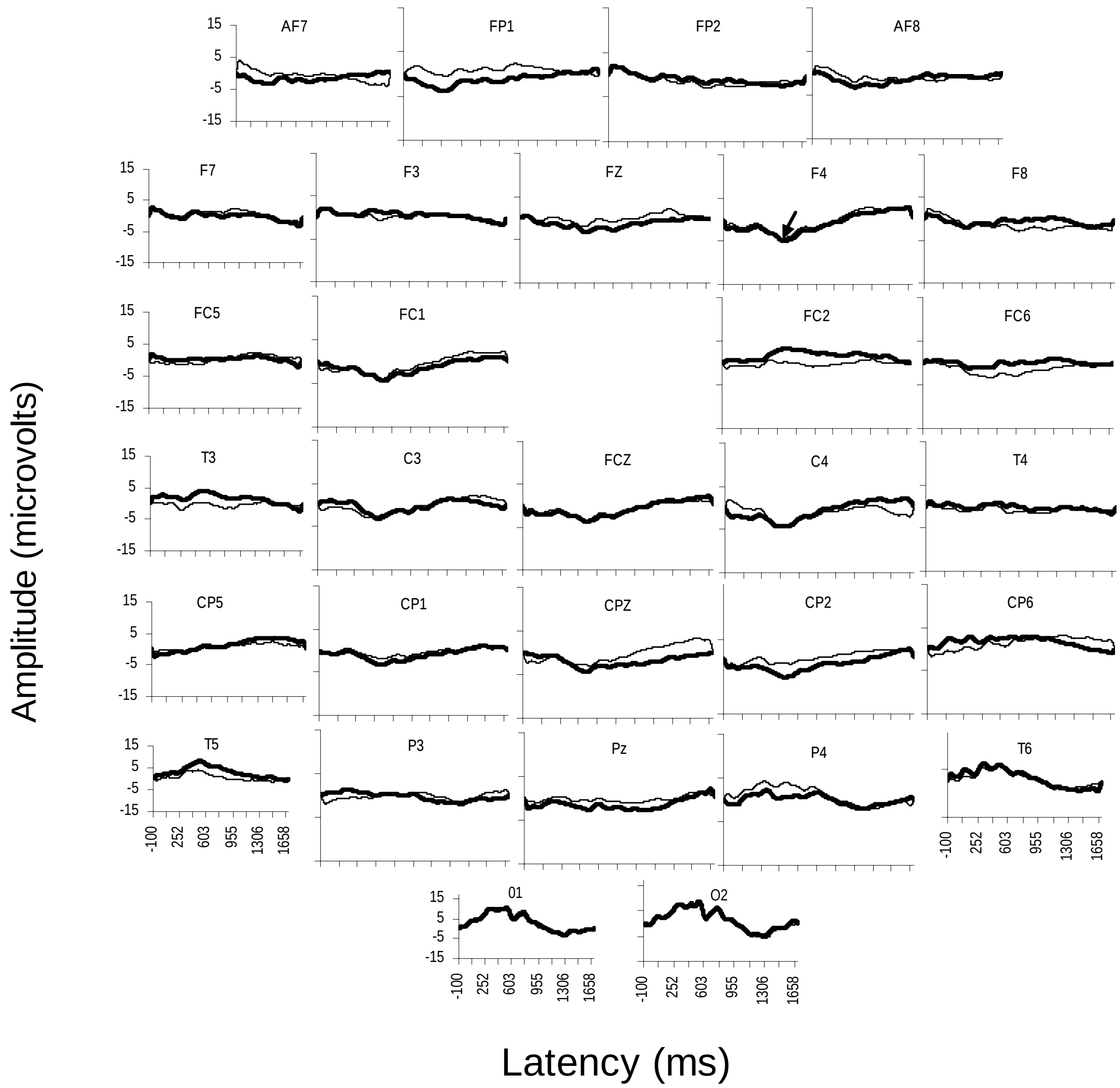
Chapter II, Figure 2. Grand Mean ERP response at each electrode averaged across subjects for both conditions. Thick black lines represent the mean waveform response to the picture of the Mother and thin lines are the response to the picture of the Stranger. Arrow at F4 lead points to the Nc component.

Chapter II, Figure 3. Relationship between Proximity-Seeking Behaviors and Nc Amplitudes in Response to Mother's Face at F3.

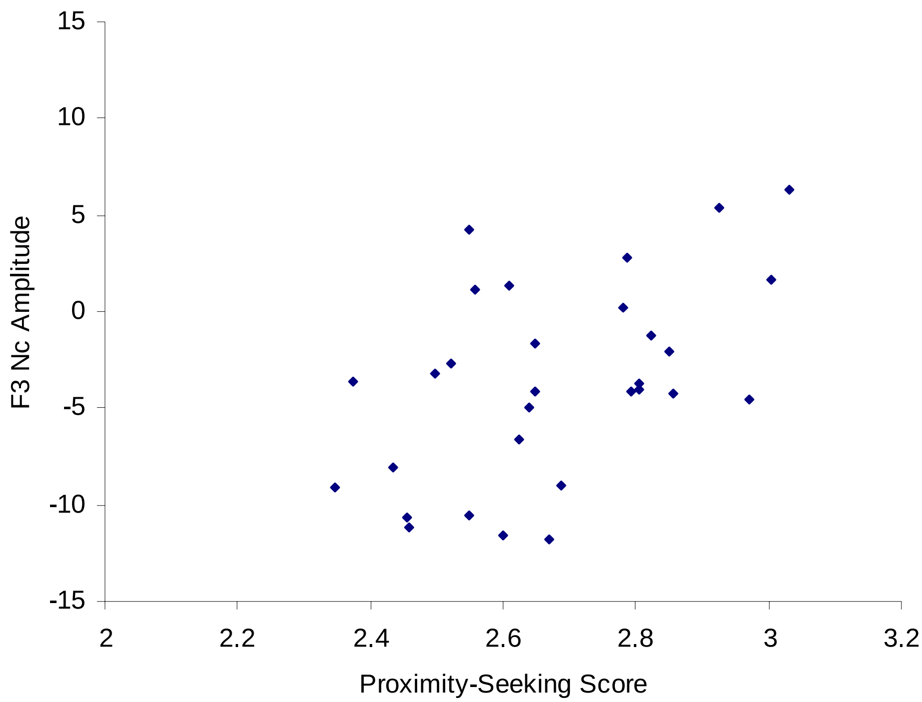
Chapter II, Figure 4. Relationship between Proximity-Seeking Behaviors and Nc Amplitudes in Response to Stranger's Face at F4.



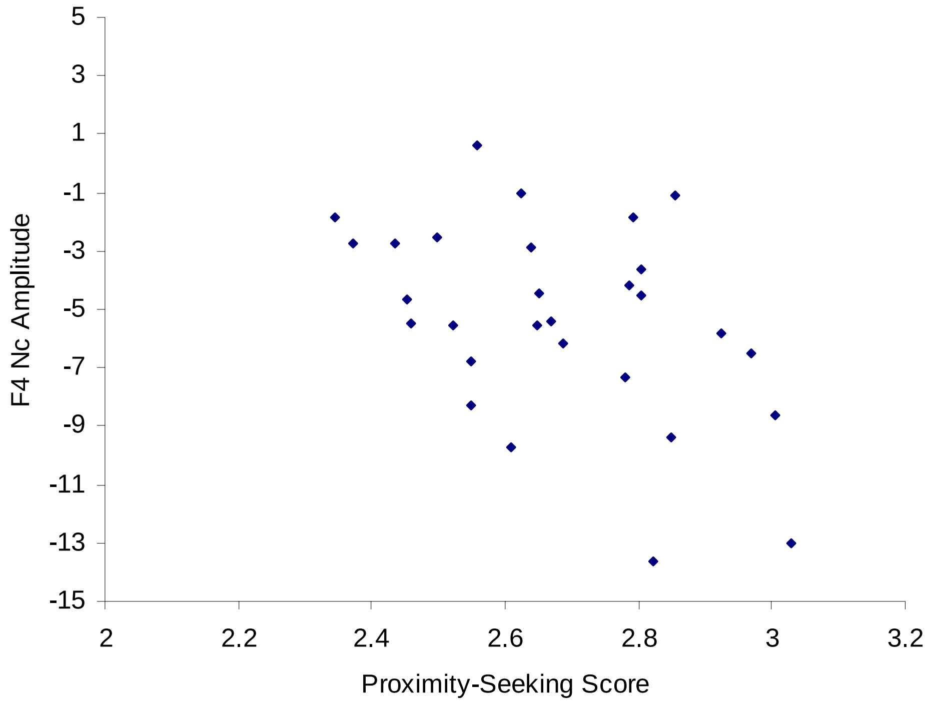
Chapter II, Figure 1. Schematic of electrode locations on the scalp.



Chapter II, Figure 2. Grand Mean ERP response at each electrode averaged across subjects for both conditions. Thick black lines represent the mean waveform response to the picture of the Mother and thin lines are the response to the picture of the Stranger. Arrow at F4 lead points to the Nc component.



Chapter II, Figure 3. Relationship between Proximity-Seeking Behaviors and Nc Amplitudes in Response to Mother's Face at F3.



Chapter II, Figure 4. Relationship between Proximity-Seeking Behaviors and Nc Amplitudes in Response to Stranger's Face at F4.

Chapter III

Brain-Behavior Correlations in the Development of the Mother-Child Relationship

Abstract

Event-related potentials (ERPs) were recorded from 6-month-olds (N=30) as they looked at pictures of their mother's face and a stranger's face. Negative component (Nc) and P400 component responses from the ERP portion of the study were correlated with infants' behavioral responses to their mothers during a series of separations and reunions with her. In the present study, we examined the relation between different caregiver-directed infant behaviors (visual attention to mother, visual search for mother when she was absent, and infant distress on separation) on infants' brain responses to pictures of the mother's face versus a stranger's face. These measures are important because they likely reflect the functioning of the emerging mother-child relationship, and inform debates about interactions between social experience and face processing. Infant distress on separation and visual search, measured as looking for mother on separation, were related to face processing ERPs, and this relationship differed across mother and stranger face presentations. In particular, distress behaviors were associated with larger amplitude responses to the mother's face in both components of the ERP. Visual attention, measured by looking at mother during interactions, related to the neural response to faces in different ways from the behaviors measured during separations. Implications for the developing mother-child relationship and face processing system are discussed.

Brain-behavior correlations in the development of the mother-child relationship

Current developmental theory acknowledges that aspects of a child's development are shaped by a cumulative experience of a co-constructed interactive process between parent and child. While this is likely the case in many domains of a child's development, this is particularly true with respect to the development of the child's relationship with primary caregivers (Hsu & Fogel, 2003; Maccoby, 1992; Sameroff & Chandler, 1975). To this end, research and theory on the development of the attachment relationship puts a special emphasis on the importance of early interactional experience between caregiver and infant (Hsu & Fogel, 2003). Indeed, it is the central tenet of attachment theory that the quality of infant attachment, most often measured at one year of life, is a reflection of the caregiver-infant interaction history (Ainsworth, Blehar, Waters & Wall, 1978). Work on the importance of coordination in parent-child interactions has led to the contention that moment-to-moment interactions between parents and children are the foundation for the development of long-term enduring relationships. Further, the quality of the resultant attachment relationship measured at one year and older is the result of these interactions and forms after the parent and child accumulate a history of interactions over time (Lollis & Kuczynski, 1997). Even infants as young as 3 months of age attempt to regulate their caregiver's behavior when confronted, for example, with a still-face manipulation (Cohn & Tronick, 1983; Tronick, 1980). Tronick (1989) proposed that the facility of infants to regulate their own and others' behavior is an important part of infants' emerging regulatory repertoire, and influences how infants interact with and respond to the emotions of their caregiver. These early interactions are thought by many theorists to lay an important foundation for later social and cognitive functioning. The purpose of the present study was to explore in detail the relation between the emerging caregiver-infant relationship and the brain organization underlying one aspect of social-cognitive functioning, namely, face processing.

Accumulated experience with a primary caregiver appears to play a role in the development of infants' face processing. A behavioral study by Quinn, Yahr, Kuhn, Slater and Pascalis (2002) provided important new information that infants' responses to faces are affected by the gender of their primary caregiver. Prior work had suggested that infants preferred looking at female rather than male faces (e.g. Leinbach & Fagot, 1993; Quinn et al., 2002). Explanations provided in the prior work for this phenomenon suggested that there is something evolutionarily "special" about female faces. However, Quinn and colleagues (2002) demonstrated that infants with a male primary caregiver showed a spontaneous visual preference for male faces rather than female faces. This finding was interpreted as evidence that infant interactions with caregivers early in development shape how they process, represent and differentially respond to faces.

Parker and colleagues (Parker, Nelson, & The Bucharest Early Intervention Project Core Group, 2005) measured ERP correlates of face processing in a control group of non-institutionalized children and a group of children raised in Romanian orphanages. The Romanian orphanage environment has been established as a generally impoverished care-giving environment (Zeanah et al., 2003). These authors recorded ERP responses to the child's primary caregiver, this was a parent for the control group and a preferred caregiver for the institutionalized group. The results showed differences between the two groups for ERP components related to face processing, including the N170 and Nc.

Although the children tested by Parker and colleagues covered a wide range of ages, the results showed a striking effect of early social experience on the face processing system. Institutionalized children had smaller and slower amplitude responses than non-institutionalized children, and although both groups differentiated familiar from unfamiliar stimuli, the developmental trajectory observed in ERP responses to faces differed between the groups. The results of Parker and colleagues' study suggest that early social interaction is important for how brain systems in general, and perhaps those involved in face processing in particular, develop.

A recent paper (Swingler, Sweet & Carver, 2007) brought research on early caregiver-infant interaction and face processing together. This study examined infants' neural responses to faces and found that individual differences in behaviors produced by 6-month-old infants correlated with the infants' event-related potential (ERP) responses to pictures of their own mother's face (the primary caregiver) and an unfamiliar mother's face. Infants who exhibited a greater number of attachment-like behaviors that maintained close proximity and continued interaction with their mother during a series of structured separations and reunions with her also showed smaller amplitude of the Nc component of the ERP in response to pictures of the mother's face than to pictures of a stranger's face. These results suggest a general relationship between behaviors infants display in the service of maintaining close proximity and interaction with the mother in early social interactions and their neural responses to her. However, that paper used a composite score of infant behaviors across separation and reunions such that higher scores indicated more proximity and interaction seeking behaviors on the part of the infant.

In addition, Swingler and colleagues included a number of theoretically important behavioral constructs to their composite measure of infant behavior, such as infants' exploratory behaviors and affective display across their behavioral situation. In the present paper, we focus exclusively on mother-child interaction variables and specifically focus on infant visual attention during interaction with the mother and visual search and distress behaviors during separation from her. Thus, Swingler et al. (2007) described very general relations between a wide range of infant behaviors and their responses to their mother's and a stranger's face. The goal of the current paper is a closer examination of the relationship between core social behaviors infants' produce that have been proposed in the literature to facilitate aspects of development ranging from socio-cognitive to socio-emotional, with a particular emphasis on their proposed importance for the developing mother-child bond in the first year of life.

Perhaps the most salient and socially relevant sensory information infants receive from the mother consistently from birth is her face. Numerous studies of face processing have shown that faces are among the most interesting and attractive stimuli for infants almost from birth (e.g., McGraw, 1943; Wolff, 1969; Fantz, 1961; Johnson, Dziurawiec, Ellis & Morton, 1991). Infants show a preference for faces in general over other types of complex visual stimuli, and show a preference for pictures of faces over schematic or blank face drawings from early in life (e.g. Goren, Sarty & Wu, 1975). Traditional views have suggested that the early preference for faces is because they are "special". That is, faces are so important that there is a dedicated system for processing them (Farah, Rabinowitz, Quinn & Liu, 2000; Kanwisher, McDermott & Chun, 1997). More recent evidence suggests that neonates' preference for faces extends to other "face-like" stimuli and even potentially non "face-like" stimuli (Simion, Macchi Cassia, Turati & Valenza, 2001; Turati, Simion, Milani, Umilta, 2002) that include anything with the spatial configuration typical of upright faces, with more features at the top of the stimulus than the bottom. Regardless of the reasons underlying the preference for faces, the preference is consistent across studies, and current theories of face-processing development suggest that the preference plays an important role in the later development of face processing systems (e.g. Nelson, 2001).

Perhaps as a result of early accumulation of experience with faces, infants also quickly begin to discriminate between faces. From 3 to 7 months, infants begin to show evidence of categorizing faces by social characteristics like familiarity, gender and facial expression (Nelson, 2001) and by six months reliably show both a behavioral and a neurophysiological preference for their mother's face over a stranger's face (e.g. de Haan & Nelson, 1997, 1999). Work by Ainsworth and Bowlby suggests that six months marks the beginning of the third phase of the attachment process in which consolidation of the relationship to the child's primary caregiver(s) takes place (e.g., Ainsworth, 1967; Bowlby, 1969/1982; Marvin & Britner, 1999). One possibility is that an innate interest in faces aids in the formation of the bond by fostering the reciprocation of the relationship on the infant's part. According to this interpretation, the developing attachment between infant and caregiver may be facilitated by the infant's increasing attention to the mother's face seen in literature on the development of eye gaze. The mother may in turn offer more security and nurturance (Ellis, 1992) and provide more opportunities for face-to-face interaction facilitating socio-cognitive and emotional development.

Eye gaze is one the earliest emerging behavioral skills available to the infant to allow them to engage in social interaction and to gather social information from these interactions. Infant's eye gaze behavior has been shown to play an important facilitative and regulatory role in the infant's early social interactions and internal physiological states—particularly as it pertains to arousal and affective processes (Field, 1981; Stern, 1974). Eye gaze also serves an important early communicative role of a readiness to engage in social interaction and informational exchange with another individual, most often the mother; thus providing what has been called a regulatory background for early experiences of mutual regulation between mother and infant (Fogel, 1993a, 1993b; Reddy, Hay, Murray & Trevarthen, 1997; Lavelli & Fogel, 2005). Developmental studies on the relationship between eye gaze and facial and vocal expressions of emotion in early communication with the mother have shown that the co-occurrence of gazing at the mother's face and specific facial and vocal expressions of positive emotion increase in frequency and stability from the second to the sixth month of life. For example, the onset of social smiling that emerges in the second month is associated with a significant increase in the duration of visual fixation to the mother's face (Lavelli & Fogel, 2005). Therefore, beginning around the second month of life an important exchange of social and emotional information between mother and infant begins to take place in the context of eye contact; infants therefore begin directing their visual attention to the mother more and more for this purpose. Behaviors such as showing distress and visual regard of the caregiver are often exhibited even in young infants when faced with an unresponsive caregiver, for example in the still face procedure (see Tronick, 1989 for a summary), and are thought to be important communicative tools for preverbal infants.

While eye gaze in general is an early emerging ability for the infant, the ability to maintain eye contact develops more slowly over the first few months. However, as it develops, the infant's increasing ability to maintain eye contact provides opportunities for gathering perceptual information about faces as well as more socio-cognitive information about social partners. From about one month of age on, eye contact serves as the base for visual inspection of areas surrounding the eyes and face outline (Blass & Camp, 2001) and leads to improvements in the infant's ability to maintain visual attention for longer periods of time (Aslin, 1987). The infant's improving eye contact abilities also provide the foundation for the infant to explore systematically the internal features of the face (Acerra, Burnod, & de Schonen, 2002) and gather perceptual cues about the partner's face and facial expressions (Rochat & Striano, 1999). The infant's behavioral changes in eye contact, visual fixation and attention are suggested to lead to the development of capabilities that are necessary for the emergence of an ability to share emotion in face-to-face interaction. Indeed, very young infants appear to regulate their relationship with their environment primarily via gaze direction changes, and in the first three months of life infant gaze becomes increasingly linked to attention on the mother's face as well as increased expression of emotion during face-to-face interactions with the mother (Lavelli & Fogel, 2005).

An important avenue of research on early mother-child interaction has examined how past interpersonal experiences may exert an influence the social cognition that occurs during these face-to-face interactions between mother and infant. Attachment theory posits that parents and infants construct mental representations or internal working models of one another and their relationship on the basis of repeated interactional experience (e.g. Pederson, Gleason, Moran & Bento, 1998; Slade, Belsky, Aber & Phelps, 1998; Hsu & Fogel, 2003). A separate line of work conceptualizing the development of close relationships in general has proposed that individuals develop cognitive structures based on regularities in interpersonal encounters, termed relational schemas (Baldwin, 1992, 1995). Importantly, a sensorimotor form of relational schemas may be available to infants before the formation of an attachment relationship during the second half of the first year of life (Hsu & Fogel, 2003). However, no studies to date have looked for neural evidence of such an internal working model or relational schema in the context of the mother-child bond. If behaviors like visual attention, eye gaze and contact that infants' produce in the context of mother-child interaction in the first year correlate with neural responses to the mother's face and a stranger's face, this may provide some initial link between behavioral and neural evidence for an internal working model.

Evidence from behavioral studies of face processing suggests infants are predisposed to behaviors that may facilitate the development of such an internal working model. For example, during the ages that comprise the proposed first phase of the mother-child attachment relationship (i.e. Bowlby, 1969/1972), from birth to almost 3 months of age, infants exhibit a preference for looking at the human face compared to other objects. In the proposed second phase, from around three months until about six months, the infant begins assuming increasing responsibility for gaining and maintaining contact with the mother either by initiating more interaction or exerting more control over the interaction through the use of increasingly complex behaviors, for example through increased visual attention to the mother's face and the use and maintenance of direct eye gaze. An important feature of this phase is that the infant also increasingly begins to differentiate his or her primary caregiver from others and preferentially directs care-soliciting behaviors to the primary caregiver(s)—behaviors that have been proposed to depend on the infant having an intact working model of the attachment figure (Bowlby, 1969). The proposed third phase (the "consolidation phase") begins between the ages of six and nine months and is when the infant is thought to consolidate attachment and specific distress and care-seeking behaviors, to the primary caregiver exclusively (Marvin & Britner, 1999). Under Bowlby's (1969/1972) theories of attachment behavior, early infant behaviors such as visual regard and visual search and distress during separation are all solicitous behaviors in the infant's behavioral repertoire that function to elicit and maintain close contact with the caregiver. In addition, the work on eye gaze and eye contact has demonstrated the importance of these behaviors for the infant and the mother-infant relationship in the first year. Therefore, individual differences in the production of these behaviors may be uniquely related to event-related potential (ERP) responses to the mother's face and a stranger's face.

ERPs are measures of brain electrical activity in response to specified discrete events, such as the presentation of a face, and are advantageous for use with infants because the method is a non-invasive and objective measure of neural response. The amplitude of the ERP is thought to reflect the summation of neural activity in which greater absolute amplitude reflects greater neural activation in response to a stimulus. In addition, because ERPs require no behavioral response on the part of infant participants it can provide valuable information where behavioral measures cannot. This fact was evident in a study that included both a visual preference test of recognition and an ERP response measure of face processing (de Haan & Nelson, 1997). Looking time proved to be a less sensitive measure of face processing than brain response; six-month-olds' looking time did not differ for the mother's face and a stranger's face, despite the fact that the amplitude of the ERP response was significantly different for the two.

Two primary ERP components have consistently been associated with face processing in infants and young children (see de Haan & Nelson, 1997, 1999; de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003). The first, the Nc component, is a middle-latency negative component that is maximal over central frontal electrodes and has been associated with increased attention, particularly to salient stimuli, (Courchesne, Ganz, & Norcia, 1981, Nelson, 1994) and with recognition memory (de Haan & Nelson, 1997, 1999; Nelson, 1994). De Haan and Nelson (1997) were the first to show that 6-month-olds' Nc component activity differentiated both a dissimilar and a similar looking strangers' face from their mothers', and that the pattern of neural activity elicited differed between these two conditions. However, the same component failed to distinguish between two stranger's faces, regardless of similarity between the two. This finding was robust even when the infants' were first familiarized to one of the faces. This suggests that different higher-order cognitive processes beyond novelty detection are activated to process a familiar, socially significant face paired with an unfamiliar face versus two unfamiliar faces, and that the Nc component is a sensitive measure of these processes. As noted above, infants' behavioral and neural responses must, in part, be the result of past experience with the mother, but these changes also likely serve the developing mother-child relationship as a result of the increasing behavioral and neural discrimination abilities of the infant. Therefore, it is hypothesized that infants who show more behavioral evidence of discriminating the mother and soliciting interaction her, will also show more evidence of neural discrimination of the mother from a stranger. Specifically, infants who show higher levels of visual attention and eye gaze directed to the mother by looking at her when she is present and looking for her when she is gone will show more evidence of discriminating her face from the stranger face in the Nc component. Similarly, infants who show higher levels of distress behavior during separations with the mother are also hypothesized to show more evidence of discriminating the mother's face from the stranger face. Because of the findings in the previous work looking at the relationship between infant behavior and neural response to mother and stranger faces (Swingler et al., 2007), it is hypothesized that the direction of this relationship will be a larger Nc component response to the stranger's face than the mother's face for infants who show more evidence of a behavioral preference for the mother.

A second ERP component has been used to index the development of face processing and has been suggested to be face specific, at least in part (de Haan, Pascalis, & Johnson, 2002, Halit, de Haan, & Johnson, 2003). This component, termed the P400 because of its latency, is a middle latency positive component localized over occipital electrodes. This component is sensitive to differences between faces and objects (de Haan and Nelson, 1999; Dawson et al., 2002), and between human and non-human faces in adults and older children, leading some researchers (de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003; de Haan, Johnson, & Halit, 2003) to suggest that it may be a developmental precursor to the N170, a face specific component seen in adults (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Although the P400 appears to be sensitive to faces and has shown variation with impairments in face processing in developmental disorders like autism, it also seems to be involved in more general aspects of object processing (Dawson et al., 2002). It may be that the P400 is a component that reflects aspects of visual attention and memory updating, and that this component is sensitive, but not specific, to face processing. However, as visual attention is of interest for this study, this component is hypothesized to correlate with measures of behavioral visual attention. Specifically, infants who show higher levels of visual attention to the mother, especially during face-to-face interaction with her when she is present, are likely to show a larger neural response indicative of discriminating the mother face from the stranger face. However, as this is the first study of its kind to examine the relationship between infant behaviors during interaction with the mother and the P400 component response to faces, the specific direction of this relationship is unknown. It is also unclear whether measures of looking for the mother during separation and infant distress behaviors during separation will be related to the P400 response to the faces.

Methods

Participants

The final sample of participants consisted of 30 full term, neurologically healthy six-month-old infants (mean age of 183.4 days; 6.1 months). All infants were recruited from an existing list of parents who volunteered to participate in research after being contacted by mail following their child's birth. Twenty-three infants were Caucasian, 3 were Hispanic, 2 were Asian and 2 were African American. The children were primarily from middle-class homes and evenly split by gender, 16 were male and 14 were female. Families were given a small toy for the infant and a printout picture of the infant wearing the electrode cap as a thank-you for participating.

An additional 25 infants were tested but not included in the final sample because they did not provide interpretable ERP data, or because an error occurred during testing: 18 infants did not provide enough artifact free data, 5 infants did not cooperate with the testing procedure, one mother talked throughout the ERP testing session, and one infant's data was lost due to experimenter error. This attrition rate is the same or lower than rates for other ERP studies conducted with the same or similar paradigm using this age group (e.g. de Haan and Nelson, 1997, 1999).

Stimuli

Each mother was photographed with a color digital camera from the neck up against a light grey background. Mothers wore the same grey scarf to obscure the neckline and clothing. Earrings and other jewelry were removed, but mothers that wore glasses were instructed to leave them on. Mothers assumed a neutral expression for the photograph. The picture of the mother's face was matched with another mother's picture so that paired faces were of the same ethnicity and mothers who wore glasses were paired together. Paired faces were chosen to be dissimilar in terms of hair color, face shape, eye color and facial features. Pictures of mothers were standardized in Microsoft Photoshop so that each face measured 18 (+/- 1) cm from the top of the head to the chin and 11 (+/- 1) cm from ear to ear.

Behavioral Procedure

The behavioral portion of the study used a paradigm inspired by the work of Ainsworth (e.g. Ainsworth, Waters, Blehar & Wall, 1978) and designed for easy elicitation and observation of infant behaviors in response to two separations and reunions with the mother. It is important to note that although this behavioral paradigm is reminiscent of the Strange Situation pioneered by Ainsworth, the Strange Situation is not valid for determining attachment quality in infants as young as those tested here. Because of this, we focus our analysis on behaviors infants show in interaction with and separation from their caregiver, and we are explicitly *not* attempting to evaluate the quality of attachment in this study. The procedure was videotaped and coded for behaviors exhibited by the infant. Each session took place in a 10' x 12' room designed for behavioral testing and equipped with a camera located in one corner of the ceiling. This camera was controlled by an experimenter in an adjacent video room who watched the camera image on a TV screen and kept the camera focused on the infant at all times. A second camera was located behind a one-way mirror on the door to the adjacent video room. This camera was also controlled by an experimenter and was kept focused on the mother and infant when the mother was in the room and the infant only when the mother was not in the room. Two large blue armchairs were the only furniture in the room. An infant blanket was placed on the floor in the center of the room and several toys were provided for the mother and infants to play with. These included a small red, squishy soccer ball, a set of 5 stacking rings and a plastic train with a squeaking top. Mothers were instructed to sit on the floor or in a chair, wherever they were most comfortable, and to interact with their infant as they normally would. We designed the behavioral assessment and coding to provide detailed information about the presence and amount (frequency, duration and intensity) of infant behaviors. See Table 1 for a detailed description of the behavioral procedure intervals. In this study, we were particularly interested in infants' mother-focused behaviors, especially during or immediately following a separation with the mother. As such, we concentrated our focus on behaviors infants' displayed on intervals 4-7.

Behavioral Coding

Two coders watched the tapes of the behavioral sessions and coded specific behaviors exhibited by each infant. The two coders were blind to the hypothesis of the study and had no knowledge of the infants' ERP data or results. Coders were trained by the first author on the original coding scheme and achieved 88% reliability with her before coding independently. Both coders coded 25% of the participants for the purposes of measuring reliability. Coding pairs achieved 87% reliability for the data on which they overlapped in this paper.

To increase precision of coding, each interval of the behavioral procedure was further sub-divided into fifteen-second segments, and behaviors were coded within each segment. Intervals of interest were those in which a separation from or reunion with the mother occurred (intervals 4 & 6, 5 & 7, respectively). For each separation interval segment, coders rated infant distress and amount of looking for mother. Distress behaviors included crying, distress vocalizations that were not crying (e.g. whining or fussing), and arm flailing, arm wiggling or kicking. In order to be coded as a distress behavior, arm failing, arm wiggling or kicking had to be accompanied by a negative vocalization and/or facial expression. Each of these 3 distress behaviors was coded as a discrete yes-no decision within each 15-second segment, and distress behaviors were summed to provide a total number of distress behaviors exhibited on each separation interval segment. Amount of looking for mother was rated on a 5-point Likert-type scale that ranged from 1 (did not look for mother) to 5 (looked for mother entire 15 seconds). Looking for mother was operationalized as looking in the direction of the room into which the mother had exited, or visually searching the rest of the room. For each reunion interval segment, coders assessed infants' amount of looking at the mother. Amount of looking at mother was also rated on a 5-point Likert-type scale that ranged from 1 (did not look at mother) to 5 (looked at mother entire 15 seconds).

Behavioral Measures

To create a single measure of each construct for each child, each measure was averaged across the 15-second segments in each interval to provide an average score on the interval and then averaged across intervals of the same type. The result was a set of three behavioral measures: infant distress upon separations, looking for mother upon separations, and looking at mother upon reunions. Infant distress upon separation scores ranged from 0 to 1.75, with an average score of 0.46 (*SD*= 0.43). The average amount of looking for mother upon separations was 1.60 (*SD*= 0.58, Range 1-3.33), while the average amount of looking at mother upon reunions was 1.79 (*SD*= 0.41, Range 1.25-2.95).

Event-related-potential (ERP) testing

Upon completion of the behavioral session, the ERP testing began in another room. The circumference of the infant's head was measured and the vertex marked. An appropriate size 32-channel electrode cap (Electro-Cap International) was fitted to the infant's head according to the manufacturer's specification. Event-related potentials were recorded from the 31 active channels placed according to the international 10/20 system of electrode placement. The following standard electrode sites were used: Pz, Fz, O1, O2, P3, P4, T5, T6, C3, C4, T7, T8, F3, F4, F7, and F8. The following non-standard sites were also used: CPz, FCz, CP5 and CP6, CP1 and CP2, FC1 and FC2, FC5 and FC6, FP7 and FP8, and AF7 and AF8 (See Figure 1 for a schematic of electrode positions on the scalp). Electrode gel was placed into each of the 32 electrodes and impedance measurements were recorded prior to testing. Scalp impedances were measured before and after testing and were always kept below 10 kilo-ohms. The mean scalp impedance before the testing procedure was 6.33 kilo-ohms, SD= 2.74 kilo-ohms. The mean of the post testing impedance measurements was 4.45 kilo-ohms, SD= 3.42. Upon entry to the ERP testing room four additional electrodes were manually placed around the infant's eyes for EOG measures of eye movements and blinking. Two electrodes were placed at the outer canthi of the eyes and two electrodes were placed above and below the right eye. Impedance measurements were also taken and recorded from these four electrodes prior to and immediately following testing. EOG impedances were ideally kept below 30 kilo-ohms, however this goal was sacrificed if the infant was becoming fussy or impatient with the testing procedure. Average impedance measurements for the Horizontal eye electrodes were 57.05 kilo-ohms before testing and 39.90 kilo-ohms after testing.

Average impedance measurements for the vertical eye electrodes were 60.88 kilo-ohms pre-test and 31.94 kilo-ohms post-testing.

Testing for all infants took place in the same sound attenuated and electrically shielded room. During the testing session the infant sat on the mother's lap about 70 cm from a computer screen that delivered the stimuli. Mothers were instructed to remain as quiet as possible during the entire ERP testing session. A large, trifold grey screen with a window cutout for the computer screen obscured the back of the monitor and part of the room from view. There were cracks between the panels of the screen through which an observer watched infants and signaled the computer via button press if the infant did not attend to the stimuli. If needed, the observer shook a rattle or squeaked a toy behind the computer screen during the inter-trial interval to attract the infant's attention to the pictures. Each trial consisted of a 100-ms baseline, 500-ms presentation of the stimulus, and 1200-ms recording period during which the computer screen was grey. Trials were separated by a randomly varying 500 to 1000 ms inter-trial interval. The order in which the stimuli were presented was randomized across infants. Data collection was terminated when the child had seen all of the 100 trials (50 mother and 50 stranger) or when the child was no longer tolerant of the testing procedure. Trials on which the child did not attend to the stimuli or during which the experimenter was attempting to attract the child's attention were removed after data collection.

EEG Recording

EEG was recorded continuously from thirty-two electrode channels. Signals were amplified and filtered through a .1 Hz high-pass filter and 100 Hz low-pass filter. A 60Hz notch filter was in place during recording. The EEG signals were amplified with a gain of 20,000 and EOG signals were amplified with a gain of 5,000. Data were recorded continuously, with a sampling rate of 284 Hz, and saved to a file in the computer-assisted scoring program (Instep) on the data collection computer. A second computer generated the stimuli and the two computers were interfaced via serial port for precise synchronization. The timing of the stimulus onset and offset was registered together with the physiological recorder for off-line segmentation of the data. Each infant's EEG data was referenced to Cz and re-referenced off-line to an average reference using the computer-assisted program. This reference was chosen primarily to replicate previous studies of face processing in infancy. Although the number of electrodes used in the present study is relatively small for an average reference, each method of referencing has advantages and disadvantages, and we chose the average reference in order to be able to compare our results to previous studies using the same paradigm (e.g. Dawson et al., 2002; Carver et al., 2003, Halit, de Haan & Johnson, 2003).

ERP Reduction

After testing, each infant's ERP data were edited off-line. Trials in which the child did not attend to the pictures were excluded from the data set. Any channels in which the EEG signal amplitude exceeded 250 μV were excluded from the trial as artifact. Trials in which EOG artifact occurred, i.e. eye blinks or large eye movement, were also excluded. Additional artifact was rejected when amplitudes exceeded A/D values, which results in clipping (flat-lining of the signal from the amplifier), and upon visual inspection. Data from trials in which more than 4 electrode sites met criteria for exclusion were not included. Only subjects with more than 10 artifact free trials in each condition were included in the final sample. The mean numbers of artifact free trials of each condition in the final data set were not different from one another (Mother condition M = 23.48, SD = 9.15; Stranger condition M = 23.03, SD = 8.98). Grand averages of the ERP data for all subjects were computed for visualization purposes.

ERP Measures.

Components of interest were identified based on previous research findings (e.g., de Haan & Nelson, 1997, 1999; Swingler et al., 2007) and upon inspection of the grand-averaged data for each condition. Grand mean ERP waveforms for all infants at electrodes of interest are presented in Figure 2. The components identified were a middle-latency negative component (Nc, see de Haan & Nelson, 1997, 1999) distributed over frontal electrode sites and a positive component peaking 300 to 500 milliseconds over occipital electrodes (P400). The Nc was defined as the maximum negative peak between 230 and 1230 ms[1], and the P400 was defined as the maximum positive peak between 260 and 855 ms. These time windows were determined by examining the data for each participant and selecting a window that captured the peak of the component for every one. A computer-assisted program calculated the peak amplitude and latency. The electrodes used in the components analyses were determined by selecting those electrodes at which the waveform morphology was prominent, and by using electrode sites comparable to those used in previous research. Dependent measures for the analyses of the P400 and Nc components were peak amplitude and latency.

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[1] This interval reflected baseline-to-baseline activity for each infant. Note that the actual peak of the Nc did not vary this broadly across infants. The average latency for the Nc component across infants was 688.23 msec. The latency ranged from 555.31 to 800.29 msec. This range suggests that the Nc likely reflected the same physiological response across infants.

Results

Repeated-measures analyses were conducted to determine if scores on the three behavioral measures were related to peak amplitude and latency of the P400 and Nc components, and to determine if these relationships differed as a function of face identity and lead location. Leads of interest were chosen based on visual inspection of the grand averaged waveforms, as well as on predictions based on previous studies of the Nc in the literature. Analyses of the Nc component were performed for the following leads: FC1, FC2, F3, F4, FC5, FC6 (see Figure 1 for a schematic of lead location). Fronto-lateral lead pairs FC1/FC2, F3/F4, and FC5/FC6 were analyzed specifically to allow for detection of possible hemisphere effects. Analyses of the P400 component were performed for occipital electrodes O1 and O2 only. Amplitude and latency were analyzed separately for each component. Only significant effects involving the behavioral measures and FACE are discussed, as these relate directly to the study hypotheses.

P400 Component

The P400 component was analyzed at occipital leads O1 and O2. Table 2 presents a breakdown of the significant results from the P400 amplitude and latency analyses, including slope estimates and associated standard errors for each FACE X LEAD condition. Analyses of the P400 component included the behavioral variable predictors of infant distress upon separation, looking for mother upon separations and looking at mother upon reunions, as well as the within-subjects variables of FACE (mother, stranger), and LEAD (O1, O2), as well as interactions of behavioral measures and FACE, LEAD.

Amplitude

The interaction between FACE identity and infant distress upon separations was significant, $F(1, 26)= 5.56$, $p= .03$, $\eta_p^2= 0.18$. This indicates that the relationship between infant distress and P400 amplitude differed significantly across the two FACE conditions. As can be seen in the top portion of Table 2, infant distress scores were significantly and positively related to P400 amplitude in the mother face condition, and slope estimates in the mother face condition were significantly larger than those in the stranger face condition. Infants who demonstrated more distress in the behavioral procedure separations also had a larger amplitude P400 response to the mother's face. This was not the case in the stranger face condition.

Latency

The interaction between FACE and looking for mother upon separations was significant, $F(1, 26)= 10.76$, $p= .003$, $\eta_p^2= 0.29$. This indicates that the relationship between looking for mother upon separations and P400 latency differed significantly across the two FACE conditions. An inspection of the bottom portion of Table 2 reveals that looking for mother upon separation scores were significantly and positively related to P400 latency in the stranger face condition, and that slope estimates were significantly larger in the stranger face condition than in the mother face condition. Higher scores on the looking for mother during separations measure predicted longer P400 latencies in response to the stranger's face. That is, children who looked more for their mothers in the behavioral procedure separations tended to have a longer latency to peak amplitude in the P400 component response to the stranger's face. This was not the case in the mother face condition.

Nc Component

Analyses of the Nc component included the behavioral variable predictors of infant distress upon separation, looking for mother upon separations and looking at mother upon reunions, as well as the within-subjects variables of FACE (mother, stranger), LEAD (FC1/FC2, F3/F4, FC5/FC6), and HEMIsphere (Left, Right). Interactions between behavioral variables and FACE, LEAD, and HEMI were also tested. Tables 3 and 4 present a breakdown of the significant results from the Nc amplitude and latency analyses, including slope estimates and associated standard errors for each FACE X HEMI X LEAD condition.

Amplitude

A marginally significant distress upon separations X FACE X HEMI X LEAD interaction emerged, $F(2, 52) = 2.54$, $p = .09$, $\eta_p^2 = 0.09$. At the left fronto-central lead FC5, more distress upon separations significantly predicted Nc amplitudes in the mother face condition; as infant distress scores increased, Nc amplitude response to the mother face condition tended to become more negative. The Nc is a negative component therefore, by definition, more negative amplitudes are indicative of a lager neural response. At the right fronto-central lead FC2, more distress upon separations also significantly predicted Nc amplitudes in the mother face condition, but in the opposite direction. As infant distress scores increased, Nc amplitudes in the mother face condition tended to become less negative, or smaller.

A visual inspection of the slope estimates presented in Table 3 suggests that it was primarily the mother/stranger difference at right hemisphere lead FC2 that drove the significant infant distress X FACE X HEMI X LEAD interaction, and follow-up FACE comparisons within each LEAD X HEMI condition confirmed this. The only significant FACE difference in the relationship between infant distress and Nc amplitude occurred at FC2, p = .01. At FC2, the relationship between distress and amplitude was significantly stronger and more positive in the mother face condition than in the stranger face condition. As scores on the infant distress measure increased, amplitude responses to the mother's face became less negative (or smaller because Nc is a negative component) in response to the mother's face at FC2. The negative relationship between infant distress and response to the stranger's face did not achieve statistical significance.

Latency

The interaction between FACE and infant distress upon separations was significant, $F(1, 26)$= 6.56, p= .02, η_p^2= 0.20. As can be seen from the top portion of Table 4, the slope estimates were significantly more positive in the mother face condition than in the stranger face condition. Higher distress upon separation scores predicted longer latencies, or time to peak amplitude, in the mother face condition. This was not the case in the stranger face condition.

The interaction between FACE and looking for mother upon separations was also significant, $F(1, 26)$= 7.62, p= .01, η_p^2= 0.23. An inspection of the slope estimates presented in the middle portion of Table 4 indicates that slopes in the mother face condition were significantly more negative than those in the stranger face condition. Higher looking for mother upon separation scores were predictive of shorter latencies, or faster responses, in the mother face condition. This was not the case in the stranger face condition.

A marginally significant interaction of looking at mother upon reunions, FACE, and HEMI also emerged, $F(1, 26)= 3.69$, $p= .07$, $\eta_p^2= 0.12$. The bottom portion of Table 4 indicates that slope estimates of the relationship between looking at mother upon reunions and Nc latency differ across FACE conditions, and that this difference is not consistent across the two hemispheres. In the left hemisphere, slope estimates were significantly more negative in the stranger face condition than in the mother face condition; in the right hemisphere, this pattern was reversed. In the left hemisphere, higher looking at mother upon reunion scores were predictive of shorter Nc latencies to peak in the stranger face condition. In the right hemisphere, more looking at mother upon reunions was predictive of shorter Nc latencies to peak in the mother face condition.

Discussion

Our goal in the current paper was to examine the multidimensional relationship between infants' behaviors during mother-child interactions and brain responses to the mother's face and a stranger's face. A previous paper (Swingler et al., 2007) found that the total amount of mother directed proximity seeking behavior 6-month-olds produced was related to the extent and morphology of neural processing observed to mother and stranger faces. However, the behavioral measure in the previous paper was a composite of a number of infant behaviors that were hypothesized to be related to the caregiver-infant relationship. This composite included a large range of infant behaviors including multi-dimensional constructs such as exploratory and affect behaviors that are likely important for the developing mother-child relationship, but also may be related to other aspects of the infant's development. In the current work, we sought to determine how three specific behaviors that have been implicated as critical in the infant's early social interactions with the mother related to brain activity in response to her face versus an unfamiliar face. Looking and distress behaviors at six months of age may be the best evidence of behavioral preference for the mother in young infants with relatively limited behavioral repertoires.

We hypothesized that measures of visual attention would be related to the P400 component response to the mother and stranger faces. Infants who showed higher levels of visual attention to the mother were hypothesized to show more evidence of discriminating the mother face from the stranger face in the P400 component. However, as this is the first study of its kind to examine the relationship between infant behaviors during interaction with the mother and the P400 component response to faces, the specific direction of this relationship was unknown. We also did not provide specific hypotheses with regard to the potential relationship between measures of looking for the mother during separation and infant distress behaviors during separation and the P400 response to the faces.

Interestingly, the P400 component response was significantly related to behavioral measures of looking for mother on separation and distress behaviors on separation, but was not related to measures of looking at mother on reunions as we had hypothesized. In addition, amplitude and latency of the P400 response were related to different behavioral measures. Amplitude of the P400 response was significantly related to the behavioral measure of infant distress on separations for the response to the mother's face only. Infants who exhibited higher levels of distress during separation from the mother also exhibited larger amplitude P400 responses to the mother's face. The behavioral measure of distress was not significantly related to the P400 response to the stranger's face. Latency of the P400 response, on the other hand, was significantly related to the behavioral measure of looking *for* mother during separations for the stranger face only. Infants who showed higher levels of looking for mother during separations also showed longer latencies to peak amplitude P400 response to the stranger's face. Therefore, infants showed more visual search for the mother when she was gone also showed slower processing of the stranger's face only in the P400 component.

The P400 component is thought to be especially sensitive to face stimuli (Halit, de Haan & Johnson, 2003), but has also been seen in response to objects. This has led some authors to suggest that the P400 is more generally associated with visual attention to a stimulus (Carver et al., 2003; Dawson et al., 2002), as well as novelty detection and memory updating processes. The relation between distress behaviors and P400 response suggests that infants who show more distress during separation from their mother also devote more visual attention to her face. This result is significant because it suggests that a brain system that at least in part seems to be specialized for processing faces (reflected in the activity of the P400) is related to the infant's social interaction with their caregiver, and may be especially related to their distress at separation.

The current study does not allow any speculation about the direction of this effect, however the results suggest that one of two equally interesting mechanisms may be at play here. It might be the case that infants whose face processing system functions in such a way that they have an increase in P400 response to their mother's face may be more sensitive to disruptions in social interaction such as separation. The alternative interpretation is equally interesting in our view. Individual differences in sensitivity to separation and resultant distress may influence how the face processing system develops, and how the system responds to relevant stimuli such as the mother's face. With the present data, we cannot separate which of these interpretations is correct; nevertheless, both lead to interesting questions about the interaction between the development of social brain systems and the face processing system, and have significance for theories about how face processing develops. The results suggest that face processing does not unfold in isolation, but that it is affected by and interacts with other social systems.

The latency of the P400, reflecting speed of processing of the facial stimuli was also related to infant behavior. Infants who looked more for their mothers had slower responses to the strangers' face. It is not immediately clear why looking for the mother would relate to how infants' process another female's face. However, one possibility is that our measure of looking for mother on separation tapped into a larger construct of separation anxiety that might have broader effects on how infants learn about other people and the neural resources they can devote to learning about another person's face. In combination, our measure of behavioral distress on separation and looking for mother on separation were both related to the P400 response to faces. Higher levels of behavioral distress predicted larger amplitude responses to the mother's face only; while higher levels of looking for the mother on separation predicted longer latency responses to the stranger's face. It may be that both of these measures were behavioral evidence of the beginnings of separation anxiety for infants and that separation anxiety influences the ways in which neural resources are allocated to process the mother's face and an unfamiliar female's face. Again, the specific direction of this relationship is not testable with these data. It would be interesting in future research to investigate whether these results maintain in older children, in whom the quality of the attachment relationship could be measured.

We also hypothesized that infants who showed higher levels of visual attention and visual search by more sustained episodes of looking *at* the mother when she was present and looking *for* her when she was absent would also show more evidence of discriminating her face from the stranger face in the Nc component of the ERP response. Similarly, we hypothesized that infants who showed higher levels of distress behavior during separations with the mother would also show more evidence of discriminating the mother's face from the stranger face in the Nc ERP response. Because of the findings in the previous paper mentioned above (Swingler et al., 2007), we hypothesized that the direction of this relationship would be a larger Nc response to the stranger's face than the mother's face for infants who showed more visual attention (looking at) during interaction with the mother and more visual search (looking for) and distress behaviors on separation.

Indeed, infants who displayed higher levels of distress behavior on separation showed an interesting cross-hemisphere interaction between scores on the distress variable and Nc response to the two faces. The left hemisphere interaction between Nc response and high scores on distress behavior was associated with larger amplitude responses to the mother's face compared to the stranger's face, while the right hemisphere relationship was associated with smaller amplitude responses to the mother's face. At the left fronto-central electrode site FC5, higher scores on the distress during separation measure predicted larger Nc amplitude responses to the mother's face only. This provided support for the idea that infants' who showed more distress (or anxiety) during separations with the mother also showed greater visual attention to her face than did infants who showed little or no distress on separation. However, at the right fronto-central electrode site, FC2, higher scores of behavioral distress during separation, predicted *smaller* amplitude responses to the mother's face in comparison to the stranger's face. A closer examination of the data suggested that the mother/stranger difference at FC2 was driving this cross-hemisphere interaction. Latency of the Nc component response to faces was also significantly related to infant distress upon separations. Infants who showed higher levels of distress upon separations also showed longer latencies to peak amplitude in response to the mother's face only.

The behavioral measures of both looking at and for mother were also significantly related to the latency of the Nc component response to the two faces. Infants with higher levels of looking for the mother upon separations also had shorter latencies to peak for the Nc component response to the mother's face, that is, they had faster responses to the mother's face only. Infants with higher scores on the looking at mother behavioral variable showed another interesting cross-hemisphere interaction between behavioral scores on this measure and latency of the Nc response to the two faces. In the left hemisphere, infants who looked longer at the mother on reunion had faster latencies to peak in response to the stranger's face only. In the right hemisphere, longer looking time at mother on reunion was associated with fast latencies to peak Nc response in the mother face condition only. Therefore, longer looking times at the mother during face-to-face interactions with her was associated with faster left hemisphere processing of the stranger's face and faster right hemisphere processing of the mother's face in the Nc component response.

The relation between infant distress during separation and hemispheric activation in response to the two faces may be reminiscent of the left hemisphere bias seen while infants view positive emotions and engage in positive interactions with the mother (Dawson, Frey, Self et al., 1999; Fox & Davidson, 1987). The relationship between caregiver and infant has been shown to mediate this effect, and may be what is reflected in our findings with infant distress behavior on separation (Dawson, Klinger, Panagiotides, & Hill, 1992; Dawson, Klinger, Panagiotides, & Spieker, 1992). The mother's face is a positive stimulus for infants, but this may be particularly true for infants who show more evidence of anxiety and distress during separation from the mother. These infants appear to show a preferential response to the mother's face in general, as evidenced by our results for the P400 component and the latency of the Nc response for infants who showed higher distress and looking for mother on separations. In addition, these infants may also show a left hemisphere bias for deeper processing of the mother's face in the Nc. Previous work using EEG and neuroimaging methods in both adults and infants has also led to the conclusion that right frontal activity is related to processing negative emotion (e.g. Davidson, 1984a, 1984b; Davidson & Fox, 1982). This may be what is reflected in the relationship between higher scores on our distress on separation variable, and a right hemisphere bias for processing the stranger's face. Perhaps infants who show behavioral evidence of anxiety during separation from the mother and a desire for her to return, are also more inclined to process an unfamiliar face, and possibly other novel stimuli as well, as potentially negative.

Interestingly, the behavioral variable of looking at mother during reunion interactions did not show the same pattern of cross-hemisphere correlations as the distress and looking for mother on separation variables did. Responses to the mother's face were faster in the right hemisphere for infants who looked longer at mother when she returned to the room; responses to the stranger's face were faster in the left hemisphere for these same infants. This suggests further potential evidence that our behavioral measures of distress on separation and looking for mother on separation were related to a larger construct of separation anxiety for infants this age. Further, these "separation anxiety" behaviors seemed to correlate with responses to the two faces in similar ways, while the looking at mother when she returned showed a different, and often opposite relationship to the neural response to the two faces. These results do not, at present, allow us to answer these questions, although they do suggest a need for further investigation of the behaviors infants show during separation and during resumed interaction with the mother. In particular, infant distress on separations was associated with larger amplitude responses for both components of the ERP investigated here. This suggests that more evidence of infant distress on separation is associated with deeper processing of the mother's face. The results on the relationship between infant behavior and latency of the two components are less consistent, and therefore, harder to interpret. Perhaps future studies could focus primarily on investigations of amplitude of component responses to faces and behavioral variables.

Possible Limitations

There are some limitations that should be considered in interpreting the results of the present study. First, the behavioral procedure that we used is new, and although it was informed by previous studies of the infant-caregiver relationship in the literature (Ainsworth, 1967; Calkins, 2004; Calkins & Hill, 2007, Field, 1996), the procedure is very similar to Ainsworth's Strange Situation (Ainsworth, Blehar, Waters & Wall, 1978). The Strange Situation is used to measure the quality of the attachment relationship. It would not be appropriate for us to attempt to draw conclusions about the quality of the attachment relationship based on our observations in infants so young. Nevertheless, future studies examining the fully emerged quality of attachment in older infants and its relation to face processing would be interesting. Another potential limitation in the present study is that the effects are correlational. In many cases, we are unable to draw strong conclusions about whether behavioral variation has led to variation in face processing, or whether differences in face processing preceded variation in behavior. Such questions would be very difficult to ask experimentally, since infants cannot be assigned to different levels of separation anxiety or distress, for example. Nevertheless, the present results are an important first step in understanding variation in infant-caregiver interaction as it relates to other social cognitive functions. What is important about our findings is that individual variation in behaviors hypothesized as highly influential in infant's early social interactions correlated with the infants' developing face processing system. This work provides new potential support for the hypothesis that as the mother-infant bond develops through an accumulation of social interactions the behavioral and neural underpinnings of this relationship also change in concert with one another.

Chapter III, Table 1

Behavioral procedure

INTERVAL	TIME (Minutes)	ACTIVITY
1	0:00-1:00	Experimenter 1 (Familiar), Mother & Infant interact.
1	1:00	Experimenter 1 exits to the video room.
2	1:00-2:00	Mother & Infant play in the testing room.
3	2:00-2:15	Experimenter 2 (Stranger) enters testing room from the video room and stands by the door.
3	2:15-3:15	Experimenter 2 approaches infant & initiates play.
3	3:15*	As cued by Experimenter 1, Mother exits to the video room.
4	3:15-4:15	Stranger continues to interact with the infant, comforts if infant distressed.
5	4:15-5:15	Mother returns to the room and resumes interaction. Stranger exits to the video room.
6	5:15-5:45*	Mother exits again to video room, infant alone in the testing room for 30 seconds or until the infant becomes upset.
7	5:45-6:45	Mother returns to testing room and resumes interaction with infant for final minute.

* Experimenter 1 cues Mother from the video room over the headphones.

Chapter III, Table 2

Mother-Child Behavioral Variables and P400

	Face			
	Mother		Stranger	
	ß	*SE*	*ß*	*SE*
Amplitude and Infant Distress upon Separations				
O1	12.90*	6.15	-2.84	3.56
O2	9.53†	5.27	-2.59	4.90
Latency and Looking for Mother Upon Separations				
O1	9.32	71.02	184.73**	66.0
O2	-55.58	75.25	247.01**	76.53

**$p < .01$, *$p \leq .05$, †$p < .10$

Chapter III, Table 3

Infant Distress upon Separations and Nc Amplitude, Lateral Leads

	Face			
	Mother		Stranger	
	ß	*SE*	*ß*	*SE*
Left Hemisphere				
FC1	-3.84	2.82	-1.31	2.52
F3	1.52	2.92	-0.37	3.05
FC5	-6.19*	2.24	-4.84	3.0
Right Hemisphere				
FC2	6.15**	2.50	-3.02	2.32
F4	-2.25	2.23	-0.43	2.32
FC6	-1.95	1.92	-2.30	2.91

** $p \leq .01$, * $p \leq .05$

Chapter III, Table 4

Mother-Child Behavioral Variables and Nc Latency, Lateral Leads

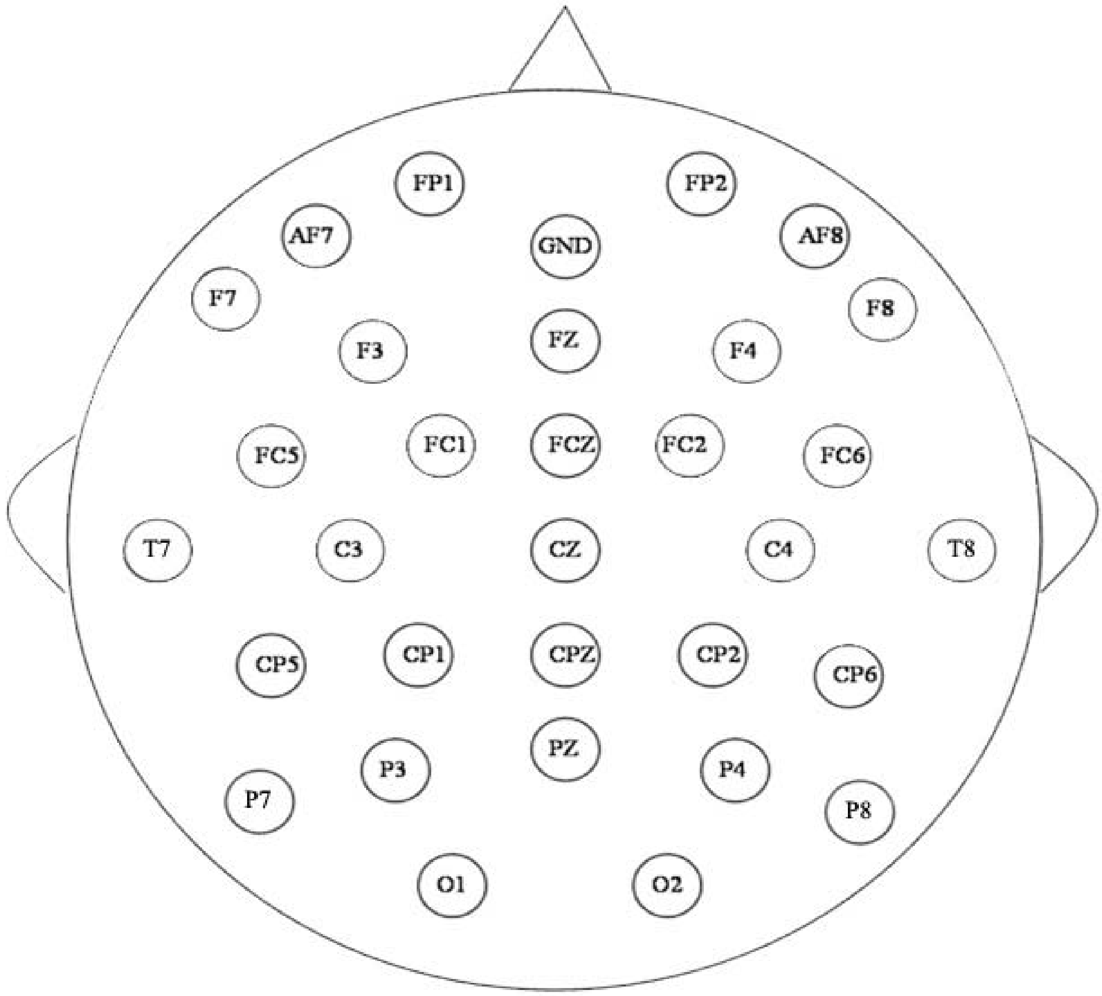
	Left Hemisphere				Right Hemisphere			
Face	Mother		Stranger		Mother		Stranger	
	β_1	*SE*	β_1	*SE*	β_1	*SE*	β_1	*SE*
Infant Distress upon Separation								
Lead								
FC1/FC2	226.25*	114.66	-12.79	132.64	84.50	207.86	90.75	180.12
F3/F4	382.64**	144.37	-164.89	182.14	23.90	105.65	74.67	106.31
FC5/FC6	139.80	188.66	-147.86	152.83	259.62	180.61	-87.16	164.41
Looking for Mother upon Separation								
Lead								
FC1/FC2	-142.64†	83.70	143.75	96.83	-107.85	151.74	-4.28	131.49
F3/F4	-134.85	105.39	126.65	132.97	0.11	77.12	9.19	77.61
FC5/FC6	-120.73	137.72	58.72	111.57	-58.61	131.84	174.29	120.01
Looking at Mother upon Reunion								
Lead								
FC1/FC2	-73.54	92.24	51.11	106.71	4.04	167.22	207.41	144.90
F3/F4	-121.42	116.14	-271.18†	146.53	-91.67	84.99	-93.67	85.52
FC5/FC6	55.86	151.77	-201.58	122.95	-339.96*	145.29	-37.74	132.26

$^{**}p < .01$, $^{*}p \leq .05$, $^{\dagger}p \leq .10$

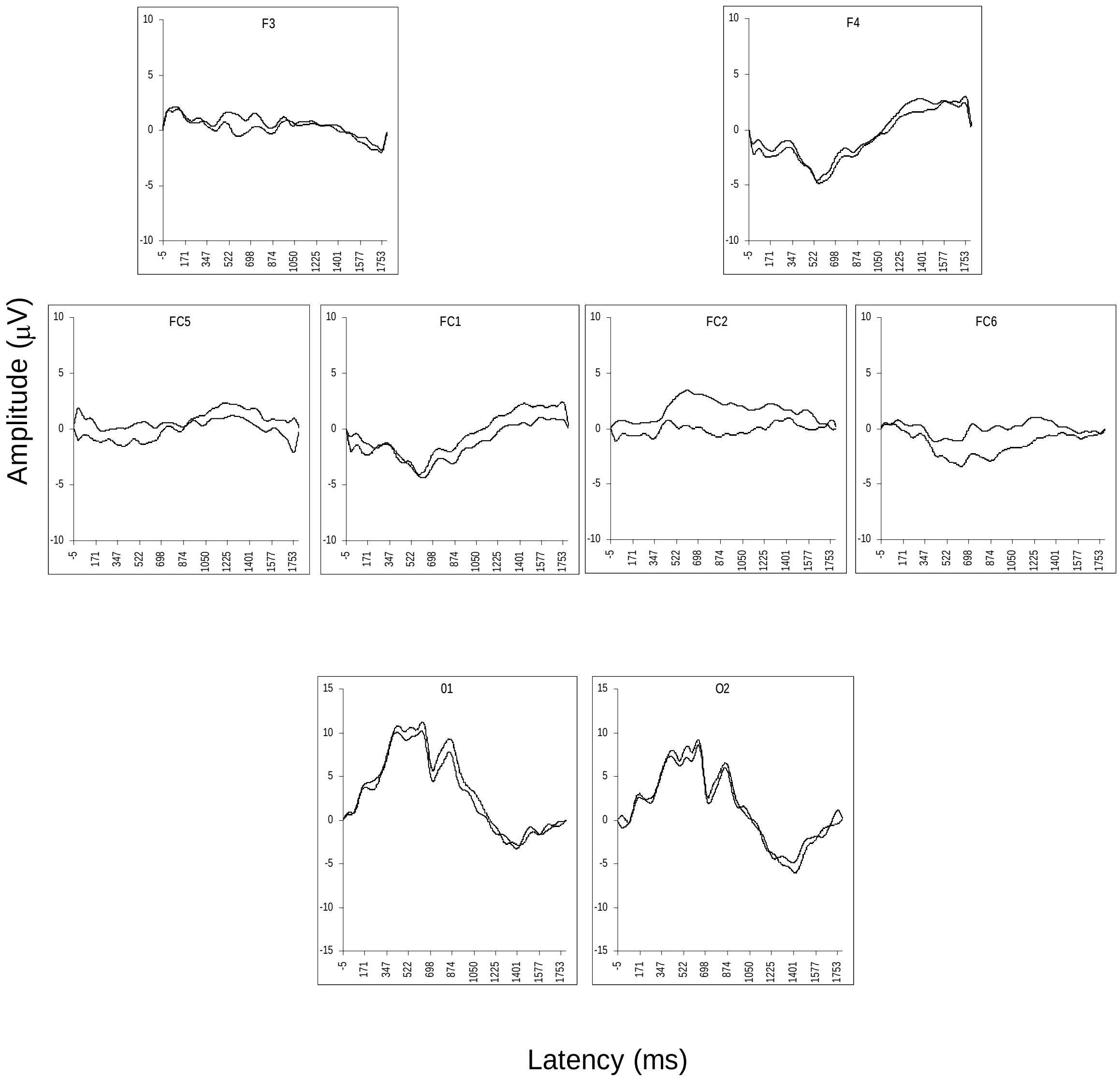
Figure Captions

Chapter III, Figure 1. Schematic of electrode locations on the scalp.

Chapter III, Figure 2. Grand Mean ERP waveforms exhibited by all subjects for both conditions over electrodes included in analyses. Amplitude (µV) is listed on the *y* axis and latency (ms) is listed on the *x* axis; (—) mother face and (- - -) stranger face. Nc component response was analyzed over fronto-lateral (F) electrode sites; P400 was analyzed over occipital (O1, O2) electrode sites.



Chapter III, Figure 1. Schematic of electrode locations on the scalp.



Chapter III, Figure 2. Grand Mean ERP waveforms exhibited by all subjects for both conditions over electrodes included in analyses. Amplitude (µV) is listed on the *y* axis and latency (ms) is listed on the *x* axis; (—) mother face and (- - -) stranger face. Nc component response was analyzed over fronto-lateral (F) electrode sites; P400 was analyzed over occipital (O1, O2) electrode sites.

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Chapter IV

Relations between Age, Behavior, and the Neural Correlates of Face Recognition in Toddlers

Abstract

Event-related potentials (ERPs) were recorded from three groups of 28- to 40-month-olds (N=47) as they looked at pictures of their mother's face and a stranger's face. A first goal of this study was to examine age-related change in the Negative component (Nc) and P400 responses to the two faces. A second goal was to explore a hypothesis of a potential relationship between the developing mother-child relationship and neural responses to the two faces. To this end, toddler behaviors were measured during a series of separations and reunions with the mother and related to Nc and P400 amplitude responses to the faces. Results indicated a decline in amplitude with age to faces in general for the Nc and P400 components of the ERP. Age-related changes in Nc responses to the mother's and stranger's faces were also found and suggest that the response to the stranger's face changes across this age range. Behavioral measures of toddler's negative affect during separations, positive affect on reunion and attachment and play behaviors during separations were also related to Nc amplitude responses to the mother's face only. The results suggest a relationship between age, behavior, and the neural correlates of face processing in 28- to 40-month-olds. The findings are discussed in the context of previous studies showing age-related changes in face processing in toddlers (Carver et al., 2003) and relations between behavior and face-processing in 6-month-olds (Swingler, Sweet & Carver, under review).

Relations between age, behavior, and neural correlates of face recognition in toddlers

The toddler years are a period of rapid developmental change in the child's linguistic, cognitive and socio-cognitive abilities, with the most dramatic shift in abilities occurring around 24 months of age (e.g. Bates, Thal, & Janowsky, 1992). The changes in the child's developing cognitive, socio-cognitive and linguistic abilities beginning at 24 months also seem to contribute significantly to changes in the mother-child relationship (Bowlby, 1969/1982; Bretherton, Bates, Benigni, Camioni & Volterra, 1979; Marvin & Greenberg, 1982) and vice versa (Cassidy, 1990). The clearest example of this is in the onset of cognitive perspective taking that occurs around 24 months of age and allows the toddler to begin to think about the mother's motivations and plans and to understand that these may be deviate from the child's plans. As a result, the child begins to attempt to induce the mother to change her plans to align more with the child's own (Marvin & Greenberg, 1982). In addition, the child's developing language abilities are rapidly improving at 24 months (Bates, Thal & Janowsky, 1992) and allow the mother and child to communicate their own goals and wishes better and help to facilitate negotiation of plans that are mutually acceptable. This results in a confidence in mutual understanding beginning around 24 months of age that allows the toddler to tolerate longer and longer separations from the mother (Ainsworth, 1989).

Research on the development of the mother-child relationship has established that by 12 months of age most children have a firmly established relationship with and representation of their mother (or primary caregiver), but that the nature of this relationship changes with age (Bowlby, 1968/1982, Ainsworth, 1989). Much of this research has been conducted by looking at behavioral responses to brief separations and reunions with the mother. Between 6 and 12 months infants are increasingly upset at separation from the mother and seek to maintain close proximity with her, especially following a separation (Cassidy & Shaver, 1999). Research on older infant and toddler responses to separations and reunions from the mother has demonstrated that 18-month-olds behave in much the same manner as 12-month-olds; most become very distressed, are not able to be comforted by another adult and seek close proximity with the mother on reunion (e.g. Cassidy, 1990; Marvin & Britner, 1999). However, beginning around 24 months of age there is a shift in the behavioral responses to separations from the mother.

While 24-month-olds do still more often than not respond with distress during separations, they also tend to rely more on calling and active search behaviors than on the crying behaviors typically seen in the younger ages (Marvin & Britner, 1999). Further, they are more likely than older toddlers to seek close proximity to the mother on reunion but this physical contact or proximity is less common than at younger ages and is often brief (Marvin, 1977). By 36 months of age, toddlers are more willing to be separated from the mother for brief amounts of time, especially when left in the company of a friendly adult. For 36-month-olds it appears that it is being left alone that is most distressing and likely to elicit a behavioral response. In addition, 36-month-olds are better able to wait out brief separations and require less contact on reunion (Marvin, 1972, 1977; Marvin & Britner, 1999). Finally, by 48 months toddlers separate easily from the mother, especially when they are prepared for this by a discussion with her before the separation occurs (Marvin & Britner, 1999).

This research suggests that the mother-child relationship begins to serve a new purpose for toddlers beginning around 24 months of age. These changes appear to be related, at least in part, to concurrent changes in the child's increased social-cognitive and affective perspective taking abilities (Marvin & Greenberg, 1982). The result of both is developmental change in toddlers' responses to separations and reunions with the mother, due at least in part to their confidence in the stability of a mutual understanding based on past interactional experiences (Ainsworth, 1989). This is often referred to in the literature as the child's working model of his or her relationship with the mother, and is proposed to develop as a result of accumulated experience in interaction with her (Bowlby, 1982; Ainsworth, 1989). Further, it has been proposed that experience in social interactions and changes in social behaviors may also be related to changes in brain areas involved in social development (e.g. Greenough, Black, & Wallace, 1987; Ainsworth, 1989; Carver et al., 2003). This suggests a hypothesis that social-emotional behavioral changes seen in the toddler years in response to the mother can be related to brain function, and that the changing role of the mother during this time period may be apparent in developmental changes in both behavioral and neural responses to her (e.g. Carver et al., 2003).

Indeed, Mary Ainsworth, a pioneer of theories surrounding the development of the mother-child relationship, noted in some of her later work that the attachment system includes not only its outward manifestations, but also an inner organization that is presumably rooted in neurophysiological processes. Further, she suggested that this inner organization is subject to developmental change because it is sensitive to environmental influences and experience, and that this change manifests in outwardly observable behaviors (Ainsworth, 1989). Therefore, as the inner organization of the mother-child relationship changes for the child in the course of development, so do outwardly observable behavioral manifestations of these changes as well as the situations in which the child displays these behaviors (Ainsworth, 1989). While the outwardly observable behavioral manifestations of developmental change in the mother-child relationship during the toddler years have been well documented, little work has explored potential measures of the inner neurophysiological processes or examined potential correlations between these processes and behavior.

One line of work that provides a potential measure of neurophysiological responses related to the developing mother-child relationship is in research examining developmental change in face processing in infants and young children. Evidence of developmental change in neural responses to the mother's face and a stranger's face has been found in research using Event-related potentials (ERPs) to measure neural responses to mother and stranger faces in infants and toddlers (e.g. de Haan & Nelson, 1997, 1999; Carver et al., 2003). Results from these studies have shown developmental shifts in ERP measures of face processing that occur at ages that have been suggested as important transitions in the mother-child relationship (e.g. Bowlby, 1969/1982; Ainsworth, 1989).

ERPs are measures of brain electrical activity in response to specified discrete events, such as the presentation of a face, and often used in developmental work because they provide a non-invasive and objective measure of neural response. The amplitude of the ERP is thought to reflect the summation of neural activity in which greater absolute amplitude reflects greater neural activation in response to a stimulus. In addition, because ERPs require no behavioral response on the part of infant and toddler participants it can provide valuable information where behavioral measures may not. Two ERP components have consistently been associated with face processing in infants and young children (see de Haan & Nelson, 1997, 1999; de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003) and are investigated in the current study.

The first component, the P400, has been used to index the development of face processing and has been suggested to be face sensitive, though it does not appear to be face specific (de Haan, Pascalis, & Johnson, 2002, Halit, de Haan, & Johnson, 2003). The P400 is a middle latency positive component localized over occipital electrodes. This component is sensitive to differences between faces and objects (de Haan and Nelson, 1999; Dawson et al., 2002), and between human and non-human faces in adults and older children, leading some researchers (de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003; de Haan, Johnson, & Halit, 2003) to suggest that it may be a developmental precursor to the N170, a face specific component seen in adults (Bentin, Allison, Puce, Perez, & McCarthy, 1996). The P400 appears to be sensitive to faces and appears to become more finely tuned to them with development (de Haan, Johnson, & Halit, 2003) and has shown variation with impairments in face processing in developmental disorders like autism. However, it also seems to be involved in more general aspects of object processing (Dawson et al, 2002). It may be that the P400 is a component that reflects aspects of visual attention and memory updating, and that this component is sensitive, but not specific, to face processing.

The second component, the Nc, is a middle-latency negative component that is maximal over central frontal electrodes and has been associated with increased attention, particularly to salient stimuli, (Courchesne, Ganz, & Norcia, 1981, Nelson, 1994) and with recognition memory (de Haan & Nelson, 1997, 1999; Nelson, 1994). de Haan and Nelson (1997) were the first to show that 6-month-olds' Nc component activity differentiated both a dissimilar and a similar looking strangers' face from their mothers', and that the pattern of neural activity elicited differed between these two conditions. However, the same component failed to distinguish between two stranger's faces, regardless of similarity between the two. This finding was robust even when the infants' were first familiarized to one of the faces. This suggests that different higher-order cognitive processes beyond novelty detection are activated to process a familiar, socially significant face paired with an unfamiliar face versus two unfamiliar faces, and that the Nc component is a sensitive measure of these processes.

A number of studies now have found that the amplitude of the Nc component response to the mother and a stranger varies with development. In the original work with six-month-olds by de Haan and Nelson (1997, 1999) the neural response to the mother's face was larger than the response to the stranger's face. Subsequent evidence from a longitudinal study using ERPs suggests that, in general, the pattern of processing the mother's face and a stranger's face reverses between 6 and 8 months and becomes larger to the stranger's face. This pattern stays stable at least through 12 months (Webb, Long, & Nelson, 2005) and is present in older (preschool age) children.

In addition, there is some evidence that the pattern may reverse again during the third year of life. A study by Carver and her colleagues (2003) found distinct, age-related changes in 18- to 54-month-olds brain responses to familiar and unfamiliar faces, but not familiar and unfamiliar objects. The youngest children in their sample, between 18 and 24 months of age, showed greater ERP responses to the mother's face than to a stranger's face. However, the oldest children in their sample, between 45 and 54 months of age, showed the opposite pattern; they had larger Nc amplitude responses to the stranger's face than the mother's. Children in the middle age group (24 to 45 months) did not show differential brain activity to the mother and stranger faces. This led to a hypothesis by Carver and colleagues (2003) that the age-related changes they observed in response to the faces were related to changes in the mother-child relationship that might also occur across the age range tested. They suggested that perhaps due to changes in the mother-child relationship at these ages the relative importance of the mother's and stranger's face may also change.

The current study investigated this hypothesis in a narrower age range of toddlers than have been examined before. The Carver study found that the younger and older age groups in their sample showed opposite patterns of neural responses to the two faces, of particular interest is the middle group (24 to 45 months) who showed no difference to the two faces. This suggested to Carver and colleagues (2003) that this may be a particularly transitional age range, not only in neural responses to the mother and stranger faces, but perhaps also in behavioral manifestations of the mother-child relationship. Therefore, the current study was conducted with 28- to 40-month-olds to examine potential age-related changes to mother and stranger faces in toddlers in the middle age range tested previously. A second goal of this study was to examine a potential relationship between behavioral responses to the mother and neural responses (ERPs) to mother and stranger faces in this age range. Toddler behaviors during structured separation and reunion interactions with their mother were measured and a potential relationship between differences in behavioral responses and neural responses to faces was examined. Twenty-four months seems to mark the beginning of an important shift in the child's understanding of the mother's goals and intentions and in responses to separations from her. This manifests itself in a new set of behavioral responses to brief separations and reunions with her that should be present in the ages tested in the current work. An examination of a potential link between behavioral responses to separations and reunions and neural responses to the two faces provides an important extension to the Carver and colleagues (2003) study conducted previously.

Methods

Participants

Participants were three groups of full-term, neurologically healthy children between the ages of 28 and 40 months: Group 1) 28- to 31-month-olds, Group 2) 32- to 35-month-olds, Group 4) 36- to 40-month-olds. See Table 1 for specific breakdown of age and gender information for each age range group. All toddlers were recruited from an existing list of parents who volunteered to participate in research after being contacted by mail following their child's birth. Thirty-three toddlers were Caucasian, 7 were Hispanic, 4 were Asian or Pacific Islander, 1 was Persian, 1 was Native American and 1 was African American. The children were primarily from middle-class homes and evenly split by gender, 25 were male and 22 were female. Families were given a small toy for the toddler and a printout picture of the toddler wearing the electrode cap as a thank-you for participating.

An additional 17 toddlers were tested but not included in the final sample because they did not provide interpretable ERP data, they would not comply with the testing procedures or because an error occurred during testing: 8 toddlers did not provide enough artifact free data to be included in analysis, 8 toddlers would not wear the ERP cap, and one toddler's data was lost due to experimenter error. This attrition rate is the same or lower than rates for other ERP studies conducted with the same or similar paradigm using this age group (e.g. Carver et al., 2003).

Stimuli

Each mother was photographed with a color digital camera from the neck up against a light grey background. Mothers wore the same grey scarf to obscure the neckline and clothing. Earrings and other jewelry were removed, but mothers that wore glasses were instructed to leave them on. Mothers assumed a neutral expression for the photograph. The picture of the mother's face was matched with another mother's picture so that paired faces were of the same ethnicity and mothers who wore glasses were paired together. Paired faces were chosen to be dissimilar in terms of hair color, face shape, eye color and facial features. Pictures of mothers were standardized in Microsoft Photoshop so that each face measured 18 (+/- 1) cm from the top of the head to the chin and 11 (+/- 1) cm from ear to ear.

Behavioral Procedure

The behavioral portion of the study used a paradigm inspired by the work of Ainsworth (e.g. Ainsworth, Waters, Blehar & Wall, 1978) and designed to measure toddler responses to the introduction of an unfamiliar adult, and two separations and reunions with the mother. Age related changes in behavioral reactions to these three situations have been observed in previous work and often used to describe characteristic changes that occur during the toddler years with regard to the changing mother-child relationship and the child's developing social interactive behaviors (Marvin & Britner, 1999). The procedure was videotaped and coded for behaviors exhibited by the toddler. Each session took place in a 10' x 12' room designed for behavioral testing and equipped with a camera located in one corner of the ceiling. This camera was controlled by an experimenter in an adjacent video room who watched the camera image on a TV screen and kept the camera focused on the toddler at all times. A second camera was located behind a one-way mirror on the door to the adjacent video room. This camera was also controlled by an experimenter and was kept focused on the mother and toddler when the mother was in the room and the toddler only when the mother was not in the room.

Two large blue armchairs were the only furniture in the room and several toys were provided for the toddlers to play with. These included a small red, squishy soccer ball, a Fisher Price© puppy with wheels that could be pulled along the ground, a large plastic school bus with a removable lid and stacking blocks inside, a Fisher Price Little People© Train with removable figures, and an interactive "fishing" puzzle with fish pieces that could be removed by a magnetized fishing pole. Mothers were instructed to sit on the floor or in a chair, wherever they were most comfortable, and to interact with their toddler as they normally would. A parenting magazine was available for mothers to read if they wanted.

The behavioral procedure was a series of eight intervals that, with two exceptions, were each two minutes in duration. See Table 2 for a description and timing of the intervals. The primary experimenter brought the mother and child into the testing room and performed consent with the mother while the child played with the toys. Following consent, the behavioral session began and the primary experimenter remained in the testing room for a one-minute interval before exiting to the adjacent video room. The mother and toddler were then alone in the testing room for two minutes before a new female (a "stranger") entered the room. The stranger entered slowly and sat quietly for at least 30 seconds before initiating interaction with the child. During this time the stranger could respond to any initiations of interaction by the child. The stranger then attempted to engage the toddler in play for two minutes. At the end of the two and a half minute interval, the mother was cued via headphones to exit to the adjacent video room. The stranger stayed in the room with the toddler and distracted or comforted the toddler if necessary. If the toddler was not distressed, the stranger waited until the mother was gone, and then pretended to be interested in reading a magazine. If the child was not distressed the stranger did not initiate interaction, but could respond to the child's bids for interaction. If the child was distressed, the stranger attempted to distract and soothe the child.

When possible, the mother remained out of the room for two minutes, however if the toddler became very upset and did not calm down the mother returned to the room early. After the mother had returned to the room and sat down, the stranger left the room and the mother and child were again alone in the room for two minutes. At the end of two minutes the mother was cued again via headphones to exit to the adjacent video room.

The child was left alone in the room for two minutes, but again this time was shortened if the child became distressed and did not calm down. At the end of this interval the stranger re-entered the room, greeted the child and sat down if the child was not distressed. If the child was distressed the stranger attempted to comfort the child and interest the child in playing with the toys. If the child was not distressed, this interval lasted two minutes before the mother returned to the room and the stranger left again. If the child was distressed and did not calm down, this interval was shortened and the mother returned early. The mother and child were alone again in the room for two minutes for the final interval of the behavioral session.

Behavioral Coding

Three coders watched the tapes of the behavioral sessions and coded toddler behaviors exhibited on three *a priori* behavioral constructs using an original coding scheme that was based on past work examining toddlers' behaviors during social interactions with the mother (NICHD Study of Early Child Care Manual, 1993) and toddlers' reactions to unfamiliar adults and separations and reunions with their mother (Greenburg & Marvin, 1989). The three coders were blind to the hypothesis of the study and had no knowledge of the toddlers' ERP data or results. Coders were trained by the primary investigator on the original coding scheme and achieved 84% reliability with her before coding independently. Coders overlapped on 25% of the participants for the purposes of measuring reliability. Coding pairs achieved 85% reliability for the data on which they overlapped in this paper.

To increase precision of coding, each of the eight intervals of the behavioral procedure was further sub-divided into fifteen-second segments, and behaviors were coded within each segment. Therefore, for an interval that lasted the full two minutes the behavior of interest was coded eight times. The behaviors measures included in this report were the following: toddler positive affect on reunions with the mother, toddler negative affect during separations from the mother, toddler play behaviors during separations from the mother and toddler attachment behaviors during separations from the mother.

Positive and negative affect coding scales were based on scales used in the NICHD Study of Early Child Care Manual for the 36-month lab visit. Positive and negative affect were coded separately such that, for example, a low score on positive affect did not indicate anything about overt negativity. The positive affect scale only assessed the presence and indications of positivity, not absence of negativity and vice versa (NICHD Study of Early Child Care Manual, 1993). Positive affect scores ranged from 1 = no explicit indicators of positivity observed, to 5 = child is clearly having a very good time, as revealed by smiles, laughter and tone of voice. A score of 2 on positive affect indicated that the child was relaxed and talking and that tone of voice was positive. A score of 3 or 4 required some evidence of pleasure via laughs and/or smiles. Positive affect was coded on reunion intervals 5 and 8.

Negative affect was also coded on a 5-point scale ranging from 1 = no evidence of negative affective expression is displayed, to 5 = child very frequently or markedly displays distress, anger, or hostility that lasts entire 15-second segment. A score of 2 on negative affect indicated that the child appeared uncomfortable or produced one or two isolated instances of a negative verbalization or act. A score of 3 on negative affect required modest evidence of negative affective expression that did not escalate into an extensive display; while a 4 indicated multiple expressions of negativity that were not isolated and escalated during the 15-second segment. Negative affect was coded during separation intervals 4, 6 and 7.

The second behavioral construct coded was toddler play behaviors. Coding of play behaviors was based on coding from the NICHD Study of Early Child Care 36-month assessment of sustained attention. Measures of play behavior included playing with toys, playing with other objects in the room (e.g. furniture), and social play. Play with toys was coded when the toddler was exploring visually and/or touching one or more of the toys provided in the room; play with other was coded when the child was exploring visually and/or touching other objects in the room (e.g. window blinds, chairs). Social play was coded when the child was interacting with the experimenter or the mother. Social play behaviors included showing objects, talking to the experimenter or mother socially or during play and/or touching the experimenter or mother socially or during play. In addition, the codes for play were not mutually exclusive, meaning that a child could have been (and often was) engaging in all three play behaviors simultaneously. Therefore, on any 15-second interval in which the child and an adult were in the room potential play behavior scores ranged from 0 to 3. Play behaviors were coded during separation intervals 4, 6 and 7.

The final behavioral construct coded was toddler attachment behaviors during separations. Attachment behaviors were defined as behaviors that predictably functioned to increase or maintain proximity or contact with the mother (Greenberg & Marvin, 1982). Specific behaviors chosen were based on attachment behaviors used in a study by Greenberg & Marvin (1982) assessing stranger wariness in toddlers. Attachment behaviors were coded every time the mother was absent from the room. Examples of attachment behaviors coded include approaching and/or banging on the door through which mother the exited, calling for mother and crying. See Table 3 for a list of attachment behaviors used on each interval. On intervals 4 and 7 of the behavioral session when the mother was absent but the stranger was present, the toddler could also potentially ask the stranger about the mother; therefore potential scores on attachment behaviors for segments of these two intervals ranged from 0 to 6. On interval 6, when the child was alone in the room, attachment behavior scores on each 15-second interval could range from 0 to 5. Attachment behaviors were coded on separation intervals 4, 6, and 7.

Behavioral Measures.

To create a single measure of each behavioral construct for each child, each measure was averaged across the 15-second segments in each interval to provide an average score on the interval and then averaged across intervals of the same type. This resulted in three separation measures: negative affect during separations, play during separations and attachment behaviors during separations. Toddler behaviors on intervals in which a separation occurred were the primary focus for this report. However, toddler's positive affect during reunion intervals was also included as positive responses to reunions have shown developmental change across these ages in work using similar behavioral paradigms (e.g. Marvin, 1977). Negative affect during separations scores ranged from 1 to 5 with an average score of 1.51 (*SD* = 1.04). The average amount of play during separations was 1.09 (*SD* =0.41, range = 0-1.75). Toddler attachment behaviors during separation scores ranged from 0 to 3.667, with an average score of 0.70

(*SD*= 0.87). Finally, scores on positive affect on reunions ranged from 1 to 2.5, with an average score of 1.81 (*SD* = .81)

Event-related-potential (ERP) testing

Upon completion of the behavioral session, the ERP testing began in another room. The circumference of the toddler's head was measured and the vertex marked. An appropriate size 32-channel electrode cap (Electro-Cap International) was fitted to the toddler's head according to the manufacturer's specification. Event-related potentials were recorded from the 31 active channels placed according to the international 10/20 system of electrode placement. The following standard electrode sites were used: Pz, Fz, O1, O2, P3, P4, T5, T6, C3, C4, T7, T8, F3, F4, F7, and F8. The following non-standard sites were also used: CPz, FCz, CP5 and CP6, CP1 and CP2, FC1 and FC2, FC5 and FC6, FP7 and FP8, and AF7 and AF8 (See Figure 1 for a schematic of electrode positions on the scalp). Electrode gel was placed into each of the 32 electrodes and impedance measurements were recorded prior to testing. Scalp impedances were measured before and after testing and were always kept below 10 kilo-ohms. Upon entry to the ERP testing room four additional electrodes were manually placed around the toddler's eyes for EOG measures of eye movements and blinking. Two electrodes were placed at the outer canthi of the eyes and two electrodes were placed above and below the right eye. Impedance measurements were also taken and recorded from these four electrodes prior to and immediately following testing. EOG impedances were ideally kept below 30 kilo-ohms, however this goal was sacrificed if the toddler was becoming impatient with the testing procedure or was bothered by the stickers on their face or close to their eyes.

Testing for all toddlers took place in the same sound attenuated and electrically shielded room. During the testing session the toddler either sat on the mother's lap or by themselves in a chair about 70 cm from a computer screen that delivered the stimuli. Mothers were instructed to remain as quiet as possible during the entire ERP testing session. A large, trifold grey screen with a window cutout for the computer screen obscured the back of the monitor and part of the room from view. There were cracks between the panels of the screen through which an observer watched toddlers and signaled the computer via button press if the toddler was not looking at the computer screen. A second experimenter was present in the room and stood behind or beside the toddler and pretended to watch the pictures with the toddler. If needed, this experimenter verbally reminded the child to look at the computer screen or tapped the computer screen during the inter-trial interval to attract the toddler's attention back to the pictures. Each trial consisted of a 100-ms baseline, 500-ms presentation of the stimulus, and 1200-ms recording period during which the computer screen was grey. Trials were separated by a randomly varying 500 to 1000 ms inter-trial interval. The order in which the stimuli were presented was randomized across infants. Data collection was terminated when the child had seen all of the 100 trials (50 mother and 50 stranger) or when the child was no longer tolerant of the testing procedure. Trials on which the child did not attend to the stimuli or during which the experimenter was attempting to attract the child's attention to the pictures were removed after data collection.

EEG Recording

EEG was recorded continuously from thirty-two electrode channels. The data from the first 24 participants were collected using Instep (Instep Systems, Ottawa, Ontario), and data from the remaining 23 participants with Neuroscan (Compumedics Neuroscan, Charlotte, NC); however the same recording parameters were used on both systems to ensure continuity of the data. Signals were amplified and filtered through a .1 Hz high-pass filter and 100 Hz low-pass filter. A 60Hz notch filter was in place during recording. The EEG signals were amplified with a gain of 20,000 and EOG signals were amplified with a gain of 5,000. Data were recorded continuously, and saved to a file in the computer-assisted scoring program on the data collection computer. A second computer generated the stimuli and the two computers were interfaced via serial port for precise synchronization. The timing of the stimulus onset and offset was registered together with the physiological recorder for off-line segmentation of the data. Each toddler's EEG data was referenced to Cz and re-referenced off-line to an average reference using the computer-assisted program. This reference was chosen primarily to replicate previous studies of face processing in toddlers. Although the number of electrodes used in the present study is relatively small for an average reference, each method of referencing has advantages and disadvantages, an average reference was chosen in order to be able to compare our results to previous studies using the same paradigm (e.g. Dawson et al., 2002; Carver et al., 2003, Halit, de Haan & Johnson, 2003).

ERP Reduction

After testing, each toddler's ERP data were edited off-line. Trials in which the child did not attend to the pictures were excluded from the data set. Any channels in which the EEG signal amplitude exceeded 250 μV were excluded from the trial as artifact. Trials in which EOG artifact occurred, i.e. eye blinks or large eye movement, were also excluded. Additional artifact was rejected when amplitudes exceeded A/D values, which results in clipping (flat-lining of the signal from the amplifier), and upon visual inspection. Only subjects with more than 10 artifact free trials in each condition were included in the final sample. The mean numbers of artifact free trials of each condition in the final data set were not different from one another (Mother condition M = 25.55, *SD* = 8.36; Stranger condition M = 29.38, *SD* = 8.73).

ERP Measures.

Components of interest were determined based on previous research findings from developmental studies of face processing (e.g., de Haan & Nelson, 1997, 1999; Swingler et al., 2007; Carver et al., 2003). For the two components of interest, the Nc was defined as the maximum negative peak recorded distributed over frontal electrode sites FCz, Fz, FC1/2, F3/4, F7/8, occurring between 360 and 920 ms following stimulus onset and the P400 was defined as the maximum positive peak over occipital electrode leads (O1 and O2) between 350 and 650 ms following stimulus onset. These time windows were based on those used in the Carver et al. (2003) study with toddlers using the same ERP paradigm. However, visual inspection of the data suggested that a narrower time window than the one used in the Carver study was necessary to capture the true peak for every subject in this sample. A computer-assisted program extracted the peak amplitude for each component specified for each subject. The electrodes used in the components analyses were determined by selecting those electrodes at which the waveform morphology was prominent, and by using electrode sites comparable to those used in previous research. Dependent measures for the analyses of the P400 and Nc components were peak amplitudes.

Results

The first goal of this paper was to look for age-related changes in three groups of toddlers in the age range of the middle age group of toddlers included in the Carver and colleagues study (2003) who did not show differences in ERP responses to mother and stranger faces. A second goal of this paper was to examine the effect of toddler's behavior during this age range on components of ERP response to the two faces. Therefore, age and behavior effects on ERP amplitudes to the mother and stranger faces were analyzed separately. Correlation analyses revealed that scores on the behavioral measures were not significantly correlated with age in our sample of toddlers: Negative affect during separations, $r = -.20$, $p = .17$; Play behaviors during separations, $r = .17$, $p = .25$; Attachment behaviors during separations, $r = -.14$, $p = .34$; Positive affect on reunions, $r = .12$, $p = .40$.

Age Effects

Repeated-measures analyses were conducted to determine if age was related to peak amplitudes of the P400 and Nc components, and to determine if this relationship differed as a function of face identity and lead location. Two separate Nc analyses were conducted; one including only midline leads, and one including only lateral leads. Lateral leads were analyzed separately by hemisphere to enable detection of potential hemisphere effects on face processing. Nc midline leads included in analysis were Fz and FCz, and lateral lead pairs included were FC1/FC2, F3/F4 and F7/F8 (see Figure 1 for lead location). Lead pairs were analyzed specifically to allow for detection of possible hemisphere effects. Analyses of the P400 component were performed for occipital electrodes O1 and O2 only.

P400 Component

A trend for a main effect of condition was observed, F (1, 42) = 2.890, *p*= .09, η_p^{2}= .064. The amplitude of the P400 response was marginally larger to the stranger's face (M = 21.56, SE = 2.05) than to the mother's face (M = 19.48, SE = 1.74) when collapsed across both occipital electrode sites. However, this marginal effect was primarily driven by a significant main effect of condition at the left occipital lead O1, F(1, 44) = 3.912, *p*= .05, η_p^2 = .082. At O1, P400 amplitude responses to the stranger's face (M = 20.95, SE = 2.07) were significantly more positive than responses to the mother's face (M = 17.19, SE = 1.91) for all toddlers. This effect was not present at the right occipital lead O2.

In addition, a significant main effect of AGE group was observed for the P400 response to both faces at the occipital leads, F (2, 42) = 4.645, *p*= .015, η_p^2 = .181. However, a significant LEAD x AGE group interaction, F (2, 42) = 4.871, *p*= .013, η_p^2 = .188 revealed that the effect of age group on amplitude of the P400 response was not the same for both electrode locations. P400 amplitudes to both faces decreased with age at both electrodes, but this was only significant at O2 (see Figure 2). At the left occipital lead, O1, the effect of age group on the P400 response to the faces was only marginally significant, F (2,44) = 2.524, *p*= .09. However, at the right occipital lead, O2, the effect of age group was significant, F (2,42) = 6.616, *p*= .003, η_p^2= .701. The mean responses to the two faces at O2 revealed that amplitude of the P400 response to the faces became smaller with age; Group 1: M = 32.26 (*SE* = 3.69), Group 2: M = 19.92 (*SE* =3.94), Group 3: M = 13.31 (*SE* = 3.81). Bonferroni-corrected pairwise comparisons revealed that the P400 response for the oldest group of toddlers (36- to 40-month-olds) was significantly different from the P400 response of the youngest age group (28- to 31-

month-olds), *p*= .05, but was not significantly different from the middle group (32- to 35-month-olds), *p*= .70. The youngest two AGE groups showed a marginally significant trend (*p*= .08) towards being significantly different from one another.

Nc Component

Midline Leads

The Nc component midline lead analysis was conducted with midline leads Fz and FCz. A 3 (AGE group: 28-31, 32- 35, 36- 40) x 2 (FACE condition: mother, stranger) x 2 (LEAD location: Fz and FCz) repeated measures ANOVA was conducted with amplitude of the Nc response at the midline leads as the dependent measure. This analysis revealed a significant FACE condition x LEAD location x AGE group interaction, $F(2,43) = 3.955$, $p = .027$, $\eta_p^2 = .155$. Follow-up analyses revealed a FACE condition x AGE group interaction that approached significance at the midline lead Fz only, $F(2,43) = 2.972$, $p = .062$, $\eta_p^2 = .121$ (see Figure 3).

Examination of the means tables for the AGE group x FACE condition interaction revealed that for the youngest group of toddlers in the sample (28 to 31 months) mean amplitude responses were larger to the stranger's face (M = -8.013, *SE* = 1.368), than to the mother's face (M = -5.823, *SE* = 1.454). The amplitude responses for toddlers in the middle age group (32 to 35 months) were not different for the stranger (M = -6.856, *SE* = 1.368) and mother (M = -6.717, *SE* = 1.454) faces. In contrast the oldest group of toddlers (36 to 40 months) showed a larger response to the mother's face (M = -5.068, *SE*=1.408) than to the stranger's face, (M = -2.676, *SE* = 1.325). The effect of AGE group was significant in the stranger face condition *only* (*p*= .018), the age groups did not significantly differ in their Nc responses to the mother face condition. Bonferroni corrected pairwise comparisons showed that the oldest group of toddlers (Group 3) significantly differed from the youngest age group (Group 1) in their Nc response to the stranger's face (*p* = .023), but not the middle age group although this effect was marginally significant (*p*= .10). The two youngest groups were not significantly different from one another.

Lateral Leads

Analyses of the Nc component at lateral leads included the between subjects variable AGE group, as well as the within-subjects variables of FACE condition (mother, stranger), LEAD pair (FC1/FC2, F3/F4, F7/F8), and HEMIsphere (left, right). The 2 (FACE) x 3 (LEAD) x 2 (HEMI) x 3 (AGE) repeated measures ANOVA revealed a significant main effect of FACE condition, $F(1,38) = 4.857$, $p= .034$, $\eta_p^2= .113$. The mean amplitude Nc response to the mother's face (M = -7.085, *SE* = .662) was significantly more negative than the response to the stranger's face (M = -6.233, *SE* =.652) at the lateral lead locations for all toddlers in the sample. A significant main effect of LEAD, $F(2,37) = 7.984$, $p=.001$, $\eta_p^2= .301$ also emerged, the mean amplitude Nc responses were significantly more negative for the frontal electrode pair F7/F8, than for the other two electrode pairs.

In addition, a significant main effect of AGE group was present for the Nc response at lateral lead locations, $F(2,38)= 10.021$, $p< .001$, $\eta_p^2 = .345$ (see Figure 4). Nc amplitudes to faces became less negative (smaller) with age: Oldest Group 1, M= -9.719 (*SE*= 1.027); Middle Group 2, M= -7.020 (*SE*= 1.200); Youngest Group 3, M= -3.239 (*SE*=1.027). Bonferroni-corrected pairwise comparisons indicated that toddlers in the oldest age group had significantly different Nc amplitude responses to faces than toddlers in the youngest age group (*p* <.001). The comparison between the oldest toddler group and the middle toddler group approached significance (*p*= .065). The youngest age groups were not significantly different from one another in these comparisons (*p*= .287).

Behavior Effects

Repeated-measures ANOVAs were conducted to determine if scores on the four behavioral measures were related to peak amplitude of the P400 and Nc components, and to determine if these relationships differed as a function of face identity and lead location. Analyses of the ERP components included the same leads as were included in the Age analyses above. Only significant and marginally significant effects involving the behavioral measures and FACE are reported, as these relate directly to the study hypotheses.

P400 Component

There were no main effects or interactions between scores on the behavioral variables and P400 amplitudes to the two faces.

Nc Component

Midline Leads

Affect

A marginally significant negative affect during separation x FACE condition (mother, stranger) x LEAD interaction emerged, $F(1,43)= 3.216$, $p= .080$, $\eta_p^2 = .048$. Follow-up analyses revealed that negative affect scores significantly interacted with FACE condition at midline lead FCz, $F(1,44)= 6.280$, $p= .016$, $\eta_p^2 = .125$. Higher scores on the negative affect variable were associated with more negative (larger) Nc component amplitudes in the mother face condition only ($\beta= -1.178$, *SE* = .684), although this association was only marginally significant, *p*= .09. No association between scores on the negative affect during separation variable and responses to the stranger's face were present.

The analyses of midline leads also revealed a marginally significant interaction between positive affect on reunions x FACE condition x LEAD, F(1,43)= 2.809, *p*= .101, η_p^2 = .061. Follow-up analyses revealed that positive affect on reunion marginally significantly interacted with FACE condition at midline lead FCz, F(1,44)= 3.299, *p*= .076, η_p^2= .070. This indicates that the relationship between positive affect on reunions and Nc amplitude at this lead differed significantly across the two FACE conditions. Positive affect on reunion scores appeared to be most related to amplitude responses to the mother's face, however this relationship did not reach statistical significance, *p* = .141.

Attachment Behaviors during Separation

A marginally significant attachment behavior x FACE condition interaction emerged, F(1,44)= 2.699, *p*= .108, η_p^2 = .058. This was primarily driven by a significant attachment behavior x FACE condition interaction at FCz, F(1,45) = 4.735, *p*= .035, η_p^2 = .095. Scores on the attachment behaviors during separation variable were significantly related to the Nc component response to the mother's face only at FCz, F(1,45)= 4.754, *p*= .034, η_p^2 = .096. Higher scores on the attachment behaviors variable were associated with more negative (larger) Nc component response to the mother's face (β= -1.765, *SE* = .809). No such relationship was present for the stranger's face.

Play Behaviors during Separation

There were no significant main effects or interactions between scores on the play behaviors during separation variable and Nc amplitudes to the two faces at midline leads.

Lateral Leads

Affect

There were no significant main effects or interactions between the scores on the negative affect during separations or positive affect on reunions behavioral variables and the Nc response to the two faces at lateral leads.

Attachment Behaviors

A significant attachment behaviors x FACE condition x HEMIsphere interaction emerged, $F(1,39)= 4.030$, $p= .052$, $\eta_p^2= .094$. This interaction was due to a significant relationship between attachment behavior scores and Nc amplitudes to the mother's face only at the left frontal electrode F7. This relationship was significant and positive ($\beta= 4.032$, $SE = 1.81$, $p= .031$). As scores on the attachment behaviors during separation variable increased, amplitude responses to the mother's face became more positive (less negative or smaller).

Play Behaviors

A marginally significant play behaviors x FACE condition x HEMIsphere interaction emerged, $F(1,39)= 3.604$, $p=.065$, $\eta_p^2= .085$. This interaction was due to a significant relationship between play behavior scores and Nc amplitudes to the mother's face only at the left frontal electrode F7. This relationship was significant and negative ($\beta= -9.184$, $SE = 3.52$, $p= .012$). As scores on the play behaviors during separation variable increased, amplitudes to the mother's face only became more negative (larger) at the left frontal lead F7.

Discussion

Age effects

This study was undertaken with two primary goals in mind. The first was to provide a follow-up to earlier work (Carver et al., 2003) on face processing that found age-related differences in the neural responses to mother and stranger faces in 18- to 24-month-olds and 45- to 54-month-olds, but not in children between 24 and 45 months of age. The authors of the previous work suggested that 24 to 45 months might be a particularly transitional point in development with regard to processing mother and stranger faces, and therefore, these ages warranted a closer examination. A second goal was to provide an extension of the earlier work by examining the hypothesis proposed by those authors (Carver et al., 2003) that age-related changes in the neural correlates of processing the two faces were related to changes in the developing mother-child relationship, and specifically to a changing role of the mother for toddlers during these ages.

With regard to the first goal, the current work found evidence of age-related change to processing both faces for both ERP components investigated. This suggests potential age related change in how faces in general are processed across the three age groups tested here. Amplitude responses to the faces tended to decrease with age for both the P400 component and the Nc component. This relationship for the P400 component was particularly evident at the right occipital electrode lead, O2. At O2, the youngest group of toddlers (28- to 31-month-olds) produced significantly larger amplitudes in response to the faces when compared with the oldest group of toddlers (36- to 40-month-olds). In addition, the comparison between the amplitudes to faces in the youngest and middle age group (32- to 35-month-olds) was marginally significant, but the middle and oldest age groups were not significantly different from one another. This suggests a general shift in the P400 responses to faces that may occur specifically between 32 and 35 months of age.

A similar shift was present in the amplitudes of the Nc component response to faces at lateral lead locations. However, the findings for this component suggest that the developmental shift in the Nc may occur slightly later than for the P400. The oldest age group produced significantly smaller amplitudes to the faces compared to the youngest age group, and marginally significantly smaller amplitudes compared to the middle age group. The youngest and middle age group amplitudes to the faces were not significantly different from one another. This suggests that there may be age-related changes for the Nc response elicited by faces between 28 and 40 months, and that these changes occur towards the latter end of the range.

This finding may provide additional support for a view that has been suggested before in face processing work with toddlers (Carver et al., 2003), that patterns of face processing in general change with increased expertise with faces. That is, with increased experience with faces the attentional, recognition and working memory resources recruited for processing them may decrease. This may be especially true with regard to distinguishing a very familiar face, like the mother's, from an unfamiliar face. Event-related potential work with adults has documented the properties of components related to the perception and recognition of faces. Findings from multiple studies have suggested that longer-latency (>400 ms after stimulus onset) components like the N400 and P600 in adults are related to recognition of facial identity (Eimer, 2000b; Itier & Taylor, 2002) and/or retrieval of semantic information related to faces (e.g. Paller et al., 2000). While relatively fewer studies have examined the neural correlates of face recognition in infants (and even fewer in toddlers), the Nc component is one of the most well-studied components of developmental cognitive ERPs. Current theories based on results from these studies hold that the Nc reflects allocation of attention and aspects of recognition and that it may reflect aspects of the adult N400 (de Haan, Johnson, & Halit, 2003). While less is known about the specific role for the P400 in the development of face processing, it appears to become more finely tuned to human faces with age (de Haan, Johnson, & Halit, 2003). Therefore, the decrease in the Nc and P400 amplitudes with age to faces seen here may indicate that with increased experience processing faces in general, and recognizing the mother's face specifically, the neural resources recruited for performing these tasks are fewer. However, further work with toddlers and older children would be necessary to test this hypothesis directly. Similar findings were not reported in the few studies of face processing in toddlers that have been conducted (e.g. Carver et al., 2003; Dawson et al., 2002), although these studies also used different paradigms and examined different age ranges.

With regard to the ERP responses to the identity of the faces in this sample, a main effect of condition was present for all toddlers, for both the Nc and P400 components. The P400 component response to the stranger's face was significantly larger than the response to the mother's face in the current sample of toddlers. This effect was particularly significant for the P400 component at the left occipital electrode O1. Conversely, Nc amplitudes to the mother's face were significantly larger than to the stranger's face. Thus, the current sample of 28- to 40-month-olds demonstrated a pattern of responding to the mother and stranger faces that was the similar to *both* the younger and older toddlers in the previous work (Carver et al., 2003). That is, the toddlers in the current work showed P400 responses to the two faces that were similar to the oldest group of toddlers in the Carver and colleagues study, but Nc responses that were similar to the youngest group in the previous work. This finding provides support for the notion that this age is particularly transitional with regard to the changing pattern of processing mother and stranger faces. More specifically, though, these results suggest that developmental change in the responses to the two faces is evident earlier in the P400 component than the Nc component and that toddlers continue to allocate more frontal attentional resources to processing the mother's face for a longer period in development. These findings may also provide further support for the influence of transitions in the mother-child relationship, especially during this age range, on patterns of face processing. It will be important to conduct future work with younger toddlers, perhaps at exactly 24 months of age, as well as between 24 and 28 months of age, to further pinpoint when these transitions in responses to the two faces first begin to occur.

In addition, the amplitude of the Nc at midline leads showed a significant interaction between face identity and age of toddlers suggesting age-related changes to the identity of the two faces. The interaction between face identity and age of the toddlers was marginally significant at the midline lead Fz. The youngest group of toddlers in our sample showed a larger amplitude Nc response to the stranger's face than to the mother's face, while the oldest group of toddlers showed a larger Nc amplitude response to the mother's face. The middle age group showed no difference in the Nc amplitudes to the two faces. Further, this effect was significant for the response to the stranger's face *only*. The oldest group of toddlers had significantly smaller amplitude responses to the stranger's face than the youngest group of toddlers, and only marginally smaller amplitudes to the stranger's face than the middle group of toddlers. The two youngest groups were not significantly different from one another in the response to the stranger's face. This finding is difficult to interpret given the results discussed above on the decline in Nc amplitude; it could be that this result could be explained simply by the general decline in Nc amplitudes to faces with increasing age. However, this same relationship was not present for the response to the mother's face. Therefore, it appears that while amplitudes of the Nc declined with age to the faces in general, this declination was not as abrupt or dramatic for the mother's face as it was for the unfamiliar stranger face. That is, the mother's face may remain a special category of stimuli for toddlers and perhaps throughout childhood. However, the current findings only suggest this hypothesis, but do not specifically address it.

Behavior effects

An interesting general finding with regard to the relationship between behaviors toddlers' produced during the separation and reunion procedure and neural responses to faces is that scores on the behavioral variables interacted with responses to the mother's face *only*. This provides some support for the hypothesis proposed in the Carver and colleagues study (2003) that the changing role of the mother in this age range should be apparent in developmental changes in the neural correlates of cognitive and social responses to her. In addition, behavior interacted with the neural responses to the mother's face for the Nc amplitude only. This is interesting because it suggests that different behavioral responses to the mother are potentially associated with more or less allocation of attentional resources to processing her face.

At the midline lead, FCz, negative affect during separations and attachment behaviors during separations were both related to Nc amplitudes to the mother's face. As scores on both of these variables increased, amplitudes to the mother's face became more negative; or larger since the Nc is a negative component. This finding suggests that toddlers who showed more distress during separations from the mother also allocated more attentional resources to processing her face. It should be acknowledged that negative affect during separations and attachment behaviors during separations were related to one another and therefore, likely represent a common construct of distress during separations. Indeed, as might be predicted, children who made many attempts to follow the mother by approaching and banging on the door through which she exited and calling for her were also showing high levels of negative affect. Therefore, in the future these two constructs may be considered together as a general distress measure.

However, the fact that toddlers who showed more affective and active distress behaviors during separations also had larger Nc component responses to the mother's face provides preliminary evidence for a potential relationship between behavioral responses indicative of transitions in the mother-child relationship and neural responses to the mother. The age of the child was not significantly related to the child's behavioral responses during the separations and reunions in this sample. Thus, it was not the case that 28-month-olds were more likely to respond to separations with distress than 40-month-olds. This suggests that potentially what we were measuring were individual differences in behavioral responses, rather than age-related changes in behaviors. Indeed, based on the prior work suggesting that 24 months begins a significant transition in the mother-child relationship (Marvin & Britner, 1999; Marvin, 1977), all of the children in our sample were likely past this transition. Therefore, it seems that it was individual differences in behavioral responses to the behavioral situation that were related to processing the mother's face. It would be beneficial in future research to extend this work to measure attachment security, which is a well-studied and validated measure of individual differences in the qualitative nature of the attachment between mother and child (Ainsworth, 1989). This assessment is most accurate and well validated at 12 months and has proven to be a powerful measure that has repeatedly been shown to be stable (Cassidy, 1990), but a number of researchers have extended its use for 18-month-olds and toddlers (e.g. Marvin, 1972, 1977).

Interestingly, distress during separations appears to correlate with neural responses to the mother's face at an earlier transition in the mother-child relationship as well. A recent paper by Swingler, Sweet & Carver (under review) reported a relationship between amounts of distress behavior 6-month-olds produced during separations from their mother and left hemisphere Nc amplitude responses to the mother's face. In line with the findings here, higher amounts of distress behavior were associated with larger amplitude responses to the mother's face at left hemisphere leads. This suggests that amount of distress during separations may be an important measure of individual differences in the developing mother-child relationship during transitional ages that shows an association with neural responses to the mother's face. Indeed, in the work with six-month-olds, distress during separations correlated significantly with both the Nc and P400 components of the ERP response to faces.

The effect of behavior was also significant at the left frontal lead, F7, although the relationship here was less intuitive. Toddlers who showed more attachment behaviors during separations also showed smaller (less negative) responses to the mother's face at this electrode. However, given the relationship between attachment behaviors and Nc responses to the mother's face at midline leads, and the nature of ERPs, it is possible that this effect is a by-product of that relationship. The Nc is maximally distributed over midline locations, suggesting that this area is the likely "source" of the electrical activity producing the signal. Since the amplitude of the ERP is a measure of summation of neural activity, in a negative component the source of the activity produces more negative amplitudes. However, as this signal propagates forward and farther from the source it becomes less negative, or more positive. Therefore, it is possible that the inverse relationship between attachment behaviors and Nc amplitudes at the midline lead FCz and the frontal lead F7 if a function of the propagation forward of the same neural response.

Play behaviors during separations was also significantly related to the amplitude of the response to the stranger's face at the left frontal lead, F7. Higher levels of play behaviors during separations were associated with more negative amplitude responses to the mother's face at F7. This relationship is somewhat puzzling. Presumably, toddlers who continued to play during separations were not distressed by the mother's absence. However, it is possible that play during separations is a strategy used by some children in order to wait out a separation from the mother. The current data do not allow for further exploration of this relationship, but it would be interesting to explore in future work.

General Discussion

The results of the current study suggested a number of interesting age-related changes in the neural responses to faces in 28- to 40-month-olds. Collapsed across age, all toddlers in this sample showed evidence of discriminating their mother's face from a stranger's face in both components of the ERP response examined here. However, the specific pattern of response in the current sample of toddlers was similar to older toddlers' P400 responses to mother and stranger faces, but younger toddlers' Nc responses to mother and stranger faces found in the Carver study (2003) and suggests developmental change in processing the mother and stranger faces occurs between 28 and 54 months of age. This confirms the idea that the time between 28 and 40 months of age is particularly transitional with regard to changing responses to mother and stranger faces. The findings also suggests a need for a closer examination of 24-month-olds and 24- to 28-month-olds as an age or age range at which transition may begin with regard to face processing and potentially with regard to a relationship between face processing and the mother-child relationship.

Preliminary evidence for a relationship between age group and the identity of the face was also found. This result was consistent with previous work showing age related change in the Nc response to mother and stranger faces. In addition, the age related change was only in the Nc responses to the stranger's face that became smaller with age. This is an opposite pattern to what was found in the Carver study (2003) with a wider age range of toddlers; age-related differences in that study were only for responses to the mother's face. However, that study included toddlers from 18 to 54 months and therefore the change was over a much broader age range. In addition, it is important to note that while this study provides an important follow-up to the Carver study, the methodologies used for collection of the ERP data were not the same. The Carver and colleagues study (2003) used a 64-channel Geodesic sensor net (EGI) for ERP data collection. Therefore, that study included many more lead locations, and this allowed for analyses using regions of interest (ROIs) which involved averaging left lateral, right lateral and midline leads of interest together. Comparisons between the two studies should take into account these differences in methodology.

In addition, preliminary evidence was found for a potential relationship between behaviors toddlers' produced during separations and reunions with the mother and amplitude of the Nc response to her face. Distress behaviors during separation appeared to have the strongest relationship with neural responses to the mother's face. This provides the first evidence of its kind in toddlers, and fits with a previous finding showing the same relationship in 6-month-olds (Swingler, Sweet & Carver, under review). Taken together, these results suggest a potential important relationship at transitional ages in the mother-child relationship between amount of distress during separations, and neural responses to the mother's face.

Chapter IV, Table 1

Age and gender information for the three groups of toddler participants

Group	**1**	**2**	**3**
Age range (months)	28 – 31	32 - 35	36 - 40
Mean age (months)	29.2	33.1	38.8
N	16	15	16
Gender (m,f)	8,8	8,7	9,7

Chapter IV, Table 2

Behavioral procedure

INTERVAL	TIME (Minutes)	ACTIVITY
1	0:00-1:00	Primary Experimenter (consent), Mother & Toddler in testing room. Primary experimenter may interact with toddler if toddler initiates.
1	1:00	Experimenter 1 exits to the video room.
2	1:00-3:00	Mother & Toddler alone in the testing room.
3	3:00-3:30	Experimenter 2 (Stranger) enters testing room from the video room slowly and sits in chair or stands by door.
3	3:30- 5:30	Experimenter 3 approaches toddler and initiates play and conversation.
3	5:30*	As cued by Primary Experimenter, Mother exits to the video room.
4	5:30-7:30	Stranger in room with Toddler. Stranger comforts or distracts if necessary, acts interested in magazine if not.
5	7:30-9:30	Mother returns to the room and resumes interaction. Stranger exits to the video room.
6	9:30-11:30*	Mother exits again to video room, Toddler alone in the testing room for 2 minutes. Interval is shortened if Toddler becomes upset.
7	11:30 – 13:30	Stranger returns to testing room, greets Toddler and sits down. Comforts or distracts if necessary.
8	13:30-15:30	Mother returns to testing room and resumes interaction with Toddler for final 2 minutes. Stranger exists to video room.

* Primary Experimenter cues Mother from the video room over the headphones.

Chapter IV, Table 3

Attachment behaviors coded on intervals of the behavioral session

Interval	Interval 6 (Toddler alone separation)	Intervals 4 and 7 (Stranger present separation)
Behaviors coded	• Looking at door through which mother exited • Approaching and/or banging on door • Calling for mother • Crying • Approaching mother's chair (where not immediately followed by retrieving a toy or playing with mother's purse)	• Looking at door through which mother exited • Approaching and/or banging on door • Calling for mother • Crying • Approaching mother's chair (where not immediately followed by retrieving a toy or playing with mother's purse) • Asking stranger about mother

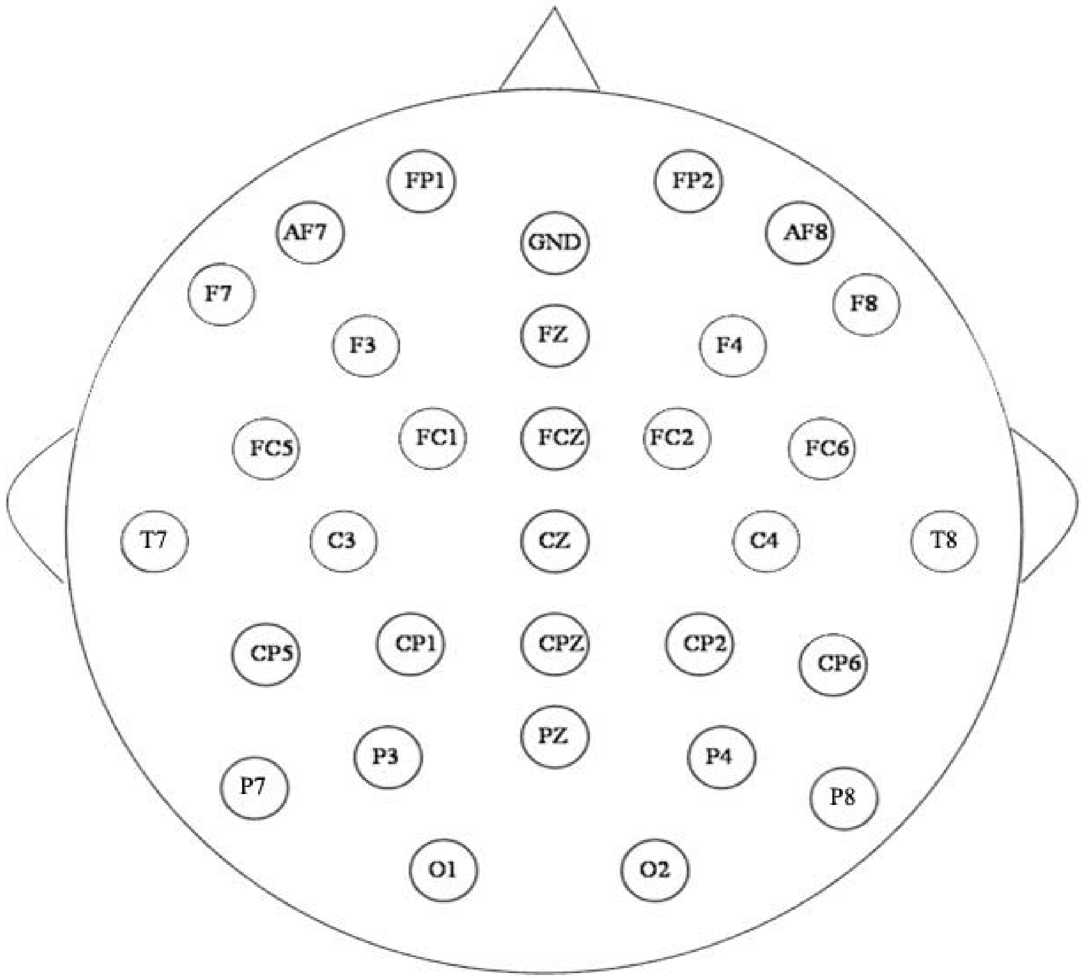
Figure Captions

Chapter IV, Figure 1. Schematic of electrode locations on the scalp.

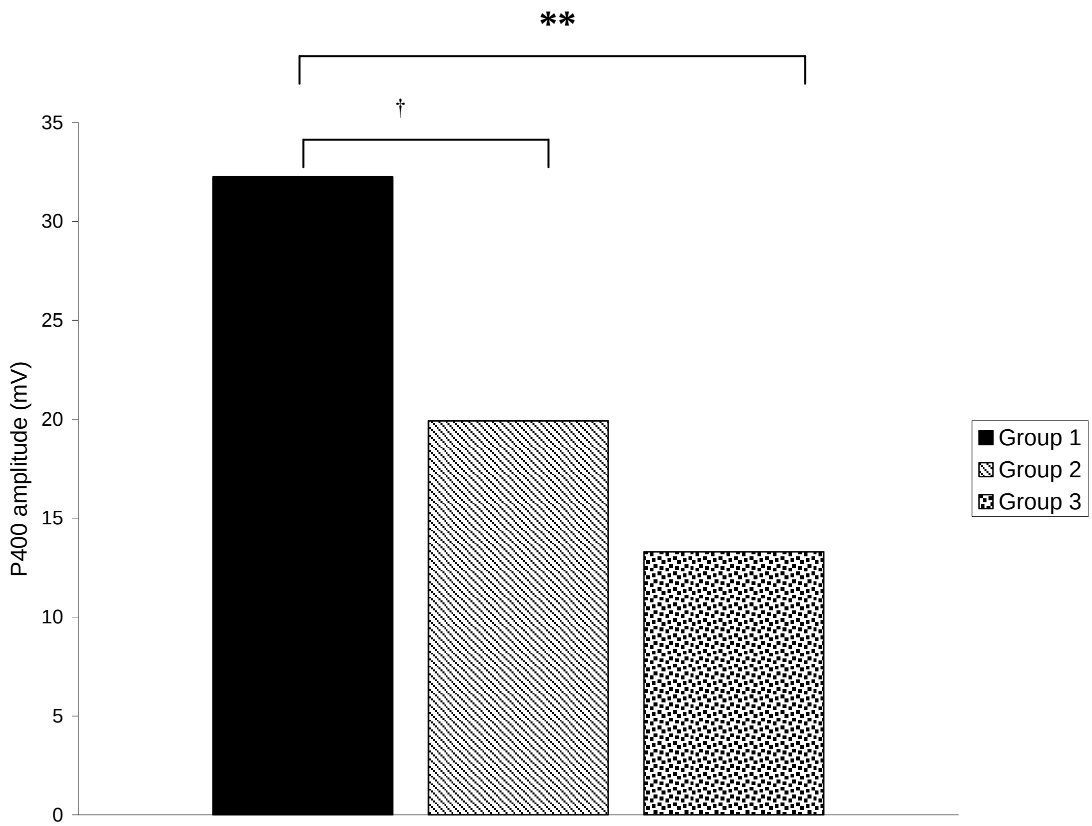
Chapter IV, Figure 2. Main effect of age group for P400 amplitude to faces at occipital lead O2.

Chapter IV, Figure 3. Face condition by age group interaction for Nc amplitude at midline lead Fz.

Chapter IV, Figure 4. Main effect of age group for Nc amplitude at lateral leads.

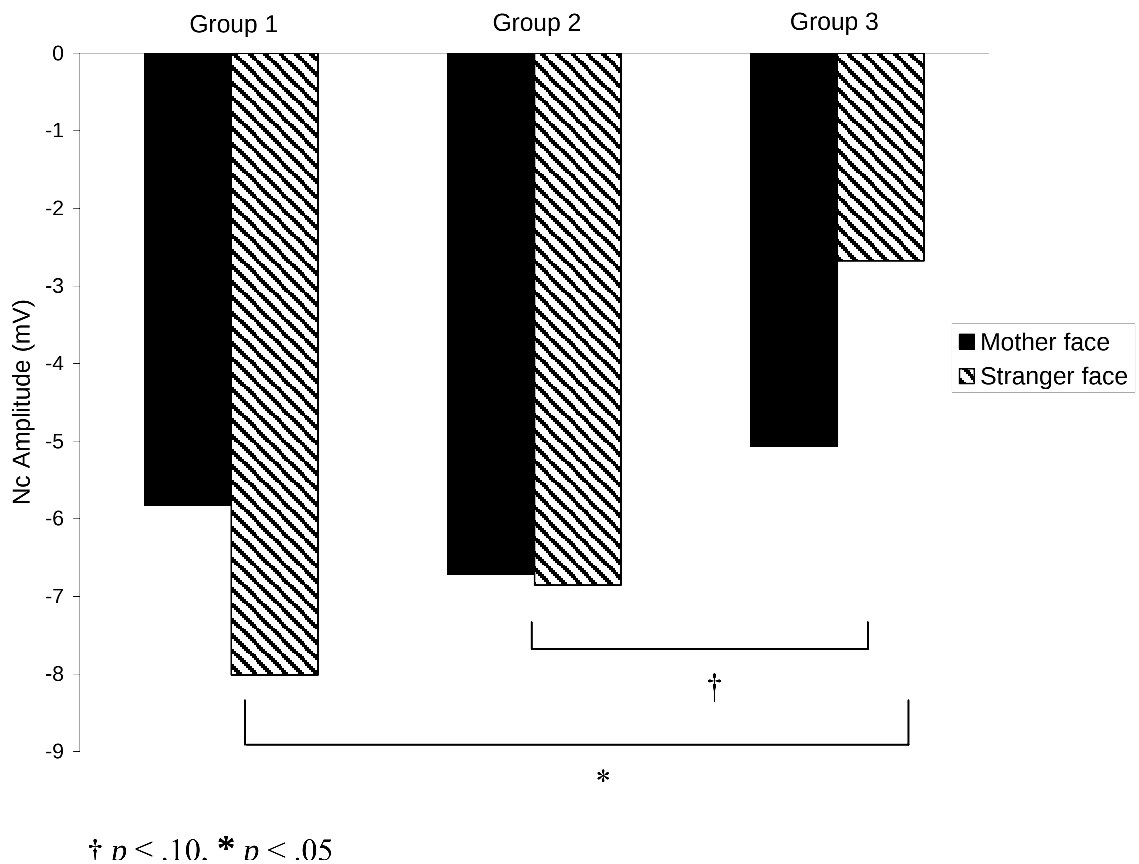


Chapter IV, Figure 1. Schematic of electrode locations on the scalp.

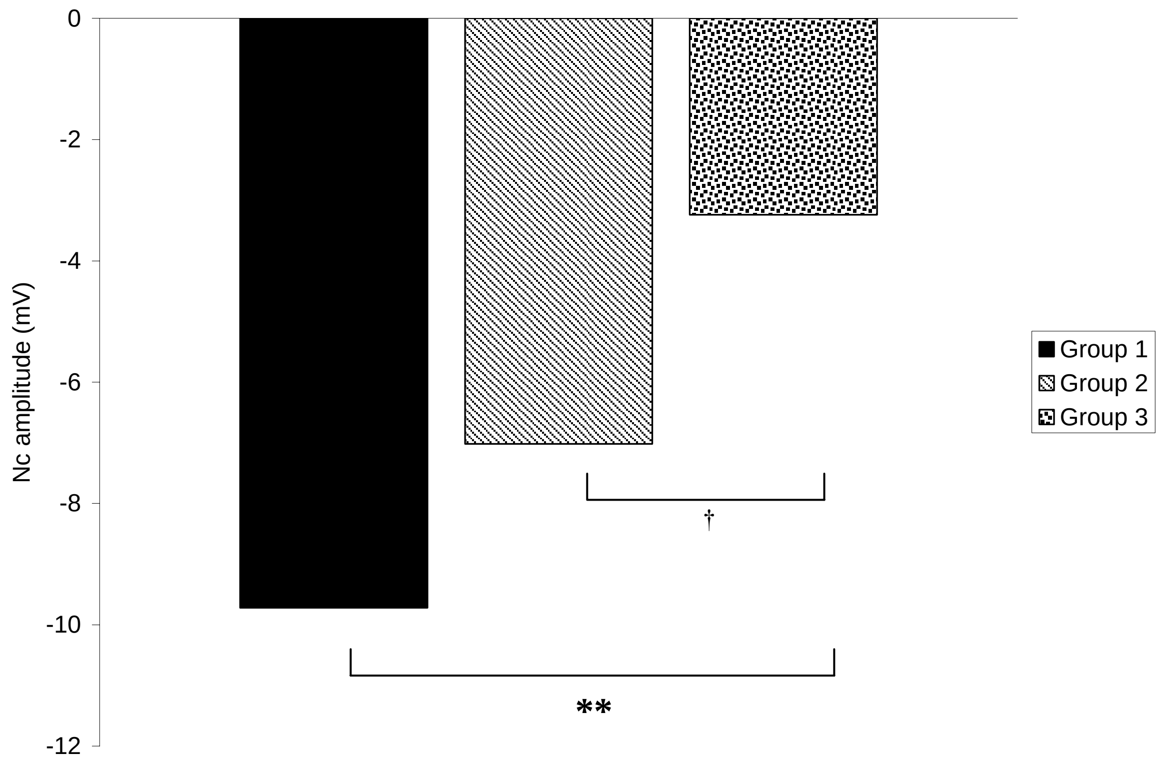


† $p < .10$, ** $p < .01$

Chapter IV, Figure 2. Main effect of age group for P400 amplitude to faces at occipital lead O2.



Chapter IV, Figure 3. Face condition by age group interaction for Nc amplitude at midline lead Fz.



† $p < .10$, ** $p < .01$

Chapter IV, Figure 4. Main effect of age group for Nc amplitude at lateral leads.

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Chapter V

General Discussion

Discussion

A potential relationship between developmental changes in the mother-child relationship and neurophysiological responses to mother and stranger faces was examined in two ages proposed as developmental transitions in the face processing literature (Webb, Long & Nelson, 2005; Carver et al., 2003) as well as the mother-child attachment literature (Bowlby 1969/1982). The studies examined behavioral responses of six-month-olds and toddlers in a behavioral paradigm inspired by the work of Ainsworth (e.g. Ainsworth, Waters, Blehar & Wall, 1978). The procedure contained two separations and reunions with the mother, and infants' and toddlers' behavioral responses to these separations and reunions were observed and investigated for a potential relationship with event-related potential responses to mother and stranger faces.

Chapter II presented data from the study of six-month-olds in which a composite measure of infant behavior was used. Scores on the composite index provided a general measure of amount of mother-focused proximity and interaction seeking behaviors 6-month-olds produced during separations and reunions with the mother in the behavioral portion of the study. A composite measure of infant behaviors was used as an important first step towards examining a relationship between infant behavioral responses to the mother and neural responses to processing the mother's face versus an unfamiliar female's face. The findings from this investigation provided the first evidence that individual differences in behavioral responses of infants during separations and reunions with the mother were related to differences in their neural responses to faces. Infants who produced more proximity and interaction seeking behaviors also produced larger Nc amplitude responses to the stranger's face than to the mother's face. Infants who produced fewer of these behaviors did not show this relationship.

Chapter III narrowed the focus on infant behavior to examine the influence of behaviors that are frequently present during face-to-face interactions between mother and infant in the first year, and which have been shown to contribute to the relationship that develops out of these interactions (e.g. Lavelli & Fogel, 2005). These behaviors were visual attention/eye gaze with the mother when she was present and visual search when she was absent. The third behavioral variable examined in this work was infant distress during separations, as increases in this behavior have been suggested in the attachment literature to mark the transition that occurs at six-months of age (e.g. Bowlby, 1969/1982). These behaviors, in particular, are theorized to be very important for an infant at six months who has relatively limited behavioral resources available with which to signal and interact with the mother. Therefore, these behaviors were hypothesized to correlate specifically and distinctly with the neural responses to the faces.

The behavioral measures did prove to be significantly related to the processing of both the mother and stranger faces in both components of the ERP response examined. The measure of amount of distress during separations was significantly related to amplitude responses of the Nc and P400 component responses, and for the mother's face only. In general, higher levels of distress during separation were associated with larger amplitude responses to the mother's face, although this effect varied by hemisphere for the Nc response. Higher levels of distress during separation were associated with larger amplitudes to the mother's face in the left hemisphere, but smaller amplitudes in the right hemisphere. In addition, higher levels of distress were associated with longer latencies for processing the mother's face. In general, this suggested a deeper level of processing and a recruiting of more neural resources associated with working memory, attention and recognition in response to the mother's face for infants who exhibited more distress during separations from her.

Interestingly, the measures of visual behaviors in response to the mother during separations and reunions were all associated with differences in the latency of the components, and the specific relationships varied by identity of the face. It is not immediately clear why infant's visual looking behaviors would be related specifically to the latency of processing faces. However, the majority of the effects of looking behaviors on latencies were associated with faster responses to mother or stranger face conditions. This may suggest that more looking behaviors in infants results in more experience with processing faces, and especially with processing the mother's face, and that this is reflected in the faster latencies to peak seen in this study. However, when the relationship between the behavioral variables and responses to the two faces for both components were examined as a whole, the behavioral measures of distress on separation and looking for mother on separation seemed to be related to a larger construct of separation anxiety for the infants' tested in this study. These "separation anxiety" behaviors correlated with responses to the two faces in similar ways, while the looking at mother when she returned variable showed a different, and often opposite relationship to the neural response to the two faces.

Finally, Chapter IV of the dissertation presents a study conducted with toddlers tested in a one year age range (28 to 40 months of age) using the same paradigm as the six month study, albeit slightly adjusted to be appropriate for use with toddlers. There were two primary questions under investigation in the toddler study. The first was whether age-related changes in processing the two faces would be present in this age range, as they have not been shown before. The findings provided evidence of age-related change to processing faces in general in this age range. There was a general decrease with age in the amplitude of both components of the ERP in response to the faces. This suggested a potential effect of expertise on the neural resources recruited for processing faces, and especially for discriminating between a very familiar face and an unfamiliar face. Perhaps with increased experience with faces, and specifically with the mother's face, toddlers begin recruiting fewer resources for recognizing the mother's face and discriminating the mother's face from an unfamiliar female's face. Alternatively, this change may be reflective of a general dampening of amplitudes of the ERP components that occurs with age. The results of this study cannot tease these two possibilities apart, but future research could address them.

When collapsed across age, Nc amplitude responses in the mother face condition were more negative than the amplitudes in the stranger face condition at lateral lead locations. This is consistent with the pattern of response to the two faces found in a younger group (18 to 24 months) but not in an older group (45 to 54 months) of toddlers, who showed an opposite pattern (Carver et al., 2003). This suggests that there is continuity between 18 and 28 months in the Nc response to processing the mother's face versus a stranger's face. Interestingly, this same pattern was not present for the P400 component responses to the two faces. Rather, the 28- to 40-month-olds in this sample showed a larger P400 response to the stranger's face than to the mother's face; a pattern that was similar to the oldest children and opposite from the youngest children, in the previous work. This suggests that developmental change in allocation of neural resources for discriminating the mother from a stranger occurs at different points in development for the Nc and P400 components. Further, it provides the strongest support for the notion that 28 to 40 months is a particularly transitional time with regard to face processing.

This seemed to be particularly true with regard to responses to the stranger's face across the ages included in the toddler study presented in Chapter IV. Amplitudes for the youngest group in the toddler study were larger in response to the stranger's face than to the mother's face, but this pattern was reversed in the oldest group, who showed larger responses to the mother's face than to the stranger's face. In addition, the middle age group showed no differences in the ERP responses to the two faces. This suggested developmental change in the processing of mother and stranger faces in this age range, although this relationship was due to changes in the response to the stranger's face only. Responses to the mother's face stayed relatively stable during this period, while amplitudes in response to the stranger's face decreased with age. Previous work examining a larger age range of toddlers found that the age related changes that occurred between 18 and 54 months were primarily due to changes in the mother's face condition only. Therefore, the relative salience of faces does appear to vacillate during these age ranges, and these changes may be occurring on a relatively short time scale. The current study examined change in toddlers spanning one year of development and patterns of age-related change found here appeared to be distinct from change found when looking at toddlers spanning three years of development (Carver et al., 2003). The results of this study support the notion that change in the salience of faces likely occurs rapidly during the toddler years, and may change often.

The second goal of this study was to examine a potential relationship between toddlers' ERP responses to the two faces and four measures of toddlers' behaviors from the separation and reunion episodes. Relationships between toddler behaviors and neural responses to the faces were significant for the response to the mother face only. This suggested that individual differences in toddlers' behavioral responses to separations and reunions with the mother were significantly related to the ways in which toddler's processed her face. In addition, like the findings for six-month-olds presented in Chapter III, distress behaviors during separations appeared to be the most significantly related to the response to the mother's face in toddlers as well. Measures of negative affect and attachment behaviors during separations were associated with larger responses to the mother's face in both components of the ERP response. This work is important because it provides evidence of developmental continuity with regard to a relationship between behavioral responses of distress to separations from the mother and neural responses to her face in both six-month-olds and toddlers.

General Conclusions

The studies contained in this dissertation have demonstrated that individual differences in behavioral responses to separations and reunions with the mother are related to the pattern of neural responses to processing her face and a stranger's face in infants and toddlers. The behavioral measures used in each study were related to the neural responses to the two faces in unique and specific ways. However, perhaps the most important finding was that there was also developmental continuity in the relationship between behavioral and neural responses for the behavioral measures of distress during separation from the mother. Both infants and toddlers who showed more evidence of distress during separations and a desire to return to close proximity with the mother also showed larger Nc and P400 component amplitudes in response to the mother's face. This suggests a potential general relationship between individual differences in behavioral responses to separations with the mother that are present at transitional ages in the mother-child relationship and neural responses to the mother's face.

Future research should examine infants and toddlers who are not at a proposed transitional age in the mother-child relationship to explore whether this relationship still holds. One possibility is that this relationship occurs because of the transitional nature of the ages tested with regard to the changing role of the mother-child relationship for the child. This would explain why the relationship was present in the infants and toddlers examined the studies presented here. However, a second explanation is that this is a measure of individual differences in behavioral responses to separations from the mother. In this case, the relationship may not be specific to transitional ages in the mother-child relationship. Another way to approach this question is to examine individual differences in quality of attachment for a potential relationship to face processing. Quality of attachment has been shown to be a stable construct and is related to both prior aspects of the mother-child relationship as well as a wide variety of later aspects of infant and child functioning (Ainsworth, Blehar, Waters & Wall, 1978; Cassidy, 1990). Therefore, individual differences in behaviors related to the quality of the attachment relationship may be related to the neural pattern of processing the mother's face, as is suggested by the findings from the studies included in this dissertation.

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