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Brain–Behavior Correlations: Relationships Between Mother–Stranger Face Processing and Infants’ Behavioral Responses to a Separation From Mother

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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 behavioral responses of the infants during a separation from their mothers. We measured the mother-directed infant behaviors of distress and visual search for mother during separation in order to determine if they were predictive of infants’ brain responses to pictures of the mother’s face versus a stranger’s face. These behavioral 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 and visual search for mother during separation were predictive of face processing ERPs, and this relationship differed across mother and stranger face presentations. In particular, distress was associated with larger amplitude P400 and Nc responses to the mother’s face, and visual search for mother was associated with longer P400 and Nc latencies to the stranger’s face. Implications for the developing mother–child relationship and face processing system are discussed.

Keywords

face processing; mother–child relationship; ERP

An important achievement of the infancy period is the ability to distinguish the primary caregiver (usually the mother) from other individuals. Several studies have been conducted on the development of recognition of the mother, and they have generally found that infants are able to distinguish the mother from other people using a variety of cues very early in development (Cernoch & Porter, 1985; Pascalis, de Schonen, Morton, Deruelle, & Fabre-Grenet, 1995; Porter & Winberg, 1999). Extensive research has focused on infants’ recognition of the mother’s face, and a number of studies have found that infants show electrophysiological brain responses that distinguish the mother’s face from that of a

stranger by 6 months of age. de Haan and Nelson (1997) developed an event-related potential (ERP) paradigm in order to compare brain responses of infants to their mother's face versus a stranger's face. They showed that infants' brain activity differed in response to the mother's face versus the stranger's face, although the specific pattern of activity varied depending on the amount of resemblance between the mother and the stranger. Recently, there has been increased interest in examining the interface between social cognitive abilities, such as face recognition, and other aspects of social and social cognitive development. We made use of the above face recognition ERP paradigm in the current study to explore in detail the relation between the emerging caregiver–infant relationship and the brain organization underlying the discrimination of the mother's face from a stranger's face in infants at 6 months of age.

Since the original studies, this paradigm has been used to test face processing in infants of a wide range of ages (Carver et al., 2003; Webb, Long, & Nelson, 2005), children with autism (Dawson et al., 2002), and infants born to diabetic mothers (Nelson et al., 2000). A number of these studies (Carver et al., 2003; Webb et al., 2005) have shown different patterns of negative component (Nc) responses to the mother's and the stranger's face depending on the age of the infant or toddler tested. The Nc is a middle-latency negative component that is maximal over central frontal electrodes and that has been associated with increased attention, particularly to salient stimuli (Courchesne, Ganz, & Norcia, 1981; Nelson, 1994), and recognition memory (de Haan & Nelson, 1997, 1999; Nelson, 1994). Because of this, likely explanations for the observed changes in brain responses to the mother's face and a stranger's face have focused on developmental change in attention to different types of faces. The goal in the present study was to test a possible explanation for these age-related changes in infant responses to the mother's face and a stranger's face in a sample of 6-month-old infants.

The literature suggests three possible explanations for developmental changes in the way infants respond to their mother's face versus a stranger's face. One possible explanation for differences in how infants respond to faces, and specifically to the mother's face, is experiential. There is accumulating evidence that experience with a primary caregiver plays a role in the development of infants' face processing. Quinn, Yahr, Kuhn, Slater, and Pascalis (2002) demonstrated that infants with a male primary caregiver showed a spontaneous visual preference for male faces rather than female faces. This provided evidence that infant interactions with caregivers early in development shape how infants process, represent, and differentially respond to faces. Parker, Nelson, and the Bucharest Early Intervention Project Core Group (2005) have provided further evidence to support the idea that social experience affects how infants process caregivers' faces. They compared ERP responses to the primary caregiver's face in two groups of children: a control group of noninstitutionalized children (primary caregiver was parent) and a group of children raised in Romanian orphanages (primary caregiver was preferred caregiver in orphanage). The results indicated striking differences between the two groups for ERP components related to face processing, including the N170 and Nc. Institutionalized children had smaller and slower amplitude responses than did noninstitutionalized children, and although both groups differentiated familiar from unfamiliar stimuli, the developmental trajectory observed in ERP responses to faces differed between the groups. These results suggest that social interaction experience is important for how behavioral and brain responses to faces develop. They raise the possibility that age-related changes in brain responses to faces could be due to some difference in the kind of experiences infants have with primary caregivers at different ages.

Another possible explanation for age-related changes in ERPs to the mother's face and a stranger's face comes from a longitudinal study of infants' responses to faces from 4 to 12

months of age. Webb et al. (2005) found that ERP responses to faces changed repeatedly with age. They suggested that these changes may be side effects of other developmental changes in cognitive abilities (e.g., memory), repeated testing, or differences in novelty preference across ages. A final possible interpretation of the differences in response to mother's face and a stranger's face was proposed by Carver et al. (2003). In a cross-sectional study of children between 18 and 54 months of age, Carver et al. found repeated changes that varied with age in ERP responses to faces. Carver et al. interpreted this finding in the context of age-related changes in sociability and attachment. They suggested, on the basis of the ages at which change in responses to faces occurred in their sample, that transitions in ERP responses to mother and stranger faces may relate to changes in the social behavior of children, particularly with their primary caregiver, that occur at the same or similar ages. However, it is important to note that Carver et al. did not measure any aspects of the mother-child relationship, and their ideas were based entirely on what is known about social development occurring in the age-groups that showed different ERP patterns in their study.

Recently, we examined individual differences in behaviors produced by 6-month-old infants in response to separations from and reunions with their mothers (Swingler, Sweet, & Carver, 2007). Infant behavior was related to the ERP responses of infants to pictures of their own mother's face (the primary caregiver) and an unfamiliar female face. Infants who exhibited a greater number of attachment-like behaviors that maintained close proximity and continued interaction with their mother tended to respond with a smaller amplitude Nc 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.

In Swingler et al. (2007), we explored the possibility that infant demonstrations of the emerging mother-child relationship might be related to brain activity in response to faces. A large number of behaviors were measured across both separations and reunions with the mother, both with a stranger present and with a stranger absent. These measures, which included infant affect, exploratory behavior, looking at and for mother, and distress, were combined to create a general measure of proximity seeking. In the present study, we further isolated those infant behaviors thought to be especially indicative of a developing bond with the mother (i.e., those evidenced when the infant is separated from her and left alone). Infant distress upon separation and visual search for the mother are traditionally thought to be early behavioral indicators of the specificity of the developing bond with her (Marvin & Britner, 1999). Here, we specifically examine how distress upon separation and looking for the mother during separation relate to the infant's brain responses to her face, as opposed to a stranger's face. In addition to narrowing our focus on more relationship-specific behaviors, we have expanded our ERP measures to include latencies, which reflect not only the extent or amount of processing but also the speed of processing. Finally, we have expanded the ERP measures by including the P400 component, which in the past has been shown to differentially respond to faces versus objects, leading to the conclusion that this component is important to face processing.

The P400 is an early to middle latency positive component localized over occipital electrodes that has been suggested to be face sensitive or face specific (de Haan, Pascalis, & Johnson, 2002; Nelson & de Haan, 1996). This component is sensitive to differences between faces and objects (Dawson et al., 2002; de Haan & Nelson, 1999) and between human and nonhuman faces in adults and older children (de Haan et al., 2002). Some researchers (de Haan, Johnson, & Halit, 2003; de Haan et al., 2002; Halit, de Haan, & Johnson, 2003) have suggested that it may be in part 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 such as 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. A second component that may also (or instead) be a precursor to the adult N170 is the N290. Because we did not analyze the N290 in this study, it is beyond the scope of this paper to discuss its contribution to infant face processing. However, as visual attention is of interest for this study, we predicted that the P400 would correlate with measures of behavioral visual attention (e.g., looking for the mother). In addition, because of the P400's sensitivity to faces, the relationships between behavior and this ERP component are likely to reflect the effects of the burgeoning mother–infant relationship on face processing more specifically than the Nc, which is likely to reflect more general attentional mechanisms.

We know from work on the development of face processing that from 3 to 7 months, infants begin to show evidence of categorizing faces by social characteristics such as familiarity, gender, and facial expression (Nelson, 2001); by 6 months, they 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). In conjunction with work on the development of face processing, research on early mother–child interaction has examined how past 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 (Hsu & Fogel, 2003; Pederson, Gleason, & Moran, 1998; Slade, Belsky, Aber, & Phelps, 1998). 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). 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). These relational schemas might be revealed in infants' emerging tendencies to note the absence of the mother, search for her, and attempt to influence her return. However, no studies to date have looked for neural correlates of a developing internal working model or relational schema in the context of the mother–child relationship. If behaviors that infants produce in the context of mother–child interaction in the first year—especially mother–child separations—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 a developing internal working model.

There is some support for the idea that age-related changes in behavior in response to separation might influence other aspects of development. Lewis and colleagues (Lewis, 1993; Lewis, Koroshczy, Douglas, & Kampe, 1997) have shown that the relations between distress upon separation and performance on sensorimotor tasks vary as a function of age. In one study, they measured infants' separation distress at 2, 6, and 10 months of age and performance on a range of sensorimotor tasks at 4, 8, and 13 months. Lewis et al. found that separation distress at 2 months was negatively related to performance on a variety of sensorimotor tasks conducted at 4 months but that separation distress at 6 months was positively related to sensorimotor performance at 8 months. In addition, distress as well as reunion behaviors predicted cognitive performance in 10-month-olds. Lewis et al. interpreted their results as indicating that emerging cognitive abilities influence infants' behavior toward the mother. In addition, relations between reunion behaviors and cognition were taken as evidence that relationship variables were also important for developing cognitive abilities.

Our purpose in the present study was to explore in detail the relation between the emerging mother–infant relationship and the brain organization underlying one aspect of social–cognitive functioning, namely, face processing. Although we were not interested in quality of attachment in this study (and, indeed, could not reliably measure it in infants this young), we were interested in this attachment relationship’s beginnings, which include distress and visual search for the mother during separation. We examined how infants responded to a separation from their mothers and how specific aspects of their behavior related to their processing of the mother’s face as opposed to a stranger’s face. Although the behavior infants display upon separation likely reflects both the temperamental profile they bring to the relationship with their caregiver and the history of interaction between the parent and infant, a larger reaction to separation is thought to be indicative of a developing bond with the mother.

Method

Participants

The final sample of participants consisted of 30 full-term, neurologically healthy 6-month-old infants (mean age = 183.4 days, or 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. Of the infants, 23 were Caucasian, three were Hispanic, two were Asian, and two were African American. The children were primarily from middle-class homes and were 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: Eighteen infants did not provide enough artifact-free data, five infants did not cooperate with the testing procedure, one mother talked throughout the ERP testing session, and one infant’s data were lost due to experimenter error. This attrition rate is the same as or lower than rates for other ERP studies conducted with the same or a 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 gray background. Mothers wore the same gray scarf to obscure the neckline and clothing. Earrings and other jewelry were removed, but mothers who 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.

Procedure

For each infant, the behavioral evaluation of response to separation occurred first. Each infant was tested individually in a paradigm involving a series of separations from and reunions with the mother (see below). This behavioral assessment took approximately 15 minutes. Immediately following behavioral testing, infants were taken to an adjacent room where ERP testing occurred. The order of behavioral and ERP testing was kept constant, so that infants would not become so distressed from the ERP testing (some infants of this age

are disinclined to wear electrode caps and can become bored or tired by watching ERP stimuli) that this affected their behavior in the separation task.

Behavioral session—The behavioral portion of this study was part of a larger behavioral evaluation reported in Swingler et al. (2007) and was based upon the work of Mary Ainsworth (e.g., Ainsworth, Blehar, Waters, & Wall, 1978). The larger behavioral evaluation contained seven intervals that varied in terms of whether the mother was in the room with the infant and/or whether a stranger was in the room. During Intervals 1 and 3, both the mother and a stranger were present in the room. During Intervals 2, 5, and 7, the mother and child were alone in the room. During Interval 4, the stranger and the infant were alone in the room, and during Interval 6 the infant was alone in the testing room. This procedure was especially designed for easy elicitation and observation of infant behaviors in response to separations from and reunions with the mother. It is important to note that although this behavioral paradigm is reminiscent of the Strange Situation pioneered by Ainsworth, we were explicitly not attempting to evaluate the quality of attachment in this study. First, the Strange Situation is not valid for determining attachment quality in infants as young as 6 months. More important, we were not at all interested in quality of attachment; rather, we were interested in observing the beginning stages of the mother–child attachment relationship. In this study we focused our analysis on Interval 6, when the infant was alone in the testing room, and on the behaviors infants are suggested to show when the mother–child relationship is forming, namely, infant distress and amount of looking for mother during separations.

Although behaviors infants exhibited when left alone after a separation from mother were the focus of interest with regard to a potential relationship with neural responses to faces, we also coded and analyzed infant distress behaviors from Interval 2, when mothers and infants were first together in the room with no stranger present. This interval was included so that we could determine if infant behaviors during the separation were more trait-like (indicating some lasting characteristic of the infant) or more situational in nature, as our hypotheses would suggest. The interval with the mother and infant together and alone in the room lasted for 1 min, and the interval when the infant was alone lasted for 30 s. The latter interval was shorter to reduce the likelihood of severe infant distress.

Each session took place in a 3 m × 4 m room designed for behavioral testing. The room included two large blue armchairs, an infant blanket placed on the floor in the center of the room, and several toys. These included a small red, squishy soccer ball, a set of five 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. Mothers were cued when to leave and when to return by the experimenter.

Sessions were videotaped and subsequently coded for infant distress behaviors and the amount of looking for mother during separation. One video camera was located in a 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.

Behavioral coding: To increase precision of coding, we subdivided each of the two intervals of interest into 15-s segments and coded behaviors within each segment. For each 15-s segment of the interval with both mother and child present, coders rated infant distress; for the separation interval, coders rated both infant distress and the amount of looking for

mother. Three types of behaviors were classified as distress behaviors: (a) crying; (b) distress vocalizations that were not crying (e.g., whining or fussing); and (c) arm flailing, arm wiggling, or kicking. In order to be coded as a distress behavior, arm flailing, arm wiggling, or kicking had to be accompanied by a negative vocalization and/or facial expression. Each of these three distress behaviors was coded as a discrete yes–no decision within each 15-s segment, and distress behaviors were summed to provide a total number of distress behaviors exhibited per segment. Individual distress behaviors were coded as yes–no distinctions, because the question of interest was whether or not the behavior occurred, not how long it occurred. Amount of looking for mother, however, was rated on a 5-point Likert-type scale ranging from 1 (*did not look for mother*) to 5 (*looked for mother entire 15 s*). We used a Likert scale for this variable because we were interested in more than whether or not a behavior occurred; we were interested in the extent to which it occurred. 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.

Interrater reliability: Two coders watched the tapes of the behavioral sessions and coded specific behaviors exhibited by each infant. The coders were blind to the hypothesis of the study and had no knowledge of the infants' ERP data or results. Coders were trained by Margaret M. Swingler on the original coding scheme and achieved 88% reliability with her before coding independently. Both coders coded 20% of the participants for the purposes of measuring reliability. Coding pairs achieved good reliability for the data on which they overlapped in this paper (κ s > .80).

Behavioral measures: Segment scores for each construct were averaged across each interval to create one score per child, per interval. Although infant distress was coded as the sum of three yes/no occurrences per segment, it was averaged across each interval to account for unequal interval lengths (i.e., the interval with the mother present lasted 1 min and that with the child alone lasted only 30 s). The result was an infant distress measure for each of the two intervals as well as a measure of the relative amount of time infants looked for their mother during the separation.

Scores for amount of looking for mother ranged from 1 to 5, with an average of 2.02 ($SD = 1.04$). Nine of the 30 children (30%) did not look for their mothers during the separation interval. Infant distress during the separation interval ranged from 0 to 2.5, with an average of 0.61 ($SD = 0.61$). Ten of the 30 children (33%) expressed no distress during the separation interval. Infant distress during the interval with mother present ranged from 0 to 1.67 and averaged 0.18 ($SD = 0.38$). Twenty-one of the 30 children (70%) expressed no distress during this interval. A repeated-measures analysis indicated that children were significantly more distressed during the separation than when the mother was present, $F(1, 29) = 14.96, p < .001$.

ERP testing—The ERP testing began in another room upon completion of the behavioral session. The circumference of the infant's head was measured, and the vertex was marked. An appropriate size 32-channel electrode cap (Electro-Cap International, Eaton, OH) was fitted to the infant's head according to the manufacturer's specification. ERPs 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 nonstandard sites were also used: CPz, FCz, CP5 and CP6, CP1 and CP2, FC1 and FC2, FC5 and FC6, FP1 and FP2, and AF7 and AF8. (See Figure 1 for a schematic of electrode positions on the scalp.) Electrode gel was placed in 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 k Ω . The mean scalp impedance before the testing procedure was 6.33 k Ω ($SD =$

2.74). The mean of the posttesting impedance measurements was 4.45 k Ω ($SD = 3.42$). Four additional electrodes were manually placed around the infant's eyes upon entry to the ERP testing room for electrooculographic (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 k Ω ; 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 k Ω before testing and 39.90 k Ω after testing. Average impedance measurements for the vertical eye electrodes were 60.88 k Ω pretest and 31.94 k Ω posttest.

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 gray 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 intertrial 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 1,200-ms recording period during which the computer screen was gray. Trials were separated by a randomly varying 500- to 1,000-ms intertrial interval. The order in which the stimuli were presented was randomized across infants. Data collection was terminated when the infant had seen all of the 100 trials (50 mother and 50 stranger) or when the infant was no longer tolerant of the testing procedure. Trials on which the infant did not attend to the stimuli or during which the experimenter was attempting to attract the infant's attention were removed after data collection.

EEG recording: EEG was recorded continuously from all 32 electrode channels. Signals were amplified and filtered through a 0.1-Hz high-pass filter and 100-Hz low-pass filter. A 60-Hz 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 offline segmentation of the data. Each infant's EEG data were referenced to Cz and rereferenced offline 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 those of previous studies using the same or a similar paradigm (Carver et al., 2003; Dawson et al., 2002; Halit et al., 2003).

ERP reduction: After testing, each infant's ERP data were edited offline. 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 μ V were excluded from the trial as artifact. Trials in which EOG artifact (i.e., eyeblinks or large eye movement) occurred were also excluded. Additional artifact was rejected when amplitudes exceeded A/D values, which results in clipping (flatlining of the signal from the amplifier), and upon visual inspection. Data from trials in which more than four electrode sites met criteria for exclusion were not

included. Only participants 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 participants were computed for visualization purposes.

ERP measures: Components of interest were identified on the basis of previous research findings (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 Nc (de Haan & Nelson, 1997, 1999) distributed over frontal electrode sites and a positive component peaking 300 to 500 ms over occipital electrodes (P400). The Nc was defined as the maximum negative peak between 230 and 1,230 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 everyone. 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 component and Nc were peak amplitude and latency.

Results

A series of mixed models was run to test the study hypotheses. Slope estimates were calculated to determine if and how scores on the two behavioral measures were related to peak amplitude and latency of the P400 and Nc, and repeated-measures analyses were included 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 were performed for the following leads: FC1, FC2, F3, F4, FC5, FC6 (see Figure 1 for a schematic of lead location). Frontolateral 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 identity are discussed, as these relate directly to the study hypotheses.

P400 Component

The P400 component was analyzed at occipital leads O1 and O2. Table 1 presents a breakdown of the significant results from the P400 amplitude and latency analyses, including slope estimates and associated standard errors for each Face $\times$ Lead condition. The slope estimates in the top portion of Table 1 reflect relationships between infant distress during separation and P400 amplitude, and the slope estimates in the bottom portion reflect relationships between looking for mother during separation and P400 latency. Analyses of the P400 component included the between-subjects behavioral variable predictors of infant distress during separation and looking for mother during separation, the within-subjects variables of face (mother, stranger) and lead (O1, O2), and interactions of behavioral measures and face, lead.

¹This 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 across infants was 688.23 ms. The latency ranged from 555.31 to 800.29 ms. This range suggests that the Nc likely reflected the same physiological response across infants.

Amplitude—The interaction between face identity and infant distress during separation was significant, $F(1, 26) = 14.39, p < .0001, \eta_p^2 = .36$. 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 1, 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 separation 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 during separation was significant, $F(1, 26) = 11.16, p = .003, \eta_p^2 = .30$. This indicates that the relationship between looking for mother during separation and P400 latency differed significantly across the two face conditions. An inspection of the bottom portion of Table 1 reveals that looking for mother during 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 separation 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 separation 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

Analyses of the Nc included the behavioral variable predictors of infant distress during separation and looking for mother during separation 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 hemisphere were also tested. Tables 2 and 3 present a breakdown of the significant results from the Nc amplitude and latency analyses, including slope estimates and associated standard errors for each Face $\times$ Hemisphere $\times$ Lead condition. The slope estimates in the top portion of Table 2 quantify the relationship between Nc amplitude and infant distress, and the slope estimates in the bottom portion of the table reflect relationships between Nc amplitude and looking for mother during separation. Table 3 presents corresponding slope estimates for the relationships between the behavioral variables and Nc latencies.

Amplitude—A significant distress during Separation $\times$ Face $\times$ Hemisphere $\times$ Lead interaction emerged, $F(2, 52) = 3.41, p = .04, \eta_p^2 = .12$. At the left frontocentral leads FC1 and FC5, more distress during separation 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 larger neural response. At the right frontocentral lead FC2, more distress during separation 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. This was reversed for the stranger face condition, where Nc amplitudes in response to the stranger's face tended to become more negative, or stronger, as infant distress scores increased.

A visual inspection of the slope estimates presented in Table 2 suggests that it was primarily the mother/stranger difference at right hemisphere lead FC2 that drove the significant Infant Distress $\times$ Face $\times$ Hemisphere $\times$ Lead interaction, and follow-up face comparisons within

each Lead $\times$ Hemisphere condition confirmed this. The only significant face difference in the relationship between infant distress and Nc amplitude occurred at FC2 ($p = .001$). At FC2, the relationship between distress and amplitude was significantly more positive in the mother face condition than in the stranger face condition or, conversely, was more negative in the stranger face condition.

In addition to this, a marginally significant Looking for Mother $\times$ Face interaction emerged, $F(1, 26) = 3.79, p = .06, \eta_p^2 = .13$, along with a significant Looking for Mother $\times$ Face $\times$ Lead interaction, $F(1, 26) = 3.24, p = .04, \eta_p^2 = .11$. At the left frontocentral lead FC5, Nc amplitudes in response to the mother's face tended to become more positive, or smaller, as the amount of looking for mother during the separation increased. This was also the case at the right frontocentral lead FC6. At FC6, however, Nc amplitudes in response to the stranger's face tended to become more negative, or larger, as infant looking for mother scores increased. A visual inspection of the slope estimates presented in Table 2 suggests that it was primarily the mother/stranger difference at lead FC5/FC6 that drove the significant Looking for Mother $\times$ Face $\times$ Lead interaction, and follow-up face comparisons within each lead condition confirmed this. The only significant face difference in the relationship between looking for mother and Nc amplitude occurred at FC5/FC6 ($p < .001$). At these leads, the relationship between looking for mother and amplitude was significantly more positive in the mother face condition than in the stranger face condition.

Latency—The interaction between face and infant distress during separation was significant, $F(1, 26) = 4.89, p = .04, \eta_p^2 = .16$. As can be seen from the top portion of Table 3, the slope estimates were significantly more positive in the mother face condition than in the stranger face condition. Higher distress during 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 during separation was also significant, $F(1, 26) = 7.61, p = .01, \eta_p^2 = .23$. An inspection of the slope estimates presented in the middle portion of Table 3 indicates that slopes in the mother face condition were significantly more negative than those in the stranger face condition. Higher scores for looking for mother during separation were predictive of shorter latencies, or faster responses, in the mother face condition. This was not the case in the stranger face condition.

Discussion

Our goal in the current paper was to examine the multidimensional relationship between infants' behaviors during separation from the mother and brain responses to the mother's face and a stranger's face. In a previous paper (Swingler et al., 2007), we found that the total amount of mother-directed proximity-seeking behavior that 6-month-olds produced during a structured interaction 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 exhibited across a series of separations and reunions that were hypothesized to be related to the developing mother–infant relationship. This composite consisted of a large range of infant behaviors, including multidimensional 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 two 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 in response to interrupted interaction may be the best evidence of behavioral preference for the mother in young infants with relatively limited behavioral repertoires.

We hypothesized that ERPs to picture of the mother's face would be related to the behavioral responses of infants to a separation from her in which they were left alone and that this would be evident in the P400 component response to the mother and stranger faces. However, because this is the first study of its kind to examine the relation between infant behaviors during separation from the mother and the P400 response to faces, we did not have specific hypotheses with regard to the nature of a potential relationship between these two variables. The P400 component response to the two faces was significantly related to both the behavioral measures of looking for mother during separation and the distress behaviors during separation in our sample of 6-month-olds. In addition, amplitude and latency of the P400 response were related to different behavioral measures, and these relationships were specific to the face that was shown. Amplitude of the P400 response was significantly related to the behavioral measure of infant distress during separations in the response to the mother's face condition 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. The latency of the P400 response, on the other hand, was significantly related to the behavioral measure of looking for mother during separations in the response to the stranger's face condition 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 who showed more evidence of looking for the mother when she was gone also showed slower processing of the stranger's face for the P400 component.

The P400 component is thought to be especially sensitive to face stimuli (Halit et al., 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 processing 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 reaction to the mother, especially with regard to exhibiting distress at her absence.

The current study does not allow any speculation about the direction of this relationship; however, the results suggest that one of two equally interesting mechanisms may be at work. It might be the case that infants whose face processing systems respond 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 is that 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.

One study has examined the effect of individual differences in emotionality and reactivity in infants on ERP responses to faces. Gunnar and Nelson (1994) measured cortisol before and

after ERPs were measured to familiarized faces and novel faces in 12-month-olds. In addition, cortisol was measured before and after a 30-min separation from the primary caregiver. Gunnar and Nelson did not examine the Nc or P400 but found that the area of a late frontal positive slow wave in response to infrequently presented faces to which the infants had previously been familiarized was related to their emotionality, both according to parent report and in response to separation from the caregiver. Infants who displayed more negative emotion during separation and who per parent report exhibited more positive emotion had larger slow wave responses to infrequently presented familiar faces. Our results show increases in activity for a highly familiar face for infants who also displayed high levels of distress during separation. Our study was different in several respects from that of Gunnar and Nelson and was conducted with a different age of participants; the Gunnar and Nelson study was conducted with 12-month-olds. First, Gunnar and Nelson measured emotionality and distress during separation in a separate session from the measure of ERPs to faces. Thus, whereas their measures likely indicated something about infant traits over long periods of time, ours measured ERPs in close temporal proximity to separation; therefore, our results might have also been influenced by the infants' states at the time of testing. In addition, Gunnar and Nelson measured ERPs to familiarized faces, and we measured them to the mother's (highly familiar) face versus a stranger's (unfamiliar) face. Finally, in addition to distress behavior, we measured the search behavior of infants in looking for their mother when she left the room. Thus, for several reasons, infants' distress in our paradigm might be more likely to be related to infants' reactions in the specific episode of separation from the caregiver. Nevertheless, infants' temperament is quite likely to be reflected in infants' distress upon separation and is also likely to influence the developing relationship with the caregiver. In future studies, it would be beneficial to couple the paradigm used in the current work with a measure of temperament in order to dissociate effects of general reactivity from the specific episode of separation from the caregiver.

The latency of the P400, which reflects speed of processing of the facial stimuli, was also related to infant behavior in our sample of infants. Infants who looked more for their mothers during a separation had slower P400 responses to the stranger's face. It is not immediately clear why looking for the mother would relate to how infants process another female face. However, one possibility is that our measure of looking for mother during separation tapped into a larger construct of distress. This construct may be related to a strengthening preference for the mother that might have broader effects on how infants learn about and respond to other people and the neural resources they can devote to learning about and responding to another person's face. In sum, our measures of behavioral distress and looking for mother during 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; higher levels of looking for the mother on separation predicted longer latency responses to the stranger's face. Although the specific directions of these relationships are 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.

Infants who displayed higher levels of distress behavior during separation also showed an interesting cross-hemisphere interaction between scores on the distress variable and Nc response to the two faces. The left hemisphere relationship between Nc response and high levels of distress was associated with larger amplitude responses to the mother's face compared to the stranger's face, and the right hemisphere relationship was associated with smaller amplitude responses to the mother's face. At the left frontocentral electrode sites FC1 and FC5, higher scores on distress during separation predicted larger Nc amplitude responses to the mother's face only. This provided support for the idea that infants who showed more distress during separations from the mother also showed greater attention and

deeper processing in response to her face than did infants who showed less distress during separation. However, at the right frontocentral 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.

The apparent association between higher levels of distress during separation and deeper left hemisphere processing of the mother's face but deeper right hemisphere processing of the stranger is consistent with past research in adults and older infants in which differences in frontal activation asymmetry are associated with experiences of positive and negative emotion (see, e.g., Davidson & Fox, 1989; Dawson, Finely, Phillips, Galpert, & Lewy, 1988; Fox & Davidson, 1987, 1988). In particular, left hemisphere activation has been associated with the expression of positive emotion and has been produced by 10-month-old infants during approach from the mother. In contrast, right hemisphere activation has been associated with expression of negative emotion and has been produced during the approach of a stranger in 10-month-old infants. In addition, frontal activation asymmetry in a baseline condition predicted 10-month-olds' distress responses to subsequent separations from the mother (Davidson & Fox, 1989). Infants with more right lateralized baseline activity were more likely to fuss and cry during a subsequent brief separation from their mother than were infants with more left lateralized baseline activity. In addition, the relationship between caregiver and infant has been shown to mediate these cross-hemisphere effects and may be what is reflected in our cross-hemisphere findings of the relationship between infant distress behavior during separation and responses to the two faces (Dawson, Grofer Klinger, Panagiotides, Hill, & Spieker, 1992; Dawson, Klinger, Panagiotides, Spieker, & Frey, 1992).

Latency of the Nc response to faces was also significantly related to infant distress during separation. Infants who showed higher levels of distress during separation also showed longer latencies to peak amplitude in both hemispheres in response to the mother's face only. Because this effect emerged most clearly when collapsing across electrodes, it would be informative for future research to use higher density recordings, to allow for discrimination of more fine-grained topographic effects. However, taken together, these results suggest an interesting general pattern in which infants who exhibited more distress during separation from the mother also showed a larger amplitude and longer latency response to her face only. This suggests a general deeper processing of the mother's face in infants who showed more evidence of distress when separated from her.

Despite the intrigue of this finding, it should be acknowledged that 6-month-olds have a fairly limited behavioral repertoire. As a result, the distress behaviors that we observed were limited to behaviors readily shown by very young infants. They included motor movements, crying, and negative facial expressions. Not every infant showed these behaviors during the separation interval, which suggests that there are individual differences in distress during separation at this age. However, most infants (70%) showed distress during separation, and, as a whole, the infants in our sample showed significantly more distress during separation from the mother than during interaction with her. Therefore, the propensity of infants toward expressing distress during separation might play an important role in their behavioral interactions with the mother, as well as in their brain response to her face and an unfamiliar female face.

Part of the motivation for this work was previous findings showing age-related changes in ERP responses to mother's face and a stranger's face. Previous research with infants at 6 months of age (de Haan & Nelson, 1997, 1999; Webb et al., 2005) has tended to find a larger ERP signature to the mother's face and a smaller response to the stranger's face. In older infants and young children, the results of have been mixed. In studies at various ages,

larger responses have sometimes been found to the stranger, sometimes to the mother; sometimes, no difference in response has been found between the two faces. One possible explanation for this effect is that at critical ages in the development of the relationship between the mother and child, there is a relative difference in the salience of the two faces. The present results suggest that although as a group infants of 6 months show differences in response to mother and stranger faces, there are substantial individual differences in these responses. The results suggest that, more than age, it may be the response of infants to the developing relationship, shown in their distress and the amount that they visually search for their mother during separation, that is related to how infants' brains process different kinds of faces.

The results from the current study raise several questions for future research. First, future studies should address changes in mother–stranger face processing across a range of ages to determine whether infants' age or behaviors during separation are more relevant for predicting individual differences in face processing. In addition, future studies should investigate relations between infants' temperaments and the patterns seen here. This might be done by obtaining parent report of temperament or, perhaps even better, by directly observing infants in nonseparation contexts. If behavioral responses when infants are confronted with a novel situation (e.g., never before experienced remote-controlled toys) are also predictive of face processing to familiar and novel faces, this would suggest that there is something more general about temperament, rather than about the developing mother–child relationship, that influences infants' neural responses to the two faces. However, we think a general temperament effect is unlikely, given that in this study, distress and visual search were differentially related to neural responses to the mother's face and a stranger's face.

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; Field, 1996), the procedure is very similar to Ainsworth's Strange Situation (Ainsworth et al., 1978). However, an important point to be made is that the Strange Situation in its traditional form 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 on the basis of our observations in infants so young, and, indeed, that was not our goal in this work. Therefore we based our behavioral procedure on the Strange Situation as a method that has been used to elicit behaviors of distress during separation in infants beginning at the age we tested here. We limited our investigation of infant distress and visual search responses to those exhibited during a second separation, in which the infant is alone in the room, as this is purported to provide the strongest evidence of distress in response to a separation from the mother (Ainsworth et al., 1978). We feel that this work does suggest that future studies examining the fully emerged quality of attachment in older infants and its relation to face processing would be interesting and potentially very informative.

Another potential limitation in the present study is that the effects are correlational. In many cases, we were 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, because, for example, infants cannot be assigned to different levels of distress. In addition, infants' distress during separation from the mother likely reflects a number of variables, including temperamental ones, as well as the accumulation of previous experience with the mother. Nevertheless, the present results are an important first step in understanding variation in the developing mother–child relationship 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.

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Figure 1.
Schematic of electrode locations on the scalp according to the international 10–20 system of electrode placement.

Figure 2.

Grand mean ERP waveforms exhibited by all participants 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; responses to mother's face and to stranger's face are shown with solid and dotted lines, respectively. Negative component (Nc) response was analyzed over frontolateral (F) electrode sites; P400 was analyzed over occipital (O1, O2) electrode sites. ERP = event-related potential.

Table 1

Mother–Child Behavioral Variables and P400

Lead	Face			
	Mother		Stranger	
	<i>B</i>	<i>SE</i>	<i>B</i>	<i>SE</i>
Amplitude and infant distress upon separation				
O1	13.41**	3.68	−0.06	2.47
O2	11.09**	3.30	−3.20	3.36
Latency and looking for mother upon separation				
O1	−2.71	37.62	96.98**	34.08
O2	−13.60	41.72	151.54***	39.58

**
 $p < .01$.

 $p < .001$.

Table 2

Mother–Child Behavioral Variables and Nc Amplitude, Lateral Leads

Face	Left hemisphere				Right hemisphere			
	Mother		Stranger		Mother		Stranger	
	<i>B_I</i>	<i>SE</i>	<i>B_I</i>	<i>SE</i>	<i>B_I</i>	<i>SE</i>	<i>B_I</i>	<i>SE</i>
Infant distress upon separation								
Lead								
FC1/FC2	-4.79**	1.87	-2.94	1.77	3.75*	1.80	-3.90*	1.44
F3/F4	-0.74	2.05	-1.13	2.11	-1.68	1.53	0.06	1.67
FC5/FC6	-4.81**	1.52	-4.01	2.06	-1.46	1.32	-1.57	2.01
Looking for mother upon separation								
Lead								
FC1/FC2	0.47	1.06	0.33	1.01	-0.39	1.02	0.10	0.82
F3/F4	1.86	1.17	-0.38	1.20	-0.78	0.87	-1.11	0.95
FC5/FC6	2.05*	0.87	1.36	1.17	1.50*	0.75	-3.17**	1.15

* $p < .05$.** $p < .01$.

Table 3

Mother–Child Behavioral Variables and Nc Latency, Lateral Leads

f	Left hemisphere				Right hemisphere			
	Mother		Stranger		Mother		Stranger	
	<i>B_I</i>	<i>SE</i>	<i>B_I</i>	<i>SE</i>	<i>B_I</i>	<i>SE</i>	<i>B_I</i>	<i>SE</i>
Infant distress upon separation								
Lead								
FC1/FC2	108.19	83.62	–58.27	89.57	89.30	145.89	22.24	132.59
F3/F4	134.44	112.13	–186.31	128.45	–11.33	75.26	–3.09	72.85
FC5/FC6	86.84	131.55	–79.05	111.91	176.41	134.2	65.10	111.83
Looking for mother upon separation								
Lead								
FC1/FC2	–65.99	47.63	116.98 *	51.02	–64.63	83.09	–0.44	75.52
F3/F4	–38.67	63.86	79.84	73.16	24.84	42.87	30.89	41.49
FC5/FC6	–64.34	74.93	18.41	63.74	–64.53	76.43	65.71	63.69

* $p < .05$.